Sapwood volume for three subalpine conifers: predictive equations and ecological implications

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Xylem conducting tissue or sapwood is an important storage organ for water, carbohydrates, and nutrients, but the living ray parenchyma cells require energy for maintenance. I examined sapwood volume for three subalpine conifers (Engelmann spruce, subalpine fir, and lodgepole pine) in relation to tree size and leaf area. Sapwood volume increases exponentially as leaf area increases, with the rate of increase determined by the ratio of leaf area to sapwood cross-sectional area. Increase in the cost of sapwood maintenance respiration relative to photosynthetic production may explain lower relative growth rates reported for large trees and older stands. Lodgepole pine showed the most rapid increase in sapwood volume with increasing leaf area, suggesting storage capacity and sapwood maintenance are important processes for this species. I also present simple equations for estimating sapwood volume.

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Le tissu conducteur du xylème ou bois d'aubier est un organe important pour l'emmagasinage de l'eau, des hydrates de carbone et des éléments nutritifs, mais les cellules vivantes du parenchyme de rayon nécessitent de l'énergie pour demeurer actives. On a étudié la relation entre le volume de bois d'aubier de trois espèces subalpines de conifères (l'Épinette d'Engelmann, le Sapin subalpin et le Pin de Murray), la taille des arbres et leur surface foliaire. Le volume de bois d'aubier augmente exponentiellement avec la surface foliaire. Le taux d'augmentation est fonction du ratio de la surface foliaire sur la surface radiale de bois d'aubier. L'augmentation du coût métabolique pour le maintien du bois d'aubier relativement à la production photosynthétique peut expliquer le taux de croissance relativement plus faible des gros arbres et des peuplements âgés. L'augmentation la plus rapide du volume de bois d'aubier en fonction de la surface foliaire a été observée chez le Pin de Murray. On peut supposer que la capacité d'emmagasinage et le maintien du bois d'aubier sont des processus importants pour cette essence. Des équations simples capables d'estimer le volume de bois d'aubier sont aussi présentées.

[Traduit par la revue]

Introduction

Sapwood in the woody tissue of trees conducts water and nutrients from roots to leaves, and leaf area is correlated with sapwood area (see Whitehead et al. (1984), Dean and Long (1986), Espinosa Bancalari et al. (1987), Long and Smith (1988) for some recent papers and reviews of the literature). The sapwood also stores carbohydrates, water, and nutrients, and sapwood storage helps buffer environmental fluctuations and may contribute to the resiliency and longevity of trees. The cost of maintenance respiration to support the living ray parenchyma cells in sapwood balances the benefits of water conduction, sapwood storage, and mechanical support. Respiration of woody tissues has been neglected in the literature (Landsberg 1986), but maintenance costs associated with sapwood can be substantial (Ryan 1988). Information on sapwood volume will help assess the costs and benefits of storage capacity.

The storage capacity of trees is considerable. Old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests can store the equivalent of 5–10 days transpiration in sapwood (Waring and Running 1978). One-third of daily transcription in 40-year-old Scots pine (*Pinus sylvestris* L.) comes from stored water in the sapwood (Waring et al. 1979). A considerable amount of fixed carbon is stored as nonstructural carbohydrate in the ray parenchyma cells in the sapwood (Kramer and Kozlowski 1979). Deciduous trees

store enough carbohydrate in sapwood to completely replace the canopy several times (McLaughlin et al. 1980), and storage in conifers may exceed annual wood production (calculated from information in Kramer and Kozlowski 1979). Sapwood can also store nutrients that become available to newly formed tissue through the conversion of sapwood to heart wood (Bamber 1976; Bamber and Fukazawa 1985). For example, Attiwell (1980) found that heart wood conversion supplied 14% of annual phosphorus demand of a *Eucalyptus* forest (31% of internal redistribution).

Indirect evidence suggests that large trees and mature stands have higher ratios of maintenance respiration to photosynthetic input than small trees and aggrading stands. For example, growth efficiency (net production per unit leaf area) commonly declines with stand age (Jarvis and Leverenz 1983) and tree size (Kaufmann and Ryan 1986). These changes may be caused by increases in respiration costs associated with sapwood as production remains constant or declines slightly (Waring and Schlesinger 1985). However, direct evidence for a mechanism is lacking.

To better understand the role of sapwood storage and its associated costs, we need to know the extent to which sapwood volume varies among species and how it changes as trees grow. My objective was to document how sapwood volume changes with tree size and in relation to tree leaf area, an index of tree productivity. I also developed regression estimators of sapwood volume for three subalpine conifers using sapwood area at breast height (1.4 m) and other mensurational variables. Armed with these allometric rela-

tionships and knowledge about the physiology and function of sapwood, we can investigate differences in sapwood storage and associated maintenance respiration for stands of various ages, structures, and species compositions.

Methods

I sampled trees from uneven-aged, mixed-species stands at the Fraser Experimental Forest near Winter Park, Colorado, U.S.A. (39°54′N, 105°52′W), where lodgepole pine (*Pinus contorta* ssp. *latifolia* (Engelm. ex Wats.) Critchfield), Engelmann spruce (*Picea engelmannii* (Parry) Engelm.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) often occur together in the Colorado subalpine zone from 2700 to 3100 m. The subalpine forests at Fraser have short growing seasons, cool night temperatures, and abundant moisture throughout the growing season (Alexander et al. 1985). The experimental forest receives an annual average of 740 mm precipitation, with two-thirds falling as snow; the annual average temperature is 2°C. Frost can limit photosynthetic activity during the spring and autumn, but summer rainstorms keep soil moisture high during the growing season so that stomatal closure associated with moisture stress is rare (Kaufmann 1982). However, nitrogen is low in the soil solution for lodgepole pine forests (Fahey and Knight 1986) and may limit photosynthetic capacity and aboveground growth. Soils are Typic Cryochrepts derived from mixed gneiss and schist.

I harvested 15–16 dominant or codominant trees of each species representing the normal range of tree size (12–50 cm dbh) and measured tree height and length of the live crown. I removed 2–3 cm thick sections at the tree base, breast height, and the base of the live crown (the middle of the internode below the first whorl with at least two live branches). Additional 2- to 3-cm sections were cut every 2 m between breast height and base of the live crown and every 2 m above the base of the live crown. Sapwood was distinguished from heart wood by illuminating the back of the thin stem sections for subalpine fir and Engelmann spruce and by staining the lodgepole pine sections with a ferric chloride solution (Kutscha and Sachs 1962).

Sapwood areas were determined for the sections by measuring two sapwood and heart wood diameters (longest diameter through the pith and then a diameter perpendicular to that). I measured the diameters to the nearest 1 mm, calculated total and heart wood cross-sectional areas using the ellipse formula (Maguire and Hann 1987), and estimated sapwood area by subtraction. For an initial sample of 15 sections, values estimated with this method were within 1% of those measured with a digital planimeter.

An additional 12–14 trees per species sampled in a leaf area study from the same site (Kaufmann and Troendle 1981) were incorporated into my data set. Kaufmann and Troendle (1981) measured sapwood cross-sectional area at breast height, base of the live crown, and also at one-third and two-thirds of the distance between the tree top and crown base.

I estimated volume using formulas for a cylinder for tree stump, neiloid frustrum (a concave solid of revolution) for stump to breast height, paraboloid frustrum for all intermediate sections, and conic paraboloid for the tree top. Sapwood volume was determined by subtracting heart wood volume from total volume inside bark. Volumes were summed over all sections to yield tree sapwood volume (Husch et al. 1982). To estimate how storage capacity or stem maintenance respiration might change in relation to leaf area as trees grow in size, I calculated the ratios of actual sapwood volume to actual leaf area for the trees sampled by Kaufmann and Troendle (1981) and actual sapwood volume to leaf area estimated from the equations of Kaufmann and Troendle (1981) for all trees. I also estimated leaf area with the equations of Long and Smith (1988) to assess the effect of a nonlinear relationship between sapwood cross-sectional area and tree leaf area.

By modifying an equation commonly used to estimate stem volume (Husch et al. 1982), I developed two equations to estimate

sapwood volume for each species. One equation included sapwood cross-sectional area at breast height and the other substituted crown length as a surrogate for leaf area or sapwood cross-sectional area. Coefficients were estimated using linear regression. Approximate R^2 values for zero-intercept models were calculated as (Schmidt 1976)

$$[1] \quad R^2 = 1 - \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^{n} (Y_i - \bar{Y})^2}$$

where Y_i is an individual volume measurement, $\hat{Y}_i$ is a volume estimated from the regression, and $\bar{Y}$ is the mean of the volume measurements. I examined the effect of pooling samples from this study and the study of Kaufmann and Troendle (1981) using a general linear model. Separate models did not explain significant ($p > 0.05$) additional variation over the model with pooled data, so the equations were fit using the combined data sets. Analysis of covariance tested differences among species in the relationship between tree size and the amount of sapwood volume supported per unit of tree leaf area.

Results

Plots of relative height above breast height ((section height − 1.4 m)/(total height − 1.4 m)) versus relative sapwood area (sapwood area of section/sapwood area at breast height) allow comparisons of sapwood taper among species and for trees of different sizes (Fig. 1). Sapwood area decreased uniformly and sapwood taper was the least variable for the two shade-tolerant conifers (subalpine fir and Engelmann spruce). In contrast, sapwood taper was more variable for lodgepole pine and changed at a relative height of about 0.5. Most trees showed sapwood area decreasing monotonically from tree base to top, but a few trees of each species showed minor (< 10%) sapwood bulges.

The ratio between sapwood volume and total leaf area is an estimate of the empirical derivative or instantaneous rate of change of the relationship between the two variables. For all three subalpine conifers, this ratio increased at a constant, linear rate as stem diameter increased (Figs. 2a, 2b). The rate of increase with tree size differed among species ($p < 0.01$) regardless of whether actual or estimated leaf area was used in the denominator. For actual leaf area, the slope for Engelmann spruce did not differ significantly from subalpine fir ($p = 0.065$), but other species combinations were significant (Fig. 2a, $p < 0.05$). For estimated leaf area, all regression slopes between the ratio sapwood volume : leaf area and stem diameter differed significantly (Fig. 2b, $p < 0.01$). Use of the equations of Long and Smith (1988) to estimate leaf area for lodgepole pine did not substantially change the relationships among leaf area, sapwood volume, and tree size.

Because stem respiration is often expressed per unit of stem surface area, I also examined how stem surface area varied as tree leaf area and tree size increased. The stem surface area to total leaf area ratio did not vary significantly with tree size for Engelmann spruce ($p = 0.99$) or subalpine fir ($p = 0.10$). Surface area per unit of leaf area did increase with tree size for lodgepole pine ($p = 0.04$), but correlation with diameter was weak ($R^2 = 0.28$).

Simple equations efficiently estimated sapwood volume for the sample trees (Tables 1 and 2):
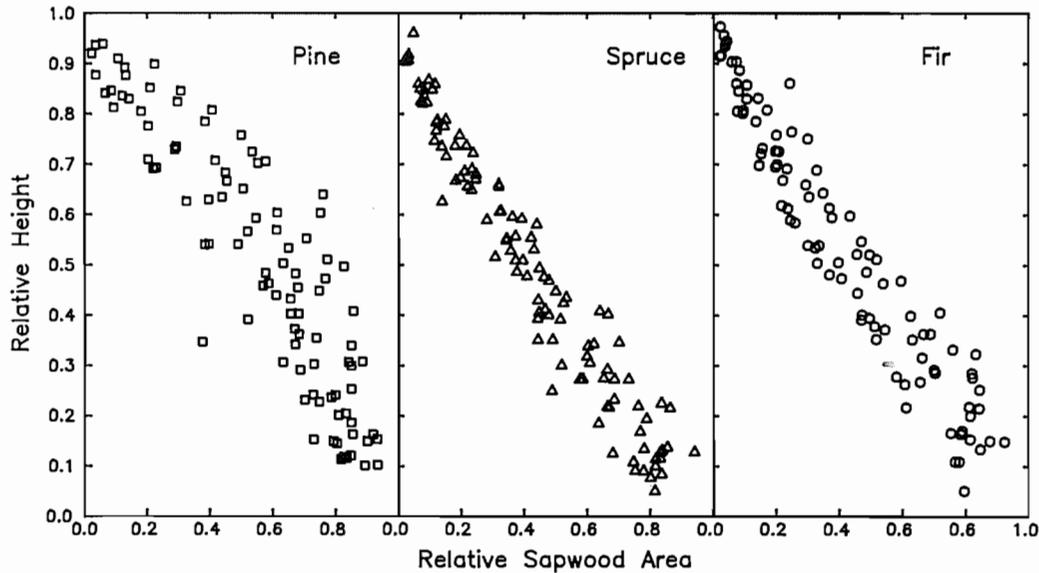
$$[2] \quad SV = B_1(D^2 H) + B_2(SA\,H)$$

FIG. 1. Sapwood taper above breast height (relative height: (section height − 1.4 m)/(total height − 1.4 m)) versus relative sapwood cross-sectional area (sapwood area of section/sapwood area at breast height) for lodgepole pine, Engelmann spruce, and subalpine fir. Values are plotted only for trees sampled in this study.

TABLE 1. Sample statistics, estimates of coefficients, and goodness-of-fit statistics for eq. 2

	Mean ± SD	n	B_1	B_2	SEE	R^2
Lodgepole pine	0.309 ± 0.409	30	4.39×10^{-6}	4.42×10^{-5}	0.055	0.982
Engelmann spruce	0.372 ± 0.548	29	7.12×10^{-6}	3.08×10^{-5}	0.037	0.995
Subalpine fir	0.117 ± 0.170	27	2.23×10^{-6}	3.59×10^{-5}	0.015	0.992

NOTE: SEE = standard error of the estimates; R^2 = approximate coefficient of determination.

TABLE 2. Estimates of the regression coefficient and goodness-of-fit statistics for eq. 3

	B_1	SEE	R^2
Lodgepole pine	2.29×10^{-5}	0.133	0.89
Engelmann spruce	2.37×10^{-5}	0.091	0.97
Subalpine fir	8.72×10^{-6}	0.034	0.96

NOTE: SEE = standard error of the estimate; R^2 = approximate coefficient of determination.

and

$$[3] \quad SV = B_1(D^2CL)$$

where SV = sapwood volume (m^3), D = tree diameter at breast height (cm), H = total tree height (m), CL = length of live crown (m), SA = sapwood area at breast height (cm^2), and B_1 and B_2 are species-specific regression coefficients. Regressions were forced through the origin, because the intercepts were rarely significant and the models with intercepts overestimated sapwood volume for small trees. The addition of other variables common in forest inventory to eq. 3 accounted for significant additional variance, but the equations were not consistent among species. Therefore, Table 2 gives the simplest consistent form. Average density of sapwood from similar lodgepole pine trees is 0.42 g·cm^{-3} and for Engelmann spruce, 0.35 g·cm^{-3} (Ryan 1988), and these factors can be used together with the equations in Tables 1 and 2 to estimate sapwood dry weight.

Discussion

Tree growth changes the relationship between the tree's photosynthetic machinery and sapwood volume, indicating potential shifts in carbon allocation and water and carbohydrate storage. Large trees have more water and carbohydrate storage capacity but require more energy for maintenance respiration relative to their ability to fix carbon than do small trees. This occurs because sapwood volume relative to leaf area and decreasing marginal energy capture both contribute to differences between small and large trees.

According to the pipe model theory (Shinozaki et al. 1964; Waring et al. 1982), leaf area is related to the cross-sectional area of the conducting xylem. Differences in the amount of foliage supported per unit of sapwood cross-sectional area explain relationships among sapwood volume, leaf area, and tree size for the three conifers. Kaufmann and Troendle (1981) show that 1-cm^2 sapwood at breast height supports a leaf area of 0.18, 0.32, and 0.75 m^2 for lodgepole pine, subalpine fir, and Engelmann spruce, respectively. Because lodgepole pine supports little leaf area per unit sapwood cross-sectional area, sapwood volume relative to leaf area increases rapidly with tree size. In contrast, subalpine fir maintains a large leaf area per unit sapwood, and sapwood volume relative to leaf area changes little as trees grow in size. For the trees in this study, nonlinearity in the relationship between leaf area and sapwood area at breast height reported by Dean and Long (1986) and Long and Smith (1988), slightly accentuated the change in sapwood volume : leaf area with increasing dbh.
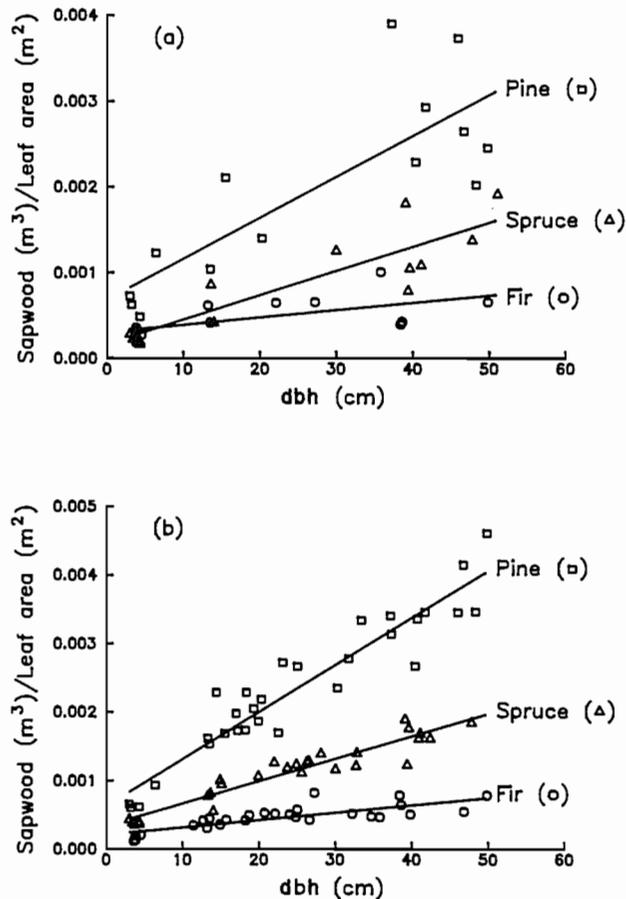
FIG. 2. (*a*) Actual sapwood volume (m³) per actual leaf area
(m²) versus dbh for trees of Kaufmann and Troendle (1981).
(*b*) Actual sapwood volume (m³) per leaf area (m²), estimated
from equations of Kaufmann and Troendle (1981) versus dbh.
Values are plotted for trees from both studies.

Large trees of any of the three species will have more sap-
wood volume : leaf area than small trees. Additionally, for
trees growing in an even-aged stand, each additional incre-
ment of leaf area absorbs less energy and produces less
photosynthate. Therefore, costs for maintenance respiration
of sapwood will likely be a larger fraction of photosynthetic
input for large trees than for small trees (Waring and
Schlesinger 1985). Because sapwood volume : leaf area
increases rapidly with tree size for lodgepole pine, sapwood
maintenance costs are likely to be more important for large
lodgepole pine than for large spruces or firs. Kaufmann and
Ryan (1986) provide indirect evidence that this is so. They
found that growth efficiency (stem wood growth per unit
leaf area) declined rapidly with increasing tree size for
lodgepole pine, but slowly declined with tree size for
Engelmann spruce and subalpine fir. Since changes in
growth efficiency indicate shifts in carbon allocation
(Waring 1983), a decrease in growth efficiency could be
explained by increasing carbon for maintenance respiration.

Small leaf area to sapwood area ratios may provide redun-
dancy needed to avoid damage from cavitation of water in
tracheids, and may also yield large water storage capacities.
Sapwood water storage also contributes to drought
avoidance (Lassoie et al. 1985). Therefore, lodgepole pine
tolerates drought partially because of a conservative leaf area
to sapwood area balance. In contrast, Engelmann spruce

and subalpine fir require moist sites to survive, to be
expected from the high leaf area to sapwood ratios and
associated relatively low storage capacities.

Sapwood tapered to 70–80% of its breast height value at
the base of the live crown for the trees in this study. Maguire
and Hann (1987) report that taper models fitted to data for
Douglas-fir estimate a taper of 39–74% from breast height
to crown base. Yang et al. (1985) and Long et al. (1981)
showed little sapwood taper (<20%) for jack pine (*Pinus
banksiana* Lamb.) and Douglas-fir. All three studies showed
that sapwood does not always decrease monotonically, but
sometimes "bulges" particularly below the crown.

Sapwood volume and leaf area are inextricably linked
through their mutual relationship with xylem conducting
area. Large trees have more sapwood volume per unit of
leaf area than small trees and consequently, can store more
water, carbohydrates, and nutrients. However, large trees
have potentially greater maintenance costs. Simple structural
analyses may help explain observed patterns in growth rate
and drought tolerance in a given environment.

Acknowledgments

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