

Patterns of change of saturated sapwood permeability and sapwood conductance with stand development

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The saturated sapwood permeability (k) of jack pine (*Pinus banksiana* Lamb.) from stands of different ages and site qualities was measured using a constant water flow apparatus. Saturated sapwood permeability at the base of the live crown (BLC) increased with age and reached a plateau just beyond $4 \times 10^{-12} \text{ m}^2$. The rate at which this plateau was reached, however, was dependent on site quality. Such age-related increases in k can partially explain how trees can maintain similar daytime leaf water potentials at different stages of stand development. Within age-classes 15 and 35, k at BLC was greater on the better-quality sites and was strongly correlated with both diameter and height growth. For age-class 120, k at BLC was not significantly different among sites. Saturated sapwood permeability at BLC could be predicted from age and site quality, using a negative exponential function ($R^2 = 0.66$). The ability to predict changes in k with stand development has potential for improving leaf area estimates derived from sapwood area - leaf area correlations. Sapwood conductance from ground level to the upper third of the crown decreased with age for good-quality sites and increased with age for poor-quality sites. It corresponded to the pattern of average annual height growth over the last 5 years ($R^2 = 0.61$). The number of annual rings contributing to the sapwood at a given age was independent of site quality. This suggests that the historical reconstruction of a tree's leaf area and growth efficiency is possible even after the formation of significant amounts of heartwood.

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La perméabilité de l'aubier saturé (k) de Pins gris (*Pinus banksiana* Lamb.) provenant de peuplements d'âges variés et de qualités de station diverses a été mesurée à l'aide d'un appareil maintenant un débit constant. Les résultats indiquent que k mesurée à la base de la cime vivante (BCV) a augmenté avec l'âge des arbres jusqu'à ce qu'elle ait atteint un plateau légèrement supérieur à $4 \times 10^{-12} \text{ m}^2$. Cependant, la vitesse d'atteinte de ce plateau a été influencée par la qualité de station. Une telle augmentation de k avec l'âge peut partiellement expliquer la constance du potentiel hydrique foliaire des arbres à divers niveaux de leur développement. Pour chacune des classes d'âge 15 et 35, k à BCV a été supérieure sur les meilleures qualités de station et a fortement été corrélée aux croissances en diamètre et en hauteur. Pour la classe d'âge 120, k à BCV n'a pas été significativement différente entre les stations. La perméabilité de l'aubier saturé pourrait être prédite par les variables âge et qualité de station en utilisant une fonction exponentielle négative ($R^2 = 0,66$). La prédiction de la variation de k en relation avec le développement des peuplements pourrait améliorer les estimations de superficie foliaire faites à partir des superficies d'aubier. La conductance de l'aubier calculée à partir du niveau du sol jusqu'au tiers supérieur de la cime, a diminué avec l'âge des peuplements sur les meilleures qualités de station mais a augmenté avec l'âge des peuplements sur les stations plus pauvres. Les valeurs moyennes de conductance de l'aubier par peuplement ont varié de façon similaire à la croissance en hauteur moyenne des 5 dernières années ($R^2 = 0,61$). Le nombre de cerne annuels dans l'aubier n'a pas significativement varié entre les qualités de station pour toutes les classes d'âge étudiées. Ce résultat suggère que la reconstruction historique de la superficie foliaire et de l'indice d'efficacité de croissance d'un arbre est possible malgré une formation importante de bois de cœur.

Introduction

Many studies have examined the efficiency with which wood can conduct fluid, i.e., its permeability. The first investigators were primarily concerned with timber utilization processes such as drying, preservation, and chemical pulping (Comstock 1965; Tesoro *et al.* 1972; Bolton and Petty 1975). Other authors have measured the permeability of wood damaged by insects or fungi in an attempt to determine the reasons for tree mortality (Puritch 1971; Gregory 1977). However, Booker (1977) reported that practically all measurements made before 1963 probably contained significant errors because the water used was not deaerated. More recently, it was found that sapwood permeability has considerable ecological relevance because of its importance in

the sapwood area - leaf area relationship of forest trees (Whitehead *et al.* 1984).

The pipe model theory developed by Huber (1928) and Shinozaki *et al.* (1964) suggested that a given unit of conducting tissue was necessary to supply water to given unit of transpiring foliage. The consequent development of sapwood area - leaf area ratios for different tree species followed for use in ecological studies (Waring *et al.* 1977, 1981, 1982; Whitehead 1978; Rogers and Hinckley 1979; Gholz 1980; Long *et al.* 1981; Kaufmann and Troendle 1981; Albrectson 1984; Marchand 1984; Keane and Weetman 1987; Oren *et al.* 1987). However, Whitehead *et al.* (1984) showed that differences in saturated sapwood permeability (k) can account for differences in the sapwood area - leaf

area ratios between species. Similarly, Espinosa Bancalari *et al.* (1987) suggested that differences in sapwood permeability may be responsible for the different sapwood area – leaf area ratios found in Douglas-fir plantations of the same age growing on different-quality sites.

Several authors have proposed proportional increases in k with increasing growth rate (Booker and Kininmonth 1978; Edwards and Jarvis 1982; Whitehead *et al.* 1984). Comstock (1965), on the other hand, found that k was not affected by differences in growth rate. These contrasting results may stem from the fact that the authors who proposed a proportional relationship between k and growth rate made their measurements on young trees of the same age, while Comstock (1965) made his measurements on older trees of different ages. This suggested to us that it would be useful to relate k to the site index curves so commonly used in forest management. As well as improving our ability to estimate stand leaf area, such a relationship had potential for providing a physiological explanation for differences in tree height growth on different-quality sites, based on the differential ability of sapwood to conduct water.

As the properties of wood produced by a tree can vary with both age and growth rate (Panshin and de Zeeuw 1980), we expected to find corresponding differences in k . We predicted that trees of similar age that are actively growing in height on different-quality sites would have sapwood of different k values, and that the trees from stands with the faster growth rates would have a greater k value. Furthermore, because the diameter growth rates of very old stands tend to be uniformly low on all sites, we predicted that trees which have approached maximum height on different-quality sites would have sapwood of similar k values.

These permeability data also allowed us to estimate the conductance through a tree stem. Because conductance to water flow through sapwood could affect the water potential and thus the turgor pressure of an expanding shoot at the top of a tree, we hypothesized that there would be a close relationship between stem conductance and height growth.

To test these hypotheses, we selected jack pine stands (*Pinus banksiana* Lamb.) of four different age-classes growing on different-quality sites in eastern Canada. Jack pine was used because it grows on a wider range of site qualities than the other major tree species found in Quebec.

Materials and methods

Study areas

Each stand that we sampled was coded using the age-class of the stand for the first number and the site class for the second number. Site classes were extrapolated from the jack pine site index curves of Plonski (1974). Each site class refers to a range of site indices. For example, site class 1 will contain all stands with a site index between 17 and 20, while site class 2 refers to stands with a site index between 14 and 17. The site index for each stand was calculated with the exponential-monomolecular function for jack pine (Lundgren and Dolid 1970)

$$[1] \quad SI = Hb_1^{-1} (1 - e^{b_2 AGE}) - b_3$$

where SI is site index (height at age 50 years), H is total height of tree in metres, AGE is age in years, $b_1 = 1.633$, $b_2 = -0.02233$, and $b_3 = 1.2419$. This equation significantly fits ($R^2 = 0.91$) the jack pine site index curves developed by Plonski (1974).

During the summer of 1987, 11 naturally established jack pine stands located in three different areas of Quebec and Ontario were

TABLE 1. Structural characteristics of jack pine stands before sampling

Stand code	No. of trees/ha	Basal area (m ² /ha)	DBH (cm)	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 to the site class derived from jack pine site index curves (Plonski 1974). Values for DBH and tree height (mean ± SE) are from three 10 × 10 m plots established in each stand before sample trees were felled.

sampled (Tables 1 and 2). Stand availability as well as limitations of time, logistics, and labor forced us to limit our sampling to these 11 stands. Seven stands (15-1, 35-1, 35-3, 35-6, 65-2, 65-3, 65-4) were in the Lac St-Jean area (48.5°N, 72.6°W) corresponding to the Laurentide-Onatchiway (B.1a) region of Rowe (1972) and to the Haute terre du lac Bouchette (8j) region of Thibault (1985). These seven stands were within 15 km of each other. The soils of these stands are of medium to coarse texture and derived from either glacial till of variable depth or fluvio-glacial sands and gravels. Three other stands (15-3, 120-3, 120-4) were in the Reserve Ashuapmushuan area (49.3°N, 73.8°W), located about 200 km farther north, which corresponds to the Chibougamau-Natashquan (B.1b) region of Rowe (1972) and the Lac Chibougamau (12b) region of Thibault (1985). The soils of this region are predominantly shallow tills. The last stand (120-2) was located near the Petawawa National Forestry Institute, Chalk River, Ontario (46.0°N, 77.4°W), within the Middle Ottawa Section (L.4c) of the Great Lakes – St. Lawrence Forest Region (Rowe 1972). This area is located about 500 km southwest of the Lac St-Jean stands. The soil of this stand is a deep, fine lacustrine sand (Burgess and Methven 1977).

Saturated sapwood permeability and sapwood conducting area

During the summer of 1987, 12 dominant or codominant trees were selected from each stand except the Petawawa stand (120-2), from which only 5 trees were available (Table 2). Selecting only dominant or codominant trees reduced the high variability typically encountered in naturally established stands. These trees were cut down between June and August 1987, and at each time, total height, length of the live crown, and the last 5 complete years of height growth were measured. At each sampling period, six trees were harvested from each of three different stands except the Petawawa stand, where only five trees were harvested. Sections 1 m long were cut at the base of the live crown (BLC) and at the bottom of the upper third of the crown for measuring k . A shorter sample was cut at 1.4 m for determining age and diameter growth at breast height. These samples were placed in plastic bags with a water-saturated atmosphere and transported to the laboratory.

Twelve samples were placed in the laboratory overnight at room temperature, and the remaining samples were stored in a refrigerator at 4°C. The following morning, 15 cm long sections were cut from each of these 12 samples, planed on each end with a hand jointer to give a smooth, clean surface, and placed between two pieces of Plexiglas on the permeability apparatus, using 6 mm thick pure gum rubber O-ring gaskets. To prepare the samples for mea-

TABLE 2. Details of sample trees within each stand

	15-1 (n = 12)	15-3 (n = 12)	35-1 (n = 12)	35-3 (n = 12)	35-6 (n = 12)	65-2 (n = 12)
Age at DBH (yr)	15.9 ± 3.2a	12.9 ± 1.4a	36.2 ± 2.8b	35.6 ± 1.5b	37.2 ± 2.3b	67.9 ± 1.7c
Total height (m)	7.2 ± 1.0b	3.6 ± 0.4a	16.1 ± 0.9e	10.5 ± 1.1c	3.7 ± 0.2a	19.7 ± 1.3g
Site index at 50 yr (m)	20.0 ± 1.8f	12.2 ± 1.1c	20.6 ± 1.4f	13.6 ± 1.2cd	4.6 ± 0.4a	16.4 ± 1.0e
DBH (cm)	10.6 ± 2.0b	2.7 ± 0.5a	17.2 ± 1.8c	11.5 ± 1.4b	4.3 ± 0.7a	22.1 ± 3.4d
Mean basal area/ tree (cm ²)	90.5 ± 32.7bc	6.0 ± 2.0a	235.1 ± 49.8e	105.6 ± 26.0cd	12.2 ± 4.6ab	393.0 ± 117.2f
Mean sapwood area/ tree at DBH (cm ²)	84.9 ± 30.5b	5.7 ± 1.8a	178.3 ± 34.2d	59.9 ± 15.3b	6.5 ± 1.8a	188.1 ± 58.6d
10-year diameter growth at DBH (cm)	7.0 ± 0.8f	2.2 ± 0.4d	3.3 ± 0.7e	1.6 ± 0.5cd	0.7 ± 0.3a	1.4 ± 0.5bc
10-year basal area growth at DBH (cm ²)	76.8 ± 21.2e	5.6 ± 1.8ab	81.8 ± 21.9e	26.3 ± 8.0c	3.7 ± 1.5a	46.2 ± 20.4d
10-year relative basal area growth rate at DBH (%/yr)	87.9 ± 10.5c	95.0 ± 4.9c	34.7 ± 4.9b	25.5 ± 8.2b	33.3 ± 14.9b	11.9 ± 4.0a
	65-3 (n = 12)	65-4 (n = 12)	120-2 (n = 5)	120-3 (n = 12)	120-4 (n = 12)	
Age at DBH (yr)	66.1 ± 1.7c	64.3 ± 2.3c	122.4 ± 13.8d	119.3 ± 2.7d	117.9 ± 3.7d	
Total height (m)	14.2 ± 1.0d	10.2 ± 1.4c	22.6 ± 3.0h	18.0 ± 1.7f	14.5 ± 1.0de	
Site index at 50 yr (m)	12.0 ± 0.8c	8.7 ± 1.1b	15.2 ± 2.6de	12.0 ± 1.1c	9.8 ± 0.7b	
DBH (cm)	15.4 ± 1.7c	17.4 ± 1.5c	34.5 ± 2.3e	20.6 ± 2.6d	17.0 ± 2.7c	
Mean basal area/ tree (cm ²)	187.5 ± 40.2de	238.0 ± 42.8e	937.1 ± 25.8g	339.2 ± 84.8f	233.0 ± 76.3e	
Mean sapwood area/ tree at DBH (cm ²)	100.5 ± 26.4bc	103.2 ± 24.3bc	275.0 ± 81.8e	140.1 ± 55.7cd	95.3 ± 29.3bc	
10-year diameter growth at DBH (cm)	1.0 ± 0.4abc	0.9 ± 0.5ab	0.9 ± 0.2ab	0.9 ± 0.3abc	0.9 ± 0.2ab	
10-year basal area growth at DBH (cm ²)	22.1 ± 10.4bc	23.3 ± 10.8bc	46.5 ± 10.1d	30.5 ± 11.4cd	22.7 ± 6.7bc	
10-year relative basal area growth rate at DBH (%/yr)	12.2 ± 5.5a	10.0 ± 5.5a	5.0 ± 1.1a	8.9 ± 2.4a	10.2 ± 3.1a	

NOTE: Values are given as mean ± SE of 12 trees, except for stand 120-2 at which only 5 trees were available. Values within a horizontal row followed by a different letter(s) are significantly different ($p < 0.05$). Multiple comparisons were calculated according to Tukey's method. *n*, number of trees selected.

surement, 0.1 μm filtered, degassed water was passed through the stem sections under a constant head of pressure until flow stabilized (Booker and Kininmonth 1978; Booker 1984). At this time, it was assumed that the sections had been saturated (Edwards and Jarvis 1982). This usually occurred in less than 15 min. The flow rate as well as the pressure and temperature differentials between the points of input and output were then measured every 3 min for a period of 9 min. The k value of the sample was calculated from the average of these three sets of measurements. As the ratio of the flow rate to the pressure differential was constant when the pressure differential was kept within the range of values experienced in nature, it is possible to compare the k values of different samples that were measured at slightly different pressure differentials (Edwards and Jarvis 1982). After this time, 0.1% rhodamine, a red dye, was passed through the samples for 5–20 min depending on the rate of dye penetration. Cutting away a 2 cm thick section allowed us to evaluate the area of sapwood actually conducting water and the number of annual rings conducting, as well as diameter growth.

Twelve more samples were measured during each of the next 2 days, for a maximum of 36 measurements per sampling period. The samples for the next day were always equilibrated to room temperature each night. Preliminary trials had indicated that we could obtain stable permeability measurements for at least 1 week with this procedure.

From the temperature of the water we could determine its viscosity (Weast 1976). The k value was calculated according to Darcy's Law

$$[2] \quad k = \frac{QL\eta}{A\Delta P}$$

where k is given in square metres, Q is the flow rate (m^3/s), L is the length of the stem section (m), η is the viscosity of the fluid ($\text{N}\cdot\text{s}\cdot\text{m}^{-2}$), A is the cross-sectional sapwood conducting area (m^2), and ΔP is the pressure differential (N/m^2).

Conductance

The conductance of a stem section to water flow is analogous to electrical resistance (Jarvis 1975) and is given by

$$[3] \quad G = \frac{1}{R} = \frac{Q}{\Delta P}$$

where G is the conductance ($\text{m}^3\cdot\text{Pa}^{-1}\cdot\text{s}^{-1}$) and R is the resistance ($\text{Pa}\cdot\text{s}\cdot\text{m}^{-3}$). By combining eq. 2 with eq. 3, the conductance becomes

$$[4] \quad G = \frac{kA}{L\eta}$$

Because we measured k only at BLC and at the beginning of the upper third of the crown ($1/3$), we can approximate the sapwood

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10-year diameter growth at DBH (cm)	7.0 ± 0.8f	2.2 ± 0.4d	3.3 ± 0.7e	1.6 ± 0.5cd	0.7 ± 0.3a	1.4 ± 0.5b
10-year basal area growth at DBH (cm ²)	76.8 ± 21.2e	5.6 ± 1.8ab	81.8 ± 21.9e	26.3 ± 8.0c	3.7 ± 1.5a	46.2 ± 20.4
10-year relative basal area growth rate at DBH (%/yr)	87.9 ± 10.5c	95.0 ± 4.9c	34.7 ± 4.9b	25.5 ± 8.2b	33.3 ± 14.9b	11.9 ± 4.0a

	65-3 (n = 12)	65-4 (n = 12)	120-2 (n = 5)	120-3 (n = 12)	120-4 (n = 12)
Age at DBH (yr)	66.1 ± 1.7c	64.3 ± 2.3c	122.4 ± 13.8d	119.3 ± 2.7d	117.9 ± 3.7d
Total height (m)	14.2 ± 1.0d	10.2 ± 1.4c	22.6 ± 3.0h	18.0 ± 1.7f	14.5 ± 1.0de
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From the temperature of the water we could determine its viscosity (Weast 1976). The k value was calculated according to Darcy's Law

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where k is given in square metres, Q is the flow rate (m^3/s), L is the length of the stem section (m), η is the viscosity of the fluid ($\text{N}\cdot\text{s}\cdot\text{m}^{-2}$), A is the cross-sectional sapwood conducting area (m^2), and ΔP is the pressure differential (N/m^2).

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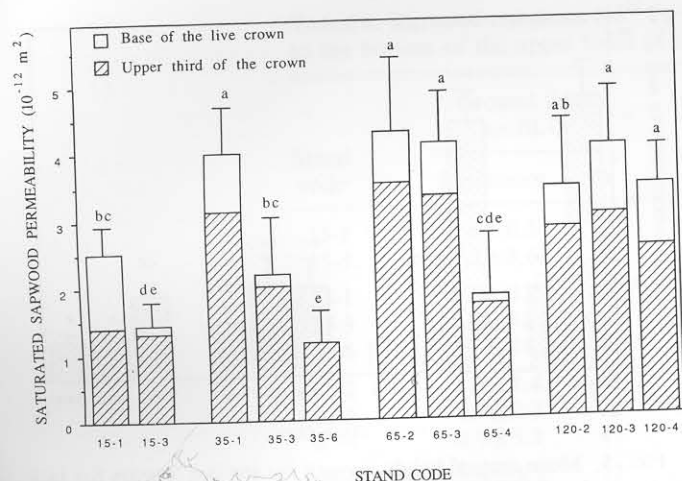


FIG. 1. Saturated sapwood permeability at the base of the live crown and at the bottom of the upper third of the crown for age-classes 15, 35, 65, and 120 on a range of site qualities. Each value is the mean of 12 trees, except that for stand 120-2, which is the mean of 5 trees. A different letter(s) indicates a significant difference for BLC at $P \leq 0.05$, using Tukey's HSD multiple comparison test. Vertical lines represent standard errors.

conductance by adding two conductances in series, i.e., from ground level to BLC and from BLC to the upper third of the crown:

$$[5] \quad \frac{1}{G_{sw}} = \frac{1}{G_{BLC}} + \frac{1}{G_{1/2}}$$

where G_{sw} is the conductance from the ground to the base of the upper third of the crown. To assess these conductances, we first assume that the product of k and A is constant below the live crown (R.E. Booker, Ministry of Forestry, New Zealand, personal communication). This assumption is also supported by the fact that $k \times A$ allows an accurate prediction of leaf area (Whitehead *et al.* 1984), and there is no leaf area below BLC. Furthermore, several authors have measured decreases in sapwood area (Huber 1928; Waring *et al.* 1982; Brix and Mitchell 1983; Dean and Long 1986; Espinosa Bancalari *et al.* 1987), as well as increases in k (Comstock 1965; Booker and Kininmonth 1978; Whitehead *et al.* 1984) from breast height to BLC. Thus, the first term in eq. 5 is

$$[6] \quad \frac{1}{G_{BLC}} = \frac{\eta L_{BLC}}{k_{BLC} A_{BLC}}$$

Secondly, we assume that $k \times A$ decreases linearly from BLC upwards to the upper third of the crown, as was found for *Pinus contorta* Dougl. and *Picea sitchensis* (Bong.) Carr. (Figs. 4a, 4b, and 4c in Whitehead *et al.* 1984). Consequently, this linear relationship between $k \times A$ and the length of the stem section (L) can be written as

$$[7] \quad kA = \alpha + \beta L$$

where α and β are the intercept and the slope, respectively, of the relationship. Thus, the second term on the right of eq. 5 is given by the definite integral from L_{BLC} to $L_{1/2}$:

$$[8] \quad \frac{1}{G_{1/2}} = \eta \int_{L_{BLC}}^{L_{1/2}} \frac{\partial L}{\alpha + \beta L} = \frac{\eta}{\beta} \left[\ln(\alpha + \beta L) \right]_{L_{BLC}}^{L_{1/2}}$$

By substitution, we find

$$[9] \quad \frac{1}{G_{1/2}} = \frac{\eta}{\beta} \ln \left(\frac{\alpha + \beta L_{1/2}}{\alpha + \beta L_{BLC}} \right) = \frac{\eta}{\beta} \ln \left(\frac{\alpha + \beta L_{1/2}}{k_{BLC} A_{BLC}} \right)$$

By combining eqs. 5, 6, and 9, we find

$$[10] \quad \frac{1}{G_{sw}} = \eta \left[\frac{L_{BLC}}{k_{BLC} A_{BLC}} + \frac{1}{\beta} \ln \left(\frac{\alpha + \beta L_{1/2}}{k_{BLC} A_{BLC}} \right) \right]$$

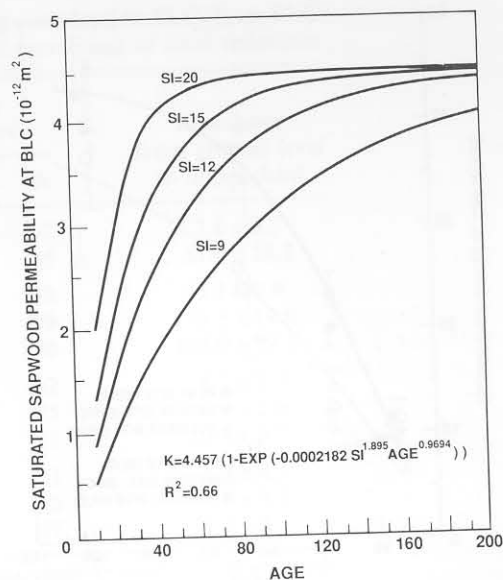


FIG. 2. Model of saturated sapwood permeability as a function of age and site quality for jack pine stands. The coefficient of determination (R^2) was computed for all trees of all stands ($n = 120$). SI, site index; BLC, base of the live crown.

Sapwood conductance is a measure of the ability of a given section of stem to conduct water from one end to the other. Thus, it is dependent on the area and the length of the sample, as well as on the viscosity of the permeating fluid. Permeability, on the other hand, is solely a property of a unit cross section of the woody stem. Permeability is therefore equivalent to relative conductivity, as defined by Heine (1971) and Jarvis (1975).

Water potential

Predawn water potentials for all stands except the one in Ontario were measured on August 3 and 4, according to the method of Ritchie and Hinckley (1975).

Statistical analysis

Analyses of variance and linear and nonlinear regressions were run on the SAS system (SAS Institute Inc. 1985). Multiple comparisons were calculated according to Tukey's honestly significant difference (HSD) test because of its ability to correct for experimental error and handle unequal cell sizes. Bartlett's test (Montgomery 1984) was used to test the equality of variances. If they were found to be heterogeneous, an appropriate data transformation was applied.

Results

Within each age-class, stands of different site qualities had clearly different basal areas, diameters, and heights (Table 1). The low values and high variability for diameter at breast height (DBH) and total height in stand 120-2 are due to its uneven age structure caused by recurrent forest fires (Burgess and Methven 1977). Within each age-class, total height, DBH, basal area, and sapwood area per tree were generally proportional to site index (Table 2). For a given site quality, the 10-year diameter growth decreased with age until age-class 65 was reached and was then constant up to age 120. Within age-classes 15 and 35, however, the 10-year diameter growth at DBH increased with site index, while for the 65- and 120-year-old stands it remained fairly constant (Table 2). Furthermore, the 10-year diameter growth at DBH showed a general decrease with age. Moreover, the 10-year relative basal area growth rates

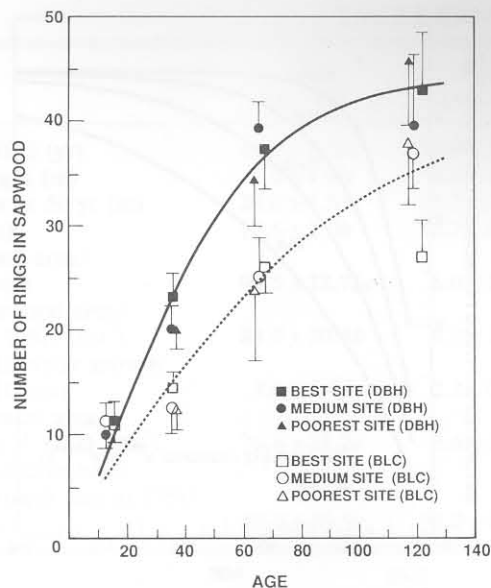


FIG. 3. Number of annual rings in the conducting sapwood of jack pine stands, according to age and site quality. Each data point represents the mean of 12 trees, except that for stand 120-2, which is the mean of 5 trees. Vertical lines represent standard errors. BLC, base of the live crown.

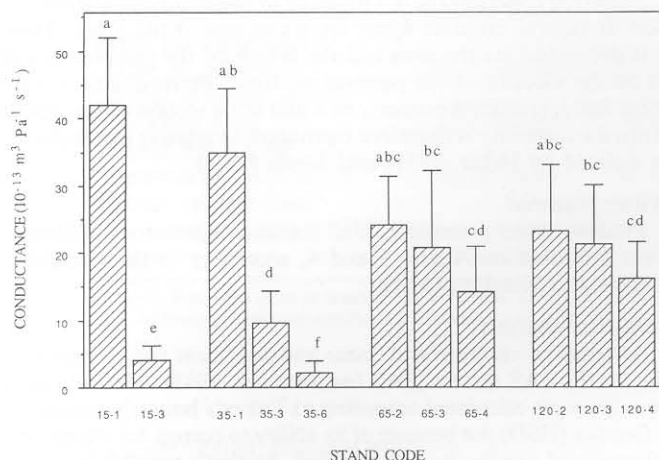


FIG. 4. Sapwood conductance from ground level to the bottom of the upper third of the tree crown for jack pine stands of different ages growing on different site qualities. Each value is the mean of 12 trees except that for stand 120-2, which is the mean of 5 trees. A different letter(s) indicates a significant difference at $P \leq 0.05$, using Tukey's HSD multiple comparison test. Vertical lines represent standard errors.

within age-classes were relatively similar and were equal within sampling error for age-classes 65 and 120.

The values of k at BLC were significantly different ($p \leq 0.05$) between sites within age-classes 15 and 35 (Fig. 1). They began to converge at age 65, and for the 120-year-old stands, were the same within sampling error on all three sites. The k values in the upper third of the crown were always lower than that at BLC, except in stand 35-6 for which the values were about equal. Saturated sapwood permeability at BLC seemed to reach a plateau just beyond $4 \times 10^{-12} \text{ m}^2$ (Fig. 1). However, the rate at which this plateau was approached depended on age and site quality (Figs. 1 and 2). The relationship of k at BLC to age and site index followed a negative exponential function (Fig. 2).

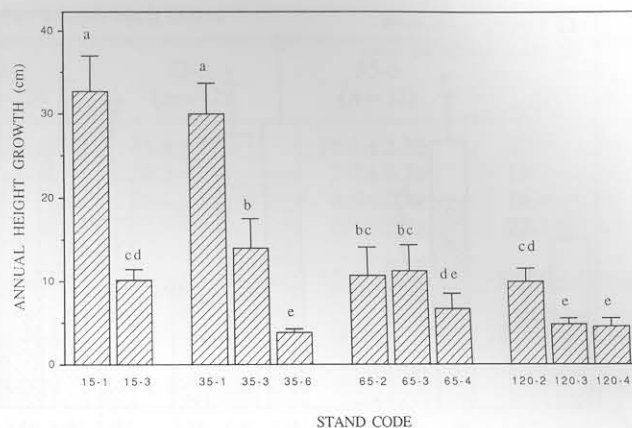


FIG. 5. Mean annual height growth for the last 5 years for jack pine stands of different ages growing on different-quality sites. Each value is the mean of 12 trees, except that for stand 120-2, which is the mean of 5 trees. A different letter(s) indicates a significant difference at $P \leq 0.05$, using Tukey's HSD multiple comparison test.

TABLE 3. Linear coefficients of determination (R^2) between saturated sapwood permeability at BLC and some growth parameters

Age-class	Total height	Height growth	10-year diam. growth at BLC	10-year basal area growth at BLC
15	0.67	0.64	0.77	0.59
35	0.76	0.72	0.75	0.74
65	0.48	0.33	0.17	0.08
120	0.04	0.00	0.07	0.13
All stands	0.61	0.01	0.00	0.09

NOTE: Linear coefficients of determination were computed for all trees of each stand; $n = 24, 36, 36$, and 29 for age-classes 15, 35, 65, and 120, respectively. BLC, base of the live crown.

Saturated sapwood permeability was well correlated with total height, height growth, diameter growth, and basal area growth within age-classes 15 and 35 (Table 3). As the trees approached 120 years in age, however, R^2 approached zero. The number of annual rings in the sapwood at DBH or at BLC was consistent within a given age-class, regardless of site quality (Fig. 3).

For good-quality sites, sapwood conductance from ground level to the upper third of the crown appeared to decrease with age, while for poor-quality sites it appeared to increase (Fig. 4). For age-classes 15 and 35, sapwood conductances were different between sites ($p \leq 0.05$). Within the two older age-classes, however, conductances were not statistically different. The overall pattern for sapwood conductance was similar to that of average annual height growth over the last 5 years (Figs. 4 and 5). The coefficients of determination (R^2) between sapwood conductance and height growth of individual trees were 0.82, 0.70, 0.15, and 0.07 for age-classes 15, 35, 65, and 120, respectively. The R^2 value for the means of all stands was 0.61.

Sapwood resistance, which is the reciprocal of sapwood conductance (eq. 3), increased with decreasing site index within age-classes 15 and 35 (Table 4). The contribution of sapwood resistance below the live crown relative to the resistance of the total pathway was lower within age-class 15 than for the older trees (Table 4).

TABLE 4. Sapwood resistance (10^{11} Pa·s·m⁻³) from ground level to BLC, from BLC to the bottom of the upper third of the crown, and percentage of total resistance

Stand code	Ground level to BLC		BLC to upper third		Resistance from ground level to upper third
	Resistance	%	Resistance	%	
15-1	0.6 ± 0.3	23	2.0 ± 0.5	77	2.6 ± 0.7
15-3	10.7 ± 8.6	35	20.3 ± 12.5	65	31.0 ± 18.2
35-1	1.9 ± 0.7	61	1.2 ± 0.3	39	3.1 ± 0.9
35-3	10.0 ± 12.2	61	6.3 ± 6.9	39	16.3 ± 19.0
35-6	73.9 ± 74.2	70	31.1 ± 37.4	30	105.0 ± 99.3
65-2	3.2 ± 1.4	68	1.5 ± 0.7	32	4.7 ± 2.0
65-3	4.4 ± 2.3	75	1.4 ± 0.5	25	5.9 ± 2.6
65-4	4.9 ± 5.3	47	5.4 ± 4.8	53	10.4 ± 9.7
120-2	4.4 ± 3.5	77	1.2 ± 0.7	23	5.7 ± 4.1
120-3	4.3 ± 2.5	74	1.6 ± 0.7	26	5.8 ± 3.1
120-4	4.5 ± 2.3	63	2.6 ± 1.1	37	7.1 ± 3.1

NOTE: Sapwood resistance is given as the mean ± SE of 12 trees, except for stand 120-2 for which only 5 trees were available. Each value was calculated according to eq. 10.

Predawn water potentials of stands ranged between 0.45 and 0.65 MPa in August.

Discussion

As predicted, trees of similar age still vigorously growing in height on different-quality sites had different k values (Figs. 1 and 2). For the 15- and 35-year-old stands, k at BLC was strongly correlated with mean diameter growth over the last 10 years (Table 3). The greater tracheid diameters generally associated with greater ring widths (Bannan 1965) could have been partially responsible for the differences in k within a single age-class.

The oldest jack pine stands had all closely approached maximum height according to Plonski's (1974) site index tables. For the last 5 years, they grew between 5 and 10 cm in height annually (Fig. 5). As predicted, the k for these trees approached a similar value, regardless of site quality (Figs. 1 and 2). As for the younger stands, this phenomenon could also be associated with the diameter of tracheids, because the diameter growth rates for all three 120-year-old sites were the same (Table 2).

Because k increases with age, comparing only diameter or basal area growth rates for trees of different age-classes does not indicate which tree has the greater k value. A 120-year-old tree on a poor site can have a greater k value than a 15-year-old tree on a very good site (Fig. 1). As the water-conducting elements of conifers are not open at their ends, the efficiency of water transport within them is closely related to the length of the tracheids and the anatomy of the bordered pits (Krahmer 1961; Comstock 1965; Bolton and Petty 1975; Schulte and Gibson 1988). For most tree species, tracheid length increases rapidly for about 20–50 years and then remains constant (Spurr and Hyvarinen 1954). Such increases in tracheid length could account for the general increase of k with age. Studies relating the wood anatomy of these jack pine stands to their saturated sapwood permeability are in progress.

The increase of k with age occurs more rapidly on better-quality sites (Fig. 1). A stand of site quality 1 had reached maximum k value by age 35, site qualities 2 and 3 by age 65, and site quality 4 by age 120. This indicates that changes in k with stand development occur faster on better-quality

sites. Saturated sapwood permeability is similar in this regard to other aspects of stand development, such as total height, accumulation of leaf area (Oren *et al.* 1987), and rates of self-thinning (Drew and Flewelling 1979).

The increases in water conduction efficiency we measured for jack pine with increasing age are supported by the results obtained by Whitehead and Jarvis (1981). They noted that the water potential gradient per metre of stem in tall trees (70–90 m) is usually one-tenth or less of that observed in shorter trees (8–20 m). Age-related increases in water conduction efficiency can explain how a tree could have about the same daytime leaf water potential at different stages of stand development yet still maintain similar maximum transpiration rates per unit leaf area.

The conductance to water flow in the main stem integrates sapwood area, length, and permeability and thus provides an estimate of the efficiency with which water can move to the upper crown of a tree (eq. 10). On good-quality sites, sapwood conductance decreased with age (Fig. 4). This could partially explain the decreases in height growth sometimes found in older stands (Fig. 5). On the poorest sites, however, sapwood conductance of a tree may improve with age (Fig. 4). When low k values typical of young stands are combined with slow rates of diameter growth, the result is a total sapwood conductance that is much lower than that found on other sites (Fig. 4). This could be related to the stagnated height growth that sometimes occurs when young trees are grown under high density or low fertility. Keane and Weetman (1987) reported that under stagnated conditions the leaf area to sapwood area ratio may be reduced by as much as 50% compared with more normally developing stands. They attributed this reduction to poor conducting properties of the wood. In our stands, k at BLC was four times greater for stand 35-1 than for stand 35-6 (Fig. 1). The trees in stand 35-1, therefore, could theoretically be four times taller and still move the same amount of water per square centimetre of sapwood for the same water potential gradient.

The conductance of the main stem to water flow is likely an important factor limiting the development of tree crowns. It even shows a significant correlation ($R^2 = 0.61$) with the height growth that trees are able to maintain at different

ages on different-quality sites. Mattson-Djos (1981) demonstrated an overall decrease in conductance with age for the entire pathway between roots and foliage for *Pinus sylvestris* L. This may be related to the fact that resistance to water flow in minor branches is 1–3 orders of magnitude greater than that of main stems (Zimmermann 1978; Thompson *et al.* 1983; Tyree *et al.* 1983; Tyree 1988). Furthermore, Tyree and Sperry (1988) concluded that transpiring trees operate near the brink of catastrophic xylem dysfunction in minor branches, which may be more responsible for the decreased height growth that occurs in older stands than the changes we found in the conducting properties of the main stem.

The ability to predict changes in k with age and site quality has considerable potential for improving estimates of leaf area derived from sapwood area – leaf area correlations. Our model (Fig. 2) was able to account for 66% of the variation in k , using age and site index. Such curves would allow a quick estimate of k in the field and make it feasible to use a more accurate predictor, such as kA or kA/L_{BLC} , for leaf area estimation. The development of such permeability curves is desirable for species for which sapwood area – leaf area coefficients are already in use.

As the number of annual rings contributing to the sapwood at any given age is independent of site quality (Fig. 3), the historical reconstruction of a tree's leaf area and growth efficiency (cf. Oren *et al.* 1987) is possible even after the formation of significant amounts of heartwood. This could be quite useful for developing more biologically based yield tables, as well as for increasing the amount of information that can be obtained from the wide range of ecological studies that attempt to reconstruct patterns of stand development over time (cf. Bormann 1965; Henry and Swan 1974; Oliver and Stephens 1977; Oliver 1981; Hibbs 1982a, 1982b; Lorimer 1985; Kelty 1986; Larson 1986). The age-dependent nature of the sapwood to heartwood conversion suggests that this process may have been controlled more by limitations on the functional life of a tracheid than by the influence of environment.

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