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Robert H. Swanson (1972)

VELOCITY DISTRIBUTION PATTERNS IN ASCENDING XYLEM SAP
DURING TRANSPIRATION.

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by

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ABSTRACT

The ascending sap stream of trees exhibits flow properties analogous to flow in pipes. Heat pulse velocity 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 parabolic distribution 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.

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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. If 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 is 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 positively 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 (Figure 1a). 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 (10-80 atmospheres) that supplies the energy for water uptake. About 2% 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 (fig. 1c). Tracheids are specialized conducting cells, 2-6 mm long, grouped together in the sapwood to form a more or less continuous channel from root to leaf (fig. 1b, d). 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. 1e).

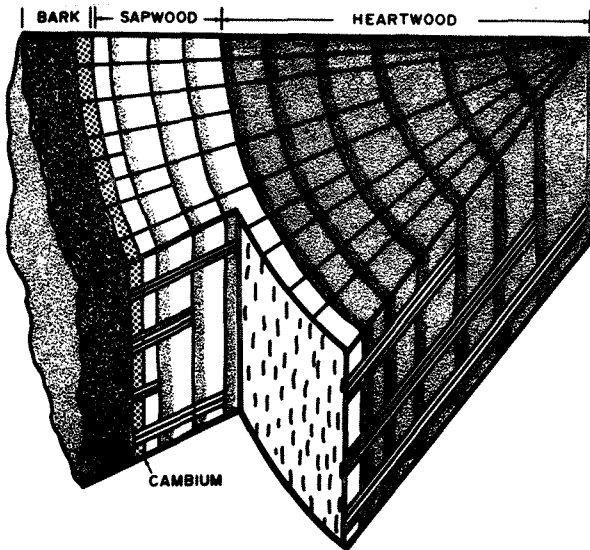
The high negative pressure created during transpiration coupled with the air-rejecting capability of bordered pits creates a hydraulic flow system that almost defies direct description or verification. Insertion of instrumentation to measure negative pressure gradients within the sapwood allows air entry 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 but known depths in the transpiration stream.

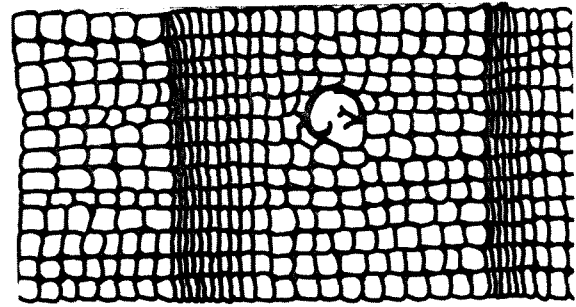
EVIDENCE OF PARABOLIC DISTRIBUTION

1. Dye staining patterns under induced flow.

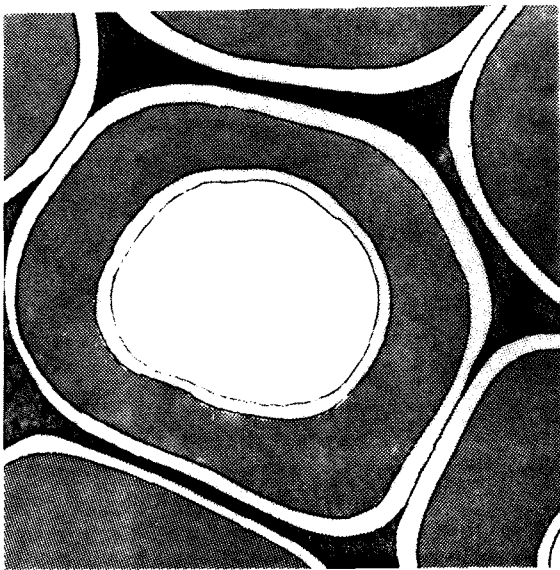
Water soluble Rhodamine B was drawn into a lodgepole pine stem section, (5 cm dia. 19.6 sq. cm. cross-section area). The stem was then cut into 1 cm long segments to ascertain the point to which the dye had travelled, (Figure 2). Dye moved through the 6 outside annual rings



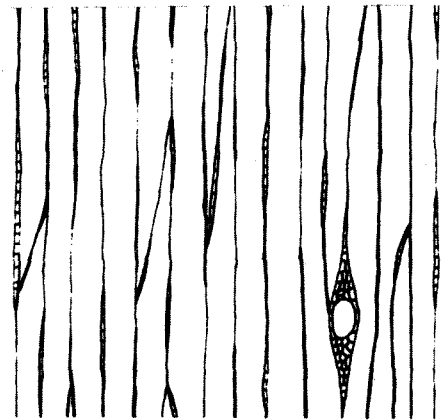
(a) Simplified stem structure, principal tissue groups only.



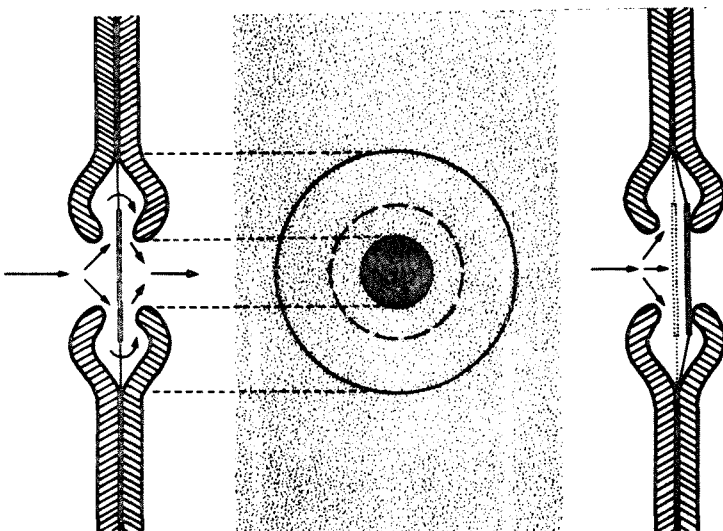
(b) Xylem (sapwood) composed of groups of tracheids. Axial view.



(c) Tracheid in cross section; central void area is lumen through which water moves.

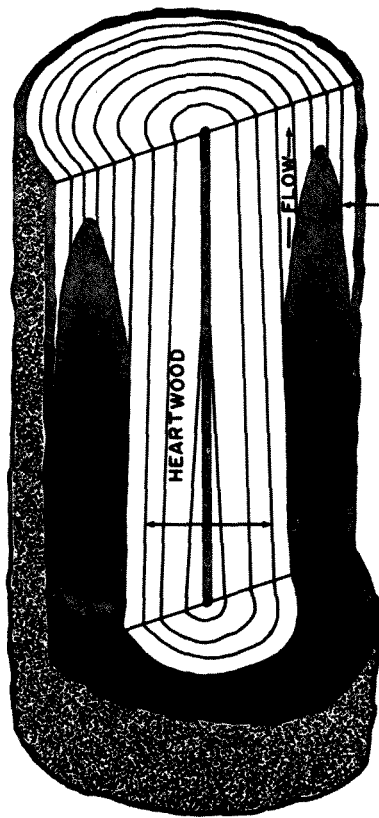


(d) Xylem in radial view. Individual tracheids overlap to give mechanical strength. Length of an average lodgepole pine tracheid is 4 mm.



(e) Diagrammatic sketch of bordered pit. Pits on adjoining tracheids meet to form pit pairs through which water moves. Pits are found all along each tracheid but tend to be more numerous near the ends.

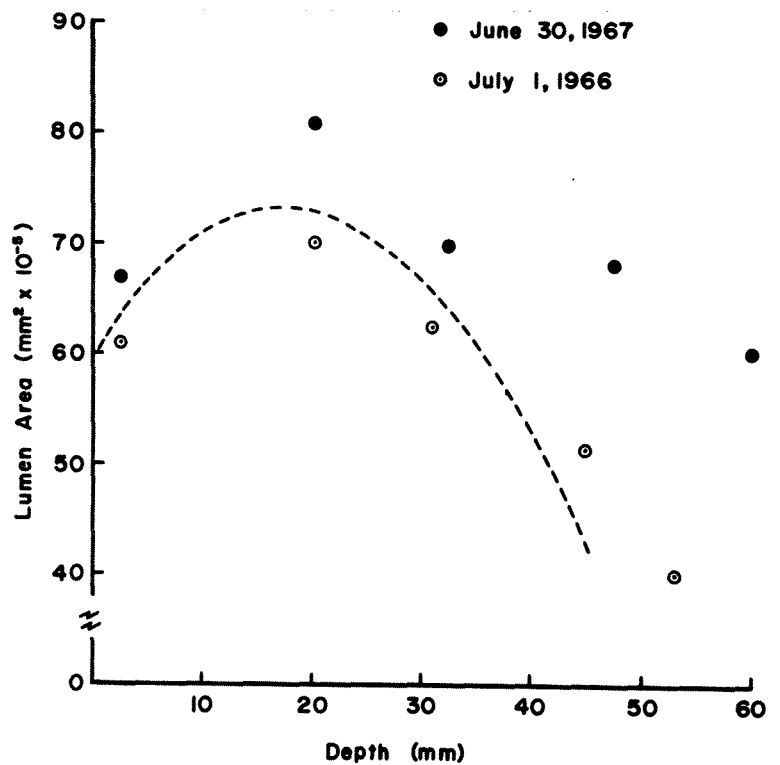
Figure One. Gross and microscopic coniferous wood anatomy.



Dye Staining
Pattern in Stem
Section

Figure Two. Diagrammatic sketch of dye staining pattern in sapwood. Not to scale.

Figure Three. Lumen area distribution with depth into sapwood in Engelmann 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 purposes.



(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.

2. 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. 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 3 shows the results of lumen area determinations at various sapwood depths.¹ 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.

3. Statistical curve fitting to empirical data.

The sapwood of trees 20-30 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 in opposite quadrants with heat pulse velocity measuring probes at 2, 5, 10, 15, 20 and 25 mm depths into the sapwood from the cambium (Figure 4).² These probes were activated and read in sequence during clear sky conditions in May and June, 1965.

Figure 5 is a graphical plot of the mean value of the data at each depth. Least squares fitting these data to a second degree linear model results in the equation:

$$\text{HPV} = 1.66 + 0.69D - 0.018D^2 \quad \text{cm/hour} \quad (1)$$

Where: HPV = heat pulse velocity.

D = depth at measurement point, mm.

For this fitting, $R = 0.685$, $n = 29$, $F = 12.8$; significant at the 99% confidence level. These statistics indicate a reasonably strong relationship between the variables. More importantly, the solution of equation (1) for the depths where HPV = 0, show that the predicted origin is approximately at zero (actually - 2.3 mm, just slightly into the bark), and at 41.3 mm, which is within the sapwood.

4. Predicted depths of movement contain 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:

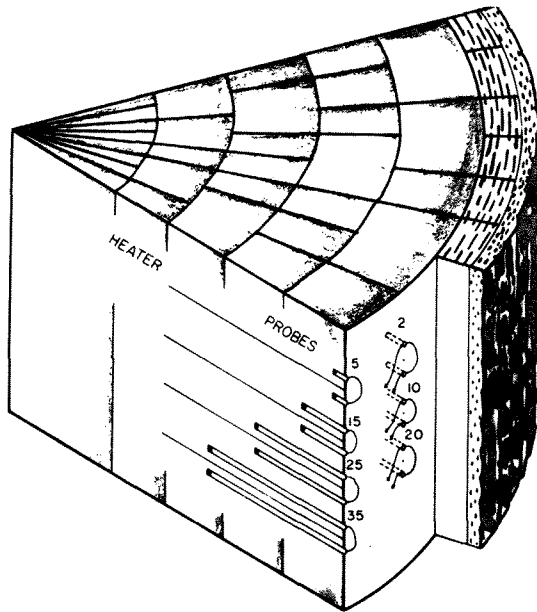


Figure Four. Sketch showing placement of heat pulse velocity measuring probes in sapwood of lodge-pole pine trees.

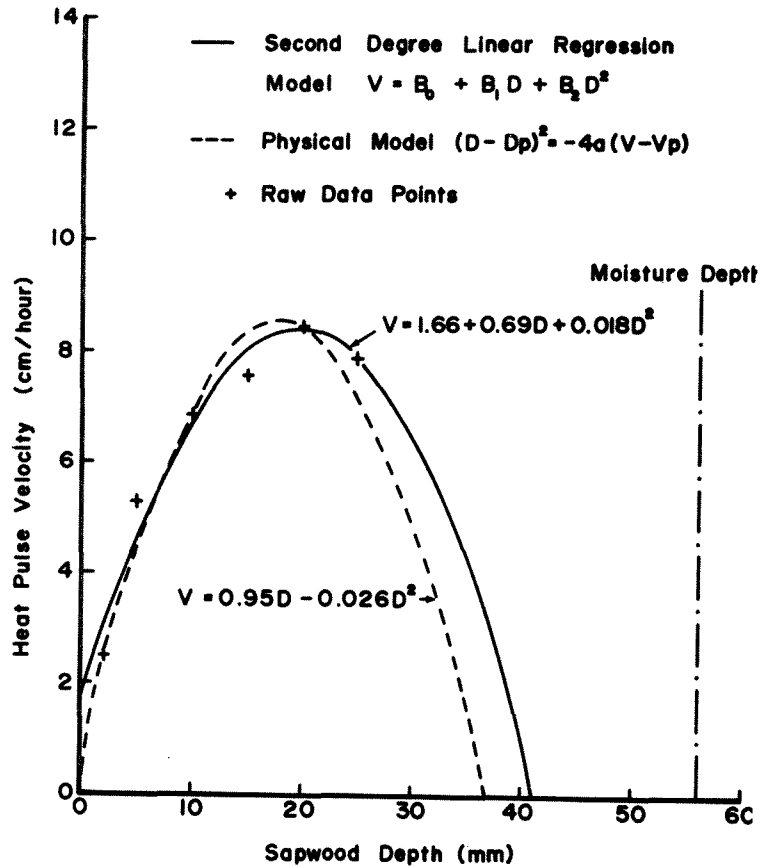


Figure Five. Graphical plot of heat pulse velocity distribution with depth into sapwood. Superimposed are statistically and physically fitted models. Data points are mean value for a least 4 determinations at that depth. Vertical line at 56 mm deep represents heartwood-sapwood boundary at which moisture content falls from 153% in sapwood to 30% in heartwood.

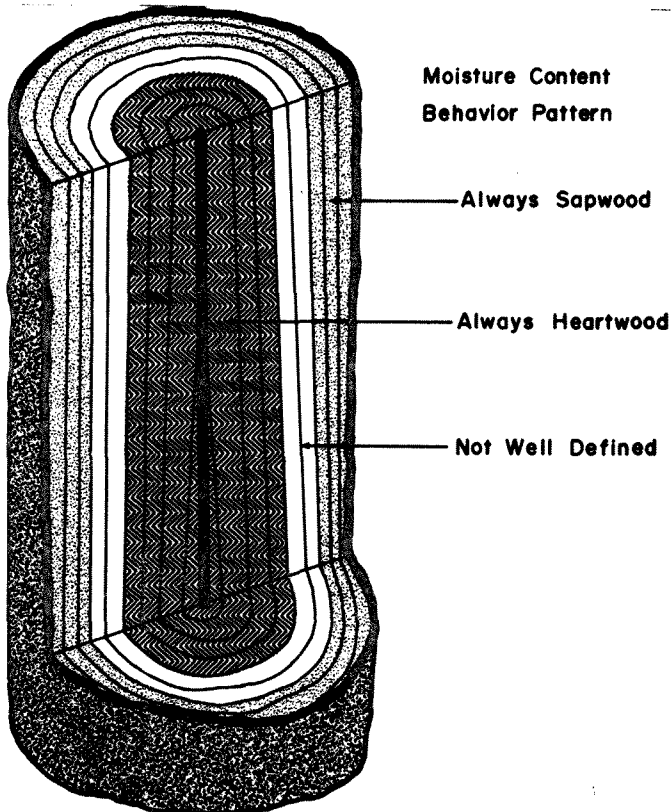


Figure Six. Stem cross section showing portions of wood usually separable into heartwood or sapwood on the basis of moisture content. The sapwood-heartwood interphase portion is not well defined by moisture content.

- a) Flow velocity at the origin (cambium) would be zero.
- b) A second point of zero movement (D_m) would fall within the sapwood at a depth equal to or less than the sapwood-heartwood interphase depth.

Mathematically, any first or higher degree equation will go through any two points, second or higher degree through any three points, and so on. A second degree parabolic model is suitable here. This model fits the empirical data, provides the necessary two points of zero movement, and is convenient as much of the theoretical work on non-compressible laminar flow in pipes can be used to advantage.

A general parabolic equation containing the relevant terminology is:

$$(D - D_p)^2 = 4a (HPV - V_p). \quad (2)$$

Where: V_p = peak heat pulse velocity.

D_p = depth at which V_p occurs.

This equation was fitted through point (0,0) and the average HPV values at 10 and 20 mm depths for the data from equation (1) above. This fitting results in

$$HPV = 0.95D - 0.026D^2 \quad \text{cm/hour} \quad (3)$$

and is plotted on figure 4 for comparison with that derived statistically. They are almost coincident.

Why use a parabolic model? Because the average heat pulse velocity across any radial cross section can be easily calculated using a standard equation, and the conducting area can be calculated by 360° rotation about the centre axis of the tree of the line segment between the two zero HPV points. This latter is most important as previous work has demonstrated that total sapwood area within a group of trees is not static.³ Seasonal changes have been noted; diurnal changes may also occur.

The sapwood must wholly contain the water conducting area, (there just isn't sufficient moisture present in the heartwood of lodgepole pine to allow any appreciable flow volume to occur there). The amount of conducting area is calculable from non-destructive samples, that is, HPV measurements, if the parabolic distribution is assumed. A necessary condition for validity is that the conducting depth calculated must be equal to or less than the total depth of sapwood. This last was tested and is reported below.

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 (based on a change in moisture content of greater than 20%) at which the sapwood-heartwood interphase commenced as determined from cores removed from the tree. The results are tabulated in table 1.

Twenty-four of twenty-seven predicted depths are less than the measured sapwood-heartwood interphase depth. 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 (Figure 6). Data taken 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%, the other two also show a similar magnitude increase. Likewise, those at depths beyond 5 cm 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 (more likely to soil moisture availability) - 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 in this instance 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.

DISCUSSION

A major weakness in the argument for a parabolic distribution for heat pulse velocities, is a lack of measurements to verify the shape between the peak velocity and the heartwood-sapwood interphase. In lodgepole pine these verifying measurements should be made in the vicinity between 2.5 and 5 cm deep. Heat pulse velocity measurements at these depths become quite inaccurate because the holes into which the sensing probes are inserted cannot be spaced with high precision. This is a mechanical problem caused by the flexibility of the necessarily-small drill bits (approximately 1 mm dia.). More rigid drill bits, better drilling techniques or the ascertainment of in-place spacing by x-ray photography may resolve this problem in the future.

The usefulness of the parabolic assumption need not await it's absolute verification. Average heat pulse velocity can be determined by a good random sampling program and suitable statistical technique; conducting

Table 1. Predicted depth into sapwood at which sap movement no longer occurs compared with measured thickness of sapwood.

<u>Tree</u>	<u>Quadrant</u>	<u>Predicted Depth</u>	<u>Measured Thickness</u>
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
		$\bar{D} = 3.69 \text{ cm}$	4.24 cm

area cannot. Sapwood area, which can be obtained from borings, is not necessarily all conducting area. Dye staining pattern may indicate the exact extent, but the technique is destructive and negates any opportunity for repeated determination from a given tree. For the present time, the only non-destructive technique is the extension of outer sapwood heat pulse velocity data to the inner sapwood by mathematical equations. The parabolic model suggested here has passed all of the tests to date. It ought to be used until proven incorrect!

CONCLUSIONS

The above evidence 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 two known and one assumed point to predict the inner depth of zero movement.

ACKNOWLEDGEMENT

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NOTES AND REFERENCES

(1) 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. 11 pp., 1967.

(2) Heat pulse velocity values are measurements related to water movement in tree stems. See Swanson, paper number 2-3-170 of these proceedings for a description of a heat pulse velocity meter.

(3) R.H. Swanson, Proceedings XIV IUFRO-Kongress, V. I, Sect. 01-02-11, 252-263. Munich, 1967.