Structure and Productivity of Juniperus occidentalis in Central Oregon [1]

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ABSTRACT: Western juniper ecosystems are well-adapted to the arid environments of central Oregon. In the stand examined, trees rarely exceeded 8 m in height and were uniformly spaced. Although foliage biomass averaged 4315.0 kg ha^{-1}, total stand leaf area was only 2.0 ha ha^{-1}. Total aboveground biomass averaged 21,161.4 kg ha^{-1}. Aboveground net primary production of the juniper was estimated at 1097 kg $ha^{-1}y^{-1}$. Juniper forests have a higher proportion of bark and a much lower stem water-storage capacity than other coniferous forests in the Pacific Northwest. The individual trees examined had leaf areas per unit of stem water-conducting tissue that were less than for fir species on more mesic sites but similar to those for two western pine species. Double sampling provided reliable estimates of means and confidence intervals for juniper biomass and leaf area.

INTRODUCTION

Western juniper (*Juniperus occidentalis* Hook. subsp. *occidentalis*) occupies the driest of all coniferous forest sites in the Pacific Northwest. In the dry forest zone of central Oregon and Washington (Franklin and Dyrness, 1973), stands of juniper merge with ponderosa pine (*Pinus ponderosa*) forests on the moister sites and border plains of big sagebrush (*Artemisia tridentata*) throughout the region. In the past, fire has controlled the spread of juniper into the adjacent shrub/steppe (Burkhardt and Tisdale, 1976), and the practice of suppressing range fires—widespread during this century—has apparently allowed juniper to invade these recently nonjuniper communities.

Because juniper can compete successfully with more palatable forbs and grasses, range managers generally regard the species as a pest. Furthermore, many of its apparent physical adaptations to this harsh environment, such as a stubby growth form with severe taper, make juniper undesirable for large-scale commercial exploitation by the forest products industry.

As a result of this management status, methods to eradicate juniper, usually to release grazable grasses and forbs (Bedell and Bunch, 1978), have been extensively researched (Martin, 1978). However, little work has focused on juniper's commercial prospects, even as a fuel, and only preliminary work has examined its role as habitat for small mammals, birds and other game animals (Maser and Gashwiler, 1978). Nothing is known of its place in the hydrology, nutrient cycles or production relations of the dry forest zone.

This study provides data from one western juniper habitat for: (1) the most important aboveground structural features of the juniper stand and the reliability with which they can be assessed; (2) the aboveground net primary production of the tree strata, and (3) the specific structural adaptations to the arid environment of the study area.

STUDY AREA

Located in central Oregon at 1356-m elevation along a NE-facing slope at the summit of Horse Ridge, the study site lies in the rain shadow of the Cascade Moun-

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tains (44°N lat, 120°W long). May to October rainfall measured 160 mm during 1976 and 80 mm during 1977. Annual snowfall averages 900 mm (Franklin *et al.*, 1972). The evaporative demand from May to October 1977, as measured with evaporimeters (Waring and Hermann, 1966), averaged 40% greater than at several sites W of the Cascades summit.

The site, adjacent to the Horse Ridge Research Natural Area described by Franklin *et al.* (1972), has been little grazed because of the absence of springs and wells along the ridge. In recent years, motorized recreational use has increased in the area, although no evidence was found for disturbances on the study site. Franklin *et al.* (1972) classified the vegetation on the upper part of Horse Ridge as the *Juniperus/Artemisia/Carex filifolia* community type. Because lack of disturbance is necessary to this type, it is restricted in area and was not described by Driscoll (1964).

Soils, derived from aerially deposited pumice, are generally shallow—65 cm to closely packed, fractured basalt bedrock. Soils on Horse Ridge have not been mapped. Pedons examined on this site were extremly stony representatives of the Torriorthent great group. Comparable soil data for other juniper habitats were given by Driscoll (1964).

The soils have low water-storage capacities. In 1977, gravimetric soil water to a depth of 1 m was never present at less than 0.1 atm tension in the spring and reached 15.0 atm by early August. In contrast, western Cascade Mountain sites had soil water at less than 0.1 atm tension in May and still had water at less than 1.0 atm in lower horizons in August, even after 6 weeks of drought. Predawn xylem water potentials averaged -30 atm in mid-August.

The vegetation on the site was sparse. Live juniper trees, averaging 246 per ha, were interspersed with big sagebrush bushes averaging 12% cover and other minor species averaging 3% cover. The juniper was uneven-aged, ranging from less than 30 years to over 350 years.

METHODS FOR DETERMINING BIOMASS AND LEAF AREA

Double sampling with regression (Cochran, 1963) of the juniper trees in the stand combines two methods of estimating plant components: (1) the complete harvest, separation and measurement of selected (n) plants, and (2) the nondestructive measurements of all plants (n′), including the plants that were destructively analyzed.

All live trees (n′) in seven 20-m-radius circular plots randomly located within a 1-ha area were nondestructively measured and recorded. Ten (n) junipers, randomly selected from three size classes (0-75, 75-150 and > 150 cm in basal circumference) within the circular plots, were destructively analyzed between June and August; four were from the small size class and three each from medium and large size classes. Based on destructive analysis from western Oregon, this sample size was considered maximum for the 8 weeks available for fieldwork. Trees judged to have less than half of a live crown were excepted from sampling with consequences that will be discussed.

Selected plants were cut off at the litter surface. Then the bole was cut into 1- or 2-m sections that were covered with a Plexiglas sheet and tissue paper so that the outlines of the heartwood, sapwood and bark could be traced. Later the tracings were cut up, and the areas were measured with a Lambda Instruments LiCor Portable Surface Area Meter (Model No. LI3000) to estimate stem volumes from extremely irregular patterns of wood and bark development (Fig. 1). All live and dead branches were cut away from the bole into 1-m lengths and grouped according to mean diameters, large (⩾ 10 cm) or small (< 10 cm). All small live branches supporting foliage were clipped below the foliage clump to create a third group of small, live, foliage-bearing twigs. Live and dead branches and foliage-bearing twigs were weighed fresh in the field to the nearest 0.5 kg.

Fig. 1.—Base of the largest juniper harvested for this study (273 cm basal circumference, 8.5 m tall). Sapwood forms a lighter discontinuous band around the outer edge, and bark inclusions commonly penetrate near the center of the stem. At the base of this tree are four isolated pockets of rot

Subsamples of small and large live and dead branches and foliage-bearing twigs were randomly selected and weighed fresh to the nearest 0.5 g in the field, then frozen for laboratory analyses. Finally, stem sections taken 1 m aboveground were cut to determine the specific gravities of the stem and bark. If rot was found, sections were taken in sound wood as near to the 1-m cut as possible. No effort was made to assess belowground biomass.

In the laboratory, branch subsamples were dried at 70 C and weighed to the nearest 0.5 g. Foliage was separated from nongreen foliage-bearing twigs, which were then weighed fresh, dried at 70 C and reweighed. Green foliage was again subsampled three times. The projected surface area of each new subsample was estimated with the LiCor meter. Each segment of green "foliage" was assumed cylindrical so that the total leaf area (all sides; Gholz *et al.*, 1976) could be computed as 3.14 times the projected area. To compensate for underestimates from Lambda-meter measurement of very small pieces of foliage, leaf areas were adjusted upward 20%, which was determined by plotting estimated vs. actual areas of paper strips 1 cm long and 1 cm to 0.05 cm wide. Subsamples were then dried at 70 C and weighed to 0.1 mg.

Stem sections were sanded smooth, their areas determined as explained, and their thicknesses measured. Bark was then separated, and wood and bark were dried at 70 C and weighed to 0.5 g.

From the moisture contents, volumes and areas of the subsamples, and from the total fresh weights in the field, 11 whole-plant components were estimated: foliage biomass and surface area, live and dead branch biomass, whole stem volume and biomass, stem bark volume and biomass, stem wood volume and biomass, and sapwood volume.

STATISTICAL ANALYSES FOR BIOMASS AND LEAF AREA DETERMINATIONS

These statistical analyses have been adapted from Uresk *et al.* (1976), after Cochran (1963), and will only be outlined here.

Data from the destructively analyzed n trees were used to compute a set of regression equations relating various plant parts (dependent variables) to basal circumference, chosen as the independent variable because it correlated highest with the most components. Circumference at breast height, crown volume, circumference at half-height, height and diameter squared times height were also evaluated as independent variables. None consistently correlated with the dependent variables as well as did basal circumference (irregular stem development makes diameters difficult to estimate accurately). The equations and the n′ nondestructive measurements were used to compute a mean component size per individual tree ($\overline{Y}_I$) and the variance [Var ($\overline{Y}_I$)].

To obtain a component total per hectare ($\overline{Y}_{tot}$), $\overline{Y}_1$ was multiplied by the mean number of plants per hectare, $\overline{Z}$:

$$\overline{Y}_{tot} = \overline{Y}_I\overline{Z} \quad (1)$$

However, the 10 component data points showed curvilinear relationships with the independent variable, as often occurs with plant biomass estimation, so both axes were log-transformed. The transform resulted in linear correlations and significantly reduced variances; therefore, the statistical analyses were completed entirely in log units, including the evaluation of the regression coefficients, $\overline{Y}_I$, Var ($\overline{Y}_I$), $\overline{Y}_{tot}$ and Var ($\overline{Y}_{tot}$). Accordingly, equation (1) was rewritten:

$$\overline{Y}_{tot} = \overline{Y}_I + \overline{Z} \quad (2)$$

where $\overline{Y}_{tot}$, $\overline{Y}_I$ and $\overline{Z}$ are all in log units. Then the variance of $\overline{Y}_{tot}$ was given by the additive relationship:

$$\mathrm{Var}(\overline{Y}_{tot}) = \mathrm{Var}(\overline{Y}_I) + \mathrm{Var}(\overline{Z}) \quad (3)$$

assuming that $\overline{Y}_I$ and $\overline{Z}$ are independent.

If the analysis is done in log units, a term must be applied before retransformation to arithmetic units (Brownlee, 1967; Baskerville, 1972) to correct the mean value $\overline{Y}_I$ for log bias. This ensures that the arithmetic value of $\overline{Y}_I$ is the mean, the parameter of interest, and not the median. $\overline{Y}_{tot}$ is composed of the already corrected $\overline{Y}_I$ and $\overline{Z}$.

Variances were not corrected. Instead, confidence limits were constructed in log units at a specified probability level, and then these limits were retransformed. The results were mean components per plant and per hectare with respective asymmetric confidence intervals around the mean that estimates the true distribution of the component (assuming that $\overline{Y}_{tot}$ is normally distributed).

If the number of samples is assumed optimal, then a reduction in variance using double sampling—rather than simple random sampling—can be calculated by equations from Cochran (1963, p. 337-339). The optimum ratio of n′ to n can also be estimated as:

$$\frac{n}{n'} = \frac{\sqrt{V_n C_{n'}}}{\sqrt{V_{n'} C_n}} \quad (7)$$

where V_n is estimated by $S^2_{y.x}$; $V_{n'}$ is estimated by S^2_y-$S^2_{y.x}$; and C_n and $C_{n'}$ are the relative costs (Uresk *et al.,* 1976).

PRODUCTION ESTIMATES

The net aboveground primary production of the juniper in the study area was estimated as the average of annual biomass increment over the last 5 years. To provide average annual increments of stem and live branch biomass (wood and bark) for the 10 destructively analyzed trees, the biomass equations were applied to current basal circumferences and circumferences corrected from stem growth measurements. Linear regressions of the 5-year increment of stem and branch biomass on basal circumference were used with the current basal circumference measured for other trees in the stand to estimate branch and stem increments (plus bark) on an area basis. Foliage production was assumed to be 30% of the total foliage biomass based on *Juniperus osteosperma* data from Utah (Mason and Hutchings, 1968). Production losses to herbivore grazing, nonfoliar litterfall and losses of current tissues to mortality were not estimated, nor was production by nonjuniper species.

RESULTS

Basal circumference of n plants destructively analyzed averaged 16 cm less than that of n′ plants measured, and the range was less for n plants than n′ plants (Table 1). Crown volumes, heights and sapwood basal areas for the n plants are also included in Table 1; sapwood basal area often is a linear estimator of leaf area

(Grier and Waring, 1974; Waring *et al.*, 1977) and, as such, is a useful variable to document. The study area had 246 ± 20 live juniper trees per ha; aerial photos indicated 194 - 321 live trees per ha within 3 km of the study area. Dead trees were not tallied.

The 12 regression equations used in this analysis represent logarithmic transformations of both variables, with consistently high r^2 values (Table 2). The lowest r^2 and greatest variance were associated with the dead branch biomass. The linear equations relating leaf surface area to sapwood basal area (Table 2) can be con-

TABLE 1.—Dimensions of live junipers on Horse Ridge: n′ = measured and n = the 10 destructively analyzed

Dimension	$\bar{X} \pm$ SE	Range	Coefficient of variation
Basal circumference (n′)	120.07 ± 7.8 cm	10.5 - 317.0 cm	0.61
Basal circumference (n)	104.10 ± 25.0 cm	14.5 - 273.0 cm	0.76
Crown volume (n)	92.21 ± 44.05 m^3	0.64 - 303.46 m^3	1.36
Height (n)	4.45 ± 0.74 m	1.00 - 8.50 m	0.52
Sapwood basal area (n)	345.56 ± 103.61 cm^2	12.34 - 1098.06 cm^2	0.95

TABLE 2.—Regression equations for estimating component biomass, volume, surface area and biomass increment for western juniper with basal circumference (cm) as the independent variable. The first 12 follow the form $\ln(Y) = A + B \cdot \ln(X)$ with variances ($S^2_{y.x}$) in logarithmic units. The last four are linear, untransformed equations with variances in arithmetic units

Dependent variable	A	B	$S^2_{y.x}$	r^2
Stem wood biomass (kg)	–8.5947	2.6389	0.029	0.995
Stem wood volume (cm^3)	–0.8568	2.6006	0.048	0.990
Stem bark biomass (kg)	–10.251	2.6333	0.152	0.974
Stem bark volume (cm^3)	–2.5414	2.6006	0.106	0.981
Whole stem biomass (kg)	–8.3939	2.6344	0.029	0.995
Whole stem volume (cm^3)	–0.6719	2.5977	0.135	0.965
Sapwood volume (cm^3)	0.7232	2.1313	0.135	0.965
Live branch biomass (kg)	–7.3115	2.3337	0.068	0.985
Dead branch biomass (kg)	–11.8460	2.8323	0.664	0.908
Leaf surface area (m^2)	–2.5917	1.5383	0.019	0.990
Leaf biomass (kg)	–4.2430	1.5606	0.024	0.988
Height (m)	–1.8616	0.7329	0.031	0.934
Leaf surface area (m^2) = 0.559 • (sapwood breast height, cm^2)			944.5	0.960
Leaf biomass (kg) = 0.140 • (sapwood breast height, cm^2)			56.6	0.966
5-year stem biomass increment (wood + bark, kg) = –0.383 + 0.0362 • (basal circumference)			0.930	0.910
5-year live branch biomass increment (wood + bark) = –0.344 + 0.0165 • (basal circumference)			0.356	0.840

TABLE 3.—Average dimensions of western juniper estimated by double sampling

Dependent variable	Units per plant ($\bar{Y}_I$)	90% confidence interval ($\bar{Y}_I$)
Stem wood biomass	30.5 kg	20.3 - 45.8 kg
Stem wood volume	59,700 cm^3	39,600 - 90,000 cm^3
Stem bark biomass	6.0 kg	3.9 - 9.4 kg
Whole stem biomass	36.5 kg	24.5 - 54.5 kg
Whole stem volume	70,812 cm^3	47,300 - 106,100 cm^3
Sapwood volume	35,600 cm^3	24,500 - 33,100 cm^3
Live branch biomass	28.0 kg	19.2 - 40.9 kg
Dead branch biomass	3.9 kg	2.1 - 7.2 kg
Leaf surface area	82.5 m^2	64.8 - 105.1 m^2
Leaf biomass	17.5 kg	13.7 - 22.5 kg
Total biomass	85.9 kg	59.5 - 125.1 kg

trasted with cited studies. Estimates of each of the 11 components (Table 3) include the means per plant ($\overline{Y}_I$) and per hectare ($\overline{Y}_{tot}$), plus 90% confidence intervals about each mean. Based on a comparison of percent cover on the study site with one sagebrush community examined nearby for a related study, sagebrush biomass was about 900 kg ha^{-1} and leaf area was 0.30 ha ha^{-1}. Biomass of other species (grasses and herbs) was judged negligible in comparison.

Specific gravities varied from tree to tree and throughout the bole. The wood averaged 0.50 g cm^{-3}, with a standard deviation of 0.05 and a range of 0.437 - 0.678 (sample size = 20). The bark mean was 0.51 g cm^{-3}, with a standard deviation of 0.07 and a range from 0.407 - 0.637 (sample size = 18).

Net production estimates for juniper were 195, 2 and 900 kg ha^{-1} y^{-1}, respectively, for stem, branch and foliar biomass increment—a total of 1097 kg ha^{-1} y^{-1}. The two regression equations used for determining stem and live branch increments are included at the bottom of Table 2. Confidence intervals for the production estimates were not constructed, but, because the estimates were derived from the biomass equations, the intervals should be comparable to those for the biomass estimates.

DISCUSSION

Biomass and leaf area.—The juniper ecosystem has much less biomass and volume than other mature coniferous forest types (Fujimori *et al.*, 1976; Gholz *et al.*, 1976; Grier and Logan, 1977; Waring *et al.*, 1978). A 2-year-old tropical forest in Colombia (Folster *et al.*, 1976) and a 16-year-old jack pine stand in New Brunswick (MacLean and Wein, 1976) have biomass equal to that of this juniper stand, which has many individuals > 200 years old. Leaf biomass of the juniper ecosystem averaged about one-third and leaf areas averaged about 0.15 of Douglas-fir and western hemlock forests in western Oregon (Gholz *et al.*, 1976; Waring *el al.*, 1978).

The values in Table 3 and biomass values from other studies should be interpreted cautiously. This analysis assumed that the measurement of basal circumference was error-free, which is not strictly true. Sixteen of the 246 live trees per ha were rejected from analysis due to poor canopy vigor (less than half a live crown); this essentially means they were measured incorrectly because their foliage biomass and area were equivalent to a tree with about two-thirds the actual measured basal circumference. Because the analysis did not deduct this difference, foliar characteristics in Table 3 may be somewhat overestimated. If we assume each of the 16 trees had one-half the foliage biomass of other trees of the same basal circumference on the plot, the foliage biomass and leaf area figures in Table 3 would be reduced 9.7% and 9.5%, respectively. Selection of samples according to predeter-

TABLE 3.—(continued)

	Units per ha ($\overline{Y}_{tot}$)	90% confidence interval ($\overline{Y}_{tot}$)
Stem wood biomass	7,505.7 kg	4,703.9 - 11,976.5 kg
Stem wood volume	14.7 m^3	9.2 - 23.5 m^3
Stem bark biomass	1,485.1 kg	897.1 - 2,458.6 kg
Whole stem biomass	8,989.7 kg	5,661.0 - 14,275.6 kg
Whole stem volume	17.4 m^3	10.9 - 27.8 m^3
Sapwood volume	8.8 m^3	5.6 - 13.7 m^3
Live branch biomass	6,894.9 kg	4,431.0 - 10,728.7 kg
Dead branch biomass	961.8 kg	500.4 - 1,848.6 kg
Leaf surface area	2.0 ha	1.5 - 2.8 ha
Leaf biomass	4,315.0 kg	3,072.9 - 6,059.4 kg
Total biomass	21,161.4 kg	13,665.3 - 32,912.3 kg

mined size classes does not invalidate the sampling technique, but does yield larger confidence intervals while better estimating the means (Uresk *et al.,* 1976). Also, no effort was made to document stem rot, prevalent in large trees, because the regressions were based on the specific gravities of sound wood. Again, this could overestimate stem wood biomass. Volumes, of course, are not so affected.

The mean ratio of hours in the field and laboratory for the destructive work (C_n) to the hours for the nondestructive work ($C_{n'}$) was estimated to be about 500:1. With the high ratio and the very high correlations between component size and basal circumference (Table 2), the double sampling effectively reduced the variances over simple random sampling. For example, Var($\overline{Y}_I$) for foliage biomass was decreased 25% over simple random sampling. The optimal ratio of n′ to n under these conditions for juniper was 21:1.

Few studies of biomass express variances associated with estimates. Comparisons with one study from western Oregon (Grier and Logan, 1977) show that the confidence intervals from double-sampling juniper are narrower than those from estimating biomass in Douglas-fir forests by standard regression techniques, even when the latter does not estimate the variation in the number of trees per hectare. Confidence intervals for juniper are larger than those calculated as 1.67 (t value at $p = 0.1$, 60 df) times the standard errors reported for a 16-year-old jack pine stand, but they are smaller than those calculated for other ages of the same vegetation (MacLean and Wein, 1976).

Specific leaf areas ($cm^2\ g^{-1}$), used to convert foliar biomass to surface area, generally are highly variable as they are extremely sensitive to light and other environmental variables (Gholz, *et al.,* 1976; Gholz, 1978). However, this was one source of variation in juniper that was unusually small. The mean specific area for n trees was 44.0 $cm^2\ g^{-1}$, with a standard deviation of only 2.0 (range from 40.0 - 46.0, sample size = 27). The low specific leaf areas reflect xeromorphic adaptations (Esau, 1960), as the juniper leaf has a thick-walled sclerenchyma-like hypodermis, a packed epidermis and several palisade layers.

Furthermore, biomass equations generally show wider scatter when a single nonfunctional parameter—such as diameter at breast height (1.3 m) or basal circumference—is used as an independent variable to estimate foliage mass. The tightness of fit of the data points in the regression analysis and the small range in specific leaf areas indicate a uniform environment for the plants on Horse Ridge and perhaps an absence of interference among trees. This, in turn, implies a system in steady state or one at least long undisturbed. Driscoll (1964) noted that the other juniper stands with N aspects and soils similar to those on this study plot had the same evenly spaced, open savannah appearance.

On a per-hectare basis, the very low leaf areas for juniper can be explained as an adaptation to a restricted water environment (Grier and Running, 1977). Contributing factors include lower precipitation, higher evaporative demand and more limited soil water availability than in western Oregon and other areas supporting higher leaf areas.

Recent studies emphasize sapwood as a water storage compartment, 350 $m^3\ ha^{-1}$ mainly in the stems of 450-year-old Douglas-fir forests (Waring and Running, 1976, 1978), which serves as a buffer during short intervals of water stress. Sapwood in the juniper forest is 2.5% of stem volume, or about 9 $m^3\ ha^{-1}$, indicating that water storage within the stems is not a major adaptive feature of juniper.

Although Douglas-fir from western Oregon can support almost twice the leaf area per unit area of stem sapwood, the ratios of leaf area to sapwood for juniper (0.56) and pine (0.51) do not differ significantly (Fig. 2). However, the total stand leaf areas for juniper are about one-third those of pine stands, juniper are much shorter with canopies nearer the ground, and maximum sapwood areas per tree are much more restricted in the juniper (700 cm^2) than in either the pine or fir (> 2000 cm^2).

Bark biomass in the juniper stand was large in relation to whole-stem biomass, averaging almost 17%. In coastal stands of western hemlock and Sitka spruce (*Picea sitchensis*), bark biomass was only 7.7% (Fujimori *et al.,* 1976). In the western Cascades, ca. 10 - 11% of the stem biomass is bark (Fujimori *et al.,* 1976; Grier and Logan, 1977). The highest value for western Oregon forests is 14% in a subalpine stand of noble fir (*Abies procera*) (Fujimori *et al.,* 1976).

Production.—Without accurate estimates of foliar production, herbivore grazing losses, nonfoliar litterfall, losses of current tissue to mortality and nonjuniper production, the "net production" values in this paper are tentative (Kira and Shidei, 1967). However, they are included as a basis for initial comparisons with other forest types.

Aboveground net production of 1097 kg ha^{-1} y^{-1} ranks this western juniper community among the least productive of the mature evergreen tree communities in the world (Art and Marks, 1971). In the United States, it is intermediate between the 650 kg ha^{-1} y^{-1} of pygmy conifer-oak scrub in the Santa Catalina Mountains of northern Arizona (Whittaker and Niering, 1975) and the 2100 kg ha^{-1} y^{-1} of *Pinus pungens* heath in the Great Smoky Mountains of Tennessee (Whittaker, 1966). The adjacent ponderosa pine communities of central Oregon annually produce twice as much dry matter as the juniper community. Western Oregon forests of

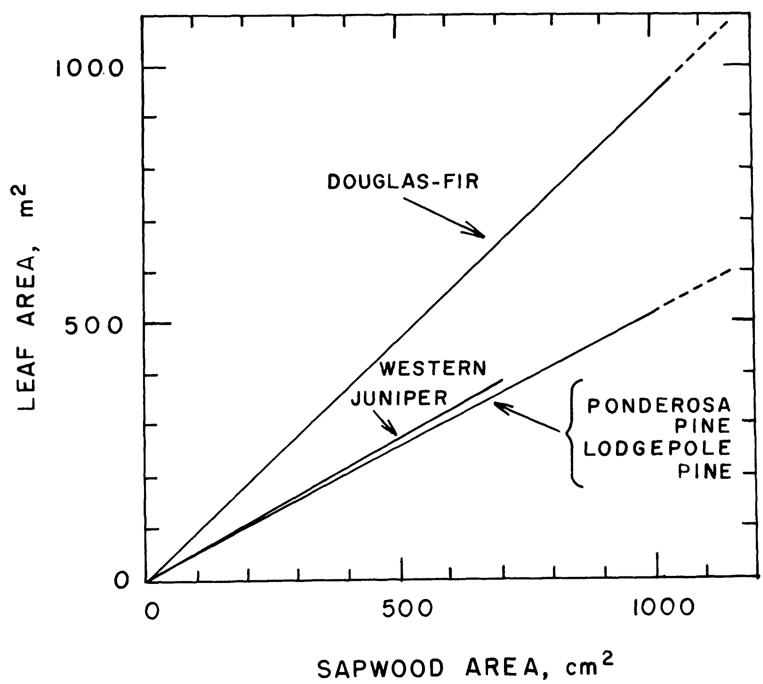

Fig. 2.—Total leaf surface area vs. sapwood cross-sectional area at breast height (1.3 m) for four western evergreens. The Douglas-fir and ponderosa pine (Grier and Waring, 1974) were converted to leaf area using constant specific leaf areas of 130 cm^2 g^{-1} and 100 cm^2 g^{-1}, respectively. Lodgepole pine data are for the Rocky Mountains (S. W. Running, pers. comm. Dep. For. Wood Sci., Colo. State Univ., Fort Collins)

Douglas-fir produce 8000 to 12,000 kg ha^{-1} y^{-1} (Fujimori *et al.*, 1976; Grier and Logan, 1977).

For the juniper, the biomass:net production ratio (biomass accumulation) is 20, the production:foliage biomass ratio is 0.24, and the production:leaf area ratio is 50—all low when compared to other forest types. However, when leaf areas are expressed on an all-side basis, the last ratio is comparable to those of the pygmy conifer-oak scrub in Arizona and a *Tsuga canadensis-Rhododendron* community from the Great Smoky Mountains (Westman and Whittaker, 1975).

The structure and production of juniper on this site reflect the relatively harsh growing conditions found at high elevations in arid regions, and juniper has many characteristics necessary for surviving drought and temperature extremes (Levitt, 1972). In fact, late summer xylem water potentials were similar to values for Douglas-fir on the drier sites in western Oregon (Zobel *et al.*, 1976), indicating that individuals here were under no more water stress than other western conifers. Individuals store little water in the stems, and thick bark covers each juniper stem. Stand leaf areas are low, foliage exhibits xeromorphic adaptations, and water-conducting tissue in the stems is minimal. Production of wood and foliage is very restricted compared with other forest types.

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LITERATURE CITED

ART, H. W. AND P. L. MARKS. 1971. A summary of biomass and net annual primary production in forest ecosystems of the world p.—*In:* H. E. Young (ed.). Forest biomass studies, Univ. Maine Press, Orono.

BASKERVILLE, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.,* **2**:49-53.

BEDELL, T. E. AND T. R. BUNCH. 1978. Effects of western juniper on forage production and livestock grazing management, p. 163-169. *In:* R. E. Martin, J. E. Dealy and D. L. Caraher (eds.). Proceedings of the western juniper ecology and management conference. U.S. Dep. Agric. For. Serv., Portland, Oregon.

BROWNLEE, K. A. 1967. Statistical theory and methodology in science and engineering. 2d ed. John Wiley and Sons, New York. 400 p.

BURKHART, J. W. AND E. W. TISDALE. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology,* **57**:472-484.

COCHRAN, W. G. 1963. Sampling techniques. 2nd ed. John Wiley and Sons, New York. 413 p.

DRISCOLL, R. S. 1964. Vegetation—soil units in the central Oregon juniper zone. *U.S. For. Serv. Res. Pap. PNW-19.* 61 p.

ESAU, K. 1960. Plant anatomy. John Wiley and Sons, New York. 376 p.

FOLSTER, H., G. DE LAS SALAS AND P. KHANNA. 1976. A tropical evergreen forest site with perched water table, Magdalena Valley, Colombia. Biomass and bioelement inventory of primary and secondary vegetation. *Ecol. Plant.,* **11**:297-320.

FRANKLIN, J. F. AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. *U.S. For. Serv. Gen. Tech. Rep. PNW-8.* 417 p.

———, F. C. HALL, C. T. DYRNESS AND C. MASER. 1972. Federal research natural areas in Oregon and Washington: a guidebook for scientists and educators. U.S. For. Serv., Portland, Oreg. Various paging.

FUJIMORI, T., S. KAWANABE, H. SITO, C. C. GRIER AND T. SHIDEI. 1976. Biomass and primary production in forests of three major vegetation zones of the northwestern United States. *J. Jap. For. Soc.,* **58**:360-373.

GHOLZ, H. L. 1978. Assessing stress in *Rhododendron macrophyllum* through an analysis of leaf physical and chemical characteristics. *Can. J. Bot.*, **56**:546-556.

———, F. K. FITZ AND R. H. WARING. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. *Can. J. For. Res.*, **6**:49-57.

GRIER, C. C. AND R. S. LOGAN. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.*, **47**:373-400.

——— AND S. W. RUNNING. 1977. Leaf area of mature northwestern coniferous forests: relations to site water balance. *Ecology*, **58**:893-899.

——— AND R. H. WARING. 1974. Conifer foliage mass related to sapwood area. *For. Sci.*, **20**: 205-206.

KIRA, T. AND T. SHIDEI. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Jap. J. Ecol.*, **70**:70-87.

LEVITT, J. S. 1972. Responses of plants to environmental stresses. Academic Press, New York. 697 p.

MACLEAN, D. A. AND R. W. WEIN. 1976. Biomass of jack pine and mixed hardwood stands in northeastern New Brunswick. *Can. J. For. Res.*, **6**:441-447.

MARTIN, R. E. 1978. Fire manipulation and effects in western juniper (*Juniperus occidentalis* Hook.), p. 121-137. *In:* R. E. Martin, J. E. Dealy and D. L. Caraher (eds.). Proceedings of the western juniper ecology and management workshop. U.S. Dep. Agric. For. Serv., Portland, Oregon.

MASER, C. AND J. S. GASHWILER. 1978. Interrelationships of wildlife and western juniper, p. 37-83. *In:* R. E. Martin, J. E. Dealy and D. L. Caraher (eds.). Proceedings of the western juniper ecology and management workshop. U.S. Dep. Agric. For. Serv., Portland, Oregon.

MASON, L. R. AND S. S. HUTCHINGS. 1968. Estimating foliage yields on Utah juniper from measurements of crown diameter. *J. Range Manage.*, **20**:161-166.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 1977. Climatological data, Oregon. Issued annually by the National Climatic Center, Environmental Data Service, Asheville, N.C.

URESK, D. W., R. O. GILBERT AND W. H. RICKARD. 1976. Sampling sagebrush for phytomass. *J. Range Manage.*, **30**:311-314.

WARING, R. H., W. H. EMMINGHAM, H. L. GHOLZ AND C. C. GRIER. 1978. Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. *For. Sci.*, **24**:131-140.

———, H. L. GHOLZ, C. C. GRIER AND M. L. PLUMMER. 1977. Evaluating stems conducting tissue as an estimator of leaf area in four woody angiosperms. *Can. J. Bot.*, **55**:1474-1477.

——— AND R. K. HERMANN. 1966. A modified Piche evaporimeter. *Ecology*, **47**:308-310.

——— AND S. W. RUNNING. 1976. Water uptake, storage, and transpiration by conifers: a physiological model, p. 189-202. *In:* O. L. Lange, L. Kappen, E.-D. Schulze (eds.). Ecological studies, analysis and synthesis, Vol. 19: Water and plant life, Springer-Verlag, Berlin.

——— AND ———. 1978. Sapwood water storage: its contribution to transpirational and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant Cell Environ.*, **1**:131-140.

WESTMAN, W. E. AND R. H. WHITTAKER. 1975. The pygmy 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.

——— AND W. A. NIERING. 1975. Vegetation of the Santa Catalina Mountains, Arizona: V. Biomass, production and diversity along the elevational gradient. *Ibid.*, **56**:771-790.

ZOBEL, D. B., A. MCKEE, G. M. HAWK AND C. T. DYRNESS. 1976. Relations of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecol. Monogr.*, **46**:135-156.

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