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Variation in Maximum Leaf Area of Coniferous Forests in Oregon and Its Ecological Significance

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Abstract. Maximum leaf areas (calculated for all surfaces) accumulated by 40 mature forest stands in western Oregon ranged from 5 to 53 m^2m^{-2}. Forests of the west-central Cascade Mountains had much more leaf area than forests in the eastern Siskiyou Mountains along the California border.

In both regions, environmental analyses correlated high maximum leaf areas with moderate air and soil temperature and with adequate soil moisture. The Siskiyou Mountains, with a more continental climate than the Cascades, had generally lower leaf areas. There the greater evaporation in the summer and colder winter temperatures apparently restrict leaf area development more than in the Cascades. In both regions, nutritional limitations may restrict the leaf areas to considerably less than the potential afforded by local climatic conditions. Forest Sci. 24:131–140.

Additional key words. Biomass, environmental gradients, photosynthesis, respiration.

As a forest community develops, leaf area increases and eventually peaks (Kira and Shidei 1967, Ovington 1957). In the northeastern United States, pioneer species may reestablish maximum leaf area within 5 years after disturbance (Marks 1974). However, in the Pacific Northwest, leaf area continues to accumulate, often for as long as 40 years (Long and Turner 1975). The resulting leaf areas are greater, often exceeding a total surface area of 40 m^2m^{-2} or a projected area of 16 m^2m^{-2} (Gholz and others 1976, Westman and Whittaker 1975). In contrast, the deciduous forests of the eastern United States typically have leaf areas of 12 m^2m^{-2} or projected areas of 6 m^2m^{-2} (Whittaker 1966).

In the west-central Cascade Mountains of Oregon, the maximum leaf areas of forest stands originating about 450 years ago can differ threefold (Gholz and others 1976). The total leaf areas of mature coniferous forests are related to a water balance at the site—that is, leaf area increases with precipitation, increased water

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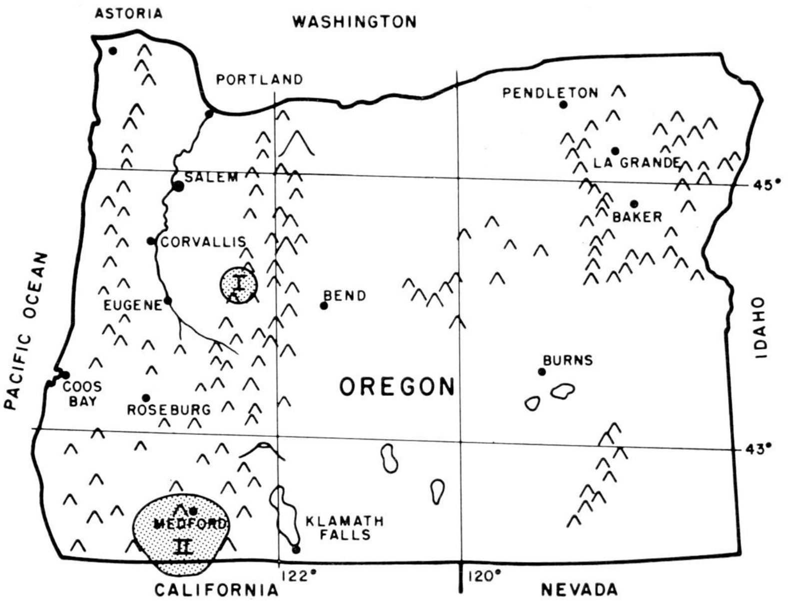

FIGURE 1. Study areas in the west central Cascade Mountains (I) and the eastern Siskiyou Mountains (II), distinct physiographic regions in Oregon.

retention in the soil, and decreased evaporation (Grier and Running 1977). However, other factors also may limit the accumulation of leaf area.

To examine how environmental factors and community structure affect total leaf area, we compared two of Oregon's major timber-producing regions, the eastern Siskiyou Mountains in southwestern Oregon and the west-central Cascade Mountains (Fig. 1). The productivity of the regions differs greatly, led by the Cascades (Beuter and others 1976). Recent studies have quantified the environments of the two regions (Waring 1969, Zobel and others 1976). By estimating leaf area (Satoo 1966, Madgwick 1970, Grier and Logan 1977), we can now link the steady-state leaf areas supported by those two regions to each area's particular environmental characteristics.

We estimated leaf area for 17 stands in the Cascades and 23 stands in the Siskiyous. All 40 stands were of natural origin, undisturbed for at least 75 years, and showed extensive natural mortality indicating that leaf areas were near maximum for steady-state conditions (Westoby 1977). We compared summer evaporative demand and winter cold stress for representative sites in both areas and used those comparisons, along with previously developed moisture and temperature indices, to interpret regional and local differences in leaf areas.

STUDY AREAS

The eastern Siskiyou Mountains straddle the California-Oregon border (Fig. 1), where the continental climate resembles that of the central Sierra Nevada Mountains in California. The west-central Cascade Mountains of Oregon have a more maritime climate than the Siskiyous, particularly during the winter.

Vegetation of the two areas differs distinctly. On drier sites in the eastern Siskiyous, the climax species is Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) mixed with hardwoods such as California black oak (*Quercus kelloggii* Newb.), canyon live oak (*Quercus chrysolepis* Liebm.), and Pacific madrone (*Arbutus menziesii* Pursh.). Midelevations commonly have mixed coniferous forests of Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.), and white fir (*Abies concolor* (Gord. & Glend.) Lindl.). At still higher elevations, forests of red fir (*Abies magnifica* var. *shastensis* Lemm.) dominate, yielding to mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) in the subalpine zone (for complete discussion, see Whittaker 1960, Waring 1969, and Franklin and Dyrness 1973).

In the western Cascades, Douglas-fir usually is succeeded by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) or western redcedar (*Thuja plicata* Donn) at lower elevations and by Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) at midelevations. None of these climax species occur in the eastern Siskiyous. At higher elevations, noble fir (*Abies procera* Rehd.) is a seral dominant succeeded by Pacific silver fir. In the Cascades subalpine zone, mountain hemlock again appears, but at elevations 300–400 m lower than in the Siskiyous. In contrast to the Siskiyous, pines are uncommon in the western Cascades although both western white pine (*Pinus monticola* Dougl.) and sugar pine do occur. In general, forests have more understory herb and shrub cover in the Cascades than in the Siskiyous. Vegetation in the Cascades has been more completely described by Zobel and others (1976), Franklin and Dyrness (1973), and Dyrness and others (1974).

METHODS

Stand Structural Analysis.—In the Cascades, 17 mature stands on 50 m × 50 m plots were measured to obtain the diameters of all trees larger than 6 cm dbh. Leaf biomass was estimated from stem diameter (Table 1) using allometric equations developed by Grier and Logan (1977). Total surface area (all surfaces of conifer needles and both sides of broadleaves) was calculated according to methods for converting biomass to area as described by Gholz and others (1976). This study excluded herbs and understory shrubs, typically 2 to 10 percent of total leaf area in western Cascade forests (Gholz and others 1976).

In the Siskiyou region, 23 stands originally described by Waring (1969) were resurveyed using variable-plot methods (Dilworth 1974) to designate trees included within a given sample. We recorded the species and diameter at dbh for each tree in each plot, then estimated foliage biomass and leaf area as we did for the Cascades. Although the allometric equations used were those developed from Cascades data, other observations led us to believe that they fairly represent the Siskiyou foliage biomass. We excluded understory plants, approximately 1 to 5 percent of total leaf area in the stands.

Analysis of Environment.—The vegetation of both the Siskiyou and Cascade regions has been classified in relation to available soil moisture and growing season temperatures (Waring 1969, Zobel and others 1976). Both studies used an index of soil drought (Waring and Cleary 1967) that compared the predawn plant water potential of reference trees at each site in August or September, near the end of the summer drought. From records of soil (20 cm depth) and air temperature (1 m height) at each site, the potential growth possible each day was assessed (Cleary and Waring 1969) for the entire growing season in both regions and summed to provide a "temperature growth index." The temperature regime was interpreted through the growth response of Douglas-fir seedlings in growth room experiments (Lavender and Overton 1972).

Because evaporative demand may also influence the development of leaf area (Grier and Running 1977), we estimated evaporation from records of air tempera-

TABLE 1. Allometric leaf biomass equations used to estimate leaf areas of forests in the Cascade and Siskiyou Mountains.[1] *Form of the equations is:* $\ln Y = a + b \ln X$ *where* Y *is leaf biomass (kg) and* X *is tree diameter (cm) at dbh.*

Species	n	SE	R^2	a	b	Reference
Abies amabilis	9	0.077	0.97	–4.5872	2.1926	This study
Abies concolor[2]	25	0.159	0.94	–3.5457	1.9278	This study
Abies magnifica				(use *A. concolor*)		
Abies procera	6	0.034	0.99	–4.8898	2.1683	This study
Acer macrophyllum				–3.765	1.617	Grier and Logan (1976)
Arbutus menziesii				(use *Castanopsis chrysophylla*)		
Castanopsis chrysophylla				–3.123	1.693	Grier and Logan (1976)
Libocedrus decurrents				(use *Thuja plicata*)		
Pinus jeffreyi				(use *P. ponderosa*)		
Pinus lambertiana				–4.023	2.032	Grier and Logan (1976)
Pinus monticola				(use *P. ponderosa*)		
Pinus ponderosa	9	0.338	0.84	–4.4302	2.0967	This study
Pseudotsuga menziesii				–4.151	1.982	Grier and Logan (1976)
Quercus spp.				$\log_{10}$ (leaf area) 3.8493 + 1.6436 $\log_{10}$ (Dia.)		Whittaker and Woodwell (1968)
Taxus brevifolia				(use *Tsuga mertensiana*)		
Thuja plicata	6	0.085	0.91	–2.6595	1.7824	This study
Tsuga heterophylla				–4.130	2.128	Grier and Logan (1976)
Tsuga mertensiana	11	0.025	0.97	–3.8294	1.9756	This study

[1] These equations differ slightly from those cited by Gholz and others (1976) based upon increased sample sizes. In particular, the equations for *Pseudotsuga* and *Tsuga heterophylla* give somewhat larger estimates of leaf area. Appropriate statistics are included for equations not published elsewhere.

[2] No specific data are available on *Abies concolor*. This equation represents data pooled from all other *Abies* species.

ture for the summer months of July, August, and September, a generally dry period comparable from year to year.

To estimate evaporation from temperature data, we used locally developed regressions (Reed and Waring 1974, Waring and others 1978) of average-day water-vapor-pressure deficits (VPD) on average-day air temperature (T). For the Siskiyous, the function between 10° and 30°C air temperature was defined as:

$$\text{VPD (mb)} = 0.484 + 0.020\,T + 0.031\,T^2 \qquad (1)$$
$$r^2 = 0.81$$

In the west-central Cascades, the function was:

$$\text{VPD (mb)} = 4.025 - 0.751\,T + 0.503\,T^2 \qquad (2)$$
$$r^2 = 0.91$$

To estimate daily evaporative demand for representative sites, we substituted average-day temperatures into the appropriate equation. VPD estimates based on mean daily temperature and on hourly averages for 3 months of summer data differed by only 7 percent, suggesting that mean daily temperatures may be used to estimate daily evaporative demand between July and September.

We converted the VPD estimates to absolute humidity deficits (AHD) using the formula (Platt and Griffiths 1965):

$$\mathrm{AHD}\left(\frac{\mathrm{mg}}{\mathrm{cm}^3}\right) = \frac{217 \times 10^{-6}\,(\mathrm{VPD})}{273.16 + T} \tag{3}$$

Then, assuming a constant stomatal conductance (K_l) of 0.25 cm $\sec^{-1}$ (Reed and Waring 1974), we calculated potential transpiration (g $\mathrm{dm}^{-2}\mathrm{day}^{-1}$) of needle surface area as:

$$\mathrm{TRAN}\ (\mathrm{mg\ dm}^{-2}\mathrm{day}^{-1}) = \mathrm{AHD} \cdot K_l \cdot A_l \cdot N \tag{4}$$

where N = day length in seconds, and
A_l = leaf area of 1 dm^2.

Relative potential transpiration was calculated as the percentage of maximum potential transpiration (749 mg dm^{-2}) estimated for Stand 3 in the Siskiyou Mountains for the period from July through September.

Daytime temperatures during dormant season are often mild enough for significant carbon fixation (Emmingham and Waring 1977), and cold nights tend to reduce fixation the next day (Larcher 1969, Neilson and others 1972). Consequently, in representative stands in both areas, we determined the frequency of frost as the percentage of nights during the three coldest months (December, January, and February) when air temperature dropped below –2°C. We selected that –2°C threshold because Douglas-fir stomata close at that temperature.[1] Finally, to evaluate energy available for evaporation, we compared daily incoming shortwave radiation from Kipp solarimeters situated in valleys at both sites.

RESULTS

The leaf area for the 23 stands in the Siskiyous and the 17 stands in the Cascades averaged 18 and 35 $\mathrm{m}^2\mathrm{m}^{-2}$. In general, leaf-area values in the Cascades were nearly twice those for sites with similar temperature and moisture coordinates in the Siskiyou Mountains (Fig. 2). The highest value, 53 $\mathrm{m}^2\mathrm{m}^{-2}$, occurred in the transition zone and lower silver fir zone of the Cascade Mountains (Fig. 2A). The lowest values occurred in the Siskiyous on a subalpine area of mountain hemlock (5 $\mathrm{m}^2\mathrm{m}^{-2}$) and on ultrabasic parent materials (6 to 8 $\mathrm{m}^2\mathrm{m}^{-2}$), sites that never support a closed-canopy forest (Fig. 2B).

The Siskiyou environments included somewhat drier and cooler sites than found in the Cascades (Fig. 2). For comparison, the plot numbers correspond to those in earlier studies (Waring 1969, Zobel and others 1976). In both regions the temperature-growth index ranges from 30 at high elevations, where the growing season began in July and ended in October, to nearly 100 at lower elevations where the growing season may begin in early April. Patterns of maximum plant-moisture stress were also similar, ranging from 5 atmospheres, where soils were deep and fine-textured or received seepage, to 25 atmospheres on shallow or coarse-textured soils.

Table 2 presents the relative potential transpiration for a range of stands from both sites. For the most extreme environments with comparable indices for moisture stress and temperature growth, the Siskiyous had a potential transpiration 32 percent greater than that for comparable sites in the Cascades. On more moderate sites, the Siskiyou region still showed evaporative demand 8 to 13 percent greater than demand in the Cascades. The Siskiyous received 20 percent more solar radiation than the Cascades during the summer. On the coolest sites, however, evaporative

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[1] Reed, K. L. 1968. The effects of sub-zero temperatures on the stomata of Douglas-fir. Unpublished M.S. Thesis, University of Washington, Seattle.

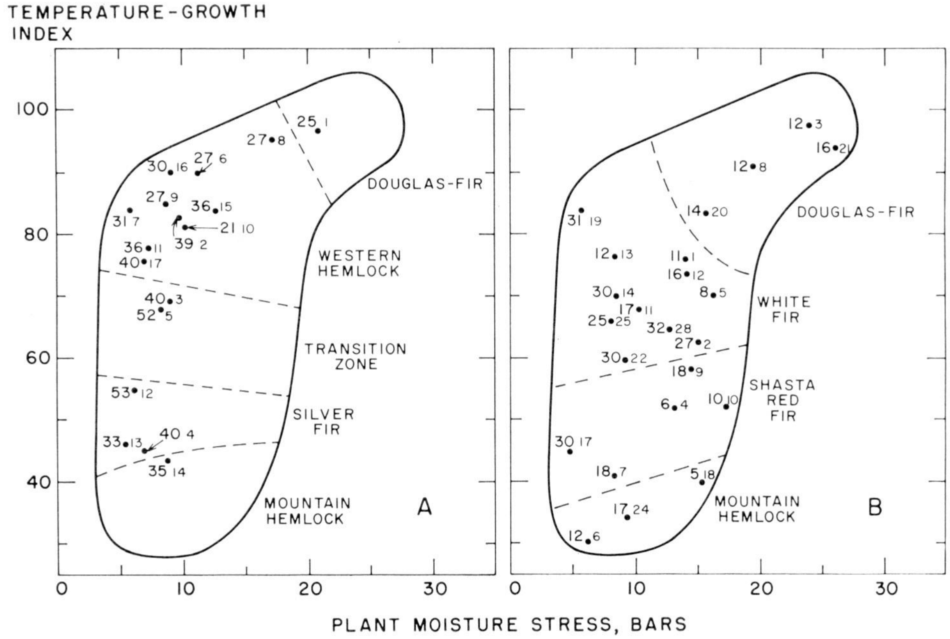

FIGURE 2. Foliage surface area (large numerals) of stands (small numerals) located in relation to predawn moisture stress and temperature growth indices for (A) the Cascade Mountains (Zobel and others 1974) and (B) the Siskiyou Mountains (Waring 1969). Foliage surface area (m^2m^{-2}) includes all surfaces of both conifer and broadleaved tree species. The enclosed areas are identical for both locations. Dotted lines represent approximate boundaries between vegetation zones. Note: Stands 4 and 5 of the Siskiyous were on ultrabasic soils.

demand was similar for both regions although the leaf area was two to three times greater in the Cascades.

In the Siskiyous, the percentage of nights with winter frost was consistently 40 to 60 percent greater than in the Cascade Mountains for sites with similar growing-season temperature indices (Table 2). For example, at the mountain hemlock site in the Siskiyous (Stand 6), 80 percent of the nights from January to March were frosty, compared to about 50 percent at the mountain hemlock site in the Cascades (Stand 14). Lower elevations showed a similar pattern.

The basal area and biomass data presented in Table 2 typify stands in both regions. Biomass for 23 stands in the Siskiyous and 17 stands in the Cascades averaged 408 and 1,016 T ha^{-1}. Basal areas measured in the Cascades were nearly double those in the Siskiyous.

DISCUSSION

The Cascade Mountains had greater leaf area than the Siskiyous (Fig. 2), and leaf area followed a definite pattern of distribution within each region. Maximum leaf areas accumulated where moisture stress was low and where the temperature growth index was between 50 and 80. The amount of leaf area supportable by a plant community fell as environments became more extreme. Thus, indices of temperature and moisture would explain many of the differences in leaf area within a region. If we compare ratios of sapwood basal area to foliage biomass (Grier and Waring 1974), the differences noted between overstory leaf areas of the Cascades and

TABLE 2. Comparison of stand characteristics for representative sites in the eastern Siskiyou and west-central Cascade Mountains.[1]

Plot	Dominant vegetation	Basal area	Biomass[2]	Leaf area	Plant moisture stress	Temperature growth index	Relative potential transpiration[3]	Frequency of winter frost[4]
		m^2 ha^{-1}	*T ha^{-1}*	*$m^2 m^{-2}$*	*atm.*			*Percent*
SISKIYOUS (1967 data)								
3	*Pinus ponderosa* *Quercus kelloggii* *Pseudotsuga menziesii*	27.5	249	12.0	24	98	100	34
1	*Pseudotsuga menziesii* *Abies concolor* *Pinus ponderosa*	27.5	205	11.0	14	74	78	57
22	*Pseudotsuga menziesii* *Abies concolor*	64.2	594	30.0	9	59	72	76
6	*Tsuga mertensiana* *Abies magnifica*	50.4	621	12.0	6	35	41	80
CASCADES (1972 data)								
1	*Pseudotsuga menziesii*	72.5	851	23.5	26	102	68	16
2	*Pseudotsuga menziesii* *Tsuga heterophylla*	98.6	1,174	38.0	11	84	65	19
5	*Pseudotsuga menziesii* *Tsuga heterophylla* *Abies amabilis*	137.0	1,773	51.5	8	67	64	27
4	*Abies procera* *Abies amabilis* *Tsuga heterophylla*	113.6	1,058	38.0	8	38	38	30
14	*Tsuga mertensiana* *Abies amabilis*	64.2	730	37.3	10	32	35	49

[1] Siskiyou data from Waring (1969); Cascade data from Zobel and others (1976).

[2] Biomass estimated with equations in Grier and Logan (1977).

[3] For July-August-September, according to procedures described by Reed and Waring (1974). 100% = 749 mg dm^{-2} of exposed foliage.

[4] Percentage of nights during December, January, and February when air temperature dropped below –2°C during 2 years (1965 and 1966 in Siskiyous; 1973 and 1974 in Cascades).

Siskiyous, using the technique of the present study, may be conservative. Including understory leaf areas would only emphasize the differences between the two regions because understory leaf area is uniformly greater in the Cascades than in the Siskiyous.

Within the midrange of the temperature axis, air temperatures remained better for photosynthesis year-around, and respiration requirements were relatively low to maintain living tissue. Thus the annual net carbon-fixation on the moist sites (plant moisture stress less than 10 b) with moderate temperatures favors both leaf area and biomass accumulations. On warmer sites, greater evaporative demand leads to depletion of soil water, stomatal closure, and lower photosynthesis rates (Emmingham and Waring 1977), as well as generally higher respiration rates (Tranquillini and Schütz 1970).

The consistently smaller leaf areas in the Siskiyou region partly resulted from greater evaporative demand during the summer, especially at warmer, lower elevation sites. High evaporative demand can cause severe water deficits in leaves, resulting in midday stomatal closure (Helms 1965). Even during early summer when soil water may be adequate, high evaporative demand can cause partial stomatal closure (Running 1976, Watt and others 1976). Thus, in two areas with similarly limited soil moisture, the area with the higher evaporative demand has less transpiring/respiring surface area.

More frequent winter frosts also may have contributed to the lower leaf areas found in the Siskiyou region. This was especially true at the high elevation sites where the evaporative demand was similar in the two regions. Even in December and January, temperatures were often above freezing at the high-elevation sites in the western Cascade Mountains. In contrast, the Siskiyou subalpine zone had 3 months of frequent frost and below-freezing temperatures. Low temperatures and high solar radiation, a condition common in the Siskiyous, can result in winter desiccation and greatly reduced photosynthesis (Tranquillini and Machl-Ebner 1971).

The more extreme winter environments in the Siskiyous could explain the abrupt reduction in leaf area from the white fir to the red fir and mountain hemlock forests. On the other hand, the milder winter temperatures associated with greater cloud cover in the Cascade Mountains may explain why leaf area differed only slightly from the transition zone to the subalpine forests.

Many of the remaining anomalies in leaf area distribution may be explained in terms of nutrition. In the Siskiyous, Stands 4 and 5—sparse forests of Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.)—developed on ultrabasic parent materials imbalanced in essential nutrients (Kruckeberg 1954). In the Cascades, all soils were derived from similar, nutritionally balanced, parent materials[2] although foliar analysis showed nitrogen stress in Stand 10 which supported little leaf area for its particular moisture stress-temperature loci (Zobel and others 1976). In Sweden additions of nitrogen and phosphorus to some soils resulted in a threefold increase in leaf area of *Picea abies* L. (Tamm 1974). Similar trends in Scotland have been reported with *Pinus nigra* var. *maritima* (Ait.) Melv. (Miller and Miller 1976). Thus nutritional deficiencies could account for otherwise unexplained low values of leaf area.

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