VELOCITY DISTRIBUTION PATTERNS IN ASCENDING XYLEM SAP DURING TRANSPIRATION

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VELOCITY DISTRIBUTION PATTERNS IN ASCENDING XYLEM SAP DURING TRANSPIRATION

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The ascending sap stream of trees exhibits flow properties analogous to flow in pipes. Data collected from lodgepole pine and Engelmann spruce from 1960 to 1970 suggests that the flow is laminar and its velocity distribution parabolic.

In coniferous trees, sap ascends through tracheids more or less uniformly distributed across a cylindrical band of comparatively wet sapwood surrounding a cylinder of physiologically inactive dry heartwood. The diameter of the void area in individual tracheids is larger at the center of this band of sapwood than at either the bark or heartwood interphases. Thus the size of the sap conducting elements are themselves distributed in a somewhat parabolic arrangement. Whether this size distribution is a result or cause of the similar velocity distribution is not known.

An important application of this finding lies in the measurement of water use by trees in forest hydrology research. Two heat pulse velocity measurements (measurements used to estimate sap flow rates) made simultaneously at specified but unequal depths are sufficient to describe both average flow velocity and the cross sectional area through which such flow occurs. Thus both the "A" and "V" of the continuity equation are described in a flow system within which the conducting cross section varies with time.

INTRODUCTION

During 1965 in New York City, water was not furnished restaurants' patrons except on demand, and then often charged for. The common 8 oz. glass of water is only 1/8 of the amount recommended for each person to drink daily. In one drinks his quota each day, he will consume about 1/20 the amount of water a tree uses each day during the summer. The method used to limit consumption in New York City was to charge for a metered amount, one glass. How, and on what basis, does one limit water use by a forest?

All trees don't use the same amount of water just as all humans don't drink their full 8 glasses. Some live where the supply in not sufficient to meet the demand. Those with enough and those without are often not clearly separated by visible evidence. If in a group where water is just exactly sufficient one is removed or dies, a surplus is created. If however, the group doesn't have enough to begin with, then the removal of one individual will have no effect: the water not used by it will be consumed by those remaining. Thus, a problem in water resource management is how to meter the amount of water consumed by trees under various environmental conditions, to compare it with that available.

The easiest way to measure the amount of water a household uses is to install a meter where the pipe goes into the house. It is possible to do the same thing in trees. A tree "uses" water in the leaves. The stem is a transmission system from the roots to the leaves. In the stem near the ground surface is a potential metering site.

THE TREE STEM IN CROSS SECTION

Flow through a tree stem cross section can be estimated from a knowledge of the area actually conducting water and the average velocity over that area. In this respect, a tree is analogous to a pipe. However, a tree stem is not a pipe and conventional metering systems won't work for it. A tree has a complex, well defined, but poorly understood water conducting system. Nothing is known about the extent of the conducting area except that it appears to be contained within the sapwood. Likewise, nothing is positively known about the velocity distribution within the conducting sapwood.

A tree stem is composed of three broad tissue groups; bark, sapwood, and heartwood (Fig. 1). The sapwood is separated from the bark by a single layer of cells called the cambium. Cells within this layer divide as the tree grows, forming wood toward the center and bark to the outside. The cambium layer is roughly 0.025 mm thick.

Tree manufactured sugar descends from the leaves via the bark tissue. There is a positive pressure head, with respect to the root zone, within the bark. By contrast, water ascends through the sapwood to the leaves. At a leaf surface, evaporation takes place creating a negative pressure (10 to 80 atmospheres) that supplies the energy for water uptake. About 2 percent of the water so lifted is used by the leaves in the manufacture of sugars. The rest is lost into the surrounding atmosphere. The evaporation process at the leaf surface is called transpiration.

The pathway through which the water to be transpired ascends in the sapwood of coniferous trees is through the lumina (void area) of tracheid elements. Tracheids are specialized conducting cells grouped together in the sapwood to form a more or less continuous channel from root to leaf. The majority of flow is longitudinal but a certain amount of lateral flow can take place due to the overlapping arrangement of the tracheids. Bordered pits at the junction of individual tracheid elements allow passage of water, but not air, from tracheid to tracheid.

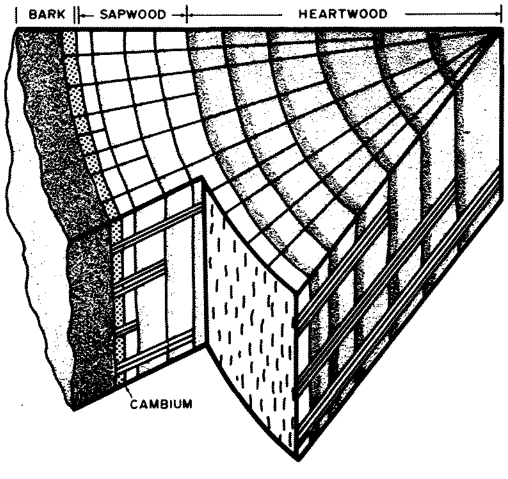

Fig. 1. Simplified stem structure showing principal tissue groups only.

The high negative pressure created during transpiration coupled with the air-rejecting capability of bordered pits creates a hydraulic flow system that almost defies direct description or verification. Insertion of instrumentation to measure negative pressure gradients within the sapwood allows air entry that blocks further water movement through the severed tracheids. Therefore, information about these flow patterns is necessarily indirect.

The evidence presented below implies that parabolic velocity distribution patterns similar to those of laminar pipe flow are present in the transpiration stream. If this description of the physical system is correct, then both conducting area and average velocity are computable from two velocity measurements made at dissimilar depths in the transpiration stream.

EVIDENCE OF PARABOLIC DISTRIBUTION

Dye Staining Patterns Under Induced Flow

Water soluble Rhodamine B was drawn into a lodgepole pine stem section. (5 cm dia. 19.6 cm^2 cross-section area). The stem was then cut into 1 cm long segments to ascertain the point to which the dye had travelled (Fig. 2). Dye moved through the 6 outside annual rings (approximately 1 cm wide band) but the "staining front" is 3 annual rings in, 7 cm further downstream than the uniformly stained area. In vertical section, the stained area appears as a parabola, 1 cm wide at the origin, 7 cm high at the vertex.

Statistical Curve Fitting to Empirical Data

The sapwood of trees 20 to 30 cm diameter is usually larger than the 1 cm band noted in the dye experiment. It is possible to indirectly measure the velocity distribution in such trees. Three lodgepole pine 26.9 cm average diameter, 590 sq. cm cross section area at 135 cm above the ground, were instrumented with heat pulse

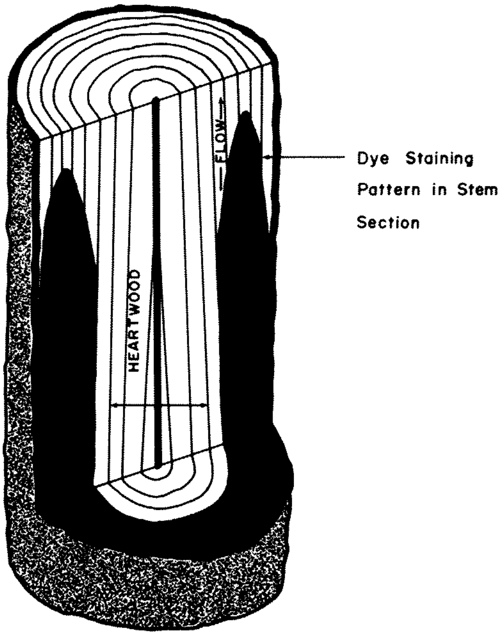

Fig. 2. Diagrammtic sketch of dye straining pattern in sapwood (not to scale).

velocity measuring probes at 2, 5, 10, 15, 20 and 25 mm depths into the sapwood from the cambium (Fig. 3).[1]

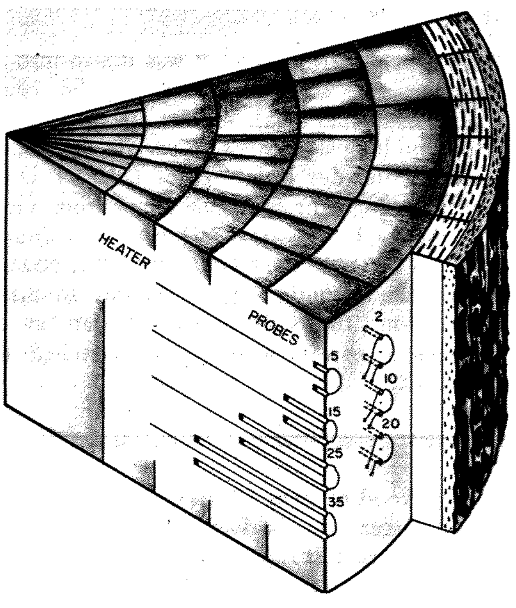

Fig. 3. Sketch showing placement of heat pulse velocity measuring probes in sapwood of lodgepole pine trees.

Figure 4 is a graphical plot of the results from these measurement points. Statistically fitting these data to a second degree linear model resulted in the parabolic equation:

$$HPV = 1.66 + 0.69D - 0.0177D^2 \text{ cm/hour} \quad (1)$$

where:

HPV = heat pulse velocity, cm/hour

D = depth at measurement, mm.

For this fitting, R = 0.685 which indicates a reasonably strong relationship between the variables. More important, the solution for the depths where HPV = 0 show that the predicted origin is at –2.3 mm; just slightly into the bark, and at 41.3 mm, well into the sapwood.

Force fitting the physical model

$$(D\text{-}h)^2 = 4a\,(HPV - K) \quad (2)$$

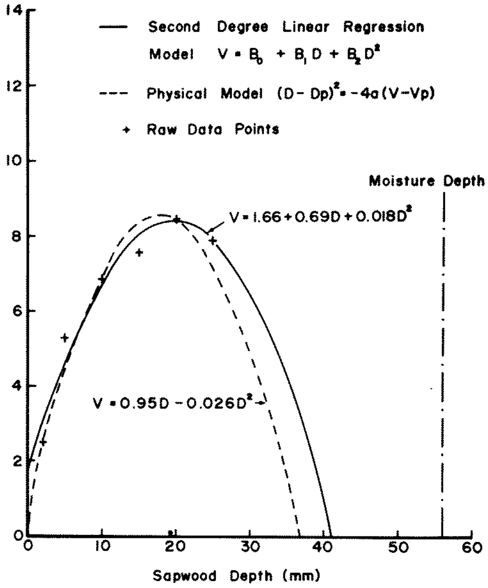

Fig. 4. Graphical plot of heat pulse velocity distribution with depth into sapwood. Superimposed are statistically and physically fitted models. Vertical line at 56 mm deep represents heartwood-sapwood boundary at which moisture content falls from 153 percent in sapwood to 30 percent in heartwood.

through points (0,0); (10, HPV_{10}); (20, HPV_{20}) yields the equation:

$$HPV = 0.96D - 0.026D^2 \text{ cm/hour} \qquad (3)$$

This equation, also displayed on Fig. 4 lies almost coincident with that derived statistically. Both second zero points (41.3 mm for the statistical model; 38.0 mm for the physical model) are of significance as they both fall within that portion of the stem cross section containing appreciable water for movement.

Wood Structure in the Sapwood of Engelmann Spruce

Fluid movement in conifers, the group to which spruce and pine belong, takes place through the lumen of tracheids.[2] A decrease in the size of the tracheids within an annual ring or within regions of sapwood hinders the upward movement of water. Therefore, the average of individual lumen areas should be larger where flow is greatest.

Figure 5 shows the results of lumen area detrimentations at various sapwood depths. The tendency is for greater lumen areas at 20 mm depths than at either the cambium sapwood interface, or the sapwood-heartwood interphase. These data also suggest a general parabolic distribution.

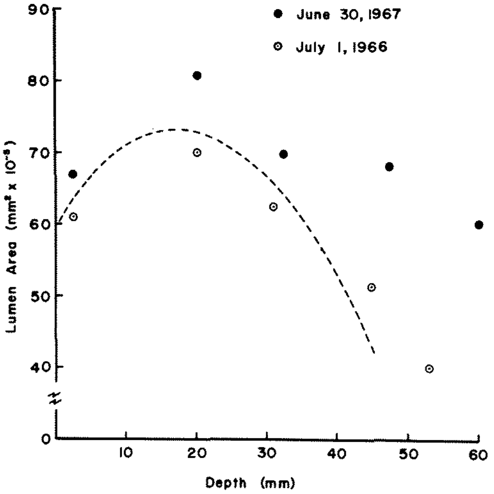

Fig. 5. Lumen area distribution with depth into sapwood in Engelman spruce. From Van Gorp, 1967. Measurements were made only at points shown. Thus no way to verify course of values between these points. Dashed curve is parabolic shown for comparative purpose.

Predicted Depths of Movement Within High Moisture Portion of Sapwood

The evidence presented above is sufficient to hypothesize parabolic velocity distribution within the transpiration stream of coniferous trees. This distribution would have the following characteristics:

1. Flow velocity at the origin (cambium) would be zero.

2. A second point of zero movement (D_m) would fail within or less than the sapwood-heartwood interphase depth.

The velocity at three known points is sufficient to define a parabola through those points.

Fifteen lodgepole pine trees average diameter 23 cm, 135 cm above the ground, were instrumented with heat pulse velocity measuring probes at 1.0 and 2.0 cm depths into the sapwood, on the east and west quadrant of each tree. The probes in each tree were simultaneously read and for each set of readings, a parabola forced through the points (0,0), (1.0, V_1), (2.0, V_2). The equation thus derived was used to predict the depth at (D_m,0). This D_m was compared with the depth at which the sapwood-heartwood interphase commenced. The results are tabulated in Table 1.

Twenty-four of twenty-seven predicted depths are less than the measured sapwood-heartwood interphase depth (based on a change in moisture content of greater than 20 percent). The average calculated depth, 3.69 cm, is well within the average interphase depth 4.24 cm. A second set of readings from the same set of measurements points one year later showed similar results: twenty-one of twenty-four calculated depths were equal to or less than the interphase depth measured. (Three sets of probes had ceased to function.)

The moisture content of the band of wood under the parabolic profile exhibits characteristics of a homogenous unit (Fig. 6). Data taken

TABLE 1. PREDICTED DEPTH INTO SAPWOOD AT WHICH SAP MOVEMENT NO LONGER OCCURS COMPARED WITH MEASURED THICKNESS OF SAPWOOD

Tree	Quadrant	Predicted Depth	Measured Thickness
1	E	4.11 cm	4.0 cm
2	E	2.26	3.0
2	W	2.36	3.5
3	E	2.34	3.5
3	W	2.32	3.5
4	E	14.80	5.0
4	W	10.16	5.0
5	E	2.35	3.8
6	E	2.84	3.2
6	W	2.67	2.7
7	E	3.23	6.0
7	W	2.85	6.0
8	E	3.81	4.0
8	W	2.38	4.1
9	E	2.68	4.6
9	W	2.54	5.5
10	E	2.46	3.4
10	W	2.50	4.4
11	E	2.73	6.0
11	W	2.80	4.7
12	E	2.94	3.8
12	W	2.63	3.4
13	E	2.64	4.5
13	W	8.80	5.6
14	E	2.65	4.3
15	E	3.00	4.0
15	W	2.94	3.1
N = 27		99.79	114.60
	$\overline{D}$ =	3.69 cm	4.24 cm

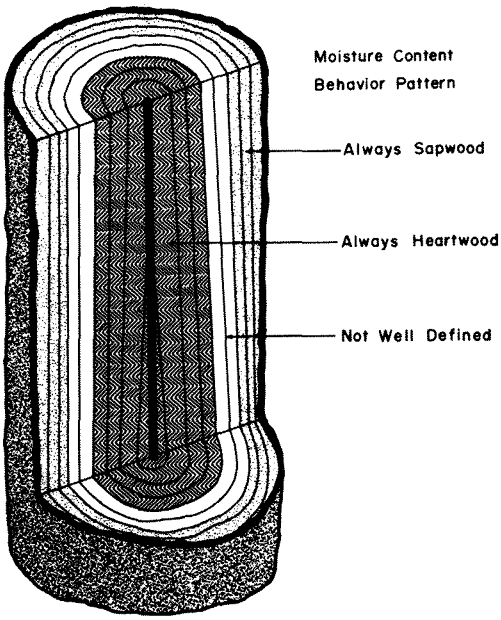

Fig. 6. Stem cross section showing portions of wood always separable into heartwood or sapwood, on the basis of moisture content. The sapwood-heartwood interphase portion is not well defined by moisture content.

from trees intermixed among the study trees shows that the first 3 cm of sapwood act together in their changes in moisture content. That is, if the moisture content of one cm segment increases by 20 percent the other two also show a similar magnitude increase. Likewise, those at depths beyond 5 cm always behave as heartwood. The 4th and 5th cm (which I have been calling sapwood-heartwood interphase) can act together as a unit neither heartwood nor sapwood, or the 4th can be an extension of the first 3 cm of sapwood; the 5th an extension of the heartwood. How the 4th or 5th cm behave appears to be related to season of the year – but the relationship is not readily apparent. The important point of the above, is that the predicted movement depth, 3.69 cm, totally encloses the section of sapwood that always behaves as sapwood, and that the 4th cm can act as part of this unit, or as part of a third unit different from either sap or heartwood.

CONCLUSIONS

The above evidence strongly suggests that the distribution of velocities from cambium to heartwood within the ascending transpiration stream is parabolic. It also suggests that an estimate of water conducting sapwood area could be made by assuming this distribution and fitting a parabola through known measurement points to predict the inner depth of zero movement.

References

[1] Heat pulse velocity values are measurements related to water movement in tree stems. See Swanson, Topic 2 of these proceedings for a description of a heat pulse velocity meter.

[2] D. Van Gorp, *Progress report on the relationship of xylary cell structure to sap movement in Engelmann spruce* (Colo. State Univ. Ref. No. 1470, 70-1605, Department of Forest and Wood Sciences, 1967).