

## Relation between the permeability and the anatomy of jack pine sapwood with stand development<sup>1</sup>

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The anatomical characteristics of sapwood from the base of the live crown of trees from 11 jack pine stands (*Pinus banksiana* Lamb.) of different age and site quality were related to the patterns of change of longitudinal sapwood permeability ( $k$ ) previously observed to occur among these stands. Tracheid length ( $L_t$ ) increased rapidly from a minimum of 1.9 mm to a plateau of around 3.6 mm as stand age and site quality (productivity class) increased. Sapwood relative water content ( $R_s$ ) measured before saturation ranged from 78 to 85% for the majority of trees. Samples taken from trees growing on poor sites, however, exhibited significantly lower values of  $R_s$ , which probably resulted in their remaining below saturation during the determination of sapwood permeability. The lower  $R_s$  values were assumed to be reflective of more adverse water balances during the growing season associated with rapidly drained and (or) shallow soils. Tracheid lumen diameter ( $D_l$ ) was positively correlated with  $k$  within age-classes 15 and 35, but not thereafter. The initial relation between  $D_l$  and  $k$  is thought to be associated with corresponding increases in the area of pit membranes, which determines the number of pores within a pit membrane. Values of  $k$  were never more than 60% of the values calculated by Poiseuille's law for ideal capillaries ( $k_c$ ) and were generally less than 40%. Values of  $k$  tended to approach  $k_c$  with increasing  $L_t$  and decreasing  $D_l$ . Overall, Poiseuille's law by itself could not explain the changes in the hydraulic properties of jack pine sapwood with stand development. However,  $L_t$  and  $R_s$  could together account for 72% of the variation in  $k$ . Young stands that had different  $k$  depending on site quality generally had corresponding differences in  $L_t$ ,  $R_s$ , and (or)  $D_l$ . Mature stands that had reached maximum  $k$  on all quality sites no longer showed differences in  $L_t$ ,  $R_s$ , or  $D_l$ .

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Les caractéristiques anatomiques de l'aubier à la base de la cime vivante d'arbres de 11 peuplements de Pin gris (*Pinus banksiana* Lamb.) de qualités de station et d'âges différents ont été reliées aux changements précédemment observés de perméabilité longitudinale de l'aubier ( $k$ ). Parallèlement à une augmentation de l'âge et de la qualité des peuplements, la longueur des trachéides ( $L_t$ ) a rapidement augmenté, passant d'une valeur minimale de 1,9 mm jusqu'à une valeur maximale d'environ 3,6 mm. Les valeurs de la teneur en eau de l'aubier ( $R_s$ ) mesurée avant saturation se sont situées entre 78 et 85% pour la plupart des arbres. Des échantillons provenant d'arbres croissant sur des stations pauvres ont eu de faibles valeurs de  $R_s$ , ce qui les a probablement maintenus en-deçà de la pleine saturation lors de la détermination de la perméabilité de l'aubier. Ces faibles valeurs de  $R_s$  sont probablement le reflet de bilans hydriques défavorables associés à des sols minces et (ou) à des drainages excessifs. Le diamètre du lumen des trachéides ( $D_l$ ) a été positivement corrélé à  $k$  pour les classes d'âges de 15 et 35 ans, mais n'a montré aucune corrélation pour les peuplements plus âgés. La relation entre  $D_l$  et  $k$  est probablement attribuable à la relation entre  $D_l$  et la taille de la membrane des ponctuations qui affecte le nombre de pores de cette membrane. Les mesures de  $k$  n'ont jamais atteint plus de 60% des valeurs calculées par la loi de Poiseuille pour des capillaires idéaux ( $k_c$ ) et ont généralement été inférieures à 40%. Les mesures de  $k$  ont approché les valeurs de  $k_c$  lorsque  $L_t$  augmentait et  $D_l$  diminuait. D'une façon générale, la loi de Poiseuille par elle-même n'a pu expliquer les changements des propriétés hydrauliques des peuplements de Pin gris survenant lors de leur développement. Cependant,  $L_t$  et  $R_s$  ont expliqué 72% de la variation totale de  $k$ . Les jeunes peuplements présentant des valeurs différentes de  $k$  en fonction des qualités de station ont généralement montré des différences correspondantes de  $L_t$ ,  $R_s$  et (ou)  $D_l$ . Toutefois, les peuplements à maturité ayant atteint une valeur maximale de  $k$  sur toutes les qualités de station n'ont pas montré de différences dans les valeurs de  $L_t$ ,  $R_s$  ou  $D_l$ .

### Introduction

The ability of sapwood to conduct fluid, i.e. its longitudinal permeability, is an important factor in the water relations of forest trees (Jarvis 1975). Whitehead *et al.* (1984)

proposed that sapwood permeability and sapwood area are major physiological factors influencing leaf area development. Pothier *et al.* (1989) demonstrated that the saturated sapwood permeability ( $k$ ) of unmanaged jack pine stands (*Pinus banksiana* Lamb.) generally increased with stand development, and increased faster on better sites. Also, younger stands on better quality sites exhibited a greater  $k$

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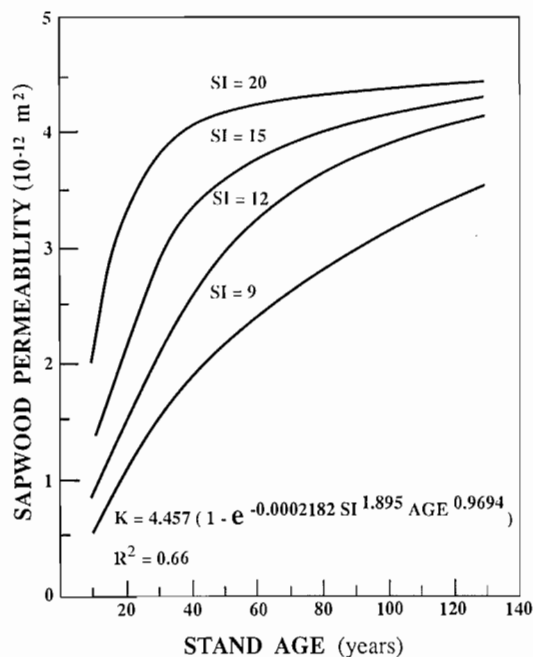


FIG. 1. Model of longitudinal sapwood permeability at the base of the live crown as a function of age and site quality for jack pine stands. Site index (SI) units are expressed in metres at age 50. The coefficient of determination ( $R^2$ ) was computed for all trees of all stands ( $n = 125$ ). (After Pothier *et al.* 1989.)

than those on poorer quality sites, whereas in older stands,  $k$  approached a common plateau (Fig. 1). We interpreted these patterns in sapwood permeability to be reflection of underlying changes in wood anatomy and report here observations supporting that contention.

Typically, 93% of conifer wood is made up of longitudinal tracheids (Panshin and de Zeeuw 1980). It is these cells that are largely responsible for the mechanical support and water transport of a living tree. Therefore, their anatomical characteristics should affect the efficiency with which sapwood can conduct water. Several attempts have been made to relate the permeability of vascular elements to a theoretical value given by Poiseuille's law. This law states that the flow rate through a cylindrical capillary is proportional to the fourth power of its diameter. However, the flow rate predicted by the Poiseuille's law tends to overestimate measured values. The extent of deviation from the theoretical value varies with species, the length of the sample specimen, and the shape and size of the vascular elements (Zimmermann 1971; Giordano *et al.* 1978; Petty 1978; Calkin *et al.* 1986; Schulte and Gibson 1988).

Poiseuille's law explicitly considers only the diameter of the tracheid lumina. Thus, the only source of resistance included in such a model is that of the lumina walls. A major source of resistance to water flow in conifers, however, is known to reside in the tracheid pits (Comstock 1970; Petty and Puritch 1970; Meyer 1971; Smith and Banks 1971; Bolton and Petty 1975, 1978; Calkin *et al.* 1986; Schulte *et al.* 1987; Schulte and Gibson 1988). According to these authors, the resistance to water flow through pits is influenced by their size and structure as well as by the number of pits per tracheid. The major source of resistance within bordered pits are the pores of the pit membrane (Bolton and Petty 1975, 1978).

TABLE 1. Structural characteristics of jack pine stands before sampling

Stand code	No. of trees/ha	Basal area (m <sup>2</sup> /ha)	Mean dbh (cm)	Mean tree height (m)
15-1	2050	9.3	7.1 ± 2.9	4.6 ± 1.1
15-3	5400	7.0	2.8 ± 3.0	2.9 ± 2.4
35-1	3833	33.7	9.9 ± 3.7	10.9 ± 2.8
35-3	3133	16.5	7.5 ± 3.4	6.8 ± 2.2
35-6	5950	8.7	3.5 ± 1.5	2.4 ± 1.4
65-2	1500	44.3	17.6 ± 8.2	15.3 ± 5.6
65-3	1433	27.1	15.1 ± 3.6	13.3 ± 1.6
65-4	925	7.3	9.1 ± 4.3	5.6 ± 2.5
120-2	2150	37.6	9.6 ± 11.6	7.8 ± 7.8
120-3	1200	31.2	17.4 ± 5.3	15.0 ± 3.8
120-4	1050	11.1	9.4 ± 6.9	7.1 ± 4.3

NOTE: The first number of the stand code refers to the age of the stand and the second number refers to the site class as derived from jack pine site index curves (Plonski 1974). Means (±SE) are from three 10 × 10 m plots established in each stand before felling sample trees (from Pothier *et al.* 1989).

Earlier studies by Krahmer (1961) and Meyer (1971) demonstrated that sapwood permeability could differ significantly between two distinct populations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). In these studies, higher sapwood permeability was associated with longer tracheids possessing large lumina and having a greater number of bordered pits than that observed in trees of lower permeability. In addition to the anatomical features mentioned, the populations with lower permeability had a higher percentage of aspirated (air-filled) pits. More pits become aspirated as sapwood moisture content falls progressively below fiber saturation point (Harris 1954). The populations sampled from a region with low precipitation had, as expected, lower permeability than those sampled from a well-watered region (Meyer 1971).

We used the results of these studies to suggest wood anatomical characteristics that might be related to the different sapwood permeabilities observed for jack pine stands of different age and site quality. In this paper, we investigate the anatomical basis of these changes in sapwood permeability on the same trees sampled in Pothier *et al.* (1989).

### Materials and methods

#### Study areas and permeability measurements

Eleven naturally established jack pine stands were sampled from three different regions of Quebec and Ontario. The structural characteristics of these stands are shown in Table 1. Details on the origin of these stands are given in Pothier *et al.* (1989). The 11 stands included two site classes for age-class 15, and three site classes each for age-classes 35, 65, and 120. Each stand that was sampled was coded using the age-class of the stand for the first number and the site class for the second number (Table 1). Site classes were extrapolated from the jack pine site index curves of Plonski (1974).

The samples used to determine longitudinal sapwood permeability ( $k$ ) were taken at the base of the live crown of 12 dominant or codominant trees in each stand, except stand 120-2 from which only 5 trees were available. All trees were harvested during the summer of 1987. For both age-classes

35 and 65, the trees were sampled during two different periods in June 1987. For each sampling period six trees from each site quality were harvested on the same morning. One metre long sections were cut at the base of the live crown, placed in plastic bags with a water-saturated atmosphere, and transported back to the laboratory at Université Laval. The same procedure was followed for stands 120-3 and 120-4 during July 1987, whereas trees from stands 15-1, 15-3, and 120-2 were sampled during only one period in July, August, and August, respectively. For stands sampled over two distinct periods, there were no differences in the permeability measurements within each stand.

The permeability apparatus as well as the method of measurement were taken from Edwards and Jarvis (1982), a modification of the method described by Booker and Kininmonth (1978) and Booker (1984). Degassed, 0.1- $\mu\text{m}$  filtered water was passed through 15 cm long stem sections ranging from 5 to 20 cm in diameter under a constant head of pressure until flow stabilized. This generally took between 10 and 60 min, but averaged around 15 min. Longitudinal sapwood permeability ( $k$ ) was calculated using Darcy's law

$$[1] \quad k = \frac{QL\eta}{A\Delta P}$$

where  $k$  is in square metres,  $Q$  is the flow rate ( $\text{m}^3/\text{s}$ ),  $L$  is the length of the stem section (m),  $\eta$  is the viscosity of the fluid ( $\text{N}\cdot\text{s}\cdot\text{m}^{-2}$ ),  $A$  is the cross-sectional sapwood conducting area ( $\text{m}^2$ ), and  $\Delta P$  is the pressure differential ( $\text{N}/\text{m}^2$ ). After the permeability measurement was completed, a disk from each sample was cut and stored in a freezer until removed for anatomical measurements.

#### Anatomical data

From each disk, a subsample was taken from the outermost rings of sapwood from the south side of the tree. These subsamples were stored in an ethanol-glycerine mixture (1:1). Transverse sections were cut to a thickness of 20  $\mu\text{m}$  and then stained with safranin. The percentage of area comprising tracheid lumina, the number of tracheids per unit area, tracheid lumen diameter, and the thickness of the radial cell walls of the tracheids were estimated in the earlywood using an image processing system at 250 $\times$  magnification. This system consisted of a Panasonic WV-CD50 camera mounted on a Leitz Wetzlar microscope. This was connected to a SUN Microsystems minicomputer, which in turn was connected to a Panasonic CT-1400MGC monitor. This monitor showed an image identical with that seen in the microscope. This image was then converted into a black and white image using a threshold algorithm and then displayed on a second monitor. On this we could easily distinguish cell wall material from lumen. Tracheid lumen cross-sectional areas took different forms ranging from nearly quadrangular to nearly circular. In all cases, however, tracheid lumen diameter was estimated as the diameter of a circle of area corresponding to the area of the tracheid lumen. At a 250 $\times$  magnification, we were able to measure tracheid diameters within an accuracy of about 1  $\mu\text{m}$ , since one pixel on the monitor screen corresponded to 0.64  $\mu\text{m}$ . Percentage of earlywood was visually estimated at 25 $\times$  magnification on three to five of the outermost rings of sapwood from the south side of the tree. Mean lumen diameter for each sample was calculated as described in Schulte and Gibson (1988):

$$[2] \quad D_l = \left[ \frac{\sum_{i=1}^n D_{li}^4}{n} \right]^{1/4}$$

The permeability of ideal capillaries ( $k_c$ ) was computed as

$$[3] \quad k_c = \frac{n\pi D_l^4}{128}$$

where  $k_c$  is in square metres,  $n$  is the number of tracheids per unit cross-sectional area ( $\text{m}^{-2}$ ), and  $D_l$  the mean tracheid lumen diameter (m) computed from eq. 2 (Siau 1984).

Another subsample located directly beside the first was taken for the evaluation of tracheid length and the number of pits per tracheid. The earlywood of the five outermost annual rings was sampled and macerated in a solution of 10% nitric acid and 10% chromic acid (1:1) for about 24 h. The tracheids were then washed and stained with safranin. Randomly selected tracheids were mounted on a slide and 10 points on the slide were then marked systematically. Around each of these points, five tracheid lengths were measured and the number of pits was counted on one of these five tracheids. Thus, for each sapwood sample of known permeability, the lengths of 50 tracheids were measured and the number of pits per tracheid was determined on 10 of these 50.

#### Sapwood relative water content and specific gravity

At the same time, the 15 cm long section at the base of the live crown was cut for the permeability measurement, a 3 cm thick cross-sectional disk was also cut for the determination of sapwood relative water content and specific gravity. From each disk, samples from the east, south, west, and north aspects were taken from the outermost rings of the sapwood. These samples were weighed, measured for volume by water displacement, and then dried in an oven at 102°C for at least 48 h. The dry mass was then determined after the samples had been placed in a desiccator containing phosphorus pentoxide.

The relative water content of sapwood ( $R_s$ ), expressed as a percentage, was calculated from

$$[4] \quad R_s = \frac{W_f - W_d}{(V_f - V_s)D_{\text{H}_2\text{O}}} \times 100$$

where  $W_f$  is the fresh weight of the wood (g),  $W_d$  is the dry weight,  $D_{\text{H}_2\text{O}}$  is the density of water ( $\text{g}/\text{cm}^3$ ),  $V_f$  is the fresh volume of the sapwood sample ( $\text{cm}^3$ ), and  $V_s$  is the volume of solid material ( $\text{cm}^3$ ), i.e., cellulose and lignin. The volume of solids was calculated from the dry weight assuming that cellulose and lignin had a constant density of 1.53  $\text{g}/\text{cm}^3$  (Siau 1984).

The specific gravity (SG) of sapwood (dimensionless) was calculated according to Siau (1984):

$$[5] \quad \text{SG} = \frac{W_d}{V_f D_{\text{H}_2\text{O}}}$$

#### Statistical analysis

Linear and nonlinear regressions as well as analyses of variance were run on the SAS system (SAS Institute Inc. 1985). Multiple comparisons were calculated according to the Tukey honestly significant difference test because of its ability to correct for experiment-wise error and handle unequal cell sizes. The Bartlett's test (Montgomery 1984)

TABLE 2. Longitudinal sapwood permeability (*k*) and characteristics of the earlywood sapwood for the sampled stands

Stand code	Longitudinal sapwood permeability ( $10^{-12} \text{ m}^2$ )	Tracheid lumen diam. ( $\mu\text{m}$ )	Tracheid length (mm)	No. of pits per tracheid	Sapwood relative water content (%)	No. of tracheids per $\text{mm}^2$ of earlywood sapwood	Specific gravity
15-1	$2.5 \pm 0.4bc$	$36 \pm 3ab$	$2.2 \pm 0.3c$	$70 \pm 14f$	$82 \pm 3a$	$718 \pm 108c$	$0.378 \pm 0.019c$
15-3	$1.4 \pm 0.4de$	$30 \pm 3cd$	$1.9 \pm 0.2c$	$75 \pm 9ef$	$78 \pm 7ab$	$966 \pm 170ab$	$0.412 \pm 0.023ab$
35-1	$4.0 \pm 0.7a$	$39 \pm 2a$	$3.0 \pm 0.3b$	$98 \pm 22cde$	$83 \pm 3a$	$651 \pm 46c$	$0.386 \pm 0.019bc$
35-3	$2.3 \pm 0.9bc$	$34 \pm 3bc$	$3.0 \pm 0.3b$	$113 \pm 13bcd$	$67 \pm 13bc$	$759 \pm 84c$	$0.411 \pm 0.018ab$
35-6	$1.0 \pm 0.6e$	$27 \pm 4d$	$2.0 \pm 0.2c$	$94 \pm 12def$	$58 \pm 11c$	$1079 \pm 281a$	$0.432 \pm 0.028a$
65-2	$4.3 \pm 1.1a$	$34 \pm 3bc$	$3.4 \pm 0.4a$	$139 \pm 19a$	$79 \pm 9a$	$723 \pm 114c$	$0.401 \pm 0.019abc$
65-3	$4.2 \pm 0.7a$	$34 \pm 4bc$	$3.2 \pm 0.2ab$	$119 \pm 27abc$	$80 \pm 8a$	$740 \pm 148c$	$0.396 \pm 0.026bc$
65-4	$1.8 \pm 1.0cde$	$33 \pm 3bc$	$3.2 \pm 0.2ab$	$117 \pm 20abcd$	$60 \pm 12c$	$796 \pm 240bc$	$0.411 \pm 0.032ab$
120-2	$3.5 \pm 1.0ab$	$38 \pm 2ab$	$3.6 \pm 0.6a$	$121 \pm 21abc$	$85 \pm 2a$	$652 \pm 91c$	$0.398 \pm 0.031abc$
120-3	$4.1 \pm 0.8a$	$35 \pm 1ab$	$3.3 \pm 0.2ab$	$124 \pm 20ab$	$83 \pm 4a$	$665 \pm 53c$	$0.388 \pm 0.028bc$
120-4	$3.6 \pm 0.5a$	$34 \pm 2b$	$3.1 \pm 0.2ab$	$138 \pm 22a$	$81 \pm 5a$	$712 \pm 88c$	$0.406 \pm 0.019abc$

NOTE: Each value is the mean ( $\pm$  SE) of 12 trees, except stand 120-2 at which only five trees were available. Values with different letters within a column are significantly different ( $p < 0.05$ ). Multiple comparisons were calculated according to the Tukey method.

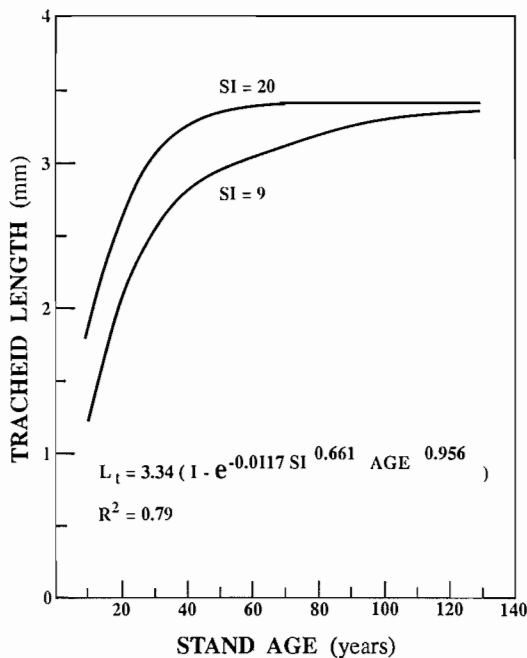


FIG. 2. Model of sapwood tracheid length as a function of age and site quality for jack pine stands. Site index (SI) units are expressed in metres at age 50. The coefficient of determination ( $R^2$ ) was computed for all trees of all stands ( $n = 125$ ).

was used to test the equality of variances. If they were found to be heterogeneous, an appropriate data transformation was applied.

**Results**

Longitudinal sapwood permeability (*k*) and tracheid lumen diameter (*D*) were significantly different among stands within age-classes 15 and 35 (Table 2). Within age-class 65, however, *k* for stand 65-4 was significantly lower than the other two 65-year-old stands, although *D*<sub>1</sub> was equal within sampling error. For age-class 120, *k* as well as all of the other anatomical characteristics of the earlywood that were measured were equal within sampling error.

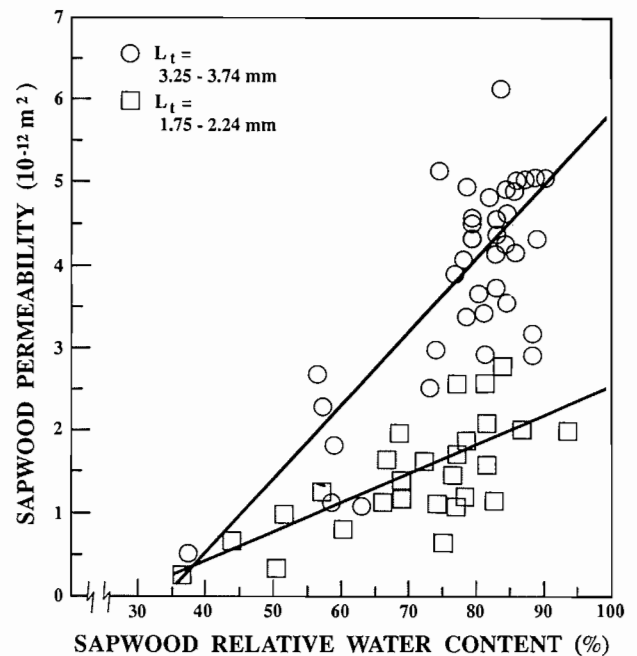


FIG. 3. Longitudinal sapwood permeability at the base of the live crown (*k*) as a function of sapwood relative water content ( $R_s$ ) for two classes of tracheid length ( $L_t$ ).

Tracheid length ( $L_t$ ) and number of pits per tracheid were equal within each age-class, except for stand 35-6, which was significantly lower than the other two 35-year-old stands (Table 2). Moreover, both  $L_t$  and number of pits per tracheid increased with stand age and seemed to reach a maximum value at age 65. The rapid increase of  $L_t$  with stand age and with site quality can be expressed by an asymptotic function (Fig. 2) similar to that used for *k* (Fig. 1).

The thickness of double radial cell walls stayed relatively constant at about 8  $\mu\text{m}$  for samples from all stands. Jack pine sapwood showed a small variation from 74 to 78% in the percentage of earlywood in an annual ring. The number of tracheids per square millimetre of earlywood of stands 15-3 and 35-6 was significantly greater than the other stands

TABLE 3. Linear coefficients of correlation ( $r$ ) between longitudinal sapwood permeability at the base of the live crown and some sapwood characteristics

Age-class	No. of sampled trees	Tracheid lumen diam. ( $D_1$ )	$k$ for ideal capillaries ( $k_c$ )	Sapwood relative water content ( $R_s$ )	Tracheid length ( $L_t$ )
15	24	0.73	0.70	0.54	0.53
35	36	0.71	0.74	0.84	0.66
65	36	-0.03	0.04	0.84	0.20
120	29	0.20	0.02	0.15	0.48
All stands	125	0.43	0.36	0.67	0.62

NOTE: Linear coefficients of correlation were computed for all trees of each stand.

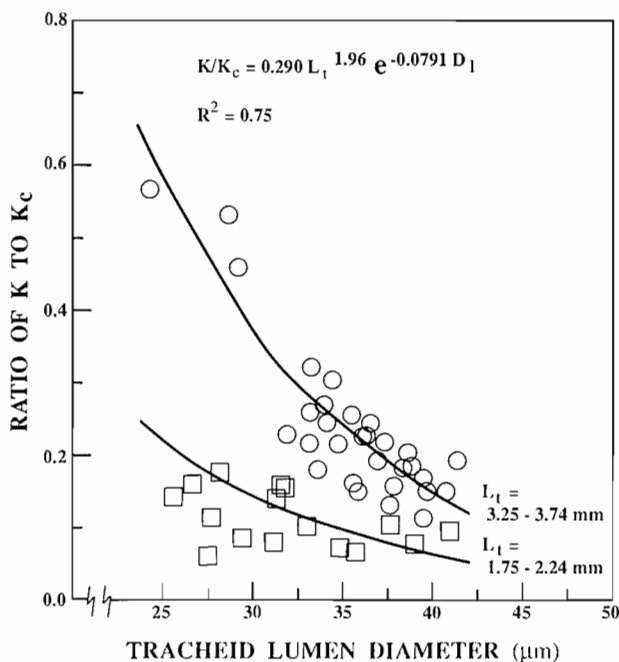


FIG. 4. Ratio of longitudinal sapwood permeability ( $k$ ) to the permeability of ideal capillaries ( $k_c$ ) as a function of tracheid lumen diameter for two tracheid length ( $L_t$ ) classes. Permeability of ideal capillaries was computed from eq. 3. The coefficient of determination ( $R^2$ ) was computed for all trees (all tracheid length classes) that had a  $R_s$  above 75% ( $n = 86$ ).

(Table 2). The percentage of sapwood area occupied by tracheid lumina ranged between 42 and 52% and tended to be proportional to the tracheid lumen diameter.

The relative water content of sapwood ( $R_s$ ) was equal within sampling error in 8 of the 11 stands (Table 2). Low values of  $R_s$  were found in stands of low site quality, i.e., stands 35-3, 35-6, and 65-4. The specific gravity of sapwood also tended to be lower on good sites than on poorer quality sites within the 15- and 35-year-old age classes (Table 2).

Within age-classes 15 and 35, there was a fair linear correlation ( $r = 0.7$ ) between both  $k$  and  $D_1$ , and  $k$  and  $k_c$  (Table 3). Within age-classes 65 and 120, these correlations diminished to near zero. For age-classes 35 and 65,  $R_s$  was well correlated with  $k$ . When all stands were analyzed together,  $k$  and tracheid length produced a linear coefficient of correlation of 0.62 (Table 3).

Of all the variables measured,  $k$  for all stands was best explained by  $L_t$  and  $R_s$  (Table 3 and Fig. 3). Within two ranges of tracheid length (1.75–2.24 mm and 2.25–3.74 mm),  $k$  was linearly related to  $R_s$ , but the slope of the relation increased as  $L_t$  increased (Fig. 3). Consequently, among all of the sapwood characteristics we measured, the best model ( $R^2 = 0.72$  and  $n = 125$ ) for predicting  $k$  was

$$[6] \quad k = -1.05 + 0.00470L_t^{0.81}R_s^{1.36}$$

The ratio of the measured  $k$  to that calculated for an ideal capillary,  $k_c$  [3], was generally below 0.4 (Fig. 4). Removing all samples that had a  $R_s$  below 75% permitted us to examine the relationship between  $L_t$  and the  $k:k_c$  ratio for sapwood with equivalent and relatively high  $R_s$ . For these samples,  $k$  tended to approach the theoretical value given by Poiseuille's law with decreasing  $D_1$  and with increasing  $L_t$  (Fig. 4). The relation took the form of a negative exponential equation having a coefficient of determination ( $R^2$ ) of 0.75 ( $n = 86$ ).

## Discussion

Pothier *et al.* (1989) related the longitudinal sapwood permeability ( $k$ ) of jack pine stands to age and site quality with an asymptotic negative exponential model (Fig. 1). This same kind of model can also relate tracheid length ( $L_t$ ) to age and site quality (contrast Figs. 1 and 2). Thus,  $L_t$  appears to be a very important anatomical characteristic affecting the changes in  $k$  that occur with stand development. Tracheid length probably affects  $k$  by determining the number of times water must pass through bordered pits, a major source of resistance to water flow in conifers (Comstock 1970; Petty and Puritch 1970; Meyer 1971; Smith and Banks 1971; Bolton and Petty 1975, 1978; Schulte and Gibson 1988). Furthermore,  $L_t$  is also indirectly related to  $k$  owing to its positive correlation with the number of pits per tracheid (Table 2). In respect to site quality, however,  $L_t$  changes much less (Table 2). Thus, whereas changes in  $L_t$  can explain the general increase of  $k$  with age, differences in  $k$  with site quality should be attributable to other factors as well.

The best variable found to explain changes in  $k$  with site quality was the relative water content of the sapwood ( $R_s$ ) measured before the samples were put on the permeability apparatus. Permeability measurements were taken when the samples had yielded stable flow rates after a period of 10 to 60 min on the permeability apparatus. Thus, it appears that for samples of low  $R_s$ , this procedure did not fully saturate

the sapwood, i.e., all cavitated tracheids could not be returned to a functional condition.

Tyree and Dixon (1986) suggested that cavitated tracheids containing only water vapor were easily reversible, whereas tracheids that contained air, i.e., embolized tracheids, were not. In embolized tracheids, water tension, along with the valve action of the torus, forces the pit membrane to become aspirated (Zimmermann 1983). Thus, the pressure gradient obtained on our permeability apparatus (0.04 MPa/m) was apparently not high enough to reverse all of the embolisms that were present. Such embolisms would remain throughout much of the growing season since recharge does not occur if there is not an extended period with wet foliage (Waring and Running 1978; Brough *et al.* 1986).

The trees in which we measured low  $R_s$  were all harvested in June, a period without soil water deficits. Furthermore, the variation of  $R_s$  between sites is well outside the 5% diurnal changes in water content measured in the lower portions of the stem (Waring and Running; Waring *et al.* 1979; Brough *et al.* 1986). Thus, we conclude that the lower  $R_s$  values observed on three sites are probably due to chronic water deficits associated with drought on rapidly drained and (or) shallow soils.

Decreasing  $R_s$  decreases  $k$  by affecting the number of pathways available for water movement (Byrne *et al.* 1977; Waring and Running 1978; Tyree and Dixon 1986). Our results show, however, that the rate of change of  $k$  with  $R_s$  depends on tracheid length, with longer tracheid classes having a steeper slope than shorter tracheid classes (Fig. 3). Thus, the advantages conferred by longer tracheids for water transport decrease with decreasing  $R_s$ . Increasing tracheid length decreases the number of tracheids per unit of sapwood volume. Consequently, an embolism in any given tracheid is much more serious for wood composed of longer tracheids (Zimmermann 1983). Indeed, in addition to the direct effect of increasing tracheid length on the number of tracheids per unit of sapwood volume, our results show that the number of tracheids per square millimetre of earlywood sapwood also decreased with increasing tracheid length (947, 757, 737, and 703 tracheids/mm<sup>2</sup> for tracheid length classes 1.75–2.24, 2.25–2.74, 2.75–3.24, and 3.25–3.74 mm, respectively).

Tracheid lumen diameter was linearly correlated with  $k$  within age-classes 15 and 35 (Table 3). This pattern is probably the result of the positive correlation between  $D_1$  and the area of pit membranes, as suggested by Schulte and Gibson (1988). The area of the pit membranes, in turn, will affect the number of pores in the pit membrane and thus the movement of water between tracheids. Within older stands, on the other hand, variation in  $D_1$  could not account for the variability in  $k$  among sites (Table 3). Moreover, for all stands combined, only 18% of the variability in  $k$  is accounted for by  $D_1$ . This emphasizes the fact that Poiseuille's law by itself is not very useful for explaining the changes in the hydraulic properties of conifer stems that occur with stand development.

Measured values of  $k$  were never higher than 60% of the values calculated for ideal capillaries,  $k_c$  (Fig. 4). Since  $k$  approached  $k_c$  as  $D_1$  decreased, the effect of  $D_1$  on the resistance to water flow could become important in trees or in parts of trees containing very narrow tracheids. Within the range of  $D_1$  found in the sapwood of jack pine trees at the base of the live crown, however,  $D_1$  was apparently not

narrow enough to exert a strong influence on  $k$  (Table 3). Measured values of  $k$  also moved toward  $k_c$  with increasing tracheid length (Fig. 4). This is to be expected, since very long tracheids will approach the open-ended form of an ideal capillary.

### Conclusions

The ability of jack pine sapwood to conduct water seems to be affected by (i) the number of tracheids through which water must pass per unit of stem length, (ii) the number of functional tracheids, and (iii) the area of pit membranes within individual tracheids. The number of times water must pass through a tracheid is directly related to the tracheid length, whereas the proportion of functional tracheids is related to the sapwood relative water content. The area of pit membranes in a tracheid is likely influenced by the tracheid diameter as well as by the number of pits per tracheid. The number of pits per tracheid, in turn, is strongly related to the tracheid length. Thus, tracheid length and sapwood relative water content are the two most important characteristics of sapwood with which we can explain the variation of sapwood permeability with stand development. Tracheid diameter, on the other hand, is important only in young stands.

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