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# ENVIRONMENTAL LIMITS ON ABOVEGROUND NET PRIMARY PRODUCTION, LEAF AREA, AND BIOMASS IN VEGETATION ZONES OF THE PACIFIC NORTHWEST<sup>1</sup>

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Abstract. Mature vegetation from eight of the 12 major vegetation zones in Oregon and Washington was sampled along a transect from the Pacific Coast to the east slopes of the Cascade Mountains. Six stands were in forests, one in woodland, and one in the shrub-steppe. Aboveground-overstory net primary production (NPP, estimated as the sum of annual stem, branch, and foliage production) ranged from <1 to 15 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>, aboveground biomass from 3 to 1500 Mg/ha, and area of all sides of leaves from 1 to 47 ha/ha; minima were in the shrub-steppe zone and maxima in the coastal forest zone.

Maximum leaf area index. biomass, and NPP were all strongly related both to a simple index of growing season water balance and to mean minimum air temperatures in January. In the subalpine conifer zone, though, cold winter temperatures apparently have a stronger influence than summer water availability. Of the water balance components, evaporative demand alone could account for >90% of the variation in leaf area index. 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. Biomass and NPP increased linearly up to a leaf area of  $\approx$ 30 ha/ha; above this point, biomass continued to increase while NPP decreased. Except in the coastal forest zones, NPP was less than maximum values reported for other mature systems elsewhere in the world for the same range in leaf area indices. Compared to other forested regions of the temperate zone with the same NPP, these systems receive more annual precipitation, and average twice the basal area and biomass.

Key words: biomass; evaporation; forest; leaf area index; net primary production; Oregon; precipitation; shrub-steppe; temperature; vegetation zone; water balance.

#### INTRODUCTION

Biomass, net primary production (NPP), and leaf area are key characteristics of autotrophic ecosystems because they define the standing crop and flux of carbon and nutrients, and set upper limits on water use through transpiration and on carbon fixation through photosynthesis. These variables or their combinations are regarded as good indices of the economic importance (Beuter et al. 1976), efficiency of solar energy use (Whittaker 1966), maturity (Bormann and Likens 1979), and stability (Odum 1969) of autotrophic ecosystems. It is becoming more important to obtain estimates at regional, national, and global levels, to assess, for example, effects on regional water quality due to silvicultural activities (EPA 1980). or effects on atmospheric CO2 levels as a result of widespread manipulation of forest lands (Woodwell 1978, Delcourt and Harris 1980).

Relationships between structural features, such as biomass or leaf area, and functional features, such as NPP, have been widely sought. Structural features are

<sup>2</sup> Present address: School of Forest Resources and Conservation, University of Florida, Gainesville, Florida 32611 USA. more easily measured, and it is reasonable to expect that production or standing biomass would be related to the photosynthesizing surface area over a range of ecosystems. However, as direct estimates of NPP or structure for even one stand are very costly and time consuming to obtain, at regional or larger levels these estimates must be made indirectly. The most promising indirect methods involve correlations with some aspects of climate, particularly precipitation and temperature (Rosenzweig 1968, Bazilevich et al. 1971, Lieth 1975, Grier and Running 1978, Box 1980).

Although the Pacific Northwest region of the United States contains a range in vegetation from desert scrub to subalpine and coastal rain forests (Franklin and Dyrness 1973), and is one of the leading timber-producing regions of the world, no studies have addressed regional patterns of NPP or biomass, and only one has generalized about leaf area (Grier and Running 1977). Because many of the forests west of the Cascade Mountains appear unique in terms of their massiveness and the longevity of individual trees, apparently as adaptations to the characteristic dry summer climate (Waring and Franklin 1979), predictions of NPP, biomass, or leaf area based on data from elsewhere in the world may not yield reliable estimates for this region.

The objective of this study was to elucidate the re-

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FIG. 1. Study sites (Roman numerals) in Oregon, superimposed on the vegetation zones from Franklin and Dyrness (1973).

lationships among ecosystem structure, as reflected in biomass and leaf area accumulation, function, as reflected by aboveground NPP, and the regional climate of the Pacific Northwest. Three main hypotheses were tested: (1) that structure and function are related over the range of natural and mature ecosystems in the Pacific Northwest, (2) that these variables can be predicted on the basis of climatic differences across this range, and (3) that the relationships derived for the Pacific Northwest are unique to the region.

### STUDY AREAS

Leaf area index and NPP increase rapidly early in secondary succession and tend to decrease to a plateau (Kira and Shidei 1967, Odum 1969, Turner and Long 1975. Bormann and Likens 1979). This plateau occurs at 40-60 yr in Pseudotsuga forests (Turner and Long 1975) and somewhat later where conditions are harsher. Stands selected for this study were old enough to have reached a plateau, but were not visibly disturbed by management, wildfire, major episodes of windthrow, insect or pathogenic outbreaks, or heavy recreational use. Furthermore, overmature stands with abundant mortality of dominant vegetation were excluded from consideration. Two final criteria were year-round accessibility and a large open area nearby to ensure comparable climatic monitoring at all sites. Those areas selected were not chosen to provide "average" values for each vegetation zone, but only as they satisfied these criteria.

Eight study sites in 8 of the 12 major vegetation zones in the Pacific Northwest (Franklin and Dyrness 1973) were selected. The sites (Fig. 1) were along a transect between 44° and 45°N latitude from the Oregon Coast (124°W longitude) 350 km east to the high desert in central Oregon (121°W longitude).

Stands in the five western zones were dominated by even-aged overstories of trees 120–200 yr old, although several stands had a few much older individuals. Eastern zone communities were uneven aged, and were mature and undisturbed based on published descriptions of the natural vegetation (Driscoll 1964, Franklin and Dyrness 1973).

Plots I (two areas, a and b) and II were in western Oregon: Plots III–V ranged from the base to the summit of the western slope of the Cascades; and Plots VI–VIII were increasingly arid in the rain shadow east of the crest of the Cascades. Table 1 contains a description of all the study sites, and four representing the full range in characteristics are presented as photographs in Fig. 2. Across the transect winters are cool and wet. and summers are dry, generally with 2–3 mo of no measurable precipitation (Franklin and Dyrness 1973). The climate becomes more continental east of the Cascade Mountains.

#### METHODS

At each site a vegetated plot from 0.25 to 0.41 ha was laid out surrounded by a buffer strip at least 25 m wide, and an open area, usually a clearcutting of

# LIMITS ON STRUCTURE AND PRODUCTION

TABLE 1. Characteristics of study sites along the transect. Physiographic provinces are from Franklin and Dyrness (1973).

					Plot				
Feature	Ia	Ib	п	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
Dominant species	Tsuga heterophylla	Tsuga heterophylla	Pseudotsuga menziesii/ Abies grandis	Pseudotsuga menziesii	Pseudotsuga menziesii, Tsuga hetero- phylla. Abies amabilis	Tsuga mertensiana	Pinus ponderosa	Juniperus occidentalis	Artemisia tridentata var. tridentata
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	
Stem density (no.)	/ha)								
<10 cm dbh	2500	1500	110	12	1250	1700	490	470	not applicable
>10 cm dbh	294	499	312	488	1005	804	215	199	0
Basal area (m²/ ha)	118.2	111.2	84.2	54.5	72.4	57.2	26.1	27.8	15.0
Soil water storage capacity (cm)	13.1	13.1	6.1	4.4	8.5	6.2	16.6	10.1	13.5
Soil subgroup (tentative)	Typic haplohumult	Typic haplohumult	Dystric xerochrept	Lithic xerumbrept	Typic haplohumult	Entic cryandept	Typic vitrandept	Typic torriorthent	typic torriorthen

the same slope, aspect, and elevation, was identified nearby.

#### Climate measurements

Specific climatic data from published sources were not uniformly available or extensive enough to describe the sites adequately for the purposes of this study. Therefore, I chose to measure precipitation, evaporation, soil water storage capacity, the degree of summer extraction of soil water, and year-round soil and air temperatures. Precipitation and evaporation were monitored in all open plots from May through October in both 1976 and 1977. Precipitation accumulated in rain gauges and was emptied at least every 3 wk; oil prevented evaporation. Relative evaporation was measured over 3-wk intervals using evaporimeters consisting of a water reservoir and a disc of pine sapwood as an evaporating surface (Gholz 1979).

Soil temperatures, at a depth of 20 cm and air temperatures 1 m above ground were measured using Partlow 30-d spring-wound thermographs installed in late fall 1975, and removed in early spring 1978. Air temperature probes were shielded from direct and reflected shortwave radiation. A temperature growth index (TGI) (Cleary and Waring 1969) was used to summarize average soil and air temperatures. The following two winter temperature indices were also computed: (1) the percentage of days from February through April with air temperature averaging  $<-2^{\circ}$  (Waring et al. 1978), and (2) the average minimum day air temperature in January.

For each site water storage capacity of the <2-mm

fraction of soils (SWC, 10-1520 kPa tension) was measured at four depths to 1 m. In 1977 just before bud burst and again in August at the peak of the typical summer drought, three soil samples from each depth were taken from two pits near the middle of each plot. Gravimetric water contents were determined and, with the laboratory determinations of 10 and 1520 kPa water contents and bulk densities, the net amount of water extracted from the soil over the "growing season" (SWE) was estimated (Waring and Major 1964). Abnormally heavy rain interrupted August sampling for sites west of Santiam Pass (Plot V); there August moisture contents were assumed to be 60% of those in the spring (Krygier 1971). These data were used with precipitation and evaporation to derive separate water balance indices (after Grier and Running 1978) for 15 May-15 October 1976 and 1977:

# WB = P - E + SWC (1976 and 1977)

or

# WB = P - E + SWE (1977 only),

where WB is the water balance (centimetres), P and E are the precipitation and evaporation (centimetres) during the period, SWC is the soil water storage capacity (centimetres), and SWE is the spring-to-August soil water extraction (centimetres).

# Biomass and leaf area index

Diameter at breast height (dbh at 1.37 m) of each tree >5 cm was measured on Plots I-VI. Total heights and the heights to the base of the live canopy of se-



FIG. 2. Four study plots characterizing the range in sites across Oregon: (A) Coastal *Tsuga heterophylla/Picea sitchensis* (Plot Ib) (United States Forest Service photo by Larry Huditz). (B) Subalpine *Tsuga mertensiana* (Plot V), December 1976, where 2-m snowpacks are present most of the winter. (C) *Pinus ponderosa* (Plot VI) on the eastern slope of the Cascade Mountains. *Artemisia tridentata* var. *tridentata* and the nitrogen-fixing shrub *Purshia tridentata* are in the understory. (D) *Juniperus occidentalis* (Plot VII, an intensive site for Gholz 1980) on a broad ridge at 1356 m in central Oregon. The largest trees are  $\approx$ 350 yr old.

lected trees spanning the size range (at least 15 per plot) were measured with an Abney level. Trees <5 cm dbh were tallied on a set of 11 smaller ( $2 \times 2$  m) subplots. All trees were tallied on Plot VI. Plot VII procedures were similar and are described in detail by Gholz (1980). At the shrub-steppe Plot (VII) maximum lengths, heights, and widths (at right angles to the lengths) were measured for the canopy of each bush on five randomly located circular subplots, each 5 m in radius.

Stem, branch, and foliage biomass for individual plants were computed for each species in each plot using the plant measurements and regression equations for species destructively sampled on diverse sites in the Pacific Northwest (Table 2). The sources of data used for these equations, sampling procedures, and other documentation are given in Gholz et al. (1979). No equations were available for *Chrysothamnus* (Plot VIII); therefore, its biomass was estimated using the *Artemisia* equations. *Pinus monticola* biomass was estimated using multispecies composite "*Pinus*" equations (Table 2). *Pinus ponderosa* equations were based on trees destructively analyzed in northern Arizona (see Gholz et al. 1979); a comparison of their diameters and heights with those of Plot VI trees indicates that the equations may have slightly underestimated *Pinus* stem biomass on Plot VI. Suitable regressions were unavailable for *Abies grandis* at Plot II, and for the few *Abies lasiocarpa* at Plot V; biomass was computed using composite "*Abies*" equations based on data from four other *Abies* species (Table 2).

Leaf area indices were computed from leaf biomass using specific leaf areas (square centimetres per gram. Gholz et al. 1976) of foliage shot from the mid-canopy with a shotgun in early August. Samples were collected from at least three dominant trees and from all

TABLE 2. Regression equations used to estimate overstory on all plots along the transect. Except where noted, all are of the form:  $\ln(Y) = a + b \ln(dbh)$ , where Y is mass in kilograms and dbh (diameter at breast height, 1.37 m) is in centimetres. Most equations without a footnote represent a composite of data from several published and unpublished sources and are more fully documented in Gholz et al. (1979). NA = not available.  $S^2_{y,x}$  = residual MS error variance.

Species	Y	а	Ь	$S^2_{y \cdot x}$	n	$r^2$
Abies (pooled)	Foliage	-3.466	1.928	0.159	25	.94
	Live branch	-4.829	2.559	0.206	26	.95
	Stem wood	-3.739	2.683	0.085	20	.97
	Stem bark	-6.192	2.880	0.057	20	.98
Abies amabilis	Foliage	-4.549	2.193	0.077	9	.97
	Live branch	-5.237	2.626	0.163	9	.96
	Stem wood	-3.506	2.571	0.018	14	.99
	Stem bark	-6.117	2.842	0.049	14	.99
Abies procesa	Foliage	-4 873	2 168	0.034	6	99
Ables proceru	Livebranch	-4.187	2 332	0.199	6	94
	Live branch	3 716	2 750	0.063	6	00
	Stem bark	-6.100	2.894	0.059	6	.99
A	Ealiaga	3 765	1.617	0.101	18	87
Acer macrophyllum <sup>+</sup>	Follage	- 5.705	2.430	0.101	10	.07
	Live branch	-4.230	1.430	1.860	10	.00
	Dead branch	-2.110	1.092	1.002	18	.15
	Stem wood	- 5.493	2.723	0.014	18	.99
	Stem bark	-4.574	2.574	0.058	18	98
Artemisia tridentata†	Foliage	Y = 43.0 + 0.	$.00000907 \cdot X$	NA	20	.68
	Wood	Y = 128.0 +	$0.000603 \cdot X$	NA	20	.80
Juniperus occidentalis‡	Foliage	-4.231	1.561	0.024	10	.99
•	Live branch	-7.278	2.334	0.068	10	.99
	Dead branch	-11.514	2.832	0.664	10	.91
	Stem wood	-8.580	2.639	0.029	10	.99
	Stem bark	-10.175	2 633	0.152	10	99
	Leaf surface (m <sup>2</sup> )	-2.754	1.536	0.019	10	.99
Picea sitchensis§	Foliage Live branch Whole stem		$log_{10} Y = 0.94log_{10} Y = 0.04log_{10} Y = 0.94$	$405 \cdot \log_{10}(X) = 55 \cdot \log_{10}(X) = 55 \cdot \log_{10}(X) = 5 \cdot \log_{1$	- 3.6343 - 3.257 - 1.207	
Dimme (mapled)	Falinga	-3 074	2 004	0.257	33	89
Finus (pooled)	Livebranch	5.200	2.652	0.216	33	.05
	Deed branch	2 707	1 743	0.120	14	53
	Dead branch	- 3. /9/	1.745	0.129	14	
	Stem bark	-4.285	2.718	0.058	14	.98
	Stelli bark	4.200	2.007	0.228	0	04
Pinus ponderosa	Foliage	-4.261	2.097	0.338	9	.84
	Live branch	-5.586	2.719	0.042	9	.99
	Dead branch	-2.577	1.444	NA	9	.64
	Stem wood	-4.491	2.759	0.031	9	.99
	Stem bark	-4.206	2.231	0.063	9	.97
Pseudotsuga menziesii	Foliage	-2.846	1.701	0.483	123	.86
	Live branch	-3.694	2.138	0.399	123	.92
	Dead branch	-3.529	1.750	0.530	85	.84
	Stem wood	-3.040	2.595	0.096	99	.99
	Stem bark	-4.310	2.430	0.104	99	.99
Tsuga heterophylla*	Foliage	-4.130	2.128	0.189	18	.96
	Live branch	-5.149	2.778	0.177	18	.98
	Dead branch	-2.409	1.312	0.641	18	.62
	Stem wood	-2.172	2.257	0.014	18	.99
	Stem bark	-4.373	2.258	0.019	18	.99
Tsuga mertensiana	Foliage	-3.8169	1.9756	0.025	11	.97
a sugar merrer istanta	Live branch	-5.2581	2.6045	0.015	11	.99
	Dead branch	-9.9449	3,2845	0.012	6	.98
	Stem wood	-4.8164	2,9308	0.052	14	.98
	Stem bark	-5 5868	2 7654	0.051	14	97
	Stem Oak	2.2000		0.051	1.4	

\* From Grier and Logan (1977).

+ From Uresk et al. (1977): Y is biomass in grams, X is crown volume in cubic centimetres.

\* From Gholz (1980); X is basal circumference in centimetres. § From Fujimori et al. (1976). No associated statistics were provided. X, here, is  $dbh^2 \times height (metres)$ ; Y for the stem equation is volume in cubic decimetres; to obtain mass for these trees multiply Y by 0.35 g/cm<sup>3</sup>.

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TABLE 3.	Climate of	study sites	from west	to east along	transect.	NA =	not available.
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	Plot									
Feature*	I	II .	III	IV	v	VI	VII	VIII		
Precipitation (cm) Average annual† Average May-Oct	246.0 41.8	120.0 15.5	157.0 30.0	200.0 32.1	230.0 39.5	40.0 7.5	25.0 9.1	20.0 7.2		
Evaporation May-Oct 1977 (cm) 1977 soil water extraction (cm)	48 23.7	76 7.2	104 5.0	71 7.6	80 9.2	100 6.5	130 3.6	127 3.5		
1976/1977 water balance index (cm)‡	24/22	-24/-49	-27/-64	-12/-64	-13/-33	-44/-88	-53/-119	-57/-118		
Winter temperature index (%)§	2	6	18	51	65	68	80	87		
Femperature growth index TGI) 1976/1977 May–Oct	58/60	78/74	80/76	65/64	46/53	82/79	91/95	89/96		
Mean air temperature (°C) Minimum. Jan 1977 Maximum. Jul 1977	2.9 11.2	-0.3 18.9	NA 20.0	-1.8 18.2	-6.0 19.0	-8.9 25.3	-8.0 25.5	-11.7 24.7		

\* Precipitation and evaporation for 1976 and 1977 were measured at each site.

+ Representing at least 10 yr of data from NOAA (1977) or other meteorological station nearest to each site.

Using soil water extraction.

§ Average percent of days with mean air temperatures  $< -2^{\circ}$ C from 1 February to 30 April 1976 and 1977.

major species in each stand. Cross-sectional adjustments (Gholz et al. 1976) were applied to convert projected leaf area indices to a total-surface basis.

### Net primary productivity

On Plots I–VI. 5-yr diameter growth at breast height was measured on increment cores from at least 25 overstory trees spanning the dbh range (bark growth was assumed directly proportional to wood growth). Dry biomass increments of stems (wood plus bark) and branches were calculated using the biomass equations (Table 2, Gholz et al. 1979) in conjunction with the current and calculated previous 5-yr dbh values.

Regressing increment values against the current dbh yielded equations that were applied to the dbh of all trees in each stand to obtain 5-yr biomass increments for the entire stand; dividing by five then yielded average annual increment. Plot VII was treated similarly (Gholz 1980). Annual production equations for branches and stems (Fujimori et al. 1976) were used for *Picea* at the two coastal plots and average annual total (wood plus foliage) aboveground production of *Artemisia*. based on a seasonal harvest method, was provided by G. Nelson (*personal communication*, compiled from long-term records at Squaw Butte Experiment Station, Burns, Oregon).

Because litterfall was not collected, new foliage produced by Plots I-V was estimated as a fixed percentage of foliage biomass; this percentage varied from 20 to 30%, depending on published values of foliage retention time (Fujimori et al. 1976, Grier and Logan 1977). Foliage production was assumed to be 25% of foliage biomass for *Pinus* (Plot VI) based on the western Oregon species and 30% for *Juniperus* (Plot VII, Mason and Hutchings 1968). Current production losses to mortality, nonfoliar litterfall, or herbivore grazing were assumed zero. Aboveground NPP for Plots I-VII was the sum of annual production by stem wood, bark, branches, and foliage.

### RESULTS

### Climate

The percentage of winter days with temperatures  $<-2^{\circ}$ C increased progressively away from the coast, while minimum day air temperatures for January decreased from  $\approx 3^{\circ}$  to  $-12^{\circ}$ C (Table 3; due to equipment failure data are unavailable for Plot III).

Average annual precipitation decreased markedly from the coast to the desert, but fluctuated greatly from site to site (Table 3). Summer precipitation averaged 13–19% of annual precipitation for the six western zones and 36% of annual precipitation in the three eastern zones. Summer precipitation in 1977 was more representative of long-term trends (10–40 yr averages, NOAA 1977) and was greater than 1976 precipitation for all plots west of the Cascades. Evaporation for all sites was uniformly higher in 1977 than in 1976.

The water balances reflect these variations (Table 3). At the coast (Plots Ia and Ib), the higher precipitation in 1977 was nearly balanced by higher evaporation. and the water balances were similar for 1976 and 1977. Evaporation increases more than offset precipitation increases from 1976 to 1977 for the rest of the transect, so that the water balances were, on the average, twice as negative as those for 1976. The water balances at the subalpine site (V) were similar to those from the transition zone (IV); otherwise, the balances

		Plot							
Feature	Ia	Ib	II	III	IV	v	VI	VII	VIII
Leaf area, all-sided (ha/ha)	31	47	18	15	22	10	7	2	1
Biomass (mg/ha)									
Foliage	23	32	16	12	18	15	7	4	1
Live branch	97	144	60	30	43	35	30	7	2
Stem	960	1316	789	407	467	228	99	9	
Biomass production (mg · ha-	-1 · yr-1)								
Stem	7	4	5	3	5	1	1	0.2	
Branch	2	1	0.5	0.2	0.5	0.2	0.2	<.1	0.3*
Foliage	6	8	5	3	4	3	1	1	
Total NPP	15	13	10.5	6.2	9.5	4.2	2.2	1.2	0.3
Total biomass:NPP	73	116	82	68	57	68	59	13	10
NPP:leaf area index	0.48	0.28	0.58	0.41	0.43	0.42	0.31	0.60	0.30

TABLE 4. Structure and production relations of study sites, from west to east across transect.

\* Stem, branch, and foliage combined.

became more negative in a linear fashion from the coast, east to the shrub-steppe site (VIII, Table 3).

### Biomass and leaf area index

Estimates of total aboveground biomass (Table 4) ranged from 3 Mg/ha in the Artemisia zone (VII) to 1500 Mg/ha in one coastal forest (Ib). Foliage biomass increased from 2 to 8% of overstory aboveground biomass in the forested zones to 21% in the Juniperus woodland (VII), and 33% in the Artemisia shrubsteppe (VIII). Likewise, live-branch biomass increased from 7–10% for the four western forest zones to 67% in the Artemisia zone (VIII), assuming Artemisia wood to be all "branches" with no "stem" biomass. Stem biomass decreased below 80% of total biomass only in Plots VI (73%) and VII (45%).

Leaf area indices varied greatly, from 1 to 47 ha/ha (projected areas of 0.5–20.0 ha/ha) again, generally decreasing from west to east (Table 4). Standing crop densities (Kira and Shidei 1967), the dry matter concentrations from the ground to the top of the canopy, decreased steadily from 2–3 kg/m<sup>3</sup> in the coastal zone (Plots Ia and b) to 0.3 kg/m<sup>3</sup> in the three rain-shadow zones (Plots VI–VIII). Canopy heights decreased from 35–55 m in the forested zones to 8 m (Plot VII) and 1 m (Plot VIII) in the two driest zones. The density of foliage in the canopies (Kira and Shidei 1967) in seven zones ranged inconsistently from 0.03 to 0.08 kg/m<sup>3</sup>. The *Pinus ponderosa* canopy (Plot VI) was the least dense (.016 kg/m<sup>3</sup> foliage).

Both biomass and leaf area index showed similar relationships with climatic variables (Table 5). Mean minimum January air temperature was the best predictor of both stand biomass ( $r^2 = .91$ ) and leaf area index ( $r^2 = .89$ , Table 5A). However, if the subalpine *Tsuga mertensiana* stand (V) was excluded, on the premise that leaf area indices on these sites are not water limited (Grier and Running 1977), then the 1977 water balance best predicted both leaf area index ( $r^2 = .97$ ) and biomass ( $r^2 = .95$ ), with very low variances

in each case (Table 5B). Relationships with the minimum temperatures did not change when Plot V was excluded; the water balance relationships became much better, with the variance for leaf area indices decreasing from 34 to 8 and for biomass from 51 000 to 15 000 (Table 5C).

The leaf area index:water balance relationships were somewhat stronger (differences were not significant) when soil water extraction rather than storage capacity was used (Table 5B), and regression slopes for 1976 and 1977 were significantly different. Of the water balance components, growing season evaporation was the best predictor of leaf area index ( $r^2 = .91$ for 1977); growing season precipitation ( $r^2 = .83$ ) and soil water extraction ( $r^2 = .82$ ) were not as good predictors (Table 5D). Soil water storage capacities had a smaller range than extraction and were not significantly correlated with leaf area index ( $r^2 = .04$ . Table 5D), and only poorly with precipitation and extraction  $(r^2 < .5)$ . In this study, leaf area index was poorly correlated with TGI ( $r^2 = .47$ , Table 5D), declining at both high and low TGI values with considerable variation.

Stand dimensional characteristics are generally less interesting for predicting stand structure and productivity at a regional level because they can only be obtained through direct field measurement. However, when all eight plots were considered, or nine if Plots Ia and b were treated separately, basal area was the best predictor of leaf area index ( $r^2 = .92$ ) and biomass ( $r^2 = .94$ ) of all the variables considered (Table 5G). Biomass was significantly correlated with leaf area index ( $r^2 = .91$ , Table 5G), so the similar patterns of correlation with climate and basal area are not surprising.

### Net primary production

NPP ranged from 0.3 to 15 Mg $\cdot$ ha<sup>-1</sup>·yr<sup>-1</sup>. Total biomass:NPP ratios declined from 95 at the coast to 12 in the eastern zones. NPP:foliage biomass ratios

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TABLE 5. Selected regressions among stand leaf area indices (ha/ha), biomass (Mg/ha) and NPP (Mg·ha<sup>-1</sup>·yr<sup>-1</sup>) across the transect in Oregon. Plots Ia and b are averaged for these analyses unless noted. All equations are of the form: Y = A + B(x).  $s^2_{yx}$  is the residual mean square error (variance). NS = not significant.

	Y	X	Α	В	r <sup>2</sup>	S <sup>2</sup> y-x
A.	Best climatic predictor	rs for all plots out of 12 individual van	riables conside	red*		
	Leaf area index	1977 Mean min. Jan air temp. (°C)	25,207	2.336	.89	22.4
	Biomass	1977 Mean min. Jan air temp. (°C)	864.62	88.323	.91	24 526.0
	NPP	1977 Mean min. Jan air temp. (°C)	10.819	1.001	.97	1.0
Β.	Best climatic predictor	rs without the subalpine Plot V:				
	Leaf area index	1976 Water balance† (cm)	29.337	0.496	.99	1.8
		1977 Water balance+ (cm)	31.680	0.263	.97	7.5
		1976 Water balance‡ (cm)	31.841	0.648	.97	7.5
	D.	1977 Water balance‡ (cm)	33.181	0.297	.95	14.0
	Biomass	1977 Water balance+ (cm)	1126.6	9.582	.95	14 626.6
	NPP	1977 May-Oct evap. (cm)	21.801	-0.166	.91	3.0
C.	Effect of removal of si	ubalpine Plot V on 1977 water balanc	et regressions:	0.221	80	24.2
	Lear area index	With Plot V	20.072	0.251	.00	34.5
	Biomass	With Plot V	991.25	8 417	78	50 497 5
	Diomass	Without Plot V	1126.6	9 582	95	14 626 6
	NPP	With Plot V	11 800	0.090	73	7.8
		Without Plot V	13.266	0.102	.88	4.0
D.	Regressions of leaf are	a index on components of the 1977 wa	ater balance (w	ithout Plot V) and	d with othe	er climatic variables
(fo	r all plots):	Mar One service (service)	52 644	0 405	01	17.0
		May-Oct evaporation (cm)	0.268	-0.405	.91	17.9
		Soil water extraction (cm)	-0.182	1 877	.05	51.2
		Soil water storage capacity (cm)	24 722	-0.802	04	227 2 NS
		1977 Mean min Jan air temp (°C)	24.722	0.002	.04	
		(with Plot V)	25.207	2.336	.89	22.4
		1977 Mean min. Jan air temp. (°C)				
		(without Plot V)	25.359	2.326	.89	110.4
		Mean May-Oct precip. (cm)	-2.906	0.983	.90	29.6
		Mean annual precip. (cm) 1976–1977 winter temp_index	-0.892	0.152	.94	16.6
		(%)	30,471	-0.322	.71	59.3
		TGI	53.691	-0.531	.47	535.3
E.	Regressions of biomas	ss on selected climatic variables:			*2	
		1977 May-Oct evan. (cm)	1829.1	-14.495	.85	40 074.0
		1977 May-Oct precip. (cm)	13.004	19.294	.57	166 822.0
		Mean May-Oct precip. (cm)	-77.175	26.733	.62	102 615.0
		Mean annual precip. (cm)	-55.408	4.549	.75	68 675.0
		1976-1977 Winter temp index (%)	1009.0	-12.085	.83	39 376.0
F.	Regressions of NPP o	n selected climatic variables:				
		1977 Mean min. Jan air temp. (°C)				
		(with Plot V)	10.819	1.001	.97	1.0
		1977 Mean min. Jan air temp (°C)	10 807	0.006	07	4.4
		(without Plot V)	10.897	0.990	.97	4.4
		Mean annual precip. (cm)	0.101	0.053	.80	4.5
		Mean May–Oct precip. (cm)	-0.108	0.308	./1	9.4
		1977 May-Oct evap. (cm) 1976-1977 winter temp index	20.403	-0.156	.02	5.2
		(%)	12.003	-0.129	.82	5.0
		1977 TGI with Plot V	21,667	-0.210	.44	95.5
		1977 TGI without Plot V	33.145	-0.346	.83	28.1
G	Regressions on stand	basal areas and leaf area indices:				
	Leaf area index	Basal area (m <sup>2</sup> /ha)	-5.258	0.336	.92	13.8
	NPP	Basal area (m <sup>2</sup> /ha)	1.834	0.137	.95	1.4
	Biomass	Basal area (m <sup>2</sup> /ha)	-277.58	12.591	.94	4.9
	Biomass	Leaf area (ha/ha)	-50.976	35.318	.91	22 066.0
	NPP	Leaf area (<30 ha/ha)	-0.377	0.492	.96	1.2
	NPP	Biomass (<1100 Mg/ha)	0.715	0.013	.97	6.3

\* Due to equipment failure 1977 Mean min. Jan air temperatures are unavailable for Plot III.

+ Based on actual extraction of soil water.

‡ Based on soil water storage capacity.

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showed a slight decline to the east (Table 4). Stem increment contributed 13-55% of NPP along the transect. Foliage production exceeded stem production on four sites.

Relationships of NPP with the climatic variables are similar to those of leaf area index and biomass with climate (Table 5). However, in this case, whether the subalpine Plot V was excluded or not, mean minimum January temperature was the best predictor of NPP. and regressions of NPP on this variable did not change significantly when Plot V was exluded (Table 5F). Even without Plot V, the water balance produced a variance four times as large as the variance associated with the January temperature regression (Table 5A), and the correlation of NPP with evaporation alone (Table 5B) was higher  $(r^2 = .91)$  than with the water balance ( $r^2 = .88$ ). Again, relationships of NPP with growing season and annual precipitation were much weaker (Table 5F). Excluding Plot V, there was a strong negative correlation of NPP with the growing season TGI, suggesting additional restrictions of NPP at plots with higher summer temperatures (Table 5F).

### DISCUSSION

# Leaf area index and biomass

There was no significant difference between the slope of the 1977 leaf area index-water balance regression line (excluding the subalpine site) and that of Grier and Running (1977), who used soil water storage capacity and long-term climatic averages with average leaf area indices from five of the same zones (excluding the subalpine zone, Fig. 3). Using water extraction rather than storage capacity to determine the water balance made little difference in the regressions (Table 5B). The agreement of these independent estimates supports a regional trend of leaf area index and water balance outside the subalpine zone.

Data for 1976 also indicate a strong relationship between leaf area index and water balance, but with a much steeper slope (Table 5B). Because needles may be retained for several years, litterfall amounts in these forests would be expected to vary  $\leq \approx 25\%$  from year to year and leaf area index ought to be nearly constant. Yet the water balance indices for sites away from the coast were often different by 100% from 1976 to 1977 (Table 4). Based on these observations I conclude that either the relationship between the transpiring leaf surface and the available water on a site reflects an adaptation to long-term hydrologic conditions rather than to the relatively large fluctuations that can occur from year to year, or that other factors exert a significant influence on site leaf area indices.

While the water balance failed to predict leaf area index accurately at subalpine Plot V, the correlations with winter cold temperature indices were high over all plots, which may reflect markedly reduced photosynthesis outside the growing season in the subalpine



FIG. 3. Leaf area index as a function of water balance during the growing season (based on equations in Table 5). Plots Ia and b are averaged in this figure. Grier and Running's (1977) regression is based on average values for five zones. (O) and ( $\bullet$ ) = subalpine Plot V.

zone (Emmingham and Waring 1977, Waring et al. 1978). TGI was of limited predictive use for leaf areas because of its restriction to the growing season and exclusion of any water considerations.

Factors other than moisture or temperature apparently may also limit maximum stand leaf area indices. For example, the presumed limitation in some coastal sites is wind damage to the developing canopy (Fujimori et al. 1976, Grier 1977, 1978). Substrate quality could also restrain leaf area index; serpentine soils in southwestern Oregon supported less leaf area than expected based on the TGI and a plant moisture index (Waring et al. 1978). Leaf areas (Gholz et al. 1976) were lower than expected in stands with very low available soil nitrogen (Zobel et al. 1976) in the western Cascades. In plantation studies, N fertilization may increase leaf area index by increasing needle retention time (Miller and Miller 1976). Whether nutrition has a direct effect on leaf area accumulation or whether it is inseparable from temperature and moisture conditions on a site cannot be answered at this point.

According to the relationships reported here, maximum leaf area indices for the Pacific Northwest are  $\approx$ 45 ha/ha, which is similar to other studies already cited.

Since biomass continues to change greatly over centuries in these forests (Waring and Franklin 1979), the close relationships of biomass with many of the climatic and stand variables (Table 5) would probably change over time. In this context the high correlations would suggest that these sites are representative of stands in similar developmental stages; they may not reflect direct causal connections between the particular variables and biomass. In some Wisconsin hardwood forests aboveground biomass was highly correlated with the product of stand basal area and mean canopy height (Crow 1978). Since stand basal areas

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and canopy heights are standard mensurational variables, and change in the same direction over time as biomass, this relationship may be useful for purposes of estimating dry matter contents of a wide range of northwestern United States forests.

### Net primary production

Although foliage production for this study was indirectly estimated, the resultant values (Table 4) compare well with litterfall estimates for other temperate conifer forests (Bray and Gorham 1964, Grier 1977, Grier and Logan 1977). NPP values calculated here seem very reasonable when compared to literature values for the coastal zone (Westman and Whittaker 1975, Fujimori et al. 1976), young, low-elevation Douglas-fir forests in Washington (Heilman 1961, Reikerk 1967, Cole et al. 1968, Turner 1975), a 100-yr-old Douglas-fir stand in western Oregon (Fujimori et al. 1976), and a subalpine *Abies amabilis* forest in northern Washington (Grier 1980).

NPP over all plots increased linearly with biomass  $(r^2 = .97, \text{Table 5G})$  to a plateau of  $\approx 15 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  at a biomass of 1100 Mg/ha. The occurrence of an NPP:biomass plateau is supported by data from oldgrowth redwood forests in northern California (Westman and Whittaker 1975). A review of "mature" forests containing no stands from the Pacific Northwest (Whittaker and Marks 1975) indicated that mature stands elsewhere in the world averaged twice the NPP per unit of biomass as stands from this study. No plateau was apparent in the review, although the largest biomass value was 600 kg/ha. less than half the maximum reported in Table 4.

NPP also increased steeply with stand basal area (Table 5G), and the correlation was high ( $r^2 = .95$ ) for the stands along the transect. No maximum NPP was indicated, although alluvial flat redwood stands in northern California at 14 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> and 250 m<sup>2</sup>/ha basal area (Westman and Whittaker 1975) no doubt represent a maximum. Compared to the average of stands in the eastern United States (Whittaker and Marks 1975), the Oregon transect stands had less than half the annual NPP at any basal area, although some eastern stands appeared comparable in this regard.

NPP was positively correlated with higher (more positive) values of the water balance (Fig. 4a), a result similar to that of Rosenzweig (1968) who used potential evapotranspiration (PET) as the independent variable, and warmer minimum winter temperatures. However, in the subalpine zone cold winter temperatures appeared to be the dominating factor in limiting NPP (Fig. 4b). This is supported by a simulation study of seasonal photosynthesis in the northwest United States (Emmingham and Waring 1977), which indicated that, while growing-season photosynthesis was greatly restricted by drought as in other forest zones, winter photosynthesis was much more restricted in the subalpine zone than elsewhere.



FIG. 4. Relationships of aboveground NPP to 1977 growing season water availability (a. using soil water extraction), and a cold winter temperature index (b; data for Plot III are unavailable). The subalpine Plot V is enclosed in parentheses. Plots Ia and b are averaged in this figure.

Are summer water or cold winter temperatures more important in controlling stand structure and production? Outside the subalpine zone these two variables are highly correlated ( $r^2 = .85$ ). When the subalpine zone is added, the correlation decreases to  $r^2 =$ .72, much lower but still highly significant. Clearly these two factors are not independent, although in the subalpine zone colder winter temperatures alone appear to exert more control even in the presence of limited summer moisture.

Given these relationships, a strong correlation between NPP and leaf area is not surprising even when average values from two old-growth redwood stands (Westman and Whittaker 1975) are included (Fig. 5). In the Pacific Northwest, where all-sided leaf area indices are <30 ha/ha (projected leaf area index of  $\approx 14$ ), NPP and leaf area index were linearly related ( $r^2 =$ .96, Fig. 5). Fig. 5 indicates the probable limits on NPP of mature tree- or woody shrub-dominated ecosystems, evergreen and deciduous, based on this study and other published reports (the dashed lines). The upper line could be regarded as "potential" NPP, representing the maximum NPP observed at any given leaf area index. A similar figure in Whittaker and



FIG. 5. Aboveground overstory NPP in relation to total stand leaf area index (all sided). • = stands from this study; RU = upslope redwood and RA = alluvial flat redwood stand (Westman and Whittaker 1975). Dashed lines indicate probable upper and lower limits on NPP by natural, mature, tree, or woody shrub dominated ecosystems at any given all-sided leaf area. Maximum previously reported leaf area indices, where NPP was also reported, are  $\approx$  30 ha/ha. For the eight transect stands with leaf area indices <31 ha/ha, treating Plots Ia and b separately. NPP = -0.377 + 0.492 (leaf area index),  $r^2 = .96$ .

Marks (1975) indicates that maximum NPP at any level of leaf area index is somewhat higher than that shown in Fig. 5, and does not show any tendency for NPP to reach a maximum or decrease at any value of leaf area index. This reflects the much smaller range in leaf area indices of studies they reviewed (all <17 ha/ha all-sided), and most important, the exclusion of demonstrably "immature" communities from this study. Immature stands (Whittaker 1966) and some lowelevation tropical rain forests (Murphy 1975) may have much higher NPP than indicated in Fig. 5. Upward corrections for underestimates of NPP based on the assumption of zero nonfoliar litter production used here might also cause results of the two studies to converge more where the data overlap in range.

As leaf area indices varied by a factor of 40, generally decreasing west to east, while NPP varied irregularly and only by a factor of 10, the regional trend in NPP was due more to changes in leaf area index than to changes in production efficiency (NPP: leaf area index, Table 4). Production efficiency ranged only from .30 to .60, with no pattern over the transect. This is considerably less than efficiencies from other regions for leaf area indices >10 (Whittaker and Marks 1975), although no other production studies of mature stands report leaf area indices as high as those reported here.

Although very old forest stands were originally excluded from this analysis, this seems unnecessary. Grier and Logan (1977) reported NPP and biomass values for five forest types in western Oregon on one small watershed dominated by *Pseudotsuga* 400–500 yr old. Leaf area indices ranged from 12 to 20 ha/ha; when plotted with NPP on Fig. 5, the points would fall very close to the line for plots of this study. This indicates that as stands in this area become decadent, as these stands were (Grier and Logan 1977), and leaf area index temporarily decreases, NPP also decreases, and a similar ratio of NPP: leaf area index is maintained.

LIMITS ON STRUCTURE AND PRODUCTION

At any given leaf area index, these Pacific Northwest ecosystems, except those in the coastal zone (Plots Ia and b, the alluvial flat redwoods from Westman and Whittaker 1977), generally seem less productive than many others throughout the world. This is due to a combination of much higher leaf area indices and somewhat lower ratio of NPP:leaf area index. However, a maximum NPP for mature temperate forests of 12–15 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> (Whittaker and Likens 1975) is supported.

For stands away from the coast, actual NPP at any leaf area index may fall short of "potential" NPP (upper dashed line in Fig. 5) because of inadequate fertility. Nitrogen is regarded as the limiting nutrient in inland conifer forests of the region (Atkinson and Morrison 1975), although data are unavailable to make a clear case for the transect stands. However, stands at the coast do not appear to be nitrogen limited (Grier 1977). Their production efficiencies are no higher than for stands elsewhere along the transect (Table 4). so if the eastern stands are N limited, inadequate nutrition must reduce NPP by reducing maximum stand leaf area indices.

A relationship of NPP with mean annual precipitation, based on production data from the eastern United States, Europe, and Asia, was used by Lieth (1975) to estimate regional NPP over the biosphere. His equation overestimates my measurements of NPP by two times (for all except Plot V) to five times (for Plot V). This comparatively inefficient water use pattern for the stands reported here is no doubt related to the great proportion of rainfall, and steady but low apparent rates of photosynthesis that may occur during the winter dormant period at sites west of the Cascade crest (Salo 1974, Emmingham and Waring 1977). under conditions less favorable than those during growing seasons elsewhere.

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