Influence of Vertical Foliage Structure on the Distribution of Stem Cross-Sectional Area Increment in Western Hemlock and Balsam Fir [For. Sci. 46(1):86–94]

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Kershaw and Maguire (2000) used pipe-model theory to derive a model for the main stem of a crown that posits a constant ratio of cross-sectional area increment to the surface area of the current annual cohort of acropetal foliage [their Equation (3)]. That the ratio proved to be decidedly variable, declining from the top to the bottom of a crown, could be viewed as a serious disagreement between theory and reality. Kershaw and Maguire (K&M) used physiological arguments unrelated to pipe-model theory to modify the model to one that allows the variable ratio. However, these physiological arguments may be unnecessary; a conventional pipe model, which uses mass as the measure of foliage and allows for reuse of sapwood, may accord with the variable ratio. I shall attempt to explain why this is so.

The original pipe model of stem form is based on observations of an approximately constant ratio between the cross-sectional area of a stem or branch and the total mass of foliage borne by that stem or branch (Shinozaki et al. 1964a,b). The constant ratio applies to points on the stem system above a certain horizon, usually the base of the live crown or the top of the zone of branch decline. K&M followed common practice by substituting leaf area for leaf mass in their interpretation of the theory. In many applications, this substitution is of little consequence. For example, the theory suggests that, across trees of a given species, total leaf mass is correlated with cross-sectional area of sapwood at the base of the live crown. Leaf area can substitute for mass because, across trees, total leaf area and total leaf mass also tend to be highly correlated. However, a constant ratio of cross-sectional area to leaf mass does not imply a constant ratio of cross-sectional area to leaf area within the crown of a tree. Specific leaf area (leaf area per unit mass) may increase significantly—about 2× in balsam fir (M.B. Lavigne, Tree Physiologist, Canadian Forest Service, Fredericton, NB, personal communication)—from the top to the bottom of a crown, i.e., from sun leaves to shade leaves. Assuming the 2× increase in specific leaf area holds, increment per unit leaf area is only one-half of the increment per unit leaf mass on low branches. Thus, a switch from leaf area to mass may reduce the variation in the ratios found by K&M. However, the switch may not eliminate the variation: a theory based on a constant ratio of total cross-sectional area to the mass of all acropetal foliage does not necessarily infer constant cross-sectional area increment per unit mass of current-year acropetal foliage.

The stem system of a pipe model of a tree is an assemblage of active and disused pipes (Shinosaki et al. 1964a). The word sapwood does not appear in either of the two original pipe-model papers by Shinozaki et al., but it is commonly assumed that active pipes of a model tree correspond to sapwood in a real tree, and the disused pipes correspond to nonconducting xylem or heartwood. In the original pipe model, each unit mass of foliage was attached to an active pipe. In most dynamic pipe models (Valentine 1985, Mäkelä 1986, et seq.), the active pipes are assumed to extend from leaves to fine roots. An assumption of constant pipe thickness within the crown provides for the constant ratio of sapwood cross-sectional area to acropetal foliar mass. Hari et al. (1986) indicated that this ratio might vary between the main stem and side branches; thus, a change in pipe thickness at the junction of a side branch and main stem may provide a more accurate model. Mäkelä et al. (1997) allowed the ratio to vary by whorl age in a model for Scots pine. Both the branch effect and the age effect transcend the original theory. Of the more recent dynamic pipe models, LIGNUM (Perttunen et al. 1996) provides the most advanced and complete description of a crown.

Kaipiainen and Hari (1985) influenced the derivations of some early dynamic pipe models with their report of good agreement between the number of sapwood rings and the number of live whorls in Scots pine. Scots pine carries two to five annual cohorts of foliage across the summer (depending on local climate) so the sapwood rings may significantly outnumber the annual cohorts of foliage. This suggests that, once branch age exceeds leaf longevity, some foliage of each new cohort connects to old sapwood. The connection of new foliage to old sapwood is inherent to most dynamic pipe models (e.g., Mäkelä 1986, Sievänen et al. 1997, Valentine et al. 1997). For example, Valentine (1988, 1990) formulated models that provide for foliar turnover—the replacement of

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senescent foliage with new foliage—on elongating active pipes. With the onset of turnover, only part of the foliage in each new cohort is attached to the new pipes that correspond to the new sapwood sheath. Thus, this “elongating-pipe model” suggests that cross-sectional area increment per unit mass (or area) of new acropetal foliage may decrease with increasing branch age, from the top to the bottom of a crown. This model seems to agree with K&M’s results. This model also seems to accord with the interpretation of pipe-model theory put forth by K&M in their Discussion, where they stated: “variability in the annual amount of stem growth versus foliation may be allowed as long as the overall balance is maintained.” K&M’s Equation (3), which posits a constant ratio of cross-sectional area increment to the surface area of the current annual cohort of acropetal foliage, corresponds to what could be called a “fixed-pipe model.” A fixed-pipe model posits that (a) all new foliage is attached to new pipes of fixed length and (b) the pipes and foliage reach senescence together. Thus, the fixed pipe model does not provide for the turnover of foliage on elongating pipes (i.e., the connection of new foliage to old sapwood). A fixed-pipe model that derives pipe-model theory (Valentine 1990) accords with K&M’s Equation (3), provided leaf mass is substituted for area. Whether a real tree agrees with a fixed-pipe model should be easy to discern. As K&M noted, the number of annual cohorts of foliage must equal the number of annual rings in the sapwood. If this constraint is met by either balsam fir or western hemlock, and the switch from leaf area to leaf mass does not furnish approximately constant increment per unit of current-year acropetal foliage, then a disagreement between theory and reality would be evident. On the other hand, if the number of sapwood rings exceeds the number of annual cohorts of foliage, then the conventional pipe model that provides for reuse of sapwood (e.g., the elongating-pipe model) may apply. In conclusion, K&M presented an interesting and thought-provoking model that relates cross-sectional area increment to the surface area of new acropetal foliage in balsam fir or western hemlock. K&M’s model is valuable and informative, but the degree to which it agrees with either a fixed-pipe model or an elongating-pipe model is difficult to discern because (a) foliage was measured in terms of surface area rather than mass and (b) information about number of cohorts of foliage and the number annual rings in sapwood was not reported. Both the fixed-pipe and elongating-pipe models accord with pipe-model theory because both models maintain the requisite constant ratio of sapwood cross-sectional area to acropetal foliar mass. The possibility remains that K&M’s model agrees with an elongating-pipe model since that latter suggests that cross-sectional area increment per unit of acropetal foliage may decrease from the top to the bottom of a crown where the annual sapwood rings outnumber the annual cohorts of foliage. More generally, it appears that observation of the number of annual cohorts of foliage, the number of sapwood rings, and the number of live nodes or whorls on the main stem of a tree may prove fruitful in connection with the advancement of models of increment along a bole.

Literature Cited