Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms[1]

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Four woody angiosperm species representing an evergreen tree (*Castanopsis chrysophylla* (Dougl.) A.DC.), a deciduous tree (*Acer macrophyllum* Pursh), an evergreen shrub (*Rhododendron macrophyllum* G.Don), and a deciduous shrub (*Acer circinatum* Pursh) were sampled to assess the relation of cross-sectional area of conducting tissue in the stem to leaf area. For the first three species listed, a linear relation between conducting area and leaf area was obtained with r^2 values ranging from 0.89 to 0.96. For *Acer circinatum* the relation only approached linearity with a log transformation of both axes with $r^2 = 0.80$.

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Quatre espèces d'angiospermes ligneuses représentant respectivement un arbre à feuilles persistantes (*Castanopsis chrysophylla* (Dougl.) A.DC.), un arbre à feuilles caduques (*Acer macrophyllum* Pursh), un arbuste à feuilles persistantes (*Rhododendron macrophyllum* G.Don) et un arbuste à feuilles caduques (*Acer circinatum* Pursh) ont été échantillonnés pour examiner la relation entre la surface des tissus conducteurs de la tige en section transversale et la surface foliaire. Dans le cas des trois premières espèces énumérées, il y a une relation linéaire entre la surface conductrice et la surface foliaire ($r^2 = 0.89$ à 0.96). Cependant chez l'*Acer circinatum* la relation n'approche la linéarité qu'avec une transformation logarithmique des deux axes ($r^2 = 0.80$).

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Introduction

In assessing the rates at which forest ecosystems recover from a disturbance, an accurate estimate of leaf area is essential (Sollins *et al.* 1974). This is particularly true when angiospermous trees or woody shrubs are present because they can transpire water and assimilate carbon dioxide at high rates (Cline and Campbell 1976; Wareing 1966; Krueger and Ruth 1965). Unfortunately, a suitably accurate means of estimating leaf area of woody angiosperms has not been available. Recent investigations with conifers (Grier and Waring 1974) and earlier studies on *Acer pseudoplatanus* L. (Dixon 1971) demonstrated that accurate estimates could be obtained from a relation between cross-sectional area of conducting tissue and foliar biomass or surface area. Our hypothesis was that a relation between conducting tissue and leaf area exists for both deciduous and evergreen angiosperms.

Study Area and Methods

An evergreen shrub (*Rhododendron macrophyllum* G. Don.), a deciduous shrub (*Acer circinatum* Pursh), and an evergreen tree (*Castanopsis chrysophylla* (Dougl.) A.DC.), and a deciduous tree (*Acer macrophyllum* Pursh) were chosen to test the general hypothesis. Sampling was completed in conjunction with other efforts to estimate component biomass of trees (Grier and Logan 1977) and a comparative study of ecosystem leaf areas (Gholz *et al.* 1976). Field research was conducted in the western Cascade Mountains of Oregon on the H.J. Andrews Experimental Forest, latitude 44° N, longitude 122° W. The forest is dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), typically with a lower stratum of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). *Acer circinatum* and *Rhododendron* are common in the understory of most plant communities as well as in open areas created by disturbances (Zobel *et al.* 1976). *Acer macrophyllum* grows along streams and beneath gaps in the canopy, but *Castanopsis* is generally restricted to the open understory of drier habitats (Zobel *et al.* 1976).

Sample plants of *Rhododendron* and *Acer circinatum*

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ranged in height from about 0.5 to 5.0 m. A selected plant was cut just above the groundline with a small handsaw and immediately placed in a container with a dilute solution of methyl red dye. After at least 2 h in the dye solution, the plant was removed and a cross section of the stem was taken from about 0.5 cm above the basal cut where the conducting tissue was clearly evident. All leaves were carefully removed and bagged for transport to the laboratory.

The conducting area of the stem as indicated by the dye was determined by photocopying (Xerox) the surface and cutting out the unstained 'heartwood' area. The area of the silhouette was determined with a Licor portable surface-area meter (Lambda Instr. Corp.) with an accuracy of $\pm 1\%$.

At least 40 leaves from each sampled plant were selected randomly. Petioles were removed and the leaf-blade area was determined with the Licor surface-area meter. Leaves and petioles were then dried at 70°C for 24 h and weighed to the nearest 0.1 mg. From these data, a conversion factor (square centimetres per gram of leaf blade) was calculated. The remaining leaves were dried and total leaf area (both surfaces) was estimated by multiplying the weight of all leaves by the appropriate conversion factor, after first subtracting the weight of petioles.

The *Acer macrophyllum* samples ranged in diameter from 7.6 cm to 35 cm at breast height (1.3 m) and were 12 to 32 m tall. The *Castanopsis* ranged from 8 cm to 36 cm at breast height and were from 4 to 17.4 m tall. For these two species, obvious color differences occur between sapwood and heartwood. Furthermore, ample evidence shows that the heartwood, as delineated by the color change, does not conduct significant amounts of water (Panshin *et al.* 1964). Sapwood thickness was measured on the cut surface along the shortest and longest radii at breast height, permitting an average cross-sectional area of sapwood to be calculated for each tree. Leaves and petioles were removed individually from *Acer macrophyllum* twigs. Fresh weights of foliage to the nearest 100 g were obtained using spring scales or beam balances. Representative subsamples were weighed in the field to the nearest 1.0 g ,then transported to the laboratory, and placed in cold storage. Water content at 70°C was determined within 4 days. The dry weight of foliage was computed from ratios of fresh to dry weight of leaves and field leaf weights. On smaller specimens of both species, all leaves were taken for drying in the laboratory.

For *Castanopsis*, twigs with attached foliage were clipped from individuals. Samples then were separated into current and older foliage plus twigs, weighed, dried, separated into current foliage, current twigs, older foliage, and older twigs, and then reweighed. Ratios were computed for each subsample and used to calculate the total weight of foliage on each tree.

Surface-area-to-weight conversions for the two trees were made from subsamples using discs 2.09 cm in diameter cut from leaves with a cork borer. The discs were oven-dried at 70°C and weighed. Area was expressed as a total of both surfaces of the discs. Procedures are described in more detail by Gholz *et al.* (1976).

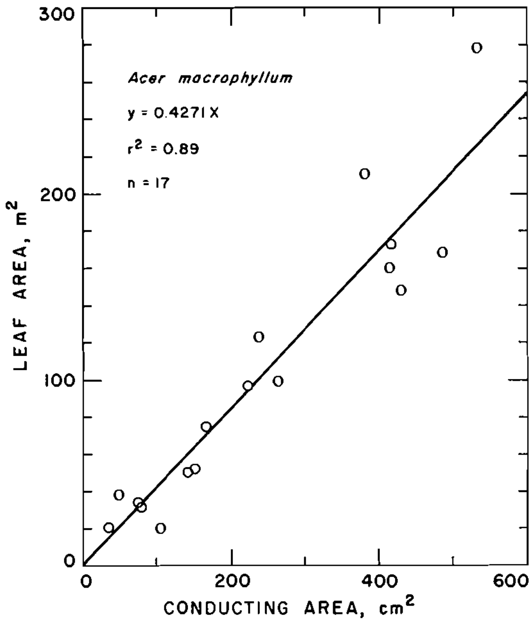

FIG. 1. Relation between cross-sectional area of conducting tissue at 1.3-m height aboveground and leaf area (in square metres) for *Acer macrophyllum*. To convert leaf area to kilograms of foliage, multiply by 0.0328.

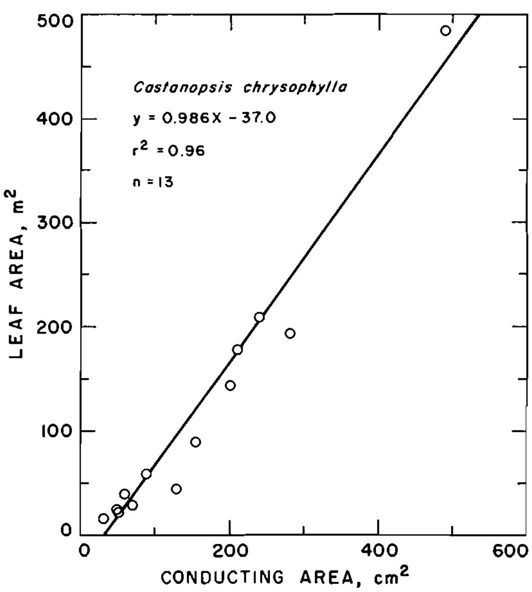

FIG. 2. Relation between cross-sectional area of conducting tissue at 1.3-m height aboveground and leaf area (in square metres) for *Castanopsis chrysophylla*. To convert leaf area to kilograms of foliage, multiply by 0.0709.

Results

The two trees *Acer macrophyllum* and *Castanopsis* showed strong linear relations between cross-sectional area of conducting tissue at 1.3-m height and leaf area (Figs. 1 and 2), with r^2

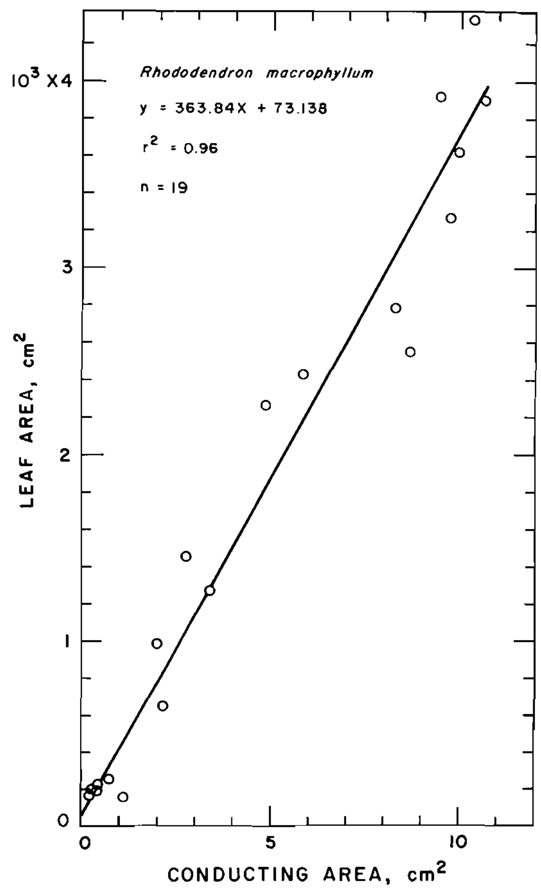

FIG. 3. Relation between cross-sectional area of conducting tissue at ground level and leaf area for *Rhododendron macrophyllum*. Note that the units for leaf area are in square centimetres.

values of 0.89 and 0.96, respectively. For a given amount of conducting area, however, *Castanopsis* had about twice the leaf area of *Acer macrophyllum*.

For the evergreen shrub *Rhododendron*, a strong linear relation ($r^2 = 0.96$) between leaf area and conducting tissue area at ground height was also evident (Fig. 3). In contrast, the deciduous shrub *Acer circinatum* showed a linear relation only when the two variables were transformed to logarithms (Fig. 4). This species exhibited a much larger variation among the plants sampled than did *Rhododendron*. *Acer circinatum* consistently carried much more leaf area than *Rhododendron* for a given amount of conducting tissue.

Discussion

Part of the variation around the regression

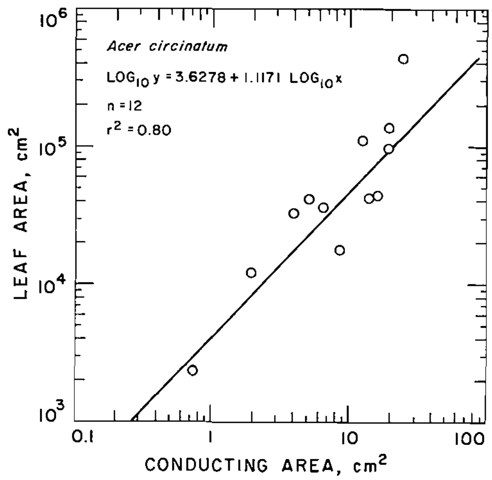

FIG. 4. Relation between cross-sectional area of conducting tissue at ground level and leaf area of *Acer circinatum*. Note that the units for leaf area are in square centimetres.

lines resulted from converting leaf weight to leaf area. The variation appeared to be greater on the shrub species, which grow under a wider range of light conditions. On 1- to 3-year-old foliage of *Rhododendron* growing under forest cover, we found a conversion factor of 200–350 $cm^2\ g^{-1}$. On the current year's foliage, the values reached 600 $cm^2\ g^{-1}$. The range in values for *Acer circinatum* was 440–890 $cm^2\ g^{-1}$.

The leaf area of the deciduous shrub *Acer circinatum* can increase greatly with only a modest change in conducting tissue area. Thus, a vegetative canopy can be reestablished quickly after disturbance. The resulting growth form, however, is spreading or reclining, permitting other species with more upright forms to achieve dominance eventually.

This research in general supports the hypothesis that cross-sectional area of conducting tissue can be used to estimate leaf area accurately on some woody angiosperms. However, these relations must be evaluated carefully for each species.

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