LEAF AREA OF MATURE NORTHWESTERN CONIFEROUS FORESTS: RELATION TO SITE WATER BALANCE[1]

CHARLES C. GRIER[2] AND STEVEN W. RUNNING[3]

School of Forestry, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. Leaf area of mature coniferous forest communities of western Oregon appears to be related primarily to site H_2O balance rather than characteristics of tree species composing the community.

Leaf areas were determined for stands in communities ranked along measured gradients of precipitation and evaporative potential. Nine coniferous and 1 deciduous tree species were found in the various stands along these gradients. Leaf areas of these stands were linearly correlated with a simple site H_2O balance index computed from measurements of growing season precipitation, open pan evaporation, and estimates of soil H_2O storage. Species composition had no apparent influence on the relation between community leaf area and site H_2O balance.

Key words: Coniferous forests; forest structure; leaf area; moisture gradients; Oregon; site water balance.

INTRODUCTION

One of the major biotic factors involved in terrestrial ecosystem production is community leaf area. The relation between leaf area and production is obvious; leaf area provides the surface across which photosynthetic gas exchange and transpiration occur. Previous studies have apparently accepted the leaf area of forest communities as an ecosystem characteristic related to a range of variables such as species composition, stand structure, tree physiology, and climatic factors (e.g., Whittaker and Niering 1975). Thus, it is known intuitively that stand leaf area decreases in areas where water is limited, but factors associated with this decrease have not been adequately examined.

The climate of the U.S. Pacific Northwest characteristically includes a relatively rainless period of varying duration and intensity beginning in late spring and ending in midautumn (Franklin and Dyrness 1973). This rainless period normally begins at the same time as the growing season of coniferous forests of the region. This means that water required by forests for growth and survival through the summer is mainly provided by water stored in the soil at the beginning of the growing season. As a consequence of this seasonal pattern of precipitation, many coniferous forests in the Pacific Northwest experience moderate to severe moisture stress in mid- to late summer (Zobel et al. 1976).

Data from an earlier study (Whittaker and Niering 1975) showed an association between net primary production (NPP) and leaf area index (LAI) in water-

[2] Present address: College of Forest Resources, University of Washington, Seattle, Washington 98195 USA.

[3] Present address: Department of Forest and Wood Sciences, Colorado State University, Fort Collins, Colorado 80521 USA.

limited ecosystems in the Santa Catalina Mountains of Arizona. Other data from this study showed associations between both LAI and NPP and a moisture stress index derived from phytosociological and climatic observations. We interpreted these data as indicating that, in primarily water-limited environments, NPP is at least as closely associated with LAI as it is with available moisture.

On forested sites where atmospheric evaporative demand during the growing season is greater than available water, trees must strike a balance between maximizing photosynthesis and maintaining a suitable internal water status. Increasing leaf area would increase photosynthetic potential but at the cost of increased transpirational water loss. To a certain extent, trees can control water loss through physiological control of stomatal aperture (Running 1976; Kramer and Kozlowski 1960). But stomatal closure restricts CO_2 exchange and thus reduces production. Tissue water potential of established coniferous trees is apparently maintained at levels > -25 bars (Ritchie and Hinckley 1975). At this point stomata of all studied conifers are continuously closed (Lopushinsky 1969). We suspect that on sites where available soil water and stomatal control are insufficient to maintain internal water potential of trees above -25 bars, leaf area is kept in balance with evaporation through reduction of leaf area. Short-term adjustments of leaf area may result from a variety of factors including changes in needle morphology due to water stress (Richter 1974) or premature senescence and loss of foliage due to high water stress (Kramer and Kozlowski 1960). However, long-term adjustments of leaf area probably result from mortality of less competitive individuals.

There is good evidence that leaf area of forest communities reaches a more or less steady state early in succession (Kira and Shidei 1967; Marks and Bormann 1972). In this paper we suggest that the magnitude of steady state leaf area of mature conifer forests in the

Pacific Northwest may be regulated by the balance between evaporative demand and water available to the stand during the growing season.

METHODS

Leaf area was determined for study plots in each of the major vegetation zones crossed by a transect line between Lincoln City and Bend, Oregon (Fig. 1). This line was chosen to cross the greatest number of vegetation zones of western central Oregon. Climate and vegetation of these zones is described by Franklin and Dyrness (1973); names of vegetation zones used in this paper generally follow their usage.

Four to 6 plots were established in stands in each of the major vegetation zones crossed by the transect. Six plots were established only in the heterogeneous vegetation zones at the eastern end of the transect. All plots in each zone were located within ±50 m of the average elevation of that zone. Elevations chosen for plots were felt to be the approximate average elevation for each vegetation zone at the latitude of the transect line. Vegetation zones in which plots were established are described in Table 1.

With few exceptions (e.g., the *Artemisia tridentata* and *Picea sitchensis* zones) plots were located in 100- to 130-year-old stands; all plots were located on mesic sites within each zone. The age of *Artemisia tridentata*
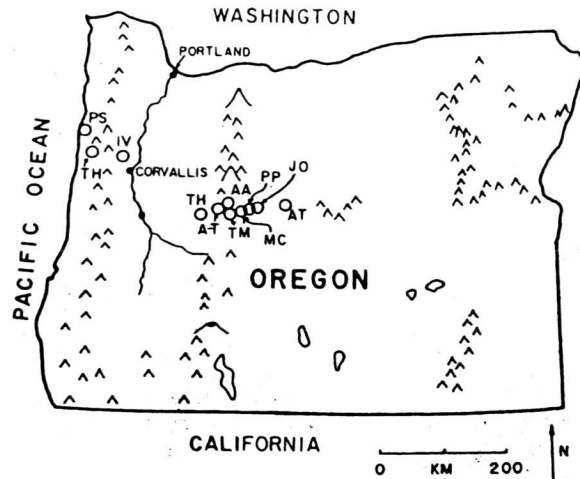

FIG. 1. Map of Oregon showing location of study plots in the various vegetation zones. Letter pairs on map refer to vegetation zones according to the usage of Franklin and Dyrness (1973). Letters identify the following zones: PS, *Picea sitchensis* zone; TH, *Tsuga heterophylla* zone; IV, Interior (Willamette) Valley zone; A-T, *Abies-Tsuga* transition zone; AA, *Abies amabilis* zone; TM, *Tsuga mertensiana* zone; MC, east slope mixed conifer zone; PP, dense *Pinus ponderosa* subzone; P-P, *Pinus ponderosa-Purshia* subzone; JO, *Juniperus occidentalis* zone; and AT, *Artemisia tridentata* zone.

TABLE 1. Climatic averages and principal tree species of the vegetation zones of western Oregon

Vegetation zones[a]	Average[b] elevation (m)	Precipitation (cm)		Mean temp (°C)		Major tree species
		Annual	Jun–Aug	Jul	Jan	
Coastal *Picea sitchensis*	90	250	20	16	5	*Tsuga heterophylla* *Picea sitchensis*
Coast range *Tsuga heterophylla*	300	200	15	16	2	*Pseudotsuga menziesii* *Tsuga heterophylla*
Interior (Williamette) valley	60	100	5	19	4	*Pseudotsuga menziesii* *Quercus garyana*
Western Cascade *Tsuga heterophylla*	350	180	10	18	1	*Pseudotsuga menziesii* *Tsuga heterophylla*
Tsuga-Abies Transition	900	200	15	15	−1	*Pseudotsuga menziesii* *Tsuga heterophylla*
Abies amabilis	1,200	240	20	14	−2	*Abies procera* *Abies amabilis* *Pseudotsuga menziesii*
Tsuga mertensiana	1,500	240	20	12	−4	*Tsuga mertensiana* *Abies amabilis*
Eastslope mixed conifer	1,300	100	4	19	−2	*Pseudotsuga menziesii* *Abies grandis* *Pinus ponderosa*
Pinus ponderosa	1,100	50	4	19	−4	*Pinus Ponderosa*
Juniperus occidentalis	1,000	30	4	19	−1	*Juniperus occidentalis*
Artemisia tridentata	1,000	20	3–4	21	−4	Treeless

[a] After Franklin and Dyrness (1973).

[b] Approximate midpoint of each elevation range.

[c] For this study, the *Pinus ponderosa* zone was divided into 2 subzones: (1) the *Pinus ponderosa-Purshia tridentata* subzone, a climax pine community, and (2) the denser *Pinus ponderosa* subzone which is probably seral or transitional to the mixed conifer zone. The *Pinus-Purshia* subzone averages ≈100 m lower in elevation that the *Pinus Ponderosa* subzones.

TABLE 2. Climatic data for a transect from west (Astoria) to east (Madras) across western Oregon. Climatic data are from U.S. Weather Bureau records for Oregon

Location	Vegetation zone[a]	Elevation (m)	July temperature (°C) $\bar{x}$	July temperature (°C) Max	Growing season precipitation (cm) Year	Growing season precipitation (cm) 1 May– 1 Oct.	Open pan evapora- tion (cm) 1 May– 1 Oct.	H_2O balance index[b] (cm)
1) Astoria	*Picea sitchensis*	70	16.0	20.6	196.7	30.1	46.9	+13.2
2) Corvallis	Interior valley	70	18.9	27.1	100.4	10.1	84.6	−44.6
3) Detroit Dam	*Tsuga heterophylla*	370	17.9	26.5	192.9	25.1	76.7	−21.6
4) Wickiup Dam	Eastslope mixed conifer	1,330	9.0	27.3	53.8	4.2	82.0	−47.8
5) Madras	*Juniperus occidentalis*	1,000	18.7	31.2	22.9	1.2	114.1	−91.2

[a] After Franklin and Dyrness (1973).

[b] H_2O balance index = $AW - E$; where AW is soil water storage plus growing season precipitation or annual precipitation if this is less than soil water storage, and E is open pan evaporation.

in plots containing this species was not determined. Plots were located in 35- to 40-year-old stands in the *Picea sitchensis* zone; older stands in this zone have their canopy biomass reduced by windstorm damage (Grier In press). Uneven-aged stands were used in the *Pinus ponderosa* and *Juniperus occidentalis* zones; these species typically occur in all-aged stands.

Plots were normally 0.25 ha but in the heterogeneous *Pinus ponderosa* and *Juniperus occidentalis* zones, they were 0.5 ha. Diameter and species of all trees on each plot was determined.

Leaf area for the forested plots was computed from regressions of leaf biomass on stem diameter and measured leaf dry weight to surface area conversions. Regressions of leaf biomass on stem diameter for *Tsuga heterophylla* and *Pseudotsuga menziesii* are from Grier and Logan (In press). Leaf biomass regressions for *Abies amabilis, Abies procera, Tsuga mertensiana,* and *Pinus ponderosa* are from previously unpublished data of the senior author. These regressions were obtained using sampling procedures outlined by Grier and Waring (1974). Leaf biomass regressions for *Pinus cembroides* (Whittaker and Neiring 1975) were used for *Juniperus occidentalis* and regressions for *Pseudotsuga menziesii* were used for *Abies grandis*. Leaf area regressions on stem diameter for *Quercus alba* (Whittaker and Woodwell 1967) were used for *Quercus garyana*.

Leaf dry weight to surface area conversions for most species are from Gholz et al. (1976). Where the appropriate conversions were lacking, values for species with similar leaf morphology were used. A weight to area conversion for *Thuja plicata* was used for *Juniperus occidentalis* and *Pseudotsuga meziesii* was used for *Abies grandis*. The weight to area conversion for *Pinus ponderosa* is from Running, personal communication.

Leaf area for the *Artemisia tridentata* plots was estimated from unpublished leaf biomass data furnished by Dr. Takao Fujimori, Kansai Branch Government Forest Experiment Stations, Kyoto, Japan. These data were obtained by plot harvest. Weight to area conversions for *Artemisia tridentata* were determined using

an optical planimeter (Gholz et al. 1976). Leaf area of *Artemisia tridentata* in the *Juniperus occidentalis* plots was estimated from cover estimates as a proportion of that in the *Artemisia tridentata* plots.

Growing season and precipitation data were obtained from U.S. Weather Bureau or U.S. Forest Service records for sites near the various plots. These data were supplemented by precipitation collectors installed in openings near many of the plots. Elevation was determined from topographic maps of the plot areas.

A site water balance index was calculated from U.S. Weather Bureau records (U.S. Environmental Data Service 1975) for those vegetation zones for which the necessary records were available. Table 2 shows characteristics of sites from which records were obtained. This index was computed by adding soil water storage to measured growing season precipitation then subtracting open pan evaporation. Growing season precipitation was defined as that falling between 1 May and 1 October. Soil water storage of the forested plots was estimated from soil profile descriptions, textural classification, and a relation between soil textural class and available soil water (Brady 1974). Soil water storage for *Juniperus* and *Artemisia* plots are from Driscoll (1964). Annual precipitation was substituted for soil water storage where storage was greater than annual precipitation.

Vegetation in the areas where open pan evaporation was measured was similar to that in the plot areas. In all cases, open pan evaporation was measured at about the same elevation as the leaf area plots; the greatest difference was 50-m elevation difference (Table 2).

RESULTS

Figure 2 shows leaf area of the various vegetation zones along the west-east transect of Oregon together with average precipitation and elevation of the zones. Rain-shadow effects can be seen in the distribution of precipitation with elevation. Storms normally cross Oregon from west to east, or from left to right in Fig. 2. Precipitation decreases substantially to the east of both the Coast and Cascade Ranges.

PS *PICEA SITCHENSIS*
TH *TSUGA HETEROPHYLLA*
IV INTERIOR VALLEY
A-T *ABIES-TSUGA* TRANSITION
AA *ABIES AMABILIS*
TM *TSUGA MERTENSIANA*
MC MIXED CONIFER-EASTSLOPE
PP *PINUS PONDEROSA*
P-A *P. PONDEROSA-PURSHIA*
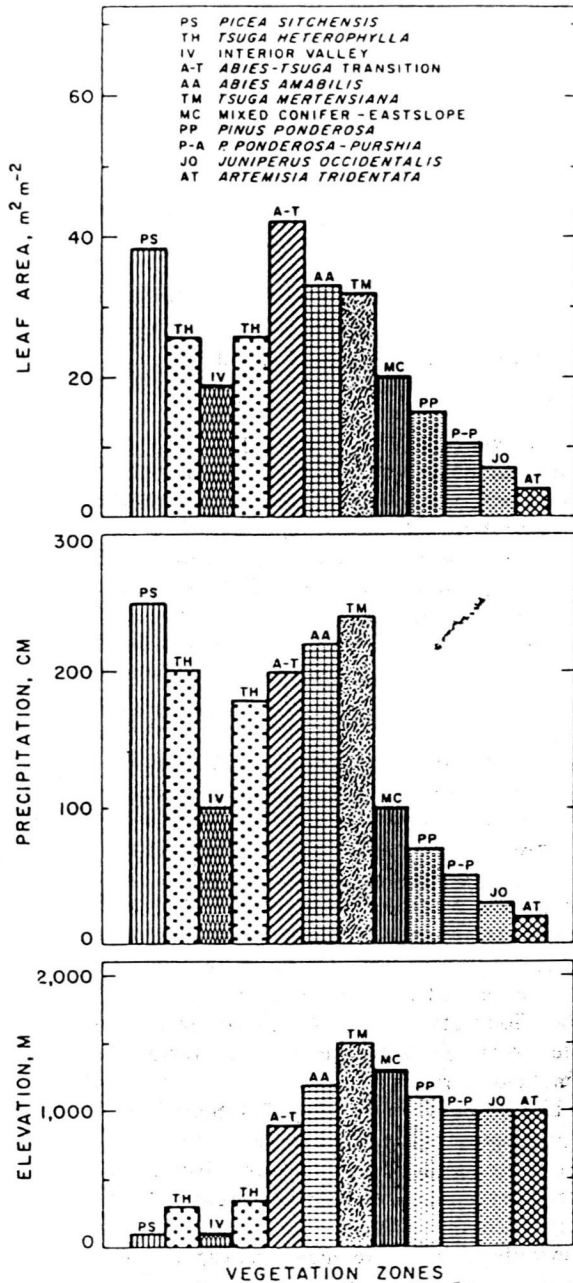JO *JUNIPERUS OCCIDENTALIS*
AT *ARTEMISIA TRIDENTATA*

FIG. 2. Leaf area of major vegetation zones of western Oregon compared with average precipitation and elevation in these zones. Zones are arranged along a transect from coast (*Picea sitchensis*) to the interior plateau (*Artemisia tridentata*). Leaf area is for all sides of leaves; values given are averages of 4–6 plots per zone. Coefficients of variation generally increased towards drier climates ranging from ≈ ±4% in the *Picea sitchensis* zone to ≈ ±30% in the highly variable *Juniperus occidentalis* zone. (Symbol for *P. ponderosa - Purshia* in legend should be P-P not P-A.)

Although not shown in Fig. 2, between-plot variability generally increased towards drier climates. Coefficients of variability for leaf area ranged from ≈ ±4% for the coastal *Picea sitchensis* and midelevation *Abies-Tsuga* transition zones to ≈ ±30% for the
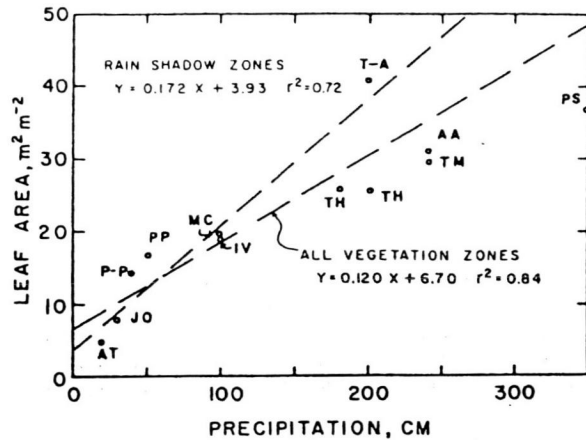

FIG. 3. Leaf area plotted against precipitation for the various vegetation zones of western Oregon. Regression lines are plotted for all vegetation zones and zones lying in the rain shadow of the Coast and Cascade ranges. Letters near plotted points identify zones. Letter codes for zones are the same as used in Fig. 2.

Juniperus occidentalis zone. Variability along the transect appeared to result from increasing stand heterogeneity toward the drier climates. This may reflect a wider range of microclimates or slower recovery from past disturbances in harsh environments. On the other hand, leaf area variability in the *Artemisia tridentata* shrub-steppe zone was ±8%, less than that of the *Pinus ponderosa* and *Juniperus occidentalis* zones.

Leaf area changes along the transect are probably more or less continuous rather than stepwise as shown in Fig. 2. The abrupt changes in leaf area from zone to zone are probably more a reflection of locating plots in the midpoint of each zone than any discontinuities in vegetation.

Figure 3 shows leaf area of the different vegetation zones plotted against annual precipitation. Regressions of leaf area on precipitation are also plotted for (1) vegetation zones lying in mountain rain shadows and (2) all vegetation zones. While leaf area clearly increases with increasing precipitation, dispersion
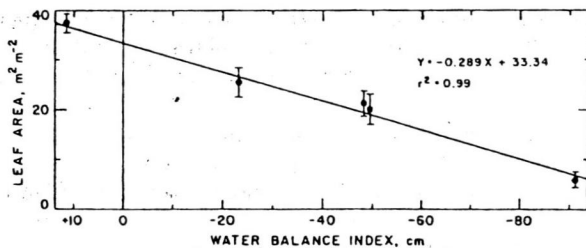

FIG. 4. Relation between water balance index (WBI) and leaf area in 5 forest zones of western Oregon. Zones plotted are, from left to right: *Picea sitchensis*, *Tsuga heterophylla*, interior (Willamette) valley, east slope mixed conifer, and *Juniperus occidentalis* (after Franklin and Dyrness 1973). Bars show range of observed leaf areas in each vegetation zone.

around both regressions is large. Linear relations between precipitation and leaf area are shown here as the simplest case, a variety of nonlinear relations might reduce the dispersion.

Figure 4 shows the relations between average leaf area of several vegetation zones and the water balance index. Negative values indicate evaporation in excess of available water (defined as stored soil water plus precipitation during the growing season) while positive values indicate available water in excess of evaporation. Vegetation zones plotted in Fig. 4 include both the wet and dry extremes of coniferous forests in Oregon.

Discussion

Leaf areas of forests in western Oregon are large, even in drier vegetation zones. However, leaf areas of coniferous forests are generally large. Earlier research by Gholz et al. (1976) has shown values generally comparable to those obtained during this study in old-growth forests of this region. Moreover, leaf areas of coniferous forests in several parts of the world are comparable to those reported here. For example, values reported by Whittaker and Neiring (1975) for some coniferous forests of the Santa Catalina Mountains of Arizona are within the range of values reported here (doubling LAI to approximate total leaf area). Similarly, Westman and Whittaker (1975) report a projected leaf area (or LAI) of 20 m^2/m^2 for coastal stands of *Sequoia sempervirens* in California, and Satoo (1974) reports mean leaf biomass for 20 stands of *Abies sachalinensis* of 14.5 tonnes ha[1]. Using cross-sectional area to LAI and surface area to dry weight ratios reported by Gholz et al. (1976), the above values convert to total leaf areas of ≈ 43 and 22 m^2/m^2 for *Sequoia* and *Abies sachalinensis* stands, respectively. Again, these values are comparable to values reported here.

Projected leaf areas of 18–20 m^2/m^2, or total leaf areas of 38–40 m^2/m^2 appear to be about the upper limit reported for coniferous forests in any environment (Gholz et al. 1976). Expansion of leaf area above this range may be restricted by levels of photosynthetically active radiation reaching the lower canopy (Kira et al. 1969). Both the *Picea sitchensis* and *Tsuga-Abies* transition zones of western Oregon are in the 38–43 m^2/m^2 range.

In contrast, leaf areas reported for nonconiferous forests are typically much less than many of the values reported here. Deciduous forests of the eastern United States typically have projected leaf areas of about 6 m^2/m^2 or total leaf areas of 12 m^2/m^2 (Whittaker 1966).

Leaf area obviously increases with increasing precipitation (Fig. 2). However, the relatively wide dispersion about the regression lines (Fig. 3) indicates that factors regulating leaf area are more complex than a simple relation to annual precipitation. Leaf area apparently has a finite upper limit; thus the idea of unlimited linear expansion of leaf area with increasing pre-

cipitation is clearly unrealistic. One of the premises of this study was that, under optimum conditions, the upper limit for projected leaf area of conifer forests at this latitude was ≈ 20 m^2/m^2. Based on this premise, lower leaf areas would result from suboptimum conditions.

Gholz et al. (1976) have proposed that maximum leaf areas in coniferous forests are found where mild summer temperatures restrict respiration rates and mild winter temperatures permit considerable photosynthesis during the dormant season. Conditions that permit high photosynthesis and low foliage respiration are found in the *Picea sitchensis* and *Abies-Tsuga* transition zones; it was observed during this study that these zones produced the highest leaf areas. But to a certain extent, conditions of high photosynthesis and low foliage respiration are also found in a large portion of the *Tsuga heterophylla* zone, yet leaf areas here are lower.

Gholz et al. (1976) have pointed out an association between high summer water stress and reduced leaf area. But summer water stress in a community is a result of a number of factors including soil water storage, summer precipitation, temperature, net radiation, humidity, wind, and physiological characteristics of species involved. Low soil temperatures can also produce water stress by restricting rates of water uptake (Hinckley and Ritchie 1972). This may be a cause of water stress in high-elevation forests. However, the relation of soil temperature to water stress would be most evident outside the growing season. No evidence of severe water stress was found in high-elevation conifer forests in Oregon during the growing season (Zobel et al. 1976).

The principal factors contributing to summer water stress are incorporated in the water balance index shown in Fig. 4. Soil water storage and growing season precipitation are explicit terms used in computing the index. Other factors such as net radiation, humidity, and wind are implicitly included in open pan evaporation. The terms as combined indicate the magnitude by which evaporative potential exceeds the amount of water available for transpiration.

There are a number of ways in which evaporation from vegetative surfaces can be reduced. The two most apparent in coniferous forests are reduced leaf area and physiological control of stomatal aperture.

Figure 4 shows leaf area of several coniferous forests plotted against the water balance index. This plot covers the full range of leaf areas and water balance values observed in coniferous forests of western Oregon. Moreover, stands plotted in this diagram are of 5 distinctly different community types including 9 different major coniferous species. This linear relation suggests that leaf area may be directly and primarily related to site water balance. A nonlinear relation, or greater dispersion about the regression line, would imply that factors such as physiological characteristics of the var-

ious species also influenced leaf area. The relatively close fit suggests that climatic factors may be dominant.

Results of several other studies tend to support this view. For example, Gholz et al. (1976) have shown total leaf area of relatively pure *Pseudotsuga menziesii* stands ranging from about 20 m^2/m^2 in xeric to 32 m^2/m^2 in cool-moist habitats. This represents a 60% increase in leaf area along a moisture gradient in stands of primarily the same species. Moreover, stomatal response to water stress appears to occur within a fairly narrow range of leaf water potential in conifers adapted to different habitats. Running (1976) has shown that stomatal response to water stress is relatively similar for *Pseudotsuga menziesii* and *Pinus ponderosa*. Yet *Pseudotsuga* is the dominant conifer in many of the more mesic climatic zones while *Pinus ponderosa* is common throughout drier zones. We recognize that physiological mechanisms serve as adaptations to dry environments; drought deciduousness and *Crassulaceae* acid metabolism are examples of these. But stomatal control of transpiration in response to water stress provides only a fairly narrow range of adaptation especially when compared to the wide range of site water balances found in coniferous forest environments.

The data in Fig. 4 are not sufficient for a rigorous test of our hypothesis; currently, data are limited by the number of sites at which open pan evaporation is measured. Moreover, the relation probably will not hold for ecosystems (1) under severe nutrient deficiency or gross nutrient imbalance such as in serpentine-derived soils; (2) in areas where mechanical damage by wind mortality or heavy snowfall has reduced canopy biomass; and (3) in areas where the combination of short growing season and low temperatures reduce productivity substantially (*Abies amabilis* and *Tsuga mertensiana* zones). Local differences in slope, aspect, and soil water storage will produce variation in the site water balance index, but leaf area should reflect these variations. Use of standardized evaporimeters (e.g., Waring and Herman 1966) in a range of communities together with detailed measurement of soil rooting zone water content should provide data for a rigorous test of the relation shown here.

Leaf area of coniferous forests may also correlate well with estimates of evapotranspiration or net radiation. The advantage of estimating water balance over either of these measures is the ease with which it can be determined with simple instruments.

Our data suggest a direct relation between environment and community photosynthetic structure. Further, these data suggest that other indices of community water stress based on observed vegetation response (Whittaker and Neiring 1975; Waring 1969) actually show the effects of factors combined in this index. For conifers, the relations between the water balance index and leaf area may be largely independent of species. This independence indicates that while the ability to exert physiological control over water loss may be a principal factor in determining which species will contribute to community leaf area, the physical water balance dictates what that potential leaf area will be.

LITERATURE CITED

Brady, N. C. 1974. The nature and properties of soils. 8th edition. MacMillan Publishing Co., New York. 639 p.

Driscoll, R. S. 1964. Vegetation-soil units in the central Oregon juniper zone. USDA For. Serv. Res. Pap. PNW-19. 60 p.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. 417 p.

Gholz, H. L., F. K. Fitz, and R. H. Waring. 1976. Leaf area difference associated with old-growth forest communities in the western Oregon Cascades. Can. J. For. Res. 6:49–57.

Grier, C. C. Biomass, productivity and nitrogen-phosphorus cycles in hemlock-spruce stands of the central Oregon coast. *In* R.J. Zososki and W. A. Atkinson [eds.] Proceedings, conference on management of western hemlock. Inst. For. Prod. Bull. No. 22. College of Forest Resources, Univ. Washington, Seattle. In press.

Grier, C. C., and R. S. Logan. 1977. Old-growth Douglas-fir forests of a western Oregon watershed: Biomass distribution and production budgets. Ecol. Monogr. In press.

Grier, C. C., and R. H. Waring. 1974. Conifer foliage mass related to sapwood area. For. Sci. 20:205–206.

Hinckley, T. M., and G. A. Ritchie. 1972. Reaction of mature *Abies* seedlings to environmental stresses. Trans. Mo. Acad. Sci. 6:24–37.

Kira, R., and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. J. Ecol. 17:70–87.

Kira, T., K. Shinozaki, and K. Hozumi. 1969. Structure of forest canopies as related to their primary productivity. Plant Cell Physiol. 10:129–142.

Kramer, P. J., and T. T. Kozlowski. 1960. Physiology of trees. McGraw-Hill, New York. 642 p.

Lopushinsky, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 130:258–263.

Marks, P. L., and F. H. Bormann. 1972. Revegetation following forest cutting: Mechanisms for return to steady state nutrient cycling. Science 176:914–915.

Richter, H. 1974. Elevated suction tensions and morphological alterations caused by transverse cuts in a *Taxus* stem. Flora 163:291–309.

Ritchie, G. A., and T. M. Hinckley. 1975. The pressure chamber as an instrument for ecological research, p. 165–254. *In* A. Macfayden [ed.] Advances in ecological research. Academic Press, New York.

Running, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. For. Res. 6:104–112.

Satoo, T. 1974. Primary production relations in a young plantation of *Abies sachalinensis* in Hokkaido: Materials

for the studies of growth in forest stands, II. Bull. Tokyo Univ. For. 66:127–137.

U.S. Environmental Data Service. 1975. Climatological data, Oregon. National Oceanographic and Atmospheric Administration, Asheville, N.C.

Waring, R. H. 1969. Forest plants of the eastern Siskiyous: Their environmental and vegetational distribution. Northwest Sci. 43:1–17.

Waring, R. H., and R. K. Hermann. 1966. A modified piche evaporimeter. Ecology 47:308–310.

Westman, W. E., and R. H. Whittaker. 1975. The pigmy forest region of northern California: Studies on biomass and primary productivity. J. Ecol. 63:493–520.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103–121.

Whittaker, R. H., and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. Ecology 56:771–790.

Whittaker, R. H., and G. M. Woodwell. 1967. Surface area relations of woody plants and forest communities. Am. J. Bot. 54:931–939.

Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46:135–156.