RELATIONSHIP OF WESTERN JUNIPER STEM CONDUCTING TISSUE AND BASAL CIRCUMFERENCE TO LEAF AREA AND BIOMASS[1]

Richard F. Miller[2], Lee E. Eddleman[3], and Raymond F. Angell[2]

ABSTRACT.—The ability to measure leaf area and biomass on a plant community basis has many important ecological applications. These include quantification of gas exchange, use of water resources on the site, nutrient pools, and construction of models simulating production and resource allocation. To test a nondestructive technique for estimating leaf area and leaf biomass of western juniper (*Juniperus occidentalis* Hook.), sapwood area and basal circumference were evaluated as predictors of total leaf biomass and leaf area. Nineteen trees, ranging in size from 9.0 to 263 cm in circumference, were destructively sampled. The entire leaf biomass was harvested and measured, and regression equations were developed. Both sapwood area and basal circumference significantly (P < .01) correlated with projected leaf area and leaf biomass (r values = 0.98).

Knowledge of leaf area and leaf biomass on a plant community basis has many important ecological applications. Leaf area is important in gas exchange, the hydrologic cycle, and models simulating production and resource allocation. Leaf area is essential in assessing recovery rates in forested ecosystems following disturbance (Sollins et al. 1974). Waring et al. (1980) also found leaf area in combination with the annual growth increment of a tree (annual growth increment cm^2:leaf area m^2) a useful index for assessing vigor in conifers. Defining leaf biomass for a dominant species describes the size of a major nutrient and carbon pool in a plant community.

Measuring leaf area, on a whole plant basis, is difficult because of a high degree of variability among plants and across sites. Leaf area measurements are also labor intensive and often require destructive sampling. As a result of these difficulties, little information is available on leaf area in range ecosystems.

Foresters have successfully used sapwood area to indirectly estimate leaf area. Shinozaki et al. (1964) concluded that a constant cross-sectional area of conducting tissue supports a given unit of leaves. Since that time, researchers have found close relationships between sapwood area and leaf area (Dixon 1971, Grier and Waring 1974, Waring et al. 1977, Snell and Brown 1978, Whitehead 1978, Kaufmann and Troendle 1981, Marchand 1984). The correlation between leaf area and area of conducting tissue is presumably a function of the physiological balance between water demand by the crown and the ability of the stem to conduct water (Kaufmann and Troendle 1981). Application of this hypothesis, sometimes called the pipe model theory, is discussed by Waring et al. (1982).

Estimating the impact of western juniper (*Juniperus occidentalis* Hook.) woodlands on nutrient resources and the hydrologic cycle

requires estimates of leaf area and biomass. The objective of this study was to develop a useful, nondestructive technique for estimating leaf area and leaf biomass of western juniper woodlands by testing the pipe model theory. To do so, we evaluated the relationship between sapwood area and basal circumference with leaf biomass and leaf area.

MATERIALS AND METHODS

The study site is at the Squaw Butte Experimental Range on the northern fringe of the Great Basin in southeastern Oregon, 57 km west of Burns. The 40-year mean precipitation for this area is 300 mm. The study site is a mountain big sagebrush/Idaho fescue (*Artemisia tridentata* ssp. *vaseyana/Festuca idahoensis*) habitat type (Winward 1970) at an elevation of 1,350 m. Soils are fine-loamy, mixed, frigid Aridic Durixerolls, approximately 112 cm deep to columnar basalt.

Thirteen healthy trees ranging from 9 to 263 cm in circumference (2.9–84 cm in diameter) at the litter surface were selected for destructive sampling. Trees selected had full canopies showing no signs of insect damage or disease. Trees were subjectively selected so four trees would fall within each of three size classes: 2.5–6 cm, 6–20 cm, and 20–45 cm in basal diameter. The thirteenth tree was selected to represent the largest trees within the stand. All trees were single stemmed. Sampling was conducted from 20 June to 1 October 1984. Maximum error caused by the duration of sampling during the growing season is estimated to be 15% (Miller and Shultz 1987). Trees were divided into two segments along the main trunk (base and midsection). Sapwood area was measured at both points, and all foliage on branches attached to the main trunk above the point of sapwood measurement and basal circumference was removed, dried at 60 C for 72 hours, and weighed. Sapwood area and basal circumference were measured at the litter surface because of tree growth form. Sapwood was easy to distinguish from heartwood, particularly after several days of air drying. A piece of acetate was laid over the stem base and the sapwood area was outlined. A cut-out of the outlined sapwood was constructed from black paper and the area of the paper measured on a leaf-area meter. All or most of the limbs were removed prior to

felling the tree. One sample of approximately 0.1 kg of fresh leaf material was harvested from each tree during defoliation, sealed in plastic bags, and stored in a freezer for later evaluation of leaf weight to leaf area relationships.

Frozen samples of foliage were thawed in the lab and their areas measured on a Li-Cor leaf-area meter. Foliage was assumed to be cylindrical, so leaf-area readings were multiplied by π to compute total exposed leaf surface. Due to partial overlapping of lower adjacent leaves, total leaf surface area is underestimated (we estimated approximately 10%). Estimates of total gas exchange, however, will not be over- or underestimated as long as measurements per unit leaf area are also based on exposed leaf area. Following leaf-area measurements, samples were dried at 60 C for 72 hours, weighed, and added to the total foliage weight for the tree. Linear regression procedures were used to establish a relationship between leaf biomass (dry weight) and leaf area for both populations of trees. These equations were then used to convert total harvested leaf biomass to total leaf area for each tree.

In the following year a second population (n = 6) of trees at two sites in central Oregon, 175 km west of Squaw Butte, was selected for study. The relationship between sapwood area and basal circumference with leaf area in the second population was compared to the first. Habitat types at both locations were similar to the site sampled at Squaw Butte. Trees, ranging in circumference from 11 to 47 cm, were sampled similarly to those in the previous year.

Values representing the ratios of leaf area (m²) to sapwood area (cm²) and leaf area (cm²) to leaf weight (g) were derived for each of the trees sampled. Student's t-test was used to test the null hypothesis that mean ratios were identical between the two populations of trees sampled. The null hypothesis was accepted and data for the two populations were pooled for final analysis.

Basal circumference, basal sapwood area, and midsection sapwood area served as independent variables in regression analysis aimed at predicting total leaf area or total leaf biomass of the supported foliage. Possible differences in relationships derived from basal sapwood areas and midsection sapwood areas

Table 1. Regression equations, standard error of estimate (Sy.x), and correlation coefficents for estimating leaf biomass and leaf area.

n	Independent variable (X)	Dependent variable (Y)	Regression equation	Sy.x	Correlation coefficient
19	Leaf wt (g)	Leaf area (cm²)	$Y = -40.566 + 65.238X$	107.010	0.978
19	Sapwood area (cm²)	Leaf biomass (kg)	$Y = 1.237 + 0.024(X) + 0.00005(X^2)$	2.735	0.987
19	Sapwood area (cm²)	Leaf area (m²)	$Y = 8.145 + 0.155(X) + 0.00035(X^2)$	17.822	0.987
19	Basal circ. (cm)	Leaf biomass (kg)	$Y = -5.381 + 0.352(X)$	3.570	0.976
19	Basal circ. (cm)	Leaf area (m²)	$Y = -35.036 + 2.296(X)$	23.294	0.976
13[1]	Sapwood area (cm²)	Leaf biomass (kg)	$Y = 0.473 + 0.040(X)$	0.445	0.938
13	Sapwood area (cm²)	Leaf area (m²)	$Y = 0.220 + 0.504(X) - 0.0024(X^2)$	3.250	0.906
13	Basal circ. (cm)	Leaf biomass (kg)	$Y = -1.046 + 0.143(X)$	0.391	0.953
13	Basal circ. (cm)	Leaf area (m²)	$Y = -4.007 + 0.767(X)$	3.763	0.862

[1] Regression equations with n = 13 were developed for trees with basal circumferences less than 50 cm.
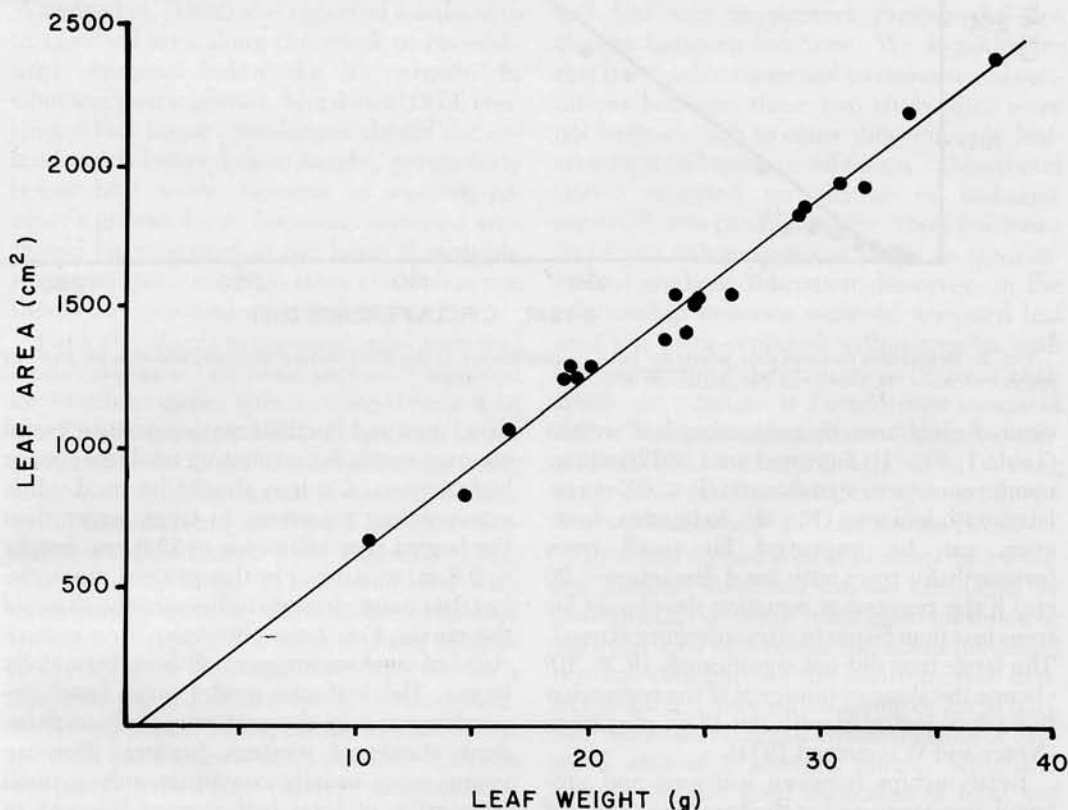

Fig. 1. Regression line and data points for leaf dry weight and leaf area for western juniper with n = 19, Sy.x = 107.010, and r = 0.978.

were evaluated by comparison of regression lines (Neter and Wasserman 1974). Regression lines were also compared between all trees sampled (n = 19) and with the big tree (263 cm in circumference) excluded. Appropriateness of the models finally selected to predict total leaf area or biomass was evaluated by ordering data in accordance with the independent variable and examining the residuals. Rank correlation of residuals with independent variables (Neter and Wasserman 1974) failed to reject the null hypothesis of constant variance (P > .05).

Results

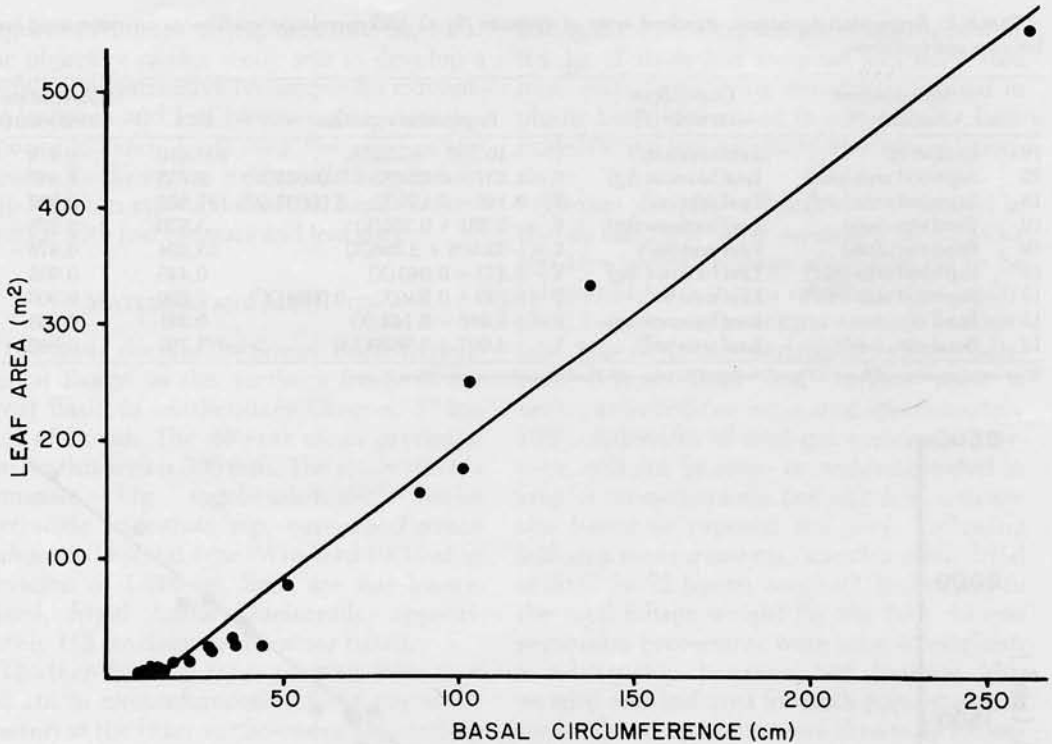A strong linear relationship between leaf weight and surface area of leaves allowed us to

Fig. 2. Regression line and data points for basal circumference at the litter surface and total leaf area for western juniper with n = 19, Sy.x = 23.294, and r = 0.976.

estimate leaf area by measuring leaf weight (Table 1, Fig. 1). Sapwood area and basal circumference were significantly (P < .01) correlated with leaf area (Fig. 2). Estimates, however, can be improved for small trees (primarily for trees with basal diameters < 20 cm) if the regression equation developed for trees less than 50 cm in circumference is used. The large tree did not significantly (P ≥ .10) change the slope or intercept of the regression line when included with the 18 smaller trees (Neter and Wasserman 1974).

Relationships between leaf area and sapwood area measured at the tree base, and leaf area and sapwood area midway up the trunk were significantly different (P < .05). At the tree base 1 cm^2 of sapwood supported 0.45 m^2 of leaf area. At the tree's midsection 1 cm^2 of sapwood supported 0.64 m^2 of leaf area. Gholz (1980) reported a leaf-area:sapwood ratio of 0.56 for western juniper when sapwood was measured at DBH.

DISCUSSION

Results of this study support use of the pipe model theory on western juniper. Both sap-

wood area and basal circumference are useful measurements for estimating total leaf area or leaf biomass. Caution should be used when extrapolating equations to trees larger than the largest tree (diameter = 82.8 cm, height = 9.8 m) measured in this project, since the last data point strongly influences the shape of the curve. Few trees, however, in a mature stand of western juniper will be substantially larger. The leaf-area model using basal circumference may also perform poorly on decadent stands of western juniper. Because young trees usually constitute only a small proportion of total leaf area or biomass in mixed-aged stands of juniper, the fact that the curve does not pass through the origin will add little error to an overall estimate of total leaf area for a western juniper woodland. If the stand is young, however, with numerous basal circumferences less than 50 cm, the regression model developed for small trees will improve the estimates.

The strong correlation between basal circumference and total leaf area is probably due to the significant (P < .01) relationship between sapwood area and basal circumference

(r = 0.98). Ovington et al. (1968) found a high correlation between bole cross-sectional area and leaf area in young *Pinus radiata*. Cross-sectional area, however, closely correlated with sapwood area since young trees have little or no heartwood.

The relationship between sapwood area and leaf area in western juniper changes above the litter surface. Less sapwood area is required to support a unit of leaf area as one moves up the trunk. This relationship, supported by both our work and that of Gholz (1980), may be partially due to butt swell. Waring et al. (1982) also reported a reduction in sapwood area along the trunk of *Pseudotsuga menziesii* below the live crown. In *Chamaecyparis obtusa*, Morikawa (1974) concluded that linear correlations should not extend much below breast height, particularly below butt swell. Because of western juniper's growth form, however, sapwood area should be measured at the base. If multiple stems are present, each stem circumference should be measured separately.

Ratio of leaf area to sapwood cross-sectional area (leaf area m^2:sapwood area cm^2) reported for 14 other conifer species ranged from 0.16 to 0.75 (Waring et al. 1982). In general, larger coefficients are found in tree species growing in more mesic environments, while trees with smaller coefficients are typical of drier environments (Kaufmann and Troendle 1981, Waring et al. 1982). When compared with other conifer species, the ratio between total leaf area to sapwood area in western juniper (0.45) is higher than might be expected for a tree growing in a relatively dry environment. Western juniper, however, has relatively low stomatal conductance rates per unit leaf area compared with other conifers and contains leaf morphological characteristics which avoid drought and reduce moisture loss (Miller and Shultz 1987). Factors reducing water loss through transpiration from the crown would reduce the amount of sapwood tissue required to support a unit of leaf area.

Gholz (1980) used basal circumference measurements to estimate leaf biomass and leaf area for western juniper. His study plots are within 1 km of our study plots, located 175 km west of Squaw Butte. His model (ln leaf biomass = −4.243 + 1.5606 ln [basal circumference]) fit our data closely for trees < 30 cm

in circumference, but consistently underestimated leaf biomass for trees 30 to 137 cm in circumference by 24 to 47%. Differences may be attributed to sampling procedures. Gholz subsampled trees (n = 10) instead of sampling entire trees. We suspect the difficulty of accurate subsampling would increase with an increase in tree size. Another source of difference between the two studies was the relationship between leaf weight and leaf surface area. Our ratios (cm^2:g) at both sites were larger than Gholz's.

The relationship between sapwood area and leaf area in western juniper did not change between locations. We hypothesize that geographic range and environmental conditions between these two study sites were not large enough to cause differences in leaf-area:sapwood-area coefficients. Marchand (1984) reported no change in leaf-area:sapwood-area coefficients for *Abies balsamea* and *Picea rubens* growing across an environmental gradient. Variation, however, in the relationship between sapwood area and leaf area has been reported within species with large geographical distributions (Waring et al. 1982). An example is *Pseudotsuga menziesii* with a leaf-area: sapwood-area (m^2/cm^2) coefficient of 0.54 for Pacific Coastal trees (Waring et al. 1982) and 0.34 for trees growing in the Rocky Mountains (Snell and Brown 1978).

Total leaf surface area or biomass for a western juniper woodland can be estimated by multiplying the mean basal circumference or sapwood area of trees in the stand (obtained through subsampling the stand) by tree density (obtained from subsampling or aerial photos). Estimates of basal circumference or sapwood area of a western juniper woodland should provide good estimates of total leaf area or leaf biomass. Estimates based on sapwood areas will probably be more reliable, especially in decadent stands of juniper, than estimates made from basal circumference. Models based on circumference, however, provide us with a nondestructive and less labor-intensive means of estimating leaf areas. Development of models estimating leaf biomass or leaf area for various plant species will enhance our ability to determine their impact on the hydrologic cycle through transpiration and to identify total carbon fixation capabilities and nutrient pools.

ACKNOWLEDGMENTS

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