DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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VARIATION IN HYDRAULIC ARCHITECTURE OF *PICEA ABIES* (L.) KARST. TREES GROWN UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

Ph. D. Thesis

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The thesis will be presented, with the permission of the Council for conferment of doctor's degrees in biology of Tartu University, for public disputation in the Council Hall at Tartu University, Ülikooli 18, on May 26, 1994.

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Variation in hydraulic architecture of *Picea abies* (L.) Karst. trees grown under different environmental conditions. Dissertationes Biologicae Universitatis Tartuensis 13. Tartu: Tartu University, 1994.

Abstract: The structure of the water transport pathway in Norway spruce [*Picea abies* (L.) Karst.] was studied on the trees grown in three habitats differing in light and soil conditions. The hydraulic architecture of the trees was characterized by relative conductivity, the Huber value, leaf-specific conductivity and transverse area of the conducting xylem. The woody parts of Norway spruce are arranged in a certain hierarchic order according to hydraulic conductivity: xylem conductivity declines in the following succession - roots, trunk, primary branches, II-order branches, III-order branches. The hydraulic hierarchy of the segments of the water-conducting system and hydraulic constriction in the base of woody organs ensure the preferential movement of water along the main axis and prevent the spread of cavitation from peripheral parts of the crown into proximal ones.

The relative conductivity of the xylem saturated with water in the trees grown under stress conditions is significantly lower as compared to the ones under favourable growth conditions. This is primarily attributable to the anatomical structure, determining xylem permeability to water. The lumen radius of tracheids explains 51-94% of the total variation in relative conductivity. Actual conductivity of the xylem depends on its water status as well: a decrease in the xylem water content may be accompanied by a drastic decline in the transport capacity of the vascular system.

Resistance to the water flow through woody parts of the trees under conditions of limited light or edaphic resources is much higher as compared to the trees grown in favourable conditions. High resistance of the vascular system in the trees growing under stress conditions is related more to a small conducting area than to low unit conductivity. The sapwood transverse area in the trunk is determined by the tree age and the radial growth rate ($R^2=0.93$). Most of the stem resistance is localized in the top. Low resistance to the water flow in the trunk, except the top, creates more equal prerequisites for water supply for the branches situated at different heights in the crown.

Sellin, Arne
Hariliku kuuse hüdraulilise arhitektuuri varieeruvus erinevates keskkonnatingimustes kasvanud puudel.
Dissertationes Biologicae Universitatis Tartuensis 13.
Tartu: Tartu Ülikool, 1994.

Kokkuvôte: Töös on uuritud kolmel valgus- ja mullatingimuste poolest erineval kasvukohal kasvavate harilike kuuskede veetranspordisüsteemi ehitust. Puude hüdraulilise arhitektuuri iseloomustamiseks kasutatakse ksüleemi suhtelist juhtivust, Huberi väärtust, erijuhtivust lehtede massiühiku kohta ja maltspuidu ristlôikepindala. Kuuse puitunud osad on teatud järjestuses vastavalt hüdraulilisele juhtivusele: ksüleemi juhtivus väheneb reas - juured, tüvi, peaoksad, II järku oksad, III järku oksad. Veejuhteteede erinevate osade hüdrauliline hierarhia ja puitunud organite basaalsete osade kõrge takistus tagavad vee eelistatud liikumise piki peatelge ja takistavad kavitatsiooni levimist võra perifeersetest osadest proksimaalsetesse.

Stressi tingimustes kasvanud puude ksüleemi suhteline juhtivus küllastatud olekus on oluliselt madalam kui puudel soodsates kasvutingimustes. See on tingitud eelkõige ksüleemi anatoomilisest ehitusest, mis määrab tema läbitavuse veele. Trahheiidide valendike raadius kirjeldab 51-94% kogu suhtelise juhtivuse varieeruvusest. Ksüleemi tegelik juhtivus sõltub ka tema veega küllastatusest: veesisalduse langemisega võib kaasneda juhteteede transpordivõime drastiline vähenemine.

Takistus vee liikumisele limiteeritud valgus- vôi edaafilistes tingimustes kasvanud puude puitunud osades on palju kôrgem kui puudel soodsates kasvutingimustes. Stressi tingimustes kasvavate puude veetranspordi-süsteemi suur takistus on rohkem tingitud ksüleemi väikesest juhtivast pindalast kui madalamast ühikulisest juhtivusest. Maltspuidu ristlôikepindala tüves on määratud puu vanuse ja radiaalse juurdekasvu kiirusega ($R^2=0.93$). Enamus tüve hüdraulilisest takistusest lokaliseerub tipuosas. Tüve, välja arvatud tema tipu, madal takistus loob võras erineval kõrgusel paiknevate okste veega varustamiseks võrdsemad eeldused.

The present thesis is a summary of the material published in the following papers, in the text referred to by Roman numbers:

I. **Sellin A.A. 1987.** Hydraulic conductivity of the water transport system in Norway spruce. - Soviet Plant Physiology, 34(3): 443-449.

II. **Sellin A.A. 1988.** Hydraulic architecture of Norway spruce. - Soviet Plant Physiology, 35(6): 839-845.

III. **Sellin A.A. 1989.** Pressure chamber determination of xylem water potential in Norway spruce shoots of different ages. - Soviet Forest Sciences, 0(1): 66-72.

IV. **Sellin A.A. 1990.** Main factors determining hydraulic conductance of the xylem of Norway spruce. - Soviet Plant Physiology, 37(3): 339-343.

V. **Sellin A.A. 1990.** Axial hydraulic conductance of roots of common spruce. - Soviet Forest Sciences, 0(5): 31-36.

VI. **Sellin A. 1991.** Hydraulic conductivity of xylem depending on water saturation level in Norway spruce (*Picea abies* (L.) Karst.). - Journal of Plant Physiology, 138(4): 466-469.

VII. **Sellin A. 1991.** Variation in sapwood thickness of *Picea abies* in Estonia depending on the tree age. - Scandinavian Journal of Forest Research, 6: 463-469.

VIII. **Sellin A. 1993.** Resistance to water flow in xylem of *Picea abies* (L.) Karst. trees grown under contrasting light conditions. - Trees, 7(4): 220-226.

IX. **Sellin A. 1994.** Sapwood - heartwood proportion related to tree diameter, age and growth rate in *Picea abies*. - Canadian Journal of Forest Research. (In press)

X. **Sellin A.** Resistance to water flow in xylem of *Picea abies* (L.) Karst trees grown in contrasting edaphic conditions. - Tree Physiology. (In prep.)

Contents

1. Introduction

The primary driving force of the water movement against the effect of the gravitational field and plant inner obstacles is a tension derived from the evaporation of water in the leaf. The water movement in vascular plants occurs mainly through the elongate conduits of the xylem - vessels and tracheids, because at maturity they offer a pathway of maximum hydraulic conductance. Although there is a continuity of liquid water between the leaf and the soil via the xylem, no rapid equalization of water potential throughout the plant can occur because of the resistance of the soil-plant-atmosphere system. Thus the water movement in the soil-plant-atmosphere continuum is governed by two fundamental factors: the driving forces and the conductance of the flow path.

Water has to move through several links of the transport path, all of which exert certain resistance to the flow: filtration resistance in the soil, resistance of epithelial tissues, bark and endodermis to water entrance to roots, frictional resistance of xylem elements, influence of gravitational field, stomatal resistance, boundary layer resistance, etc. In the present study, attention is focused on the long-distance water transport in sapwood, by which water and nutrients move from roots to leaves. In conifers, unlike other groups of vascular plants, the xylem makes a considerable contribution to the total resistance to water flow (Jarvis 1975; Tyree et al. 1975; Tyree 1988; Tyree & Sperry 1989). This observation could be explained by morpho-anatomical peculiarities of coniferous trees: water is transported across long distances (dozens of metres), and it is only tracheids that participate in the axial water flow.

The water-conduction efficiency of the vascular system depends primarily on the inner properties of the plant, the most important of which are the water status (Sperry et al. 1988; Jones 1989; Pothier et al. 1989b; Sperry & Tyree 1990; Tyree & Yang 1992; Huang & Nobel 1993) and the anatomical structure of the wood (Legge 1985; Calkin et al. 1986; Schulte & Gibson 1988; Pothier et al. 1989b). Wood is formed in the process of xylogenesis under a simultaneous impact of a multitude of environmental factors. Thus, all climatic, edaphic, meteorological and biotic factors, which the course of xylogenesis depends on, can affect indirectly the hydraulic conductivity of the xylem. The wood anatomical structure mediated by the plant water status, in turn, is an essential factor in plant competition and survival

(Zimmermann & Milburn 1982; Tyree & Sperry 1988).

Efforts have been made during the two last decades to interpret the wood structure in terms of an adaptive value (Carlquist & Hoekman 1985; Ewers 1985; Baas & Schweingruber 1987; Guthrie 1989; Chiu & Ewers 1992; Sperry & Sullivan 1992). The investigation of xylem properties under different environmental conditions helps to find meaningful relationships between the xylem structure and plant water relations. Concerning the long-distance water transport in plants, it is relevant to observe the construction of the vascular system as a whole. To mark a pattern of xylem hydraulic properties throughout the tree Zimmermann (1978) has coined the term "hydraulic architecture".

This thesis presents a summary of the studies on hydraulic architecture of *Picea abies* (L.) Karst., an important commercial tree species in Estonia. The investigation was undertaken with the following purposes:

1. Establishing of the main traits of the hydraulic architecture of Norway spruce and its implication in plant water relations.
2. Determination of the variability of the hydraulic architecture of the trees growing under different light and edaphic conditions.
3. Disclosing of the nexus between the transport capacity of the xylem and its anatomical structure and water status.

2. Material and methods

2.1. Material

The experimental work on Norway spruce [*Picea abies* (L.) Karst.] trees was carried out at Vooremaa Ecology Station, East Estonia, in 1985-1990. A detailed description of the climate, relief, soil and vegetation of the study area has been published formerly (Frey 1977). Three middle-aged trees from different sites served as the main material for permeability measurements (Table 1). The sample trees were chosen so that 2 pairs of sites with contrasting growth conditions could be involved in the analysis: (1) a tree grown in a rich well-drained soil and exposed to solar radiation, i.e. under favourable edaphic and light conditions; (2) a tree grown in a rich well-drained soil under a dense canopy of higher trees, i.e. under limited light conditions; (3) a tree grown in a poor waterlogged soil and exposed to sunlight, i.e. under limited edaphic conditions. The trunk, 2 to 3 sample roots, and 3 sample branches from each tree were divided into 10 sections. From each section one xylem segment was cut for permeability measurements.

Table 1. Characterization of the sample trees for permeability measurements.

Tree no.	Age, years	Height, m	Number of primary branches	Number of primary roots	Forest site type	Light conditions	Soil conditions
1	40	14.84	183	14	*Hepatica*	exposed to sunlight	well-drained brown forest soil
2	50	4.29	38	7	*Hepatica*	under dense canopy	well-drained brown forest soil
3	78	7.65	119	13	raised bog	exposed to sunlight	water-logged highbog soil

To establish general traits of the hydraulic architecture in spruce four trees of 9, 18, 33 and 38 years of age were additionally sampled. Xylem specimens were taken likewise from different parts of several young trees in order to establish relative conductivity depending on the tracheid diameter. Variations in sapwood transverse area in relation to the tree diameter, age, growth rate and dominance class were examined on 125 intact (4- to 117-year-old) trees growing in uneven-aged stands in *Hepatica* and *Oxalis* forest site types.

2.2. Methods

Xylem permeability was determined on the excised wood segments by a method based on Darcy's law, according to which the volume of water moving in a unit of time over a xylem segment is proportional to the pressure gradient (Nobel 1991):

$$J_v = -L \times \frac{\delta P}{\delta x} \text{ ,} \tag{1}$$

where J_v is the volume flux density ($m^3s^{-1}m^{-2}$); **L**, the hydraulic conductivity coefficient ($m^2Pa^{-1}s^{-1}$); $-\delta P/\delta x$, the gradient of the hydrostatic pressure ($Pa\ m^{-1}$). The experimental technique was adopted from Booker & Kininmonth (1978) and Zimmermann (1978). We established a fine proportionality between the volume flux density and the pressure gradient for the xylem of Norway spruce (Fig. 1).

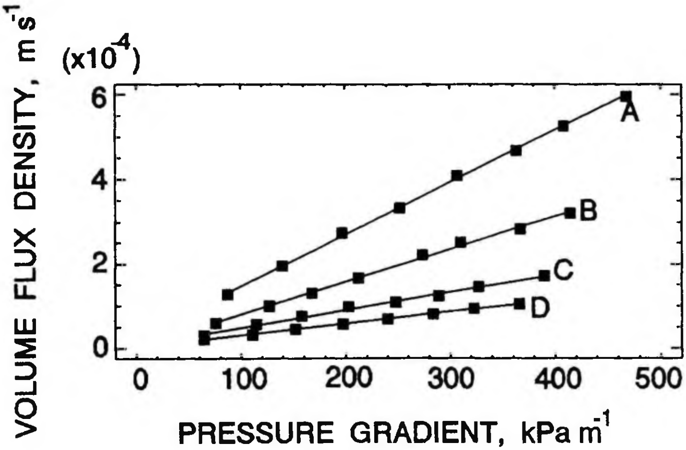

Fig. 1. Volume flux density of water versus the gradient of hydrostatic pressure for 4 specimens of branchwood (**A** to **D**) taken from different Norway spruce trees. The values of the hydraulic conductivity coefficient for specimens: **A** - 1.23×10^{-6}, **B** - 7.77×10^{-7}, **C** - 4.24×10^{-7}, **D** - 2.82×10^{-7} $m^2Pa^{-1}s^{-1}$.

The volume flow rate of water, **q** (m^3s^{-1}), is defined as

$$q = -L \times A \times \frac{\delta P}{\delta x} \text{ ,} \tag{2}$$

where **A** is the transverse area of the conducting xylem, i.e. sapwood (m^2). In experimental studies usually the term "relative conductivity" is used instead of the "hydraulic conductivity coefficient". It takes into consideration the viscosity of the permeating fluid as well (Jarvis et al. 1981):

$$k = \frac{q \times l \times \eta}{\Delta P \times A} , \tag{3}$$

where **k** is the relative conductivity of the xylem (m^2); **l**, the length of the xylem specimen (m); **η**, the dynamic viscosity of water ($N\ s\ m^{-2}$), and **ΔP**, the applied pressure difference across the specimen (Pa). Relative conductivity indicates the water conduction efficiency of the xylem per area unit.

In order to characterize the xylem conduction capacity in relation to the foliage amount that is supported by the xylem leaf-specific conductivity, **LSC** ($m^4 g^{-1}$), is used:

$$LSC = \frac{q \times l \times \eta}{\Delta P \times m} , \tag{4}$$

where **m** is the leaf dry weight (g). The Huber value, **HV** ($m^2 g^{-1}$), indicates the ratio of the sapwood transverse area to the leaf dry weight (Ewers & Zimmermann 1984a, 1984b):

$$HV = \frac{A}{m} . \tag{5}$$

HV is related more directly to mechanical properties than to hydraulic properties of stems or branches. However, the producing of more wood per unit of the foliage amount is one way of enhancing the water supply.

According to the Ohm's law analogy, the resistance to the water flow through a plant or certain part of the plant, **R** ($Pa\ s\ m^{-3}$), is defined by the following ratio (Richter 1973; Fitter & Hay 1987):

$$R = \frac{\Delta \Psi}{q} , \tag{6}$$

where **ΔΨ** is the water potential difference (Pa) between two points in the plant. In experiments on excised xylem segments **ΔΨ** is replaced by the applied pressure difference **ΔP** (Pa):

$$R = \frac{\Delta P}{q} . \tag{7}$$

The substitution of **q** from Eq. 3 into Eq. 7 yields

$$R = \frac{l \times \eta}{k \times A} . \tag{8}$$

The length of xylem segments is a distinct and easily measurable characteristic, while the dynamic viscosity is a function of the fluid temperature. Therefore, the attention in our study was focused on the xylem relative conductivity and the sapwood transverse area, the most relevant characteristics responsible for the resistance to the long-distance water transport. The total resistance (**R_t**) of the branch and root system was estimated by adding reciprocals of the resistances linked in parallel way (Fitter & Hay 1987):

$$R_t = \frac{1}{\sum_{i=1}^{n} \frac{1}{R_i}}, \qquad (9)$$

where **R_i** is the resistance of the *i*th branch or root.

The sapwood transverse area on intact trees was estimated by 4 increment cores extracted from each tree at the breast height along stem radii at 90° angles. Sapwood - heartwood border was identified by using a differential translucence (Waring et al. 1982), differential absorption and aniline pencil methods (Münster-Swendsen 1987). Xylem anatomical measurements were made with an ocular micrometer under light microscope by using a 400-fold magnification.

3. Variation in hydraulic characteristics of xylem

3.1. Spatial variation within a tree (I, II, III)

The woody organs of Norway spruce differ significantly with respect to relative conductivity. The farther away from the soil (a source of water) the organ is located, the lower is its hydraulic conductivity. Thus, different parts of the tree are arranged in the following order according to the decrease in relative conductivity: roots, trunk, primary branches, II-order branches, III-order branches. This sequence is completed by leaf petioles in deciduous trees and palms (Zimmermann 1978; Zimmermann & Sperry 1983), and probably by vascular bundles connecting mesophyll cells with cells of shoot axes in conifers. One explanation of the differences in the xylem water potential observed between spruce shoots of different age may be the resistance to water movement from tracheids of the shoot axis to the mesophyll cells, increasing with the shoot age. An analogous hierarchical arrangement of the segments of the water-conducting pathway was observed with respect to leaf-specific conductivity (**LSC**): the highest values of **LSC** were observed in the trunk, lower values in primary branches, and still lower, in II-order branches.

The relative conductivity was always lower in the base of the branches than in the trunk or main branch at the point of the branch attachment, and also lower than in more distal sections of the same branch. Basal parts of roots also demonstrated low relative conductivity. The spatial variation of relative conductivity was of an universal pattern for the trunk, branches as well as roots: the values were maximal in the middle of the organ, and declined in both basal and apical direction (Fig. 2). The same regularity was characteristic of all the investigated trees regardless of their age and growth conditions. The Huber value (**HV**) was more or less constant along most of the trunk, but increased sharply in the top of the tree. **HV** in primary branches at first decreased slightly in the direction from the base to the middle part of the branch and started to increase again on approaching to the apex, whereas in II-order branches it increased steadily from base to top. Consequently, the decline in unit efficiency of the xylem water conduction in apical direction is compensated by the increase of the sapwood transverse area in relation to the foliage amount to enable the water supply for distal parts of the crown. As regards **LSC**, there were distinct differences in its spatial pattern between the trees from contrasting sites.

The hydraulic constriction in the basal section of organs, called a "bottleneck" (Ewers & Zimmermann 1984a, 1984b), is of a paramount physiological importance: the constriction ensures the preferential movement of water along the main axes. On the other hand, high resistance of basal sections of branches prevents a spread of cavitation from lateral branches into the main axis. Thus, the hierarchical arrangement of the segments of the water-conducting system, the hydraulic hierarchy, and the phenomenon of "bottleneck" contribute to the tree's survival under severe water deficit (Tyree & Sperry 1988, 1989). According to Zimmermann's concept of plant segmentation, peripheral parts of plants are subjected to low xylem pressures with a concomitant risk of xylem embolism, while proximal parts function at considerably more moderate pressure potentials. If the water stress is severe, peripheral parts of the crown could be sacrificed to reduce the transpiring area of the foliage, and the trunk and the main branches remain functional (Zimmermann 1983). Besides, the hydraulic architecture of the tree described above is a basis for the realization of apical dominance by promoting a water supply for apical leaves and buds.

3.2. Variation between the trees growing under different environmental conditions (VIII, X)

The trees growing under contrasting environmental conditions differ in absolute values of the hydraulic characteristics of the xylem. A comparison of middle sections of primary roots, branches and trunks revealed that in a tree grown under favourable light and edaphic conditions, the relative conductivity of rootwood was approximately 1.4-fold ($P<0.001$), of branchwood, 1.8-fold ($P<0.001$), and of stemwood, 3.1-fold ($P<0.001$) higher than that in a tree from under a dense canopy. These values exceeded by 2.2 ($P<0.01$), 1.2 (n.s.*) and 1.1 (n.s.) times the respective values of relative conductivity for a tree grown in poor soil conditions. Thus, the xylem in the trees under favourable growth conditions is more efficient in water conducting as compared with the trees growing under limited resources conditions.

The Huber value, relatively constant along most of the trunk, also differed significantly in absolute values from site to site. **HV** averaged (the topmost section excluded) 0.70×10^{-6} m^2g^{-1} for the trunk of the tree under favourable growth conditions, 0.43×10^{-6} m^2g^{-1} for that of the bog-grown tree, and 1.45×10^{-6} m^2g^{-1} for that of the shade-grown tree. Consequently, there is the largest amount of needles supported by the unit area of sapwood for the tree grown under waterlogged conditions. The largest sapwood transverse area in relation to the foliage amount in the shade tree can be treated as a compensation for the lowest unit efficiency of the water conduction of the xylem.

The vertical course of the **LSC** within the trunk, in contrast to that of relative conductivity and **HV**, differed in the spatial pattern as well as in numeric values at the sites (Fig. 2). Under favourable growth conditions **LSC** was relatively uniform in most of the stem with the exception of a sharp increase in the top. In the shade- and bog-grown trees **LSC** declined in the apical direction. The mean values of **LSC**

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* the difference between the arithmetic means is not statistically significant at the level of probability 0.05

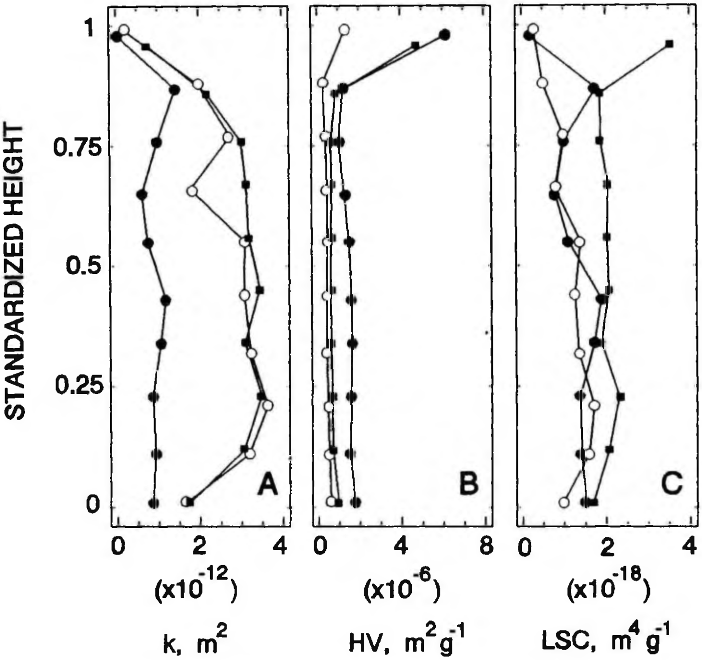

Fig. 2. Vertical variation of xylem hydraulic characteristics in the trunks of the trees grown under contrasting environmental conditions: in a rich well-drained soil and sunlight exposure (*squares*), in a rich well-drained soil and shade (*filled circles*), in a poor waterlogged soil and sunlight exposure (*empty circles*). **A** - relative conductivity, **B** - Huber value, **C** - leaf-specific conductivity.

were 2.14x10^{-18}, 1.27x10^{-18} and 1.09x10^{-18} m^{4}g^{-1}, respectively. The potential water transport capacity of the stem per unit amount of foliage was at an average 2-fold higher for the tree grown under favourable conditions as compared to the one grown under water-logged conditions. Such striking difference in **LSC** between the trees is explicable by the degree of the risk of water deficit that could lead to a catastrophic xylem dysfunction due to embolism and the consequent desiccation-induced leaf loss (Tyree & Sperry 1988, 1989). Trees in a well-drained soil growing at a greater risk of water stress, have a water transport system with a larger margin of safety, i.e. larger conducting area of the xylem per unit amount of foliage. The trees growing in a waterlogged soil, on the contrary, do not face the unavailability of water, and neither the redundant sapwood area nor a high relative conductivity are required.

According to the pipe model theory each unit of foliage requires a unit pipeline of wood to conduct water from the roots and to provide physical support (Shinozaki et al. 1964a, 1964b). The pipe model presumes that the sapwood area at the height x is proportional to the foliage amount above x, i.e. a constancy of **HV**. Our data show that **HV** is not a species-specific constant, but an environment-dependent variable. Furthermore, the relationship between the sapwood transverse area and the cumulative foliage area varies within a tree. The inconsistency follows from the variation of the conduction efficiency of the xylem, which cannot be ignored in the physiological studies comprising sapwood as a transport channel. This statement is supported by Whitehead et al. (1984) who have shown that in *Picea sitchensis* and *Pinus contorta* the foliage amount is more closely related to the product of sapwood area × hydraulic conductivity than to the sapwood area alone.

The conducting system of the roots, stem and branches, being responsible for water supply for leaves, has a functional nexus to CO_2 assimilation which is mediated by leaf water potential. Thus, xylem hydraulic properties can be related to the photosynthetic activity of the tree. The mathematical form of the relationship has been proposed by Mäkelä (1986):

$$\sigma_W \times A = \Pi_W \times \sigma_C \times m \ , \qquad \mathbf{(10)}$$

where $\boldsymbol{\sigma_w}$ is the water conductivity of sapwood (kg $yr^{-1}m^{-2}$); **A**, the sapwood transverse area (m^2); $\boldsymbol{\Pi_w}$, the water use efficiency (kg_{water} kg_C^{-1}); $\boldsymbol{\sigma_C}$, the specific photosynthetic activity (kg yr^{-1} kg^{-1}), and **m**, the total foliage biomass (kg).

In a stable environment the stem conducting area and amount of leaves are mutually adjusted for given ecological conditions. Abrupt changes of growth conditions (radiation regime, soil water status, nutrient availability, etc.) have direct consequences on plant water relations through altered water losses from the foliage or the uptake by roots. In conifers stem conduction capacity remains critical for some years until new balance between the sapwood area and the transpiring leaf area will be established. In pruning experiments on *Pinus sylvestris* Långsröm & Hellqvist (1991) observed that the adjustment of a conducting xylem was still incomplete four years after treatment.

4. Main factors determining xylem relative conductivity

4.1. Water saturation level of the xylem (IV, VI)

Variation in hydraulic conductivity of the xylem in relation to water saturation level was examined on spruce branchwood. The values of relative conductivity (**k**) ranged from 0.03×10^{-12} to 1.62×10^{-12} m^2 depending on the xylem water status and the specimen origin. Relative conductivity declined with the decrease in xylem water content according to the logistic curve: the reduction in the relative water content from the saturated state to 85% caused conductivity fall by a factor of 2, with the reduction to 75% the conductivity fell by one order of magnitude. This result is in accordance with the data on conductivity loss depending on the xylem water potential reported for other tree species (Tyree & Dixon 1986; Tyree & Sperry 1989; Cochard & Tyree 1990; Cochard 1992; Cochard et al. 1992). The logistic form of the relationship between **k** and the xylem water content established for Norway spruce is a fair mirror image of the xylem vulnerability curve that expresses the percentage loss of conductivity versus the minimum water potential. Consequently, the water saturation level is one of the main determinants of xylem hydraulic conductivity.

The actual conductivity as a function of saturated conductivity and the xylem water content in Norway spruce is described by the following empiric model:

$$k = \frac{1.06\,k_{sat}}{1 + e^{15.4-0.18\theta}}, \quad R^2=0.94, \quad P<0.001, \quad \mathbf{(11)}$$

where **k** is relative conductivity at a given water content (m^2); $\mathbf{k_{sat}}$, relative conductivity at full saturation (m^2), and θ, relative water content of the xylem (%). The higher the relative conductivity at full saturation is, the more permeable the xylem is at any water content. The model explains 94% of the total variation in the actual conductivity of spruce branchwood.

The decline of hydraulic conductivity as well as water transport capacity of the xylem with the reduction of the water content is expected to be caused by cavitation of tracheids, which reduces the number of flow paths. The water in the xylem is transported under tension, i.e. in a physically metastable state. Cavitation is a rupture of liquid water columns and an explosive transition of the water to an equilibrium vapour phase in xylem conduits under negative pressures. A steeper decline of permeability in xylem specimens with higher $\mathbf{k}_{sat}$, and also with wider tracheids (see below), could be explained by the fact that larger xylem conduits are more susceptible to water stress, as they tend to cavitate at lower tensions (Boyer 1985; Lewis & Tyree 1985; Tyree & Dixon 1986; Cochard & Tyree 1990; Lo Gullo & Salleo 1993). There is considerable evidence that water-stress-induced embolism occurs by air seeding at pores in the intervessel (or intertracheid) pit membranes (Zimmermann 1983; Sperry & Tyree 1988). It is the pit membrane pore diameter rather than the conduit diameter that determines a conduit's vulnerability; the larger the pore, the more vulnerable the conduit to water stress. The fact that larger tracheids tend to be more vulnerable within a species results from a correlation between the conduit size and the pit membrane pore size (Tyree & Sperry 1989).

In a saturated xylem of Norway spruce the bulk of water is transported by large earlywood cells, and the cavitation of a few large tracheids is responsible for a considerable decline in permeability. Consequently, reduction in the xylem water content can cause a drastic decline in the water-conduction capacity of the vascular system, and, if it is severe enough, it will likely limit the leaf water supply, gas exchange and growth. This is confirmed by the experiments performed on broadleaved species. The hydraulic conductance limitations imposed in *Acer saccharum* by roots, shoots and petioles do not allow trees to attain maximum stomatal conductance at midday even without soil water stress (Yang & Tyree 1993). The growing of xylem resistance with water deficit has been observed to cause leaf water potential in *Vitis vinifera* to drop to the level sufficient to completely inhibit the shoot growth (Schultz & Matthews 1988).

4.2. Anatomical structure of the xylem (IV, V, VIII)

The flow rate of liquid volume through ideal capillaries, as defined by Hagen-Poiseuille's law, is proportional to the fourth power of the capillary radius (Zimmermann 1983; Nobel 1991):

$$q = -\frac{\pi \times \sum_{i=1}^{n} r_i^4}{8\,\eta} \times \frac{\delta P}{\delta x}\,, \qquad (12)$$

where **q** is the volume flow rate (m^3s^{-1}); **r_i**, the radius of the *i*th capillary; ***η***, the dynamic viscosity of the liquid (Pa s), and **$-\delta P/\delta x$**, the gradient of the hydrostatic pressure (Pa m^{-1}). Therefore, from a theoretical standpoint, the flow rate through the xylem should primarily be a function of the tracheid radius. Our studies on Norway spruce revealed a close relationship between relative conductivity and the inner radius of the largest tracheids measured in outermost growth rings: R^2 was 0.51-0.94 for stemwood, 0.76-0.93 for rootwood and 0.69-0.85 for branchwood, depending on the site type. The narrower the tracheids are, the lower is the xylem permeability to water. The decrease in the tracheid diameter is accompanied by an increase of the share of cell walls in the cross-section, and, consequently, by the increase in wood density. Thus, the relative conductivity is related to wood density as well (Fig. 3). Our results on spatial variation in relative conductivity are consistent with the data reported on wood density changes in Norway spruce: the density is low in the middle part of the trunk and increases in both basal and apical direction

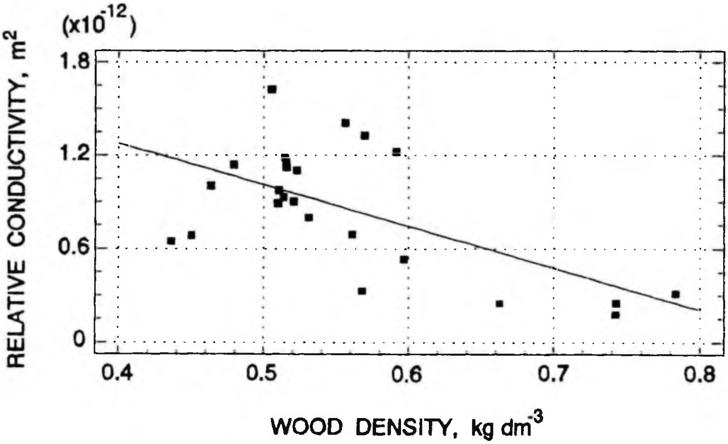

Fig. 3. Relative conductivity (**k**) versus wood density (**ρ**) in branches of Norway spruce. The regression equation: **k** = $-2.68\times10^{-12}\rho + 2.35\times10^{-12}$, $R^2=0.38$, $P<0.01$.

(Nekrasova et al. 1985; Poluboyarinov & Nekrasova 1986).

Low relative conductivity of the xylem in the trees grown under limited resources as compared to a tree under favourable growth conditions may be attributed to narrow tracheids. On the other hand, some reports suggest that the lumen is not the main constituent of resistance to fluid flow through a tracheid (Petty 1970; Bolton & Petty 1975; Calkin et al. 1986). Model simulations have indicated that only 21.4% of the resistance in tracheids of *Podocarpus nagi* is attributable to lumina (Schulte & Gibson 1988). Petty & Puritch (1970) have shown that 39% of the resistance to the flow through tracheids in *Abies grandis* is accounted for by resistance in the lumen, the rest being sited in the margo of the bordered pits. Nevertheless, it has been suggested that in the first-formed earlywood, with its relatively large number of large bordered pits, the lumina may cause more than half of the resistance.

The good correlation between the relative conductivity of the xylem and the radius of the largest tracheids observed in Norway spruce can be explained in view of the following facts. First, a few outer growth rings play a dominant role in the long-distance water transport in Norway spruce. Though the permeability of coniferous wood is preserved for many years, the contribution of the inner sapwood to the total water flow is considerably less than that of outer annual rings. Second, under sufficient water supply (i.e. in a saturated xylem) the bulk of water is transported through large-diameter earlywood tracheids. Third, the radius of xylem elements has been found to be correlated with several other anatomical characteristics of wood (Buchmüller 1986; Calkin et al. 1986; Jinxing 1989; Ewers et al. 1990).

The relationship between relative conductivity and the tracheid radius observed in this study is of a correlative rather than a causative nature, as it is not strictly consistent with Hagen-Poiseuille's equation. However, the close correlation no doubt indicates a structural-functional basis of the relationship. Regardless of the anatomical complexity of wood structure, the tracheid diameter is an important determinant of xylem permeability. Thus, the ecological conditions of a site exert significant influence on the water conduction capacity of the xylem through wood structure.

5. Variation in the conducting area of the xylem (VII, IX)

The transverse area of the water-conducting xylem has been found to be related to the amount of foliage distal to the transverse section (Bormann 1990; Coyea & Margolis 1992; Robichaud & Methven 1992; Usoltsev 1993; van Hees & Bartelink 1993), which follows from the physiological balance between the water demand by the crown and the ability of the stem to conduct water. Thus, the sapwood area is a characteristic of the stem conduction capacity, being an input variable in the modelling of tree water relations (Waring & Running 1976; Hatheway & Winter 1981; Čermák et al. 1984; Edwards et al. 1986). The sapwood transverse area in Norway spruce varied depending on the tree diameter, age, dominance class and habitat. The tree diameter measured inside the bark describes 91% of the total variation in the sapwood area and might serve as a means of predicting the amount of sapwood.

$$A = 2.19\, d^{1.575}, \quad R^2=0.91, \quad P<0.001, \qquad \mathbf{(13)}$$

where **A** is the sapwood basal area (cm^2) and **d**, the tree diameter inside the bark (cm). Although the sapwood area increases also with tree age ($R^2=0.40\text{-}0.72$), the age cannot be used as a predictor of the sapwood area because of great differences in the width of growth rings by trees, especially in the trees from different sites or dominance classes. Therefore, it is expedient to take into consideration tree growth rate as well.

The tree age and radial growth rate combined describe the sapwood transverse area more precisely as compared to the age, diameter or growth rate taken alone:

$$A = \frac{387\, I_R^{1.33}}{1 + e^{3.82-0.0677\,a}}, \quad R^2=0.93, \quad P<0.001, \qquad \mathbf{(14)}$$

where $\mathbf{I_R}$ is the radial growth rate of the trunk (mm yr^{-1}) during the last life period corresponding to the sapwood zone, and **a**, the tree age (years). The age is one of the main factors determining the number of sapwood rings in *Picea abies*, *Picea mariana* (Hazenberg & Yang 1991), *Pinus banksiana* (Yang & Hazenberg 1991) and *Pinus contorta* (Yang & Murchison 1992). Moreover, the number of annual rings contributing to sapwood at a given age is independent of the site quality (Pothier et al. 1989a), tree vigour (Kaufmann & Watkins 1990) and crown class. Thus, the tree age controls the increase of the sapwood band according to the addition of new rings, but the actual sapwood area in adult trees is determined also by the growth rate. The influence of ecological factors (resulting from either dominance relations or site quality) on sapwood amount is mediated by the radial growth rate.

The spruce trees from contrasting sites differed drastically in the sapwood amount in terms of both the absolute and the relative area (Fig. 4). However, the vertical variation in sapwood area along the trunk was of the same pattern for all trees: the area was the largest at the trunk base and declined steadily in the apical direction. The share of sapwood in the spruce trees growing under the conditions of scanty resources was substantially less than for the trees under favourable

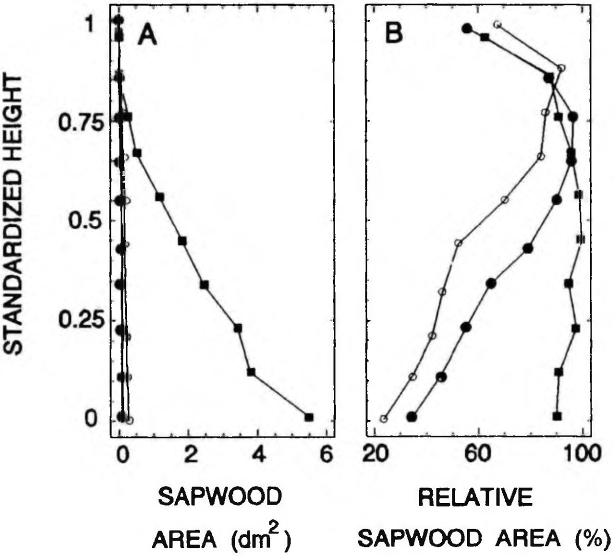

Fig. 4. Vertical variation of the sapwood transverse area in the trunks of the trees grown under contrasting environmental conditions: in a rich well-drained soil and sunlight exposure (*squares*), in a rich well-drained soil and shade (*filled circles*), in a poor waterlogged soil and sunlight exposure (*empty circles*). **A** - absolute sapwood area, **B** - relative sapwood area.

growth conditions. The sapwood - heartwood proportion is formed as a result of balance between two critical functions of tree boles, mechanical support of the crown and water supply to the foliage. As a tree grows, the number of branches as well as the leaf area increase. At the same time, the sapwood volume enlarges exponentially with the leaf area growth, accompanied by a proportionate increase of maintenance respiration (Ryan 1989). Consequently, the tree normal growth is accompanied by the decline in the ratio of photosynthetic to respiring tissues (Valentine 1985; Mäkelä 1986). From a certain tree's size onwards, the growing respiration costs begin to limit the further increase of sapwood. It causes the cease of the sapwood enlargement and some time later the growth of the whole tree will be stagnated. This happens substantially earlier in the trees growing under harsh environmental conditions, because carbohydrate reserves are as a rule lower in the trees under stress conditions (Waring 1987). This process explains the decrease in the sapwood relative portion with the age of the trees. The costs of maintenance respiration to support the living parenchyma cells in sapwood balances the benefits of water conduction, sapwood storage and mechanical support (Ryan 1989).

6. Distribution of xylem frictional resistance to the water flow within a tree (VIII, X)

Because of both the less sapwood area and low relative conductivity in the spruce trees growing under scanty resources conditions, the resistance to water movement through their trunk, root and branches is many times higher than in the trees in favourable growth conditions. The summed resistance (i.e. primary roots, branches and trunk all together) was 0.5×10^{14}, 18.1×10^{14} and 122.4×10^{14} Pa s m^{-3} for an open-, bog- and shade-grown tree, respectively. The largest share of the total xylem resistance resides in the trunk for the trees grown in favourable edaphic conditions and in the root system for the trees grown in a waterlogged soil.

The greatest differences in xylem resistance in open- and shade-grown trees under favourable soil conditions occurred in the trunk. Under low level of resources available, the amount of the substrate allocated to the stem depends on the reserves left after the tree has met root, foliage and reproductive commitments (Waring 1980, 1987).

Low levels of resources available for the trunk growth, in turn, result in both a smaller conducting area and narrower tracheids. Thus, the high resistance of the trunk in shade-grown trees is attributable to light competition from higher trees. For bog-grown trees, on the contrary, limiting ecological factors are connected with severe edaphic environment. The hypoxia and low nutrient availability - the factors combined in bog soils, result in low productivity of trees as compared with those in well-drained mineral soils. Severe edaphic conditions have the greatest impact on the formation of the root system - the part of the tree which is under the immediate influence of stress factors.

Our results contradict the position that the bulk of tree's hydraulic resistance is localized in branches (Ewers & Zimmermann 1984a, 1984b; Tyree 1988; Yang & Tyree 1993). The data show that there is no unique distribution pattern of xylem resistance in the stem, primary roots and branches for all trees in whatever ecological situation, but it seems to be influenced by growth conditions. We are of the opinion that the relative distribution of xylem resistance should be considered a dynamic rather than a static phenomenon. The spatial pattern of hydraulic resistances within the tree, being dependent on xylem water status, will change as soon as water deficit develops. However, our data do not rule out the occurrence of the largest resistance in minor branches of higher orders.

The distribution of resistance within the trunk is of the common regularity for trees from all sites: most of the stem resistance is localized in the top. Ikeda & Suzaki (1984) have reported similar results for several hardwood species - hydraulic conductivity of the current-year increment of the stem is very small. The resistance of the topmost section of the trunk in Norway spruce is of the same magnitude as the resistance of primary branches. Low resistance to water flow throughout most of the trunk, except the top, creates more equal prerequisites for water supply for branches situated at different heights in the crown. Otherwise, the branches near the base of the tree would be hydraulically favoured over the branches at the apex, and the shoots at tree's top would be subjected to a chronical water deficit due to the long distance from the water source and the gravitational force. The vascular system of spruce trees "must have been constructed" in a way that resistance to the water movement to the topmost shoots will not exceed the resistance on the pathway from roots to the shoots in the lower part of the crown.

7. Concluding remarks

The present investigation expands our understanding of the plant's internal factors affecting tree water relations. The spruce trees growing under contrasting environmental conditions differ significantly in relative conductivity, Huber value, leaf-specific conductivity and conducting area of the xylem. The resistance to the water flow through woody parts of trees under limited light or edaphic resources is many times higher as compared to the trees grown under favourable conditions. High resistance of the vascular system of these trees is related more to a small conducting area than to low relative conductivity of the xylem. In any case, both the transverse area and conductivity of the sapwood have to be considered in the studies comprising long-distance water transport.

The sapwood amount (transverse area, volume) is more important a characteristic for trees than it may seem at the first glance. Sapwood is one of the links between different physiological processes. A tree requires a sufficiently large sapwood area to compensate evaporative water losses from leaves, otherwise, the photosynthetic activity will be limited by stomatal resistance. The lowered rate of CO_2 assimilation, in turn, has a negative impact on the growth rate including that of sapwood. On the other hand, the growing sapwood volume requires more and more resources for maintenance respiration, and sooner or later the respiration costs start to limit the growth.

The spatial distribution of resistances to the water flow within the spruce tree favors the preferential movement of water along the main axes. Such a structure of the conducting system ensures the ascent of water to the top of the tree, where the most important leaves in terms of productivity are situated. In this way the hydraulic architecture is involved in the mechanisms responsible for a strong apical dominance typical of Norway spruce. Higher activity of the apical meristem and higher growth rate of the top in comparison with lateral branches are possible only if the top is provided adequately with water and nutrients.

Environmental conditions have a dual influence on water-conduction capacity of the vascular system of trees. First, a direct impact of water availability from the soil and the atmospheric evaporative demand on relative conductivity through the xylem water content. The direct effects of ecological factors can cause quick changes in xylem hydraulic conductivity, that are comparable in the time scale with the fluctuations occurring in the overall plant water status. Second, an impact of ecological factors on xylogenesis determining both the wood amount and its anatomical structure, which in turn control hydraulic properties of the tree. Therefore, the indirect effects of environment on xylem conductivity are observable in a long-term scale and they are of a more static nature. The indirect influences are particularly relevant for coniferous species, because their xylem remains conductive for many years.

8. Acknowledgements

The investigation was performed at the former Laboratory of Ecosystems, Tartu University. I wish to express my gratitude to my supervisor Prof. Toomas Frey and to the whole staff of the Laboratory for good co-operation and support. Also, I am grateful to Dr. Andres Koppel, Institute of Zoology and Botany, and Dr. Olevi Kull, Institute of Ecology, Estonian Academy of Sciences, for fruitful ideas and critical remarks on my work. Special thanks are due to Mrs. Evi Vaik for improving the English text.

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APPENDIX

I. Soviet Plant Physiology, 1987, 34(3): 443-449

HYDRAULIC CONDUCTIVITY OF THE WATER TRANSPORT SYSTEM IN NORWAY SPRUCE*

A. A. Sellin

UDC 581.112.2

We investigated characteristics of the water-conducting capability of stem xylem in Norway spruce (<u>Picea abies</u> L.) in relation to peculiarities of tree architecture. The region and regularities of changes in three quantitative characteristics of hydraulic conductivity were determined experimentally, viz., relative conductivity (K), the Huber value (HV), and leaf-specific conductivity (LSC). It is demonstrated that K varies along the stem basically in conformity with the same regularity regardless of tree age and conditions of the habitat. Support is obtained for the assumption that the nature of changes in hydraulic conductivity along the stem plays a significant role in the phenomenon of apical control. Increase of HV and LSC in the direction of the tree top can be considered a reflection of strong apical control.

KEY WORDS: Norway spruce; xylem; hydraulic conductivity; apical control; tree architecture.

The provisioning of overground organs of the plant with water depends not only on environmental conditions, but also in large measure upon conductivity of the water transport system. In the generally accepted view, cell walls and membranes exert the main resistance to water movement in trees, xylem resistance being considered of secondary importance here. However, it has been demonstrated in certain investigations [1, 2] that the share of xylem resistance in water transport has been underestimated to date, despite the fact that a fairly large number of studies have been published since the 1920's on hydraulic conductivity of the xylem in different species of conifers [3-8].

Hydraulic conductivity or water conductivity of the xylem is a characteristic that indicates the ease of water translocation in the transport system. Relative conductivity indicates the volume of water translocated per unit of time in the presence of a given gradient of pressure through a xylem segment of definite length and cross section. The value of K as a rule is half as great in coniferous trees as in evergreen broad-leaved species, in which it is in turn half as great as in deciduous trees. Roots with their broad vessels and vines conduct water especially well [9, p. 228].

The value of K of the xylem is not a constant species trait, but rather one that varies both among separate plants and among different parts of the same plant [2, 6-8, 10, 11]. A fairly detailed analysis of xylem conductivity is given in certain studies [6-8, 10]. Characteristics of water conductivity are linked with peculiarities of tree architecture in these studies. The special term "hydraulic architecture" has been proposed [10] to signify the pattern of spatial variability of xylem water conductivity in different parts of the plant.

The paths of water transport in a tree from sucking roots to leaves can be regarded as a unified balanced system where all elements (roots, stem, branches, leaves) possess the ability to conduct an equal amount of water. Regardless of the fact that these organs on the strength of anatomical peculiarities can possess different conductivity, the relationship between their water-conducting areas is functionally determined [12]. On the basis of analogous assumptions, a hydraulic model, the so-called "pipe model," has been proposed to describe tree structure [13, 14]. According to this model, a tree is regarded as a complex

*<u>Abbreviations</u>: K) Relative conductivity of xylem; HV) Huber value; LSC) leaf-specific conductivity of xylem.

Tartu State University. Translated from Fiziologiya Rastenii, Vol. 34, No. 3, pp. 545-553, May-June, 1987. Original article submitted May 6, 1986.

0038-5719/87/3403-0443 $12.50

of individual systems of pipes or bundles (in more slender-stemmed plants) where each subsystem supplies water to a certain number of consumers (leaves). New subsystems are added to existing ones with growth in the form of annual rings. The model is based on the observation that the area of conducting xylem in many woody species is proportional to the amount of foliage located apical to the site of area measuring [13-17].

Huber [18] introduced the concept of "relative xylem conducting surface," i.e., the ratio of water-conducting area of xylem to area or mass of foilage. This characteristic is currently known as the Huber value. According to the "pipe model," HV should be constant not only in all trees of the same species, but also in different parts of an individual tree. However, data have been published in the literature indicating variability of HV in certain species [7, 8, 10, 18]. Leaf-specific conductivity has been used to estimate efficiency of the xylem as a water transport system, LSC being an index that characterizes the potential capacity of xylem to supply foliage with water [6-8, 10].

The purpose of the present work was to determine quantitative characteristics of the water-conducting capacity of Norway spruce xylem in relation to peculiarities of tree architecture. Results of investigating the hydraulic conductivity of stem xylem are examined in the present communication.

METHOD

Experimental investigations were conducted at the Vooremaaskaya Ecological Station (Estonian SSR) of Tartu State University from May to October of 1985. A characterization of the climate, relief, soils, and vegetation of the test plot was published previously [19]. The objects of investigation consisted of four young trees of Norway spruce [Picea abies (L.) Karst.]: 38 years old and 4.34 m tall, tree No. 1 formerly grew in a dense stand, but for the last six years grew under relatively good light conditions; 18 years old and 4.61 m tall, tree No. 2 grew on the edge of a cleared strip under favorable light conditions; 33 years old and 1.80 m tall, tree No. 3 grew under a dense canopy of taller trees; and nine years old and 1.83 m tall, tree No. 4 grew on a felling site under favorable light conditions.

Xylem hydraulic conductivity was studied by a method based on an analog of Ohm's law, according to which the volume of water translocated per unit of time through a xylem segment is proportional to the gradient of pressure. The method is described and analyzed in the works of Comstock [20], Booker and Kininmonth [21], and Zimmermann [10]. Our investigations were conducted with stem segments saturated with water under a vacuum using a 10 mM aqueous solution of KCl deaerated before the experiment. The difference of pressure between ends of the segment lay within the limits of $(1.47\text{-}1.57)\cdot 10^4$ Pa. The dye method was used to measure conducting area of the xylem. Three indices characterizing the water-conducting capacity of xylem were determined:

1) Relative conductivity

$$K = \frac{ql\eta}{\Delta p A}\ (\mathrm{m}^2), \tag{1}$$

where q is the rate of translocation of solutions, $\mathrm{m}^3\cdot\mathrm{sec}^{-1}$; ℓ is length of the segment, m; η is dynamic viscosity of the solution, $\mathrm{N}\cdot\mathrm{sec}\cdot\mathrm{m}^{-2}$; Δp is the difference of pressure, Pa; and A is the conducting area of xylem, m^2.

2) The Huber value

$$HV = \frac{A}{m}\ (\mathrm{m}^2\cdot\mathrm{g}^{-1}), \tag{2}$$

where m is absolutely dry leaf mass, g.

3) Conductivity per unit of leaf mass or leaf-specific conductivity

$$LSC = \frac{ql\eta}{\Delta p m}\ (\mathrm{m}^4\cdot\mathrm{g}^{-1}). \tag{3}$$

The following relationship exists between these characteristics:

$$LSC = K\cdot HV. \tag{4}$$

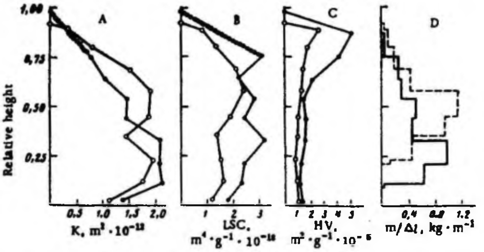

Fig. 1. Hydraulic conductivity of stem xylem. Light circles) tree No. 1; dark circles) tree No. 2. A) Relative conductivity; B) leaf-specific conductivity (dotted line indicating interpolation to point 1.0); C) Huber value; D) vertical distribution of needle mass (dashed line representing tree No. 1, solid line representing tree No. 2).

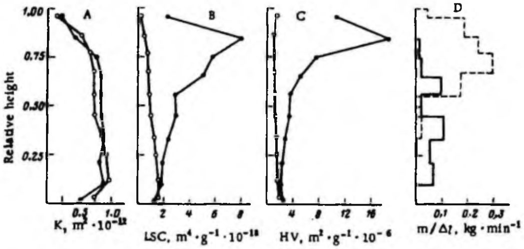

Fig. 2. Hydraulic conductivity of stem xylem in spruce trees No. 3 (light circles) and No. 4 (dark circles). Other designations are the same as on Fig. 1.

RESULTS

Maximum values of relative xylem conductivity comprised more than $2 \cdot 10^{-12}$ m² in the large spruce trees (Nos. 1 and 2) and up to $1 \cdot 10^{-12}$ m² in the small ones (Nos. 3 and 4), while K varied along the stem in conformity with the same regularity (Figs. 1A and 2A). The value of K increased in the direction of the top in the basal part of the stem, then was constant over a certain interval, and declined smoothly with approach to the top. In spruce trees that grew under favorable light conditions (Nos. 1, 2, and 4), K turned out to be highest on the stem sector with the greatest mass of foliage (Figs. 1D and 2D). The obtained results coincide with previously published data [3, 7, 8]. There are also data in the literature indicating increase of stem K from base to top [20, 21].

Xylem water conductivity in spruce tree No. 1 was determined at the beginning of July, when growth in height was not yet completed. No part of the apical increment of the current year conducted water intensively, since the entire xylem was composed of living cells. Spruce tree No. 2 was analyzed two weeks later, at which time it was clarified that the base of the current year increment (400 cm from the ground surface level) already conducts water, whereas the upper part (450 cm) does not yet do so. It follows that young wood becomes water-conducting tissue gradually with cessation of growth and death of tracheids. Interest is aroused by the fact that the K value of such young xylem turned out to be many times higher (not shown on Fig. 1) than the highest values of K in the older part of the stem The K value of water-saturated xylem is determined by its anatomical structure. It follows that K depends upon those ecological factors which affect wood formation. Influence of the

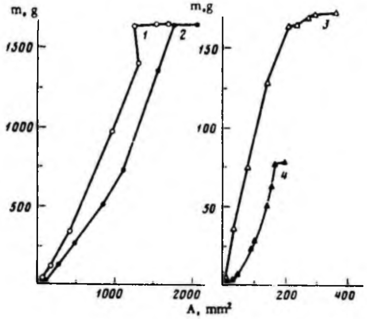

Fig. 3. Needle mass as a function of xylem conducting area. Spruce trees Nos. 1 (1), 2 (2), 3 (3) and 4 (4).

habitat conditions on xylem water conductivity is clearly manifested from a comparison of spruce trees Nos. 1 and 3 (Table 1). Spruce tree No. 3 represents a suppressed tree that for years resided under conditions of strong competition. Its annual rings were narrow, and tracheid clearances also turned out to be narrower in it. The value of K in all parts of the stem on the average was half as great as in spruce tree No. 1, which grew up under relatively favorable conditions.

The Huber value in spruce trees that grew under favorable conditions increased monotonically in the apical direction (Figs. 1C and 2C). Such a structure of the water-conducting system should provide the top of the tree with a water supply at least equivalent to that available to lower parts of the crown. The higher the shoots in the crown, the greater the hydrostatic pressure-determined resistance that must be overcome by the flow on its way to them. Increase of HV in the apical direction probably represents one of the means by which adequate compensation of water loss in shoots located far from the source of water and under more stressed conditions of radiation is realized.

The apical bud in spruce usually opens before lateral buds, and the top grows faster and longer than the branches. Such a growth rhythm is repeated from year to year, with the result that the crown takes on a conical form, which is illustrated by the vertical distribution of needle mass (Figs. 1D and 2D). Increase of HV in the apical direction is probably associated with the phenomenonon of apical control. This tendency is manifested especially strongly in the youngest (No. 4) of the investigated spruce trees (Fig. 2C), in which HV attained the highest values, viz., $18.87 \cdot 10^{-6}\ m^2 \cdot g^{-1}$. Such a hypothesis is in agreement with data indicating that apical control is strongest in young trees and undergoes weakening with the years [22, pp. 132-135]. The value of HV decreases with age more rapidly in the upper part of the stem, due to which the curve describing changes of HV with height approaches the vertical axis.

The powerfully suppressed spruce tree (No. 3) differed qualitatively in regard to the nature of HV changes with height (Fig. 2C). The value of HV turned out to be highest ($2.13 \cdot 10^{-6}\ m^2 \cdot g^{-1}$) in the base of the stem and decreased slightly in the direction of the top. Increase in height was very slight in this tree, the top was poorly developed, and apical control was weakly expressed. The upper branches were relatively long, and virtually the entire mass of needles was located in the upper part of the tree (Fig. 2D). It may be hypothesized on the basis of our results that HV values in older trees and in suppressed trees with weak apical control remain low and relatively stable throughout the entire stem.

The area of conducting xylem did not turn out to be proportional to the amount of needles in Norway spruce. As was to be expected, the curve describing the dependence between needle mass and xylem conducting area (Fig. 3) most closely approached a straight line in spruce tree No. 3.

Leaf-specific conductivity of the xylem in spruce tree No. 4 (which possessed the strong-

TABLE 1. Relative Hydraulic Conductivity of Stem Xylem ($\cdot 10^{-12}$ m^2) in Spruce Trees That Grew under Different Ecological Conditions (tree No. 1 grew under relatively favorable light conditions, whereas tree No. 3 grew under a dense canopy of taller trees)

Tree No.	Time age, years	Basal part	Middle part		Apical part
			region of variation	mean value* ± standard error	
1	38	1.15	1.43—1.98	1.75±0.13	0.32
3	33	0.74	0.72—0.86	0.74±0.04	0.13

*The difference of means is statistically significant at a 99.9% level of confidence.

TABLE 2. Leaf-Specific Conductivity of Stem Xylem ($\cdot 10^{-18}$ $m^4 \cdot g^{-1}$) as a Function of Tree Age

Tree No.	Tree age, years	Mean value* ± standard error	Maximum value
1	38	1.60 a±0.18	2.44
2	18	2.56 b±0.19	3.26
4	9	3.44 b±0.72	8.07

*The difference of means is statistically significant at 99.9% (a) and 99% (b) levels of confidence.

est apical control) increased smoothly in the apical direction (Fig. 2B) in keeping with HV. In spruce trees Nos. 1 and 2, LSC was highest in the middle or upper part of the stem (Fig. 1B). A completely different nature of LSC changes with height was recorded in spruce tree No. 3: maximum values were observed in the base of the stem, after which LSC decreased smoothly in the direction of the top. Values of LSC in the upper part of the stem differed more than 10-fold in spruce trees Nos. 3 and 4. Thus, the potential water supply available to the top was more than 10 times more favorable in spruce tree No. 4 than in spruce tree No. 3. This represents one of the factors behind desiccation of spruce trees on the margins of felling sites: the water-conducting system of trees that formerly grew under the canopy of a closed stand cannot make good the water losses incurred at higher radiation intensity. Analogous differences of LSC between dominant and suppressed trees were recorded in *Abies balsamea* [7] and *Tsuga candensis* [8].

As Table 2 indicates, LSC of the stem decreases with age.

DISCUSSION

The value of K depends upon age of the wood, topographical location of the section, and ecological factors, which together determine anatomical structure of the xylem. It follows from this that the origin of analyzed material must be precisely fixed in determining xylem hydraulic conductance. Caution must be shown in drawing conclusions about the hydraulic architecture of mature trees on the basis of data obtained on seedlings or stool shoots [3].

In all of the spruce trees we investigated, K increased in the lower part of the stem, but decreased in the direction of the top in the upper part of the stem. Such a pattern of K changes with height seems to be universal. Published data describing a tendency of this parameter to change in only one direction were apparently dictated by the fact that the stem was not analyzed throughout its entire length.

Booker and Kininmonth [21] critically approach values below $2 \cdot 10^{-12}$ m^2. However, the limits they established in comparing hydraulic properties of the xylem of different species are apparently too arbitrary. The majority of data we obtained lie below this limit, but are close to results published for several coniferous species, viz., $2.05 \cdot 10^{-12}$ m^2 [23] and $2.62 \cdot 10^{-12}$ m^{-2} [5] for *Pinus contorta*; $2.38 \cdot 10^{-12}$ m^2 for *Pseudotsuga menziesii* [5]; $2.74 \cdot 10^{-12}$ m^2 for *Tsuga canadensis** [8]; and $2.77 \cdot 10^{-12}$ m^2 for *Picea engelmannii* [5]. The

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*For conversion to the same measuring units, the value of dynamic viscosity of water was assumed to be equal to $1 \cdot 10^3$ $N \cdot sec \cdot m^{-2}$.

listed values for the most part were measured in the lower part of the stem of old trees and therefore represent the higher values possible for these tree species. Age of the spruce trees we studied did not exceed 40 years. Farmer [3] concluded that relative conductivity of the xylem in well developed tall trees can greatly exceed the K value of young trees.

It is known that apical control is realized as a result of the interaction of many physiological processes in which phytohormones play a guiding role. However, it is obvious that more active functioning of apical meristem and growth of the top in comparison with the branches are possible only in the presence of adequate provisioning with water and mineral substances. More favorable water supply of apical parts of the plant is not only a result of apical control, but also a condition for it. As we were able to convince ourselves, K varies along the stem basically in conformity with the same regularity regardless of age and conditions of the habitat. In young trees possessing strong apical control, better water supply and faster growth of the top are achieved by means of increase in relative conducting area of the xylem, which compensates for decline of K in the apical direction.

Both its radial increment and growth in height decline with aging of a tree. The crucial factor from the viewpoint of water supply is precisely the indicated decline of radial increment, as a result of which increase of xylem conducting area can no longer compensate for the increase of resistance during transport of water to the upper parts of the crown. Owing to this, the top begins to lose its hydraulic superiority in comparison with lateral shoots. In old coniferous trees (especially in many species of pine), the crowns become sprawling and the main axis loses its dominant position with the passage of time due to increase in overall size of the trees, aggravation of competition between branches, and lengthening of the pathways of transport of water and mineral substances [22, p. 135].

The apical bud periodically dies in certain woody species, and this causes simultaneous development of lateral buds. The shoots of lateral buds grow parallelly, but one of them usually attains preeminence eventually. The shoot which becomes dominant in this competition is one that is in a preferred position from the viewpoint of water supply, i.e., a shoot possessing higher K [3] or higher LSC or HV [7]. As was established by Farmer [3], K turned out to be lower in the main shoot than in neighboring shoots in ash and certain other plant species. Such results become comprehensible when we examine the material on which Farmer experimented. He worked mainly on segments of root suckers, stool shoots, and branches, in which dominance relations are not yet composed or are very weakly expressed. Moreover, ash belongs to the category of species with weak apical control.

Stem LSC in spruce varied within the limits of $(0.20\text{-}8.07)\cdot 10^{-18}\ m^4\cdot g^{-1}$, values which coincide with data obtained for other conifers,* viz., $(0.10\text{-}3.40)\cdot 10^{-18}\ m^4\cdot g^{-1}$ for *Thuja occidentalis* [6]; $(0.27\text{-}8.14)\cdot 10^{-18}\ m^4\cdot g^{-1}$ for *Tsuga canadensis* [8]; and $(0.08\text{-}16.73)\cdot 10^{-18}\ m^4\cdot g^{-1}$ for *Abies balsamea* [7]. Changes of HV and LSC with height possess a certain diagnostic value: the more they increase in the direction of the top, the stronger the apical control of the tree. It may be hypothesized that HV will prove to be relatively constant in stems of old and suppressed trees, the curves describing changes of it with height approaching a straight line. This hypothesis is supported by data obtained for *Abies balsamea* [7]. In dominant trees of this species, HV exceeded $50\cdot 10^{-6} m^2\cdot g^{-1}$, whereas it comprised $4.5\cdot 10^{-6}\ m^2\cdot g^{-1}$ on the average in suppressed trees. In comparison with the above species, *Tsuga canadensis* possesses weak apical control, the range of HV values lying within the limits of $(6.5\text{-}2.5)\cdot 10^{-6}\ m^2\cdot g^{-1}$ [8].

Conclusions as to a relatively linear rate of water translocation in different parts of the stem may be drawn on the basis of HV values. The lower the LSC, the higher the rate of xylem flow through this sector of xylem must be and the steeper the water potential gradient [10]. If it is postulated that uniform transpiration conditions prevail throughout the entire crown and the rate of transpiration per unit of foliage mass is constant, the linear rate of the ascending flow should then be proportional to the LSC of this sector. Thus, the linear rate of xylem flow can differ markedly in different points of the stem at one and the same time. This circumstance must be taken into account in comparing flow rate data obtained by the thermoimpulse method.

Finally, let us dwell on the contradiction noted by Ewers and Zimmermann [7, 8] in connection with the question as to whether the ratio of xylem conducting area to foliage mass

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*See footnote on previous page.

is constant (as follows from the "pipe model") or not. It is not constant in Norway spruce, but varies both among separate trees and within the same tree. The area of conducting xylem can represent a satisfactory estimate of foliage mass or area in investigation of water exchange on the stand level, especially in the case of stands composed of trees of the same age or ones homogeneous in the sense of age class. Such an estimate apparently remains imprecise for individual trees, although HV can be relatively constant within stem limits in certain cases (weak apical control, old or suppressed trees).

The results of our investigation support the position that the hydraulic architecture of a tree is associated with peculiarities of form of the tree in a concrete ecological situation. The nature of spatial changes in hydraulic conductivity of the xylem plays a significant role in the phenomenon of apical control.

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HYDRAULIC ARCHITECTURE OF NORWAY SPRUCE

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UDC 581.824.1

We studied the spatial variability of xylem hydraulic conductivity in lignified parts (trunk, branches, roots) of Norway spruce [*Picea abies* (L.) Karst.]. Xylem waterconducting capacity was determined on the basis of relative conductivity (K), the Huber value (HV), and leaf-specific conductivity (LSC).* The spatial distribution of K was identical in all of the investigated organs, K being maximal in the middle of the organ and declining in the basal and apical directions. The different organs differed significantly in absolute values of water conductivity characteristics. Values of K decreased in the following series: roots—trunk—rank I branches—rank II branches—rank III branches. Water conductivity in bases of branches of any rank turned out to be significantly lower than in the trunk at a corresponding height or in the main branch at a corresponding distance from the trunk, a situation that creates the prerequisites for preferential movement of water along the axial organ. It is hypothesized that the hydraulic hierarchy of different parts of the tree and high resistance of the base of branches also play a definite role in the phenomenon of apical control.

KEY WORDS: Norway spruce; xylem; hydraulic conductivity; hydraulic architecture.

In the soil—plant—atmosphere system, water travels the greatest distance through the xylem of roots, trunk, and branches. Structure of the xylem of these organs differs slightly: tracheids of root xylem have greater length and width than tracheids of the trunk and branches [1, p. 71; 2, p. 20].

As a result of anatomical peculiarities, these organs also differ in hydraulic conductivity. It has been established that the relative conductivity (K) of tree roots is much higher than in trunks [3], root conductivity growing with increase of distance from the trunk base [4, 5]. The value of K in branches and shoots is in turn lower than in the trunk [6; 7, p. 386; 8; 9]. With respect to values of leaf-specific conductivity (LSC), an index which characterizes the potential capacity of xylem to supply the leaf with water, different parts of the tree are arranged in a definite order called the hydraulic hierarchy. From the viewpoint of water supply, the trunk holds sway over rank I branches, while the latter are in turn ahead of rank II branches [8-11].

In a previous study [12], we obtained quantitative characteristics of hydraulic conductivity in trunk xylem of Norway spruce. The purpose of the present work was to determine characteristics of the water-conducting capacity of branches and roots, clarify regularities of changes in these characteristics, and analyze the physiological significance of the hydraulic hierarchy of spruce.

METHOD

Investigations were conducted in the Estonian SSR at the Vooremaa Ecological Station of Tartu State University from May to October of 1985. The test plot (a characterization of which was compiled in 1979) is located at an elevation of 90 m above sea level in the middle of a gradual (2-3°) northeastern slope of the Kallivere drumlin with brown pseudopodzolic soil and humus horizon thickness of 20-30 cm. The forest in question is a 40-yr-old spruce forest of complex type with stand composition of 10 S + B, P, As. Median tree height comprises 18.6 m, average diameter at chest height comprises 19.4 cm, trunk density exhibits a value of 1550/ha,

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*Abbreviations: K) Relative conductivity of xylem; LSC) leaf-specific conductivity of xylem; HV) Huber value.

Tartu State University. Translated from Fiziologiya Rastenii, Vol. 35, No. 6, pp. 1099-1107, November-December, 1988. Original article submitted March 3, 1987; revision submitted June 18, 1987.

0038-5719/88/3506-0839$12.50

TABLE 1. Relative Hydraulic Conductivity of Stem and Branch Xylem ($\times 10^{-12}$ m^2)

Tree No.	Investigated part of organ	Trunk		Rank I branches	
		Range of variation	$\bar{x}\pm S$*	Range of variation	$\bar{x}\pm S$
1	Basal	1,15		0,08—0,38	0,26±0,05
	Middle	1,43—1,98	1,75±0,13	0,28—0,91	0,61±0,09
	Apical	0,32		0,02—0,34	0,24±0,05
2	Basal	1,40		0,03—0,35	0,22±0,05
	Middle	1,08—2,11	1,64±0,22	0,15—0,83	0,63±0,09
	Apical	0,76**		0,10—0,65	0,38±0,08

Tree No.	Investigated part of organ	Rank II branches		Rank III branches	
		Range of variation	$\bar{x}\pm S$	Range of variation	$\bar{x}\pm S$
1	Basal	0,04—0,24	0,15±0,02		
	Middle	0,11—0,32	0,22±0,03	0,03—0,16	0,09±0,02
	Apical	0,05—0,09	0,07±0,01		
2	Basal	0,04—0,26	0,15±0,02		
	Middle	0,15—0,31	0,24±0,02	0,04—0,09	0,07±0,01
	Apical	0,02—0,23	0,10±0,05		

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*$\bar{x}$) Arithmetic mean; S) standard error. In the case of branches, arithmetic means were calculated from measurements on all studied branches of the corresponding rank. Arithmetic means in the trunk (middle part) were calculated from five measurements on a single trunk.

**Does not include the unusually high value ($38.19 \cdot 10^{-12}$ m^2) measured in spruce No. 2 in the base of apical increment of the current year.

and the sum of trunk cross section areas comprises 48.9 m$^2\cdot$ha^{-1}. Absolutely dry mass of the overground part of the stand comprises 232.2 tons$\cdot$ha^{-1} (192.0 tons in the technical part of trunks), while that of the underground part comprises 48.3 tons$\cdot$ha^{-1}.

The main objects of investigation consisted of two young trees of Norway spruce [*Picea abies* (L.) Karst.]: No. 1 with an age of 38 yr and height of 4.34 m formerly grew in a closed stand, but spent the last 6 yr under relatively good light conditions; and No. 2 with an age of 18 yr and height of 4.61 m grew on the edge of a ride under favorable light conditions. Seven main branches from different crown height were studied in both trees, three or four test segments being sawed off from each. Two or three rank II branches were selected in all of the investigated main branches, and three test segments were sawed off from each of them. One rank III branch as a rule was selected for study on rank II branches, and one test segment was sawed off from it.

The following individual branches and roots were additionally analyzed (10 test segments from each) for a detailed study of hydraulic architecture: three rank I branches of southern exposure from a height of 2-4 m above the ground from 40-yr-old trees at the edge of the forest; three rank II branches of southern exposure from a height of 2 m above the ground from a 70-yr-old tree at an open locality; and four lateral roots of middle-aged trees in a closed stand.

The experimental procedure employed has been described in the studies of Comstock [13], Booker and Kininmonth [14], and Zimmermann [10]. We used xylem segments with a length of 2-4 cm in the experiments. A 10 mM aqueous solution of KCl was used to saturate the segments under a vacuum. This solution (deaerated just before the experiment) was also passed through the test segments. The difference in pressure between ends of the segment was within the limits of $(1.47\text{-}1.57)\cdot 10^4$ Pa. Conducting area of the xylem was measured by the dye method.

RESULTS

Hydraulic Conductivity of Branch Xylem. No distinct differences were clarified in values of hydraulic conductivity characteristics in the two trees we investigated (Tables 1 and 2). In the case of rank I branches, K attained its highest values in the middle part, being two to three times greater there than K in the branch base. In rank II branches, K attained its highest values in the middle part, being two to three times greater there than K values in the branch base. This difference turned out to be smaller in rank II branches. Values of K in the base of branches were much lower than K of the trunk at a corresponding height (Table 3). For technical reasons, test segments of branch base xylem as a rule were sawed off at a distance of 1-2 cm from the trunk. However, spatial differences of K were especially great in this part of branches. Thus, in two segments sawed off close to the trunk, K turned out to be 66 and 22 times less than K values at a corresponding height in the trunk. It follows from what has been said that the branch base offers significant resistance to entry of water into the branch, thereby creating the prerequisites for preferential movement of water along the main axis of transport pathways.

A curious regularity was clarified in comparing mean values of K: The value of K in rank I branches on the average turned out to be 2.7 times lower than in the trunk, K in rank II branches was in turn 2.7 times lower than in rank I branches, and K in rank III branches was likewise ~2.7 times lower than in rank II branches. Rank I branches and the trunk also differed in LSC values (Table 2), which were several times higher in the trunk than in branches. The Huber value (HV) was also higher at the top of the trunk than in the apical part of branches.

Detailed analysis of the hydraulic conductivity characteristics of branches indicated that the curve of changes in K of rank I branches (Fig. 1A) is similar ro the corresponding curve for the trunk [12]. An analogous tendency (although to a lesser extent) was also clarified in rank II branches. Figure 2 illustrates changes in xylem hydraulic conductivity characteristics along rank II branches, branch age on the horizontal axis being recorded at the place of taking of the test segment. Since annual increments in rank II branches were similar in length, the nature of the curve was not qualitatively altered as a result of this replacement.

The nature of changes in the value of LSC along rank I and II branches differed significantly (see Figs. 1B and 2B). The value of LSC turned out to be very low in the base of rank I branches. It increased sharply in the distal direction, attaining maximal values at a distance comprising 1/4 of the entire length of the branch. The value of LSC declined again further on in the direction of the apex. The value of LSC was relatively constant in rank II branches, mean values varying within narrow limits, viz., $(0.16–0.25)\cdot10^{-10}\cdot m^4\cdot g^{-1}$. The value of HV increased smoothly in the apical direction in rank II branches (Fig. 2C), whereas HV in rank I branches at first decreased slightly in the direction from the base to the middle part of the branch and started to increase only with approach to the apex (Fig. 1C).

Hydraulic Conductivity of Root Xylem. Relative conductivity of the xylem (K) of Norway spruce roots varied within very wide limits, $(0.06–10.32)\cdot10^{-12}\cdot m^2$, while its spatial variability (Fig. 3) in general features turned out to be analogous to tendencies exhibited by K changes in the trunk and branches. The highest K values occurred in the central part of the roots, and K turned out to be lower in the proximal and distal parts. The value of K in the roots on the average was five times greater than K values in the trunk.

DISCUSSION

The lignified organs of Norway spruce differ significantly in the value of K. The farther away from the ground (the source of water) an organ is located, the lower its hydraulic conductivity. Thus, different parts of the tree can be arranged in the following order with respect to decrease of K values: roots—trunk—rank I branches—rank II branches—rank III branches. This series is completed by leaf petioles in deciduous trees and palms [10, 15] and probably by bundles of xylem elements connecting needle tracheids with water-conducting pathways of shoot axes in conifers. An analogous series is formed with respect to LSC values: The highest values of LSC were observed in the trunk, lower values were encountered in rank I branches, and still lower values occurred in rank II branches. The hydraulic hierarchy of tree organs is composed on the basis of water conductivity. The results we obtained in general features agree with data published for *Abies balsamea* [8], *Tsuga canadensis* [9], and certain deciduous species [10]. The hydraulic hierarchy is expressed especially clearly in spruce, a species possessing powerful apical control.

In the case of spruce, the value of K in roots is ~5 times greater than K of the trunk. Stone and Stone [5] stress the ecological significance of high water conductivity of the root xylem in woody plants. A high value of K creates conditions for better transport of water from any part of the root system, ensuring a more stable water supply for overground organs

TABLE 2. Xylem Leaf-Specific Conductivity (LSC) and Huber Value (HV) of Trunk and Rank I Branches*

Tree No.	Investigated part of organ	Trunk			
		LSC (×$10^{-16}\cdot m^4\cdot g^{-1}$		*HV* (×$10^{-4}\cdot m^2\cdot g^{-1}$)	
		range of variation	$\bar{x}\pm S$	range of variation	$\bar{x}\pm S$
1	Basal	1,19	1,88±0,22	1,04	1,08±0,13
	Middle	1,36—2,44		0,77—1,40	
	Apical	0,84		2,63	
2	Basal	1,80	2,63±0,21	1.28	1,68±0,17
	Middle	2,20—3,28		1,17—2,08	
	Apical	3,14**		5,13	

Tree No.	Investigated part of organ	Rank I branches			
		LSC (×$10^{-16}\cdot m^4\cdot g^{-1}$)		*HV* (×$10^{-4}\cdot m^2\cdot g^{-1}$)	
		range of variation	$\bar{x}\pm S$	range of variation	$\bar{x}\pm S$
1	Basal	0,16—0,37	0,26±0,03	0,70—2,73	1,21±0,30
	Middle	0,56—1,34	0,80±0,13	0,64—3,19	1,70±0,41
	Apical	0,42—1,08	0,72±0,10	0,80—3,81	1,96±0,46
2	Basal	0,08—0,34	0,24±0,04	0,80—3,74	1,46±0,42
	Middle	0,62—1,27	0,83±0,15	0,81+1,82	1,16±0,21
	Apical	0,37—1,68	1,02±0,23	1,40—2,58	2,07±0,24

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*See footnote to Table 1.

**Not included in the Table is the unusually high LSC value ($196\cdot 10^{-16}\cdot m^4\cdot g^{-1}$) measured in spruce No. 2 in the base of apical increment of the current year.

TABLE 3. Relative Hydraulic Conductivity (K) of Xylem of the Trunk and Branch Base

Tree No.	Trunk		Branch base	
	height from ground, cm	K, ×$10^{-12}\cdot m^2$	distance from trunk, cm	K, ×$10^{-12}\cdot m^2$
1	93	1,96	1	0,23
	126	1,68	7	0,38
	185	1,80	2	0,36
	213	1,91	2	0,36
	272	1,74	1	0,19
	318	1,23	1	0,24
	360	0,63	1	0,08
2	40	1,97	0	0,03
	95	2,08	2	0,32
	130	2,10	1	0,35
	194	1,57	0	0,07
	219	1,47	1	0,22
	272	1,27	1	0,30
	315	0,94	1	0,23

of the tree under changing ecological conditions, since the availability of ground water to plants can vary significantly.

The K values we obtained for spruce roots coincide with data published by other investigators for a number of coniferous species: $0.52\cdot 10^{-12}\cdot m^2$ for *Taxus baccata* [16]; $(0.77-11.37)\cdot 10^{-12}\cdot m^2$ for *Picea abies*, $1.15\cdot 10^{-12}\cdot m^2$ for *Larix decidua*, and $2.74\cdot 10^{-12}\cdot m^2$ for *Pinus sylvestris* [4]; and $(6.71-25.45)\cdot 10^{-12}\cdot m^2$ for *Pinus resinosa* [5]. Certain authors [4, 5] record that the K of roots increases with increase in distance away from the base of the trunk. Although our investigations corroborate this, the indicated authors apparently did not analyze roots throughout their entire length.

The low value of K in the root base is determined by small diameters of the tracheids, which lends greater mechanical strength to the wood. For the most part performing the function of fixing the tree in the ground, anchor roots are attached precisely to the basal part of lateral roots. In all of the roots we investigated, a definite K minimum was observed at

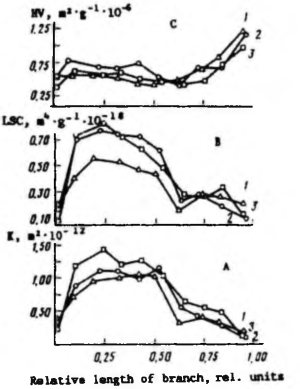

Fig. 1

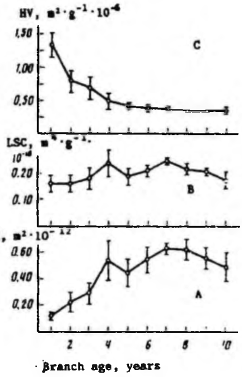

Fig. 2

Fig. 1. Hydraulic conductivity of xylem in rank I branches. A) Relative conductivity (K); B) leaf-specific conductivity (LSC); C) Huber value (HV). 1-3) Branches 2.12, 2.24, and 2.57 m long, respectively.

Fig. 2. Hydraulic conductivity of xylem in rank II branches. Each point on the figure represents the arithmetic mean of measurements on three branches (the bars signify the standard error). A-C) Same as on Fig. 1.

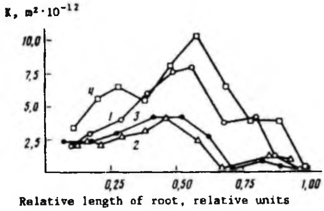

Fig. 3. Relative hydraulic conductivity of root xylem. 1-4) Roots 1.77, 2.14, 2.41, and 3.58 m long, respectively.

a distance of 1/4 of the way from the root tip. It may be hypothesized that such a minimum is associated with morphological characteristics of the roots and exists in the event of root tip death resulting in replacement of the main axis by a lateral root, in whose base the value of K is lower (sympodial growth is observed relatively often in spruce roots).

Values of the characteristics of xylem hydraulic conductivity we investigated were lower in the base of branches than on the corresponding sectors of the trunk or main stem, and also lower than on sectors of the same branches removed from the base. High resistance of organ bases is determined by shrinkage of tracheid internal diameters, as well as by reduction in the share of xylem elements that intensively conduct water [10]. Such anatomical structure ensures preferential movement of water along the main axis of the conducting system and apparently is one of the mechanisms by means of which apical control is realized. This phenomenon is called a "bottleneck" in the literature [8-10].

Spatial variability in the value of K along the stem, branches, and roots is universal in nature and primarily determined by differences in the rate of xylem cell formation. The dimensions of tracheids are determined by the rate of differentiation of the cells, their final diameter depending upon length of the growing season. Contradictory opinions exist in regard to influence of the auxin concentration gradient down the organ on differentiation of xylem elements [1, pp. 76-77; 17]. The higher the rate of cell differentiation, the smaller the diameter of tracheids that are formed, and consequently the higher the density of the wood and the lower its water conductivity. The investigations of Booker and Kininmonth [14] on Monterrey pine confirm that the value of K is inversely proportional to xylem density.

Our results agree nicely with previously obtained data on wood density changes throughout height of the trunk in Norway spruce [18]. The parabolas approximating wood density changes are oppositely directed in relation to the curve characterizing the distribution of K throughout trunk height [12]. An analogous regularity of spatial changes in wood density probably extends to branches and roots. The bases of trunks, branches, and roots are subjected to greater mechanical stress than are their distal parts. The high mechanical strength of wood is primarily achieved due to the small diameter and greater thickness of tracheid cell walls.

According to the Hagen-Poiseuille law, the volume of water transported in a unit of time through a capillary is proportional to the fourth power of its radius [19, p. 190]. It may be hypothesized that the value of K also depends to the greatest extent upon tracheid diameter. Since the value of K declines and HV values increase in the apical direction in the trunk [12] and in branches, adequate provisioning of distal shoots with water is realized as a result of increase in the relative area of the water-conducting xylem, i.e., the number of tracheids per unit of needle mass, not as a result of increased tracheid size.

The water potential of leaves depends not only upon environmental parameters, but also on internal characteristics of the tree and its hydraulic architecture. Values of the water potential in one part or another of the tree in any ecological situation are inseparably linked with structure of the water transport system. The water-conducting pathways (which constitute the structural basis of water exchange processes) apparently are so constructed that total resistance to water movement up to the highest shoots in the tip does not exceed resistance on the pathway from the roots to shoots in the lower part of the crown. Differences in K and HV compensate for differences of resistance caused by different distances in the place of consumption of water from its source. Precisely this accounts for the very low values of the water potential vertical gradient detected in tall coniferous trees of North America [20, 21]. Differences of the water potential appearing in measurements performed on shoots of lateral branches cannot give an adequate picture that would enable us to judge the water potential vertical gradient in the trunk [10, 11, 22]. These factors apparently explain the opposite water potential gradient detected in *Picea sitchensis* [23].

Since the water potential gradient under definite conditions is inversely proportional to the value of xylem LSC, the steepest gradient is therefore observed in slender branches. The higher the rank of a branch, the steeper the water potential gradient in it and lower the absolute values achieved by the water potential at a high rate of transpiration. It has been hypothesized that the hydraulic hierarchy of different parts of the tree under conditions of prolonged drought can in a certain sense turn out to be a protective mechanism preventing rapid death of the tree [10]. The water potential under conditions of a water deficit declines to the greatest extent in peripheral shoots, causing irreversible cavitation in their xylem elements [24]. The death of lateral shoots results in decrease of the transpiring area and tree's water loss. The central water-conducting pathways, i.e. trunk xylem, will be subjected to the danger of embolization in the very last order.

The hydraulic hierarchy of axial organs and the resistance of branch bases probably play a significant role in the phenomenon of apical control in spruce. Characteristics of hydraulic architecture constitute the structural basis of water exchange reactions during adaptation of the tree to changing environmental conditions.

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III. Soviet Forest Sciences, 1989, 0(1): 66-72

PRESSURE CHAMBER DETERMINATION OF XYLEM WATER POTENTIAL IN NORWAY SPRUCE SHOOTS OF DIFFERENT AGES

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Lesovedenie, No. 1, pp. 62-68, 1989

UDC 630*161.13:630*174.755

Xylem water pressure was studied as a function of the age of Norway spruce shoots. Theoretical and methodological problems occurring when measuring the water potential in conifers by a pressure chamber are discussed.

Many different methods have been developed for studying components of the water potential (ψ) in plants: compensation method in the liquid phase, compensation in the gas phase, psychrometric method, dew point method (thermocouple hygrometer), hanging-drop method (volumetric tensiometer), cryoscopic method, pressure chamber method, and hydraulic press method [1,10,15,21]. The majority of methods are labor-intensive and technically complex, and therefore it is difficult to use them under field conditions. Satisfactory technical solutions for measuring the xylem ψ in shoots of coniferous trees have still not been developed in any of the aforementioned methods.

In ecological investigations the pressure chamber found the widest use for measuring the ψ of leaves and shoots of plants, starting with the works of Scholander et al. [19]. The principle of measuring ψ by a pressure chamber is based on the assumption that the negative hydrostatic pressure (tension) in the xylem of leaves reflects ψ of the entire leaf. In comparison with others, this method is technically simple, enables rapid measurements in many replications, the apparatus is portable and convenient for use under field conditions. The pressure chamber was such a reliable instrument that it is used in calibrating other, sometimes technically more perfect apparatuses measuring ψ [7, 10,13,14,18,25].

The pressure chamber method also has its shortcomings. We are essentially dealing with a destructive method, since the leaves or shoots, the ψ of which is being measured, are separated from the plants. Furthermore, there is information that the pressure in the chamber has a damaging effect on cells [2]. The pressure chamber does not enable continuous tracking of the changes in ψ. Certain errors due to the anatomic and morphological characteristics of the species are possible in this method [2,3,5,17,24,26].

Our investigation was undertaken to determine the dependence of xylem ψ on the age of Norway spruce shoots. It was of interest to establish a difference in the values of ψ between shoots of different ages at the same time under the same conditions of evapotranspiration. Attention was devoted also to the following problems. First, how the results of measuring ψ depend on the ratio of the needle mass (m_n) to the mass of the shoot axis (m_a), i.e., on the relation of tissues with different functions. Second, whether the axial hydraulic conductivity of xylem of the shoot axis affects the value of ψ in shoots of different ages. In the article are discussed also certain theoretical and methodological problems encountered when measuring the xylem ψ of coniferous trees by the pressure chamber method and also when interpreting the results.

OBJECTS AND METHODS

The investigations were conducted at the Vooremaa Ecological Station of Tartu State University (Estonia) during the 1985 growing season. The characteristics of the sample plot were published earlier [22]. The objects of investigation were two middle-aged Norway spruce trees (*Picea abies* (L.) Karst.) growing on an open site. We studied 47 secondary branches from a height of 2 m from the ground consisting of shoots of different ages but relatively the same in length growing next to one another. We measured the pressure potential in xylem of shoots aged 1-4 years and current-year shoots in dry weather in the daytime, using a pressure chamber and being guided in so doing by the methodological instructions of G. A. Ritchie and T. M. Hinckley [17] and T. A. Sasonova [3]. Since the osmotic potential of sap in spruce is minimum, we can consider that the values obtained by the pressure chamber express the entire ψ of the shoots [9].

Before the investigation we conducted two series of methodological experiments to reveal possible distortions of the measurement results due to cutting old shoots from both ends. The first series of experiments was conducted with current-year shoots, both whole ones and with a cut apex, in half of the shoots we applied polyvinyl acetate adhesive on the cut and in the other half the cut was left clean. In both series of experiments no statistically significant differences in the values of ψ were found.

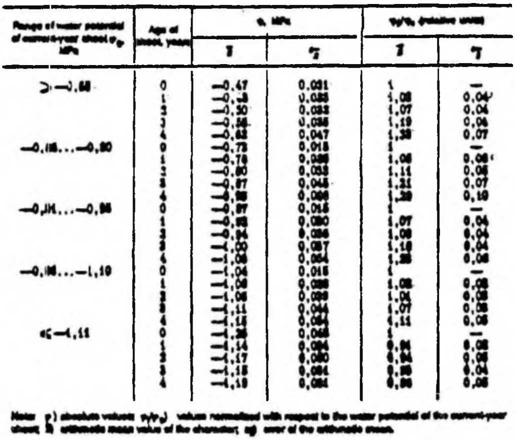
The shoots were cut from twigs immediately before placing them in the chamber; the rate of increasing the pressure in the chamber was less than 0.1 MPa/sec. After measuring ψ the shoots were dried at a temperature of 100°C to a constant mass and the needles and shoot axes were weighed separately. In three additional branches we determined three characteristics of hydraulic conductivity of xylem (relative and leaf-specific conductivity and Huber's value) of the shoot axes, using the method published earlier [4]. The experimental data were subjected to mathematical treatment, statistical methods and a stepwise multiple regression analysis were used.

RESULTS AND DISCUSSION

Table 1 gives the results of measuring the xylem ψ of Norway spruce shoots of different ages. The values of ψ of the different branches were grouped according to the value of the water potential of the current-year shoots (ψ_0) and then the arithmetic means were calculated for individual years, as a result of which a family of curves was obtained (Fig. 1). An explicit regularity was found: the older the shoot, the lower its ψ. The relative differences between shoots of different ages decrease with decrease of the absolute values of (Table 2). In the range of ψ_0 between 0 and -0.95 MPa (curves a-c in Fig. 1A) ψ changes quite regularly depending on age. Curves d and e ($\psi_0 < -0.95$ MPa) move away from the other curves. This indicates a possible qualitative difference of water exchange at different values of ψ, presumably due to the phenomenon of cavitation of tracheids [6]. For ψ_0 less than -1.10 MPa the lowest values were not observed in the 4-year-old shoots but, conversely, in the current-year shoots.

Table 1

Xylem Water Potential in Shoots of Different Ages



Range of water potential of current-year shoot ψ_0, MPa	Age of shoot, years	ψ, MPa		ψ/ψ_0 (relative units)	
		$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$
≥−0,68	0	−0,47	0,031	1	—
	1	−0,48	0,035	1,08	0,04
	2	−0,50	0,032	1,07	0,04
	3	−0,56	0,036	1,19	0,06
	4	−0,62	0,047	1,33	0,07
−0,69...−0,80	0	−0,73	0,015	1	—
	1	−0,78	0,028	1,06	0,06
	2	−0,80	0,033	1,11	0,06
	3	−0,87	0,045	1,21	0,07
	4	−0,95	0,066	1,30	0,10
−0,81...−0,95	0	−0,87	0,015	1	—
	1	−0,93	0,030	1,07	0,04
	2	−0,94	0,036	1,08	0,04
	3	−1,00	0,037	1,16	0,04
	4	−1,08	0,064	1,26	0,06
−0,96...−1,10	0	−1,04	0,015	1	—
	1	−1,06	0,038	1,02	0,03
	2	−1,06	0,039	1,04	0,03
	3	−1,11	0,044	1,07	0,03
	4	−1,15	0,054	1,11	0,05
≤−1,11	0	−1,26	0,068	1	—
	1	−1,14	0,084	0,91	0,03
	2	−1,17	0,080	0,94	0,03
	3	−1,15	0,084	0,95	0,04
	4	−1,19	0,084	0,96	0,05

Note: ψ) absolute values; ψ/ψ_0) values normalized with respect to the water potential of the current-year shoot; $\bar{x}$) arithmetic mean value of the character; $s_{\bar{x}}$) error of the arithmetic mean.

With age the ratio of m_n to m_a decreases, since a new annual ring of xylem is added each year (Table 3). The quantitative relation of m_n and m_a in a particular year depends both on the weather conditions of the current year and on the meteorological character of preceding years. Atmospheric pollution affects the number of needles, especially in the past decade, substantially shortening the life of the needles.

A number of characteristics expressing differently the quantitative relation of m_n and m_a were subjected to a correlation regression analysis. The analysis included data only of those branches (23 branches) for which ψ_0 was higher than -0.95 MPa, since below this value, obviously, qualitative changes in water transport begin in Norway spruce shoots. A weak correlation was found between the normalized values of the water potential (ψ_1/ψ_0) and relation of m_n and m_a. The highest coefficient of determination (r^2) was observed for the following characteristics: $(m_a/m_n)^2$, m_a/m_n, $(m_n - m_a)$, the values of r^2 were respectively 0.30, 0.28, and 0.23. Consequently, the relation of m_n and m_a describes less than one-third of the entire variation of ψ_1/ψ_0. Therefore the differences in the relation of m_n and m_a can hardly cause the distinctly expressed age-related tendency toward a decrease of the value of the shoot ψ. It follows from the aforesaid that the use of the pressure chamber for determining ψ in spruce shoots is valid and an artifact is not noted in the results. Shoots of different ages actually differ in ψ.

Table 2

Difference of the Mean Values of the Water Potential of 4-Year-Old Shoots and Current-Year Shoots

Range of water potential of current-year shoots ψ_0, MPa	Difference in absolute values, MPa	Difference in normalized values (relative units)
>−0.85	0.15	0.33
−0.86...−0.90	0.21	0.39
−0.91...−0.95	0.19	0.33
−0.96...−1.10	0.11	0.11
≤−1.11	−0.08*	−0.04*

*The 4-year-old shoots have a higher water potential than the current-year shoots, i.e., a difference of opposite direction.

Table 3

Ratio of Bone-Dry Needle Mass to Mass of Shoot Axis

Age of shoot, years	$\bar{x}$	$s_{\bar{x}}$
0	4.90 a	0.18
1	3.23 b	0.10
2	2.38 c	0.12
3	2.47 c	0.13
4	1.80 d	0.08

Note: $\bar{x}$ and $s_{\bar{x}}$ see Table 1. The difference of the means, marked by different letters, is statistically significant at the 99.9% confidence level.

With age the characteristics of the hydraulic conductivity of xylem of the shoot axes change completely regularly (Fig. 2). The relative conductivity (K), expressing the water conductivity of a unit area of a segment of xylem of a certain length, increases, and Huber's value (HV), characterizing the relative water-conducting area of the xylem, conversely, decreases with shoot age. The potential capacity of the xylem to supply leaves with water is determined by the leaf-specific conductivity (LSC) - the product of K and HV. In the branches investigated by us LSC was relatively constant, its values varied only within narrow limits, $(0.12\text{-}0.31)\cdot 10^{-18}$ m^4/g (Fig. 2B). In the LSC values is observed a tendency toward a decrease along the branch in the apical direction, i.e., the younger the branch, the lower the LSC of the shoot axis and the worse the potential water supply. Consequently, axial water conductivity of shoot axes cannot serve as the cause of our established differences in ψ between shoots of different ages.

Our results confirm the presence of an explicit dependence of xylem ψ on shoot age - the older the shoot, the lower its ψ. However, this regularity is noted only in the case of a sufficient water supply of the shoots, i.e., when ψ_0 is higher than -1.10 MPa.

In many works attention was called to methodological problems occurring when using a pressure chamber for determining ψ. Filling of the pith cells with water upon an increase of pressure in the chamber, as a consequence of which a higher pressure is necessary to return the xylem sap to the cut surface of the shoot, is suggested as one of the possible sources of errors [5,16]. In experiments with Norway spruce shoots of different ages we can eliminate the hypothesis of the pith as a water reservoir, since the proportion of pith decreases with age of the shoot.

In certain plant species the volume of the twig or shoot placed in the chamber affects the results of measuring xylem ψ. However, it has been proved that in conifers the volume of the shoot is not critical [3,17,26]. The volume of that part of the shoot axis which remains outside the chamber during measurement is essential. In our experiments the length of the shoot axis outside the chamber was the same and did not exceed 4-5 mm.

External pressure increases the pressure potential in needle cells, as a consequence of which the water is pressed out from them back into the xylem. The process of equalization between the xylem and mesophyll cells lasts a certain time, but, taking into account the rate of increase in pressure in our ex-

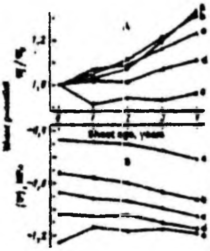


Fig. 1

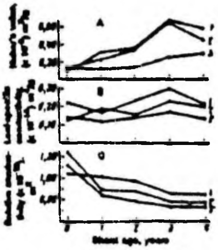


Fig. 2

Fig. 1. Dependence of the xylem water potential on shoot age: A) values of the water potential normalised with respect to the water potential of the current-year shoot (ψ_1/ψ_0); B) absolute values of the water potential (ψ); a) $\psi_0 \geq -0.65$; b) $-0.66 \geq \psi_0 \geq -0.80$; c) $-0.81 \geq \psi_0 \geq -0.95$; d) $-0.96 \geq \psi_0 \geq -1.10$; e) $-1.11 \geq \psi_0$.

Fig. 2. Hydraulic conductivity of xylem of shoot axes of three branches: A) relative conductivity; B) leaf-specific conducivity; C) Huber's value; 1-3) numbers of branches.

periments, this cannot affect the measurement results. J. Hellkviet et al. [9] came to the conclusion that in the Sitka spruce, *Picea sitchensis* Carr., the results of measuring xylem ψ do not depend on the rate of pressure change in the chamber.

With age the ratio of m_n to m_a decreases and, consequently, the relation of volumes of tissues of different type also changes. From this follow the differences in the content of apoplast and symplast water, which in certain cases affects the characteristics of water exchange of plants [12]. For this same reason shoots of different ages differ in total water content upon complete saturation of the tissues. The results of our investigations indicate that in Norway spruce the relation of m_n and m_a negligibly affects the value of ψ, describing less than one-third of the entire variation of ψ. Consequently, the differences in ψ of shoots of different ages are natural, which indicates a more intense water supply of older shoots in comparison with young ones.

This statement is confirmed by investigations in which ψ was measured directly on needles [8,23]. E Sucoff [23], determining ψ in bundles of red pine needles, established during the morning decrease and afternoon increase of ψ its dependence on the age of the needles - in old needles ψ was lower. At noon in the presence of a strong water deficit such a tendency was not observed, and the data obtained were characterized by a large scatter. The author attributed this to a variable cloud cover in the midday hours, but it seems to us that he encountered the same such phenomenon as we did in our experiments for ψ_0 lower than -1.10 MPa.

Water losses by needles cannot cause such differences, since the resistance of stomata increases with age in conifers and the transpiration rate decreases [11]. Consequently, the cause lies in water supply - old needles are supplied with less water than young ones. Our data indicate that such a difference is not due to the axial hydraulic conductivity of the xylem of the shoot axes. We suggest that the main cause of the differences in ψ is an increase with shoot age of the resistance of the radial bundle of xylem elements connecting the mesophyll cells with axial water-conducting paths of the shoot axis. This occurs due to elongation of the said path, plugging of the tracheids by residual metabolic products, gas bubbles, and resin [8], or as a result of both processes. According to our ideas about the hydraulic architecture of the Norway spruce, this section of the xylem has the lowest relative conductivity. A greater drop of ψ is observed in the link of the transport system having a higher resistance. The osmotic component of ψ presumably also plays a greater role in the formation of ψ in older shoots.

The regularities presented above were found as a result of measurements of the xylem ψ in two middle-aged trees in an open site and therefore they cannot be directly transferred to trees growing in a dense stand. Thus considerable work still lies ahead in order to establish more detailed regularities of the variability of ψ of shoots in relation to the radiation and water regimes of the stand, as well as to the age of the tree.

CONCLUSIONS

1. The xylem water potential in Norway spruce shoots depends on the shoot age - the older the shoot, the lower its ψ. However, this regularity is found only in the case of sufficient water supply of the shoots.

2. The xylem water potential is practically independent of the relation of m_n and m_a. The lower values of ψ in older shoots are not due to the longitudinal hydraulic conductivity of xylem of the shoot axis.

3. The measured values of ψ are natural, they are not due to characteristics of the pressure chamber method. It is assumed that the main cause of the differences of xylem ψ between shoots of different ages is an increase with time of the resistance to water transport in the section from the axial xylem elements of the shoot axis to the mesophyll cells.

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MAIN FACTORS DETERMINING HYDRAULIC CONDUCTANCE OF THE XYLEM OF NORWAY SPRUCE

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UDC 581.116

*We investigated hydraulic conductance of the xylem of Norway spruce [*Picea abies *(L.) Karst.] in relation to the level of xylem saturation with water and tracheid diameter. It is established that K declines exponentially with decrease of θ in the xylem. In the saturated state, K of the xylem depends upon its anatomical structure, especially upon tracheid diameter. The average R_h of the largest tracheids described 79-85% of all variation of K in saturated xylem. The outer annual rings play a leading role in far transport of water in spruce xylem. Under conditions of adequate water supply, water transport occurs for the most part through the large tracheids of early wood.*

KEY WORDS: Norway spruce; xylem; hydraulic conductance; tracheid; hydraulic radius.

The flow of water in the course of its movement in the soil—plant—atmosphere system overcomes a whole series of resistances: resistance of the soil; resistance of cover tissues, cortex, and endodermis (during entry of water into the root); frictional resistance in xylem elements; action of gravitational force; diffusion resistance of stomates; resistance of the boundary layer; etc. Among different phylogenetic groups of plants, the share of xylem resistance in water transport is most significant in coniferous trees in view of the fact that water in them is transported through the xylem over great distances (tens of meters) and the wood consists solely of conducting elements of a primitive type — tracheids [1, p. 15; 2, p. 136].

The capacity of xylem for water transport is determined by its hydraulic conductance, which characterizes efficiency of the water-conducting system. The structure of wood is fairly complex, and the question of factors determining its hydraulic conductance is therefore enormously significant in understanding water transport mechanisms. It is known that the water conductance of freshly cut wood is higher than in seasoned wood [3, 4]. Moreover, it has been demonstrated that the water conductance of xylem rises with an increase in the degree of its saturation with water [5-8]. The level of saturation of the water-conducting pathways is probably one of the main factors affecting conductance of the xylem.

According to the Hagen—Poiseuille formula [9], the rate of flow of a liquid in ideal capillaries is proportional to the sum of their radii to the fourth power (ΣR^4). Thus, the rate of water flow through plant xylem should theoretically be a function of the radius of xylem elements. However, the conducting system in coniferous trees is not an ideal capillary system, its hydraulic conductance being determined by a whole complex of anatomical characteritics of the xylem. To be specific, water conductance of the xylem depends not only upon the diameter of tracheal elements [10-13], but also upon their length [14], the ratio of early and late wood [5, 15], xylem density [3, 5, 15, 16], the number of pores in end walls of tracheal elements [14, 17], the presence of tyloses in tracheal elements [18, 19], wood density [15], size of the aperture and density of bordered pits[12, 13], and the nature of the closing membrane and size of the pores in it [10-13]. In view of the fact that wood structure is composed in the process of morphogenesis under the combined influence of many environmental factors, the climatic and meteorological conditions and biotic factors on which the course of xylogenesis depends likewise affect — albeit indirectly (through anatomical structure) — hydraulic conductance of the xylem.

The present work was undertaken in order to establish the extent to which relative hydraulic conductance of the xylem of Norway spruce depends upon the level of saturation with water and diameter of the tracheids.

Abbreviations: K) Relative conductance of xylem; θ) relative content of water; R_h) hydraulic radius of tracheid.

Laboratory of Ecosystems, Tartu University, Tartu. Translated from Fiziologiya Rastenii, Vol. 37, No. 3, pp. 450-456, May-June, 1990. Original article submitted May 22, 1989; revision submitted September 18, 1989.

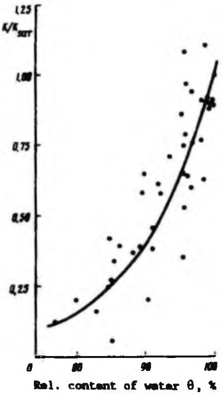

Fig. 1

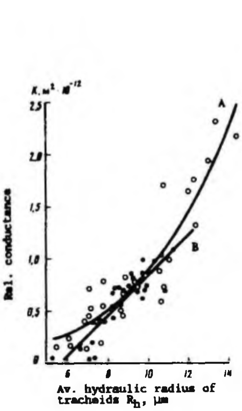

Fig. 2

Fig. 1. Hydraulic conductance in relation to level of saturation of the xylem with water. K/K_{sat}) Value of relative conductance normalized with respect to relative conductance of xylem in the saturated state.

Fig. 2. Xylem K in relation to R_h of the largest tracheids. A) Xylem of trees that developed under normal illumination conditions; B) xylem of trees that developed under conditions of shading.

METHOD

Experimental investigations were conducted at the Vooremaaskaya Ecological Station (Estonian SSR) of Tartu University during the growing seasons of 1986 and 1988. Characteristics of the climate, relief, soils, and vegetation of the test plot were discussed in a previous study [20]. Main branches of young and mature trees of Norway spruce [*Picea abies* (L.) Karst.] served as the objects of investigation.

Hydraulic conductance of the xylem was determined by a method based on D'Arcy's law, according to which the volume of water transported in a unit of time over a segment of xylem is proportional to the pressure gradient. The procedure is described in the studies of Booker and Kininmonth [15] and Zimmermann [21]. The index of relative conductance (m^2) [9] was used for quantitative characterization of xylem water-conducting capacity:

$$K = \frac{ql\eta}{\Delta PA},$$

where q is the rate of transport of an aqueous solution ($m^3 \cdot sec^{-1}$); l is length of the xylem segment (m); η is dynamic viscosity of the solution ($N \cdot sec \cdot m^{-2}$); ΔP is the difference of pressure (Pa); and A is conducting area of the xylem (m^2).

Our experiments were conducted with xylem segments 2-3 cm long. The conducting part of the xylem was established by means of staining. Its cross-sectional area was determined from photographs with the aid of an electronic planimeter on a graphic signal panel connected to an Apple II Europlus personal computer (USA). Mathematical processing of the experimental data was conducted using programs for personal computers.

In order to determine influence of the level of water saturation on xylem hydraulic conductance, we determined K in segments of eight branches (six segments from each branch) saturated for different lengths of time with a 10 mM aqueous solution of KCl under a vacuum. The same solution — deaerated just before the experiment — was also used for measuring. The difference in pressure between ends of the segments was within the limits of (3.6-7.1) · 10^3 Pa. Branch segments whose xylem possessed the highest conductance [22] were used in the work. Using segments from a definite region of branches, we presumed that anatomical differences between segments of the same branch are insignificant and can be ignored. Relative content of water was determined by the weight method.

In order to clarify the dependence between hydraulic conductance of the xylem and tracheid diameter, we studied branches of trees located under different illumination conditions: in a glade under favorable light conditions and under a canopy of taller trees. Completely saturated segments of branches were used in this experiment (saturation lasted not less than 4 h). The difference in pressure between ends of the segments as a function of conductance was (0.4-1.6) · 10^4 Pa. The minor and major diameters of 10 of the largest tracheids in 10 (in trees located under favorable illumination conditions) or three (in trees under a canopy) outer annual layers were measured with the aid of a light microscope in 30 segments.

RESULTS

Dependence of Relative Conductance (K) upon Level of Xylem Saturation. Branch segments possessing the highest value of θ were considered saturated. For separate branches, the value of K of segments with different water content was normalized with respect to relative conductance of a saturated segment (K_{sat}). It turned out that K is closely dependent upon θ of the xylem (Fig. 1). The relatively great scattering of data is dictated by the fact that the segments were not all anatomically identical. For this reason, the value of K in a saturated segment in one of the branches was not very high and the two normalized values of relative conductance (K/K_{sat}) exceeded 1.0.

The relation between K/K_{sat} and θ of the xylem is approximated by an exponential function, the regression formula being

$$K/K_{sat} = 1{,}05 \cdot 10^{-4} e^{9{,}17 \cdot 10^{-2}\theta},\ r^2 = 0{,}72,\ P < 0{,}001 .$$

where r^2 is the coefficient of determination and P the level of significance. Within limits of the values we obtained, the investigated dependence was better approximated by linear and exponential functions, but they turned out to be essentially dissimilar. The line of regression intersects the abscissa axis at an argument value of 78.3 for the linear function, but at a lower argument value for the exponential functions, i.e., K would be equal to zero at such a high θ in the xylem. In reality though, K first declines sharply with decrease of θ in the xylem during lowering of xylem water content, then begins to approach zero, but without ever becoming equal to zero.

Dependence of Relative Conductance upon Tracheid Diameter. The clearances of tracheids are not round in form, but are sooner ellipsoid or polygonal. Moreover, tracheids do not have a constant diameter, but taper at the ends, and the entire cavity of the tracheid takes part in water transport in varying degrees. We therefore employed the concept of the hydraulic radius (R_h), which expresses the hydraulic effective radius of xylem elements. Of the formulas of R_h employed for other plant species [17, 23], the following expression of R_h (μm) turned out to be most suitable for the xylem of spruce branches:

$$R_h = \frac{2 \cdot R_s R_l}{R_s + R_l} ,$$

where R_s and R_l respectively signify the smaller and larger internal radii of the tracheid.

Average R_h was calculated from the diameters of tracheids in the outermost annual layer, in the annual layer with the largest tracheids, in the three outer annual layers, and in all measured annual layers (up to 10). In the course of correlation-regression analysis, a close relationship was established between K and R_h of the largest tracheids. The closest correlation was detected in calculating the average R_h of tracheids in the outer annual layer. This enables us to postulate that although the water-conducting capacity of xylem in coniferous trees is preserved for a period of many years, the main role in far transport of water is played solely by the outermost layers.

In trees that grew under favorable light conditions, better results of approximating K in relation to R_h are yielded by a cubic parabola (Fig. 2), the regression formula being

$$K = 7{,}72 \cdot 10^{-16} R_h^3 + 1{,}01 \cdot 10^{-13};\ r^2 = 0{,}85,\ P < 0{,}001 .$$

Where a straight line is employed, the value of the coefficient is lower than $r^2 = 0.81$. In xylem of trees located under conditions of shading, the range of R_h values is narrower, but the scattering of data is the same as in trees that developed under normal illumination conditions. The dependence between K and R_h is therefore weaker and better approximated by a linear function, the regression formula being

$$K = 1{,}94 \cdot 10^{-13} R_h - 1{,}10 \cdot 10^{-12}, \; r^2 = 0{,}79. \quad P < 0{,}001.$$

Figure 2 presents the data of all xylem segments in which tracheid diameters were measured.

DISCUSSION

Our investigation supported the position that the level of saturation of water-conducting pathways with water is the paramount factor determining K of the xylem. In Norway spruce K of branch xylem declines twofold with decrease of θ to 92.5% of the saturated state and by an order of magnitude with decrease of θ to 75%. Comstock [5] established a linear dependence of K upon absolute water content in the xylem of eastern hemlock [*Tsuga canadensis* (L.) Carr.]. However, the correlation between these characteristics turned out to be weak ($r^2 = 0.40$), apparently due to anatomical differences between segments. Regions of xylem with different anatomical characteristics are difficult to compare in this regard because xylem structure is the second main factor on which K depends. The flow of water in tracheids is interrupted with lowering of water content in the xylem, and the tracheids (depending upon their diameter) lose their water-conducting capacity [24].

In stem xylem of *Pinus contorta* Dougl., decrease of θ from 97 to 94% caused a decline of K by approximately one order of magnitude [8]. Exponential decline of K with decrease of xylem θ has also been recorded in *Abies grandis* (Dougl.) Lindl. [6] and *Taxodium distichum* (L.) Rich. [7]. Legge [17] expressed doubt that such an insignificant change of θ can dictate such a pronounced decline of water conductance. However, our investigation corroborates the above-cited results, although the decline of K as a function of the level of xylem saturation was not so sharp in spruce.

Decline of hydraulic conductance (and consequently of the water-transport capacity) with decrease of θ is caused by cavitation of tracheal elements, as a result of which there is a reduction in the number of conducting channels. The exponential nature of this pocess is attributable to the fact that the bulk of water during far transport moves through large (spring) xylem cells. This follows from the Hagen—Poiseuille law, which holds that insignificant differences in the radius of xylem elements are accompanied by significant differences of water conductance. However, it has been demonstrated that the greater the diameter of tracheal elements, the higher the probability of disruption of the water flow in them [24]. Thus, cavitation of large tracheids is accompanied by significant decrease in K of the xylem. The greater the diameter of tracheids and the higher the K of the xylem, the faster the decline of water conductance under conditions of a water deficiency in the xylem.

The close dependence we established between K and R_h of the largest tracheids also serves as evidence in support of these deliberations. If the effect of water content on K is excluded, then hydraulic conductance of the xylem will depend solely upon its anatomical structure. Since the average R_h in the saturated state of xylem in spruce described 79-85% of all variation of K, it may be concluded that tracheid diameter is one of the main anatomical factors determining xylem water conductance. The obtained dependence in its nature is not strictly functional and in conformity with the Hagen—Poiseuille law, but probably is a correlative relationship. On the other hand, the close correlation between relative hydraulic conductance and average radius of the largest tracheids unquestionably indicates a physiological basis for this dependence.

Hydraulic conductance of the xylem depends not only upon tracheid diameter, but on other anatomical characteristics as well. The close dependence between K and average R_h of the largest tracheids as measured only in the latest annual layer is attributable to a number of circumstances. Thus, the outer annual rings play a leading role in far transport of water in the xylem. The inner rings lose their water-conducting capacity with time due to plugging of tracheids with resin and residual products of metabolism, as well as owing to aspiration of bordered pits [25]. Within the limits of a separate annual ring under conditions of adequate water supply, i.e., in the saturated state, the bulk of water moves through the large tracheids of early wood.

It may be concluded from what has been said that K of xylem in the water-saturated state is determined by its anatomical state. Among anatomical characteritics of the xylem, tracheid diameter exerts the most significant influence on K. In the presence of intensive transpiration, the water flow begins to be interrupted in large tracheids, hydration of the xylem declines, and resistance to water movement rises sharply. It follows that the conducting capacity of xylem also depends upon the value of θ. Thus, the diameter of tracheids and the level of saturation of the xylem are the main factors determining variation of hydraulic conductance of the xylem in spruce.

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V. Soviet Forest Sciences, 1990, 0(5): 31-36

AXIAL HYDRAULIC CONDUCTANCE OF ROOTS OF COMMON SPRUCE

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Lesovedenie,
No. 5, pp. 39-45, 1990

UDC 630*161.12:630*174.755

The author studied the spatial and age variability of axial hydraulic conductance of the xylem of roots of common spruce and its dependence on the diameter of tracheids. With the tree's age, the roots' relative conductance rises. Since the relative conductance of the roots' xylem decreases in a radial direction with distance from the cambium, the main role in long-distance transport of water is played by outer annual rings of the sapwood. In a water-saturated state, the xylem's relative conductance depends to a significant extent on the diameter of tracheids.

COMMON SPRUCE, ROOT, XYLEM, HYDRAULIC CONDUCTANCE

Many problems of woody plants' water metabolism are connected with the mechanism of long-distance transport of water. Movement of water and mineral elements from the roots to the leaves occurs through the lumina of dead xylem cells: vessels and tracheids. According to the latest ideas, long-distance transport of water in plants is seen as a passive process, the motive force of which is the gradient of water potential in the soil-plant-atmosphere system [1, p. 192; 2, p. 302; 8]. However, the rate of water's movement in a plant depends not only on environmental conditions, but also on internal factors of the plant determining resistance to ascending flow.

Among the various phylogenetic groups of plants, the portion of xylem resistance in water transport is more significant in conifers. In coniferous trees, first of all, water is transported through the xylem over large distances (tens of meters), and secondly, coniferous wood consists only of conducting elements of a primitive type: tracheids [4, pp. 15-16; 5, p. 136].

The path of water is also considerable along roots. The xylem's capability of water transport is determined by its hydraulic conductance [16,17]:

$$G = \frac{q}{\Delta\psi}, \qquad (1)$$

where G is the xylem's hydraulic conductance, $m^3 \cdot sec^{-1} \cdot Pa^{-1}$; q is the volumetric rate of movement of sap in the xylem; and $\Delta\psi$ is the difference in water potentials, Pa.

The purpose of the present work was to study spatial and age variability of axial hydraulic conductance of the xylem of common-spruce roots and to establish its dependence on the diameter of tracheids.

OBJECTS AND PROCEDURE

Experimental investigations were conducted at the Vooremaa Ecological Station (ESSR) of Tartu University over the course of the vegetation periods of 1986 and 1988. Characteristics of the climate, relief, soils, and vegetation of the test area have been published previously [23]. The basic objects of the investigations were the main roots of two middle-aged common-spruce trees (*Picea abies* (L.) Karst.) grown in sharply opposite light conditions, and heavily depressed tree 2 under the canopy of taller trees (Table 1). In addition, we also studied the roots of several young trees grown in favorable light conditions (Table 2).

The xylem's hydraulic conductance was determined by a method based on analogy of Ohm's law, according to which the volume of water moving per unit of time through a segment of the xylem is proportional to the pressure gradient. In intact plants, the pressure gradient corresponds to the water-potential gradient, which has the same dimensionality. The procedure is described in the works of R. Booker and J. Kininmonth [7], and M.

Table 1

Relative Conductance of Root Xylem for Middle-Aged Spruce Grown in Opposite Light Conditions

Tree number	Age of tree, years	Height of tree, m	Length of root, m	Relative conductance, $\cdot 10^{-12}$ m^2			
				base of root	middle part of root		apical part of root
					range of values	$\bar{x} \pm s_{\bar{x}}$	
1	40	14,84	5,43	1,43	7,91—12,44	11,07±1,06	2,24
			5,70	0,78	10,32—12,07	11,18±0,38	2,04
2	50	4,29	2,40	0,66	5,91—7,33	6,71±0,32	0,12
			2,81	0,24	3,88—8,27	6,75±1,03	1,42
			3,23	0,89	8,31—10,80	9,65±0,61	1,35

Note. $\bar{x}$ - Arithmetic mean value (computed according to four measurements in middle part of the root); $s_{\bar{x}}$ - arithmetic mean error.

Table 2

Dependence of Relative Conductance of Root Xylem on Age of Trees

Age of trees, years	Length of root, m	Relative conductance, $\cdot 10^{-12}$ m^2			
		base of root	middle part of root		apical part of root
			range of values	$\bar{x} \pm s_{\bar{x}}$	
4	—	0,016	0,007	—	0,003
4	—	0,028	0,093	—	0,031
5	—	0,022	0,013	—	0,006
7	>0,32	0,21	0,65—0,92	0,78±0,08	0,90
	0,37	0,49	1,31—2,12	1,68±0,24	1,34
8	0,32	0,39	0,65—1,15	0,95±0,15	0,38
	>0,34	0,86	1,18—2,17	1,77±0,30	2,02
16	1,18	0,51	1,51—3,78	2,83*±0,48	0,13
	1,51	0,40	3,20—3,79	3,49*±0,16	0,02
	1,80	1,09	3,88—5,48	4,56*±0,34	0,01

Note. $\bar{x} \pm s_{\bar{x}}$ - See note to Table 1. Arithmetic means marked with an asterisk were computed according to four measurements; the rest, according to three measurements in the middle part of the root.

Zimmermann [24]. In the tests, we used segments of xylem 2-3 cm long, saturated under a vacuum with a 10-mmole aqueous solution of KCl. The same solution, deaerated immediately before the experiment, was passed through the test segments; the difference in pressure between the ends of the segment, depending on conductance, was $(0.4\text{-}1.6) \cdot 10^4$ Pa.

The conducting part of the xylem was recognized by passing dyes through the xylem segments. The area of its cross section was determined from a photograph with the help of an electronic planimeter connected to an Apple II Euoplus personal computer. With a light microscope, we measured the smaller and larger diameters of the 10 largest tracheids in 3 (depressed tree) or 10 (viable) outer annual layers.

For quantitative characterization of the xylem's water-conducting ability, we used the index of relative conductance [16,17].

$$K = \frac{ql\eta}{\Delta PA}, \tag{2}$$

where K is relative conductance, m^2; q is the rate of movement of the solution, m$^3 \cdot$sec^{-1}; l is the length of the segment of xylem, m; η is the solution's dynamic viscosity, N$\cdot$sec$\cdot$m^{-2}; ΔP is the pressure difference, Pa; and A is the conducting area of xylem, m^2.

The xylem's hydraulic conductance (G) is proportional to its relative conductance (K).

RESULTS AND DISCUSSION

Variation of root xylem's relative conductance. The relative conductance of the xylem (K) of spruce roots varied over a very wide range: for 4-5-year old seedlings $(0.003\text{-}0.093)\cdot 10^{-12}$ m^2, for young trees $(0.010\text{-}5.48)\cdot 10^{-12}$, and for middle-aged trees $(0.01\text{-}12.44)\cdot 10^{-12}$ m^2. The roots' K rises with the tree's age (Tables 1 and 2). In all likelihood, the rise in K continues to a certain age. In old trees, for which growth decreases, tracheids with smaller diameter are formed, and consequently, the xylem possesses less conductance. At the base and tip of roots, this tendency is not clearly expressed, since K is low for these parts of the roots, and its spatial variability is high. The apical part of growth roots did not conduct water intensively (values of K were lower than the limit of our measuring system's sensitivity): the xylem consisted of live cells containing cytoplasm. The basal, partially lignified part of the same roots did conduct water: K was $(0.014\text{-}0.024)\cdot 10^{-12}$ m^2.

The main limiting ecological factor for depressed trees under the canopy of tall trees is solar radiation. Due to the trees' reduced net production, radial growth and growth in length is restrained in the roots (Table 1). For such a spruce (no. 2), in the middle part of the root K was approximately 1.5 times lower than for a spruce of the same age in favorable conditions of illumination (no. 1). At the bases of the roots, the trees did not differ clearly in values of K, but in the distal part of the roots K for the depressed tree was also lower in comparison with spruce 1. Consequently, resistance to the movement of water in the root xylem of depressed trees is higher than in the roots of trees growing separately or dominant in the stand.

In spite of significant variation in absolute values of K between roots, as well as within the bounds of a single root, along the roots K changes according to the same pattern. The highest values of K were measured in the central part of the roots, and they diminished in the proximal and distal directions [3] (Fig. 1). However, the conducting part of the root's xylem is inhomogeneous in its hydraulic properties at some certain distance from the stump: there is radial variation in K. Within the bounds of individual disks of wood sawed from the bases of large roots, values of the sapwood's K varied by as much as 36 times. As a rule, K decreased with distance from the cambium. This is the result of obstruction of the tracheids in time with residual products of metabolism, resin, and gas bubbles. The tracheids gradually cease to function as conducting elements, and heartwood finally forms [5, p. 117; 19]. Consequently, the contribution of inner annual layers to long-distance transport of water decreases in time in accordance with the reduction in K and the relative area of their cross section.

Thus, on the strength of high longitudinal and radial variability of K, evaluation of the water conductance of the whole root's xylem is a complex problem, especially together with lateral roots. It should be recognized that reliance on average values of hydraulic conductance in models of trees' water metabolism is highly doubtful.

Dependence of relative conductance on the diameter of tracheids. The structure of wood is fairly complex; therefore, the question of factors determining its hydraulic conductance is of enormous significance in understanding the mechanisms of water transport. The results of measurement of the diameters of tracheids revealed a tendency analogous to changes in K along the roots (Fig. 1). By dividing the measured diameters by two, we got the tracheid's smaller (R_s) and larger (R_l) radii, which correspond to semiaxes of an ellipse. In their form, the lumina of tracheids are not round, but rather elliptical or angular; therefore, the problem arises of what to take as the tracheid's radius. Moreover, tracheids do not have a constant diameter; they taper at the ends. The tracheid's inner space does not all participate the same in water transport; therefore, the concept of the hydraulically effective radius (R_e) is used, which expresses the radius of the effectively conducting part of the xylem element's cavity. For other plant species, several different approximations of R_e are used:

$$R_s\ [10,\ 11,\ 14],\ \frac{R_s+R_l}{2}\ [12,\ 13],\ \frac{2R_sR_l}{R_s+R_l}\ [9],\ (R_sR_l)^{1/2}\ [21],\ \left(\frac{2R_s^3R_l^3}{R_s^2+R_l^2}\right)^{1/4}\qquad [20].$$

In the course of mathematical processing of data, it was revealed that a more suitable approximation of R_e for the root xylem of spruce is the arithmetic mean of the tracheid's smaller and large inner radius.

We established a close correlation between K and the average R_e of the largest tracheids in roots of common spruce (Fig. 2). For trees grown in favorable light conditions, the closest correlation was revealed between K and R_e^3 ($r^2 = 0.93$); the relationship between K and R_e was weaker ($r^2 = 0.87$). For the depressed tree 2, the

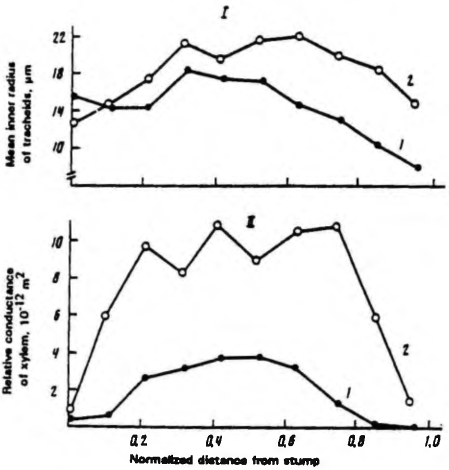

Fig. 1. Changes in mean inner radius of largest tracheids (I) and relative conductance of xylem (II) along roots: 1) root 1.51 m long (age of tree 16 years, height 4.28 m); 2) root 3.23 m long (50 years, 4.29 m).

spread of data was greater, the correlation was weaker, and the dependence under investigations was better approximated by a linear function ($r^2 = 0.77$).

In comparison with viable trees in favorable light conditions, for depressed spruces the roots' K is lower due to the tracheids' narrower lumina. Comparison of curves (Fig. 2) discloses a curious tendency: with equal radii of the largest tracheids, K of depressed trees' roots is higher. Here, we have not ruled out the presence of a distinctive compensation mechanism providing adequate water supply for the depressed tree. In order to compensate for increased resistance due to a decrease in the diameter of tracheids, the resistance of other anatomical components of the xylem is less. Thus, all of this allows us to suggest that the root system of depressed and viable trees differ in other anatomical characteristics besides the diameter of tracheids.

According to the Hagen-Poiseuille formula, the volume of water moving per unit of time through ideal capillaries is proportional to the sum of their radii to the fourth power [17;25, p. 190]. Consequently, our results do not correspond to the Hagen-Poiseuille law, for various reasons, perhaps. Firstly, as regards the structure of tracheids, they probably cannot be identified with ideal capillaries due to the irregular form of cells, barriers in the form of bordered pits, unevenness of the cell walls' inner surface, etc. Secondly, in each annual layer only the 10 largest tracheids were measured, not all conducting tracheids. The discrepancy with the Hagen-Poiseuille law may also be due to other factors [15].

The closest correlation between relative conductivity and the radius of tracheids was noted in computing R_e according to the dimensions of measured tracheids in the three outer annual layers, not in the last one or in all of them. Indirectly, this once again confirms the proposition that, although the conducting ability of coniferous xylem is preserved for many years, the role of the inner part of the sapwood in water transport is significantly less in comparison with the role of the outer part.

The mean R_e of the largest tracheids describes 77-93% of the whole variation in K in roots of common spruce. We can draw the conclusion that in a saturated state of the xylem K depends, to a significant extent, on the diameter of xylem elements. However, in some investigations [6,11,22], it was shown that the tracheids' lumina do not constitute the main portion of total resistance to water flow in the xylem. In our opinion, the given results do

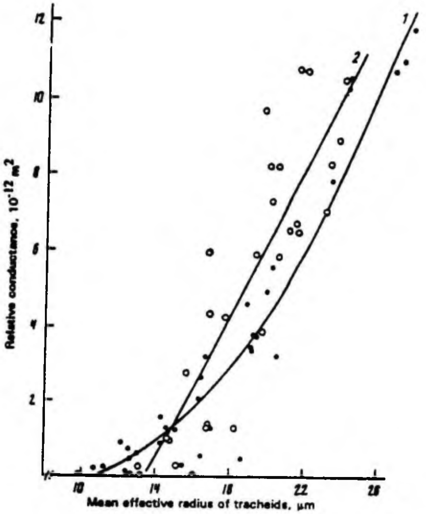

Fig. 2. Dependence of relative conductance (K) of xylem on mean effective radius (R_e) of largest tracheids: 1) xylem of viable trees, regression formula: $K = 6.46 \cdot 10^{-16} R_e^3 - 7.69 \cdot 10^{-13}$, $r^2 = 0.93$. Level of regression's significance $P < 0.001$; 2) xylem of depressed trees, regression formula: $K = 9.69 \cdot 10^{-13} R_e - 1.30 \cdot 10^{-11}$, $r^2 = 0.77$, $P < 0.001$.

not contradict sources in the literature. If other anatomical components of tracheids (the pore channel, pore chamber, marginal pores) account for the greater part of the total resistance to the movement of water in the xylem, then they vary less in their dimensions. An anatomical investigation conducted by R. Krahmer [18] with two forms of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) differing in the xylem's conductance confirms our proposition. The two forms' xylem differs in diameter and length of the tracheids, but not in the dimensions of parts of the bordered pits. The structure and surface density of bordered pits determine the order of magnitude of the xylem's water conductance characteristic of the species as a whole. But variation in the xylem's hydraulic conductance within the bounds of a certain tree or between trees depends significantly on the diameter of the tracheids.

CONCLUSIONS

1. Axial hydraulic conductance of the xylem of common-spruce roots varies over a wide range depending on the age of the tree and ecological factors; the roots' K increases with the tree's age.

2. Resistance to the movement of water in the root system of depressed spruces is higher than for viable trees, due to narrower tracheids. Besides the tracheids' diameter, differences in the roots' K between depressed and viable trees are also due to other anatomical characteristics of the xylem.

3. Axial conductance of the roots' xylem decreases in a radial direction with distance from the cambium. The basic role in long-distance transport of water is player by outer annual rings of the sapwood.

4. The diameter of xylem elements is one of the main anatomical factors determining the xylem's water conductance. The mean R_e of the largest tracheids describes 77-93% of the whole variation in K in water-

saturated roots of common spruce.

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10 November 1989

Tartu University, Tartu

VI. Journal of Plant Physiology, 1991,

138(4): 466-469

J. Plant Physiol. Vol. 138. pp. 466–469 (1991)

Hydraulic Conductivity of Xylem Depending on Water Saturation Level in Norway Spruce (*Picea Abies* (L.) Karst.)

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Received October 23, 1990 · Accepted March 8, 1991

Summary

The influence of xylem water content on the hydraulic conductivity of sapwood was measured on branch sections of *Picea abies*. Relative conductivity of the branchwood ranged from 0.03×10^{-12} to $1.62 \times 10^{-12}\,m^2$ depending on water saturation level. A reduction in relative water content from 100 to 75 % caused permeability to fall curvilinearly by about one order of magnitude. The higher the relative conductivity at full saturation, the steeper the decline in permeability in the case of reduction of xylem water content. An empiric model was derived that relates actual values of relative conductivity to saturated conductivity and relative water content. It describes 94 % of the total variation of relative conductivity.

Key words: Picea abies, relative conductivity, relative water content, sapwood, xylem.

Abbreviations: K = relative conductivity; K_{sat} = relative conductivity at full saturation; Θ = relative water content.

Introduction

An important determinant of leaf water potential is the capacity of the vascular system to supply water to leaves, determined by the hydraulic conductivity of xylem. Xylem conductivity depends primarily on inner factors of the plant, the most substantial of which are anatomical structure (Bolton and Petty, 1975; Ewers and Zimmermann, 1984; Parker and Pallardy, 1985; Calkin et al., 1986; Schulte and Gibson, 1988) and water saturation level of the wood (Comstock, 1965; Passioura, 1982; Boyer, 1985).

The mechanisms by which the resistance to the water flow through plants changes depending on xylem water saturation is basic to the understanding of plant water relations. There is increasing evidence that large variations in resistance to water flow in plants may be caused by emptying and refilling of xylem conduits. A reduction in relative water content in stem sapwood of *Pinus contorta* from 100 to 90 % caused permeability to fall to about 10 % of the saturated value (Edwards and Jarvis, 1982). The fall in permeability at low water content was assumed to be the result of cavitation of tracheids. A similar steep decline of hydraulic conductivity due to reduction in xylem water saturation has also been observed in *Abies grandis* (Puritch, 1971) and *Taxodium distichum* (Tesoro et al., 1974).

The effect of reduction in water content on permeability of the sapwood to water is important in modelling water transport through trees. The aim of this study was to investigate the dependence of xylem permeability on relative water content at different conductivities in Norway spruce.

Materials and Methods

Plant material

The investigations were carried out in September 1989 on primary branches of Norway spruce (*Picea abies* (L.) Karst.) trees at Vooremaa Ecology Station, East Estonia. A detailed description of climate, relief, soil and vegetation of the site has been published previously (Frey, 1977). Twelve branches cut in dry weather from trees of various age were allowed to dry for at least 24 hours. Segments of 20 to 30 mm in length were cut from each branch: two segments for conductivity measurements and two adjacent segments for determination of sapwood transverse area. Diameter inside the bark of the branch segments ranged from 3 to 17 mm. All segments were prepared for the experiment by removing the bark and recutting the faces of the specimens to remove torn and clogged tracheid ends.

Conductivity measurements

Hydraulic conductivity of xylem was measured by forcing water through specimens following the methods of Booker and Kininmonth (1978) and Zimmermann (1978). The measurements were made after saturation of the specimens under vacuum during 0, 3, 6, 15 min, and 1 and 6 h. The permeating fluid was a 10 mM solution of KCl in freshly distilled water, prepared immediately prior to measurements and deaerated under vacuum. The solution was supplied to specimens at a constant pressure by using a fluid column of definite height. The pressure difference between the sample faces, measured by a mercury manometer, was held at 6 kPa. After each saturation-permeation cycle the weight increment of the specimens was established gravimetrically. After the treatment, specimens were dried to constant weight at 102 °C. Relative water content of specimens was calculated according to the following equation:

$$\Theta = (W_f - W_d) * 100/(W_s - W_d), \qquad (1)$$

where Θ is relative water content (%),

W_f – actual weight of the specimen (g),
W_d – specimen dry weight (g),
W_s – specimen saturated weight (g).

Specimens saturated for 6 h were considered fully saturated.

Measuring xylem transverse area

Area of the conducting xylem was identified on double segments, saturated for 6 h, by perfusion with crystal violet (0.5 % w/v aqueous solution). Coloured specimens were photocopied and the total and sapwood transverse areas were determined from enlarged photographs with a graphics tablet (HIPAD DIGITIZER, Houston Instrument, USA) attached to a personal computer.

Calculation of relative conductivity

Relative conductivity of specimens at different saturation levels was calculated according to Darcy's equation (Comstock, 1967; Edwards and Jarvis, 1982), viz,

$$K = q * l * \eta/(\Delta P * A), \qquad (2)$$

where K is relative hydraulic conductivity (m^2),

q – volume flow rate ($m^3 s^{-1}$),
l – length of a specimen (m),
η – dynamic viscosity of the liquid ($N s m^{-2}$),
ΔP – pressure difference (Pa),
A – transverse area of the conducting xylem (m^2).

Results and Discussion

Relative conductivity (K) of the branchwood of Norway spruce ranged from 0.03×10^{-12} to 1.62×10^{-12} m^2 depending on water saturation level and segment origin. Our previous studies (Sellin, 1988) showed that K is largely influenced by the location of the segment in the branch and by the height of the branch in the crown. Relative conductivity of saturated specimens (K_{sat}) was between 0.17×10^{-12} and 1.62×10^{-12} m^2 in our material. The higher the relative conductivity at full saturation, the more permeable the xylem at any water content. Saturated conductivity is determined by xylem structure and depends on diameter and length of xylem elements, number, size and condition of bordered pits and other anatomical components (Petty, 1970; Petty and Puritch, 1970; Bolton and Petty, 1975; Ewers and Zimmermann, 1984; Gibson et al., 1984; Calkin et al., 1986; Sellin, 1990).

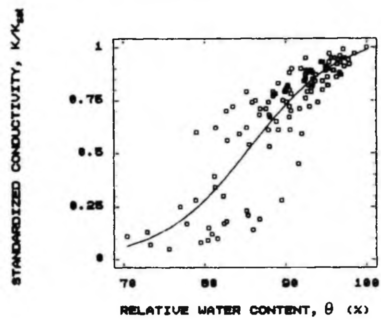

Fig. 1: Relationship between relative conductivity of xylem and relative water content. K/K_{sat} – actual relative conductivity standardized by saturated conductivity, Θ – relative water content of xylem (%). The equation of the regression line: $K/K_{sat} = 1.06/(1 + e^{15.4 - 0.180 * \Theta})$, $r^2 = 0.78$, $P < 0.001$.

The values of K at all water contents were standardized relative to the corresponding values at saturation in order to make the data of different specimens comparable. It became evident that K depends curvilinearly on xylem saturation level (Fig. 1). Non-linear regression analysis proved that the best approximation for the relationship is the logistic function:

$$K/K_{sat} = 1.06/(1 + e^{15.4 - 0.180 * \Theta}), \qquad (3)$$

where K is relative conductivity at a given water content (m^2), K_{sat} – relative conductivity at full saturation (m^2), and Θ – relative water content of the xylem (%). With a reduction of Θ from saturated state to 85 % the permeability of xylem decreased by a factor of about 2; with a reduction to 75 % the permeability fell by one order of magnitude. With further reduction in Θ the permeability approached zero. Thus, it must be concluded that water saturation level is one of the main determinants of xylem hydraulic conductivity.

Expressing K from equation (3) gives an empiric model relating actual values of K to K_{sat} and Θ:

$$K = 1.06 * K_{sat}/(1 + e^{15.4 - 0.180 * \Theta}). \qquad (4)$$

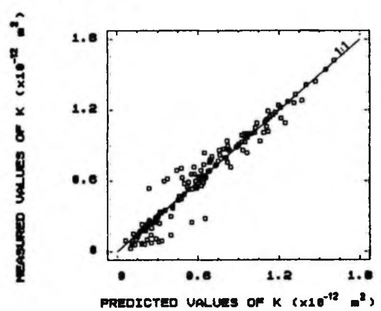

Fig. 2: Comparison of predicted and measured values of relative conductivity. $r^2 = 0.94$, $P < 0.001$.

There was good agreement ($r^2 = 0.94$, $P < 0.001$) between predicted and observed values of K (Fig. 2). The model describes 94 % of the total variation of relative conductivity in spruce branchwood. In Fig. 3 the model is presented in the form of a surface plot. The higher the K_{sat}, the steeper the decline in K in the case of reduction of Θ. The decline of hydraulic conductivity as well as the water transport capacity of xylem with a reduction in water content is expected to be caused by cavitation of tracheids, which reduces the number of flow paths. A steeper decline of permeability in the xylem specimens with higher K_{sat} and, consequently, having wider tracheids as well, could be explained by the fact that larger xylem conduits are more susceptible to water stress, because they tend to embolize at higher water potentials (Boyer, 1985; Lewis and Tyree, 1985). In saturated spruce xylem the bulk of water is transported by large earlywood cells (Sellin, 1990). Therefore, the cavitation of a few large tracheids is responsible for a considerable decline in permeability.

There are data in the literature (Puritch, 1971; Tesoro et al., 1974; Edwards and Jarvis, 1982) on an even sharper (exponential) decline of conductivity due to reduction in xylem water content. These results were obtained on stem xylem of different coniferous species using other methods. Legge (1985), however, has doubted that such a sharp drop in conductivity could be attributed merely to slight changes in xylem water content. The gravimetric method used to determine the water content in the present study did not permit separate measurement of the Θ of sapwood from that of the whole specimen. Besides wide sapwood cells being primarily responsible for axial waterflow, branch segments also contain heartwood not participating in water transport, and narrow tracheids of compression and latewood with very thick cell walls. Due to their anatomical peculiarities the absolute water content at full saturation is lower in these types of tissues. Therefore, the gravimetric method probably underestimated values for sapwood water content to some extent and influenced the shape of the permeability curve.

Thus, the results presented here suggest that water saturation level is one of the primary factors determining xylem hydraulic conductivity. Reduction in relative water content of xylem can cause a drastic decline in the water transport capacity of the vascular system, resulting in leaf water potential decrease.

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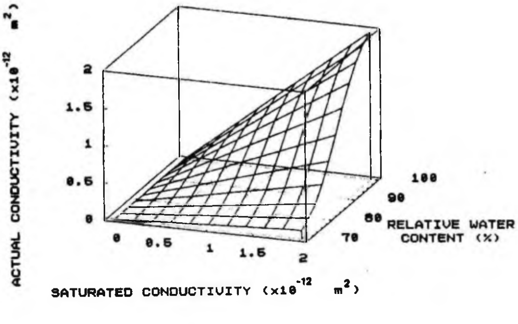

Fig. 3: Graphic model expressing dependence of actual values of relative conductivity (K) on saturated conductivity (K_{sat}) and xylem relative water content (Θ).

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VII. Scandinavian Journal of Forest Research, 1991, 6: 463-469

Scand. J. For. Res. 6: 463–469, 1991

Variation in Sapwood Thickness of *Picea abies* in Estonia Depending on the Tree Age

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Scandinavian Journal of Forest Research

Sellin, A. (Laboratory of Ecosystems, Tartu University, 202400 Tartu, Estonia, USSR). Variation in sapwood thickness of *Picea abies* in Estonia depending on the tree age. Accepted Jan. 5, 1991 Scand. J. For. Res. 6: 463–469, 1991.

Variation of sapwood thickness in terms of a linear measurement and a growth ring count with reference to the age was studied in dominant and suppressed Norway spruce trees. In the trees of both dominance classes the sapwood thickness increased in absolute terms, while its relative portion decreased with the age of the trees growing. Great differences were found in sapwood thickness between dominant and suppressed trees in linear measurements but not in the number of sapwood rings or the rate of the heartwood formation. The number of sapwood growth rings reached 40 in old trees. The index of vigour differed considerably in dominant and suppressed trees. *Key words: Norway spruce, sapwood thickness, heartwood formation, index of vigour, crown class.*

INTRODUCTION

Sapwood is a physiologically active zone of xylem, in which tracheids constitute a water transport system and parenchyma serves as a reserve tissue. Heartwood does not act in life processes, it has retained only its function as a mechanical support. Thus, the sapwood-heartwood relationship is of interest as an indicator of the physiological state of a tree. Sapwood increment should express the tree vigour. The index of tree vigour presented by Waring, Thies & Muscato (1980), is based on the measurements of the transverse area of the outermost annual ring and of the sapwood basal area. The sapwood-heartwood proportion is of more than barely an academic interest, as the two zones of wood differ substantially in their technological properties and appearance. Numerous practical applications, such as preservative treatment, pulping, and drying of wood, exist in case sapwood makes a more or less desirable portion of the stem.

The width of the sapwood band varies considerably among different conifers (Trendelenburg, 1939; Lassen & Okkonen, 1969; Rupert & Graham, 1974; Yang et al., 1985). The sapwood thickness is not only under genetic control but it is also affected by various environmental factors (Trendelenburg, 1939; Harris, 1953; Lassen & Okkonen, 1969; Hillis & Ditchburne, 1974). The transition from sapwood to heartwood is influenced by the tree vigour (Werberg, 1930; Wellwood & Jurazs, 1968; Münster-Swendsen, 1987), growth rate (Wellwood & Jurazs, 1968; Lassen & Okkonen, 1969), tree size (Trendelenburg, 1939; Smith et al., 1966; Hillis & Ditchburne, 1974) and age (Werberg, 1930; Yang et al., 1985; Münster-Swendsen, 1987). However, in some species the sapwood thickness has been found not to depend significantly on the tree age (Smith et al., 1966; Wellwood & Jurazs, 1968). The sapwood width varies also with respect to the aspect of the stem in conifers (Werberg, 1930; Yang et al., 1985). In the course of two last decades the environmental pollution has become a determinant of sapwood-heartwood relationship (Bauch, 1986; Frühwald, 1986; Rademacher et al., 1986).

The aim of this study was to establish the variation in the sapwood thickness at the stem base of Norway spruce with respect to the tree age. The sapwood width, sapwood-heartwood proportion and vigour index of the trees depending on the crown class have also been discussed.

MATERIALS AND METHODS

The measurements were carried out in June and July, 1989 on Norway spruce (*Picea abies* (L.) Karst.) trees growing under contrasting light conditions at Vooremaa Ecology Station, Estonia. A detailed description of the climate, relief, soil and vegetation of the study area has been published formerly (Frey, 1977). We sampled 65 (4- to 117-year-old dominant) trees well exposed to solar radiation and 60 (4- to 98-year-old suppressed) trees grown under dense forest canopy. Saplings were taken from the forest culture and from under the dense canopy of higher trees and the forest understory. For simplicity we name all of them dominant and suppressed trees, respectively. The trees were chosen on a principle that the full range of ages from uneven-aged stands in *Hepatica* and *Oxalis* forest site types, situated on rich brown pseudopodzolic soil be covered. The trees were sampled at the stem base: the saplings were cut off and cross-sectional disks were cut from the stems above the root collar, in older trees 4 increment cores were extracted at the breast height (1.3 m above the ground) along stem radii at 90° angles. The sapwood-heartwood border both on fresh increment cores and stem disks was identified by using differential translucence method, doubled by aniline pencil method (Münster-Swendsen, 1987) when needed.

The sapwood thickness was estimated in two ways: by a linear measurement and by counting the number of sapwood growth rings. The widths of heart- (w) and sapwood (W) were measured by a ruler, the width of annual ring of the previous year (r) and the number of growth rings, under a light microscope. The number of growth rings at the stem base was taken as the tree age. All measurements were made along the radii for 4 aspects of the stems, excluding the current annual ring as the growth had not been completed by that time. Approximating the stem transverse section to an ellipse, the transverse area of sapwood (g_s) was calculated for each tree as follows:

$$g_s = (\pi/4)[(R_n + R_s)\,(R_w + R_e) - (w_n + w_s)\,(w_w + w_e)]$$

where R_n, R_s, R_w, R_e are the north, south, west and east radii of the stem, and w_n, w_s, w_w, w_e are the respective widths of the heartwood band. The area of the last growth ring (g_l) was calculated as

$$g_l = (\pi/4)[(R_n + R_s)\,(R_w + R_e) - (R_n + R_s - r_n - r_s)\,(R_w + R_e - r_w - r_e)]$$

where r_n, r_s, r_w and r_e are the widths of the last growth ring at the respective aspects. The index of vigour (IOV) is expressed as

$$\mathrm{IOV} = g_l/g_s.$$

For data processing simple and nonlinear regression procedures based on the least squares method were used.

RESULTS

Sapwood thickness

The sapwood band at the stem base of Norway spruce thickened with the growing age, attaining obviously constant values from a definite age (Fig. 1). Actually, by single trees there are probably differences from this pattern. In dominant trees of the age over 40 years the sapwood width ranged 4–13 cm, in suppressed trees, 0.4–4.5 cm. The mean width of the

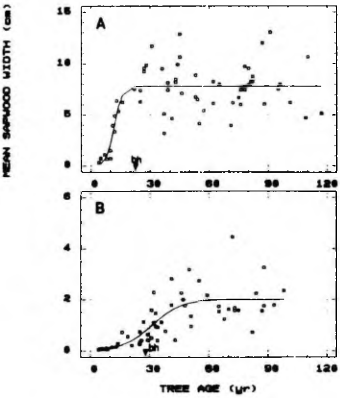

Fig. 1. Mean sapwood thickness (y) expressed by linear measurement versus tree age (x). A—dominant trees, regression equation: $y = 7.82/(1 + e^{5.98-0.505*x})$; determination coefficient, $R^2 = 0.63$; probability level, $p < 0.001$; standard error of estimate, S.E.E. = 2.00. B—suppressed trees, regression equation: $y = 2.02/(1 + e^{4.13-0.132*x})$; $R^2 = 0.60$; $p < 0.001$; S.E.E. = 0.63. The arrow indicates the age from which the trees were sampled at the breast height (bh).

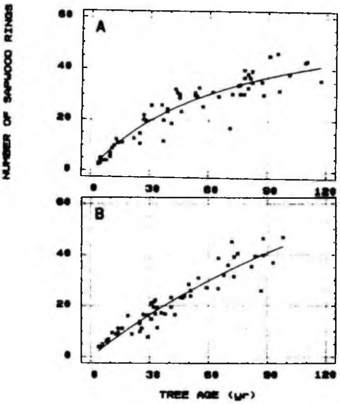

Fig. 2. Mean sapwood thickness (y) expressed by the number of growth rings versus tree age (x). A—dominant trees, regression equation: $y = 65.7*x/(x + 70.1)$; $R^2 = 0.89$; $p < 0.001$; S.E.E. = 4.3. B—suppressed trees, regression equation: $y = 159*x/(x + 260)$; $R^2 = 0.90$; $p < 0.001$; S.E.E. = 4.0.

sapwood growth rings was 2.84 ± 0.15 (S.E.) and 0.49 ± 0.04 mm, respectively. In the saplings the sapwood band did not thicken equivalently to the addition of new annual rings as it might be expected. One or two innermost growth rings were transformed into heartwood already 3–6 years after their formation. The number of annual rings covered by sapwood was almost the same in dominant and suppressed trees (Fig. 2). In old trees the number of sapwood rings reached 40 or even more.

A borderline between sap and heartwood turned out to be of an irregular shape and differences were observed in sapwood thickness at different aspects of the stems. Dominant trees had the thickest sapwood layer in the northern side, exceeding on an average 14% that of the southern ($p < 0.01$) and western sides ($p < 0.01$) and 9% that of the eastern side (not significant). The mean number of sapwood rings was also the highest in the northern side and the lowest in the eastern side. In suppressed trees there were no statistically significant differences in this respect at the level of probability 0.05.

Relative sapwood portion

The characteristics expressing the relative sapwood portion indicate also a sapwood-heartwood relationship, except in seedlings in which pith constitutes a remarkable part of the stem. For this reason, the relative thickness of sapwood expressed as a percentage of the diameter inside bark (d.i.b), was less than 100% in seedlings. In older trees the portion of pith was negligible. The relative sapwood width steadily decreased with the tree age, while the decline was more rapid in suppressed trees (Fig. 3). In this respect the differences were found to be especially great in young trees. For example, in 30-year-old dominant trees

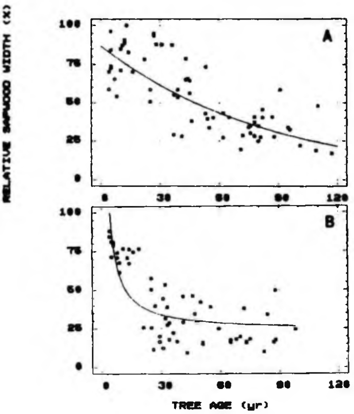

Fig. 3. Relative sapwood thickness (y) expressed as a percentage of the diameter inside bark versus tree age (x). A—dominant trees, regression equation: $y = e^{-0.0116^{*}x + 4.47}$; $R^2 = 0.62$; $p < 0.001$; S.E.E. = 14.8. B—suppressed trees, regression equation: $y = (x + 13.6)/(0.0426^{*}x)$; $R^2 = 0.62$; $p < 0.001$; S.E.E. = 15.0.

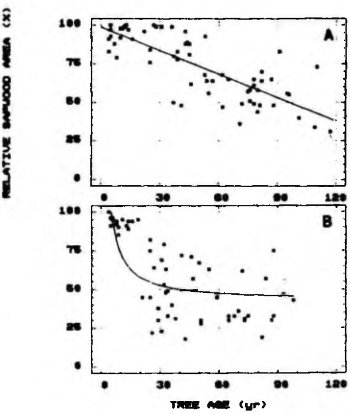

Fig. 4. Relative sapwood area (y) expressed as a percentage of the total wood cross-sectional area versus tree age (x). A—dominant trees, regression equation: $y = -0.509^{*}x + 99.0$; $R^2 = 0.63$; $p < 0.001$; S.E.E. = 12.6. B—suppressed trees, regression equation: $y = (x + 7.32)/(0.0236^{*}x)$; $R^2 = 0.50$; $p < 0.001$; S.E.E. = 18.6.

sapwood covered on an average 62% of d.i.b., in suppressed trees, only 34%. In the relative number of sapwood rings no such difference was observed.

The relative sapwood area expressed as a percentage of the total transverse area of the wood, decreased linearly with the age in dominant trees (Fig. 4). Suppressed trees exhibited another variation pattern: the relative sapwood area reduced rapidly in young trees and remained almost steady when the tree age exceeded 40 years. The steady level corresponds on an average to 45–50% of the total transverse area of the wood. In adult dominant trees the relative sapwood area was considerably larger, ranging from 48–79%, depending on the tree age.

As the tree age is strongly correlated with the d.i.b. within the crown classes (R_2 was 0.91 for dominant and 0.93 for suppressed trees), a close relationship was found to exist also between d.i.b. and all the observed characteristics expressing the sapwood thickness.

Index of vigour

The index of vigour showed a strong dependence on the tree age, R^2 was 0.90 for dominant and 0.72 for suppressed trees. In the trees of both crown classes IOV reduced curvilinearly, especially sharply in saplings, with the increase of the tree age. After the 20th year the reduction of IOV decelerated, attaining almost constant values as the tree reached 40 years of age. Excluding the trees younger than 40 years old, the mean value of IOV was 0.038 ± 0.002 (S. E.) for the dominant and 0.023 ± 0.003 for the suppressed class.

DISCUSSION

The sapwood thickness at the stem base of Norway spruce increased curvilinearly with the tree age depending on the ratio between the wood radial increment and the heartwood formation rate. At a certain age of the tree the rates of these two processes equalize and the sapwood width becomes more or less constant. In adult dominant trees the mean sapwood thickness was 7.8 ± 0.37 (S. E.) cm, by other authors, 5.2–6.8 cm (Trendelenburg, 1939; Frühwald, 1986; Schmidt-Vogt, 1986). Norway spruce, as compared to other conifers (Trendelenburg, 1939; Wellwood & Jurazs, 1968; Lassen & Okkonen, 1969; Ruppert & Graham, 1974; Yang et al., 1985), belongs to the species having a sapwood band of intermediate thickness. The differences between the species exist also concerning the number of sapwood rings.

In old trees of both crown classes the mean number of sapwood rings at the stem base reached 40 at Vooremaa, Estonia. A similar range of sapwood rings has been reported for spruce trees growing in Schwarzwald, Germany (Trendelenburg, 1939). According to Münster-Swendsen (1987), in North Zealand, Denmark, sapwood covered about 20 annual rings at the tree age of 40 years and it seemed to remain at this level as the tree grew older. He expected the heartwood formation to begin when the tree is about 18–20 years old. The discrepancy between our data and those of Münster-Swendsen (1987) can be explained by the differences in age range of sampled trees and/or in the rate of heartwood formation due to environmental peculiarities on the sites.

Nevertheless, the processes resulting in heartwood formation in conifers (pit aspiration, pit membrane incrustation, etc.) start immediately after the wood maturation (Harris, 1953; Mark & Crews, 1973). Our measurements suggest that in Norway spruce they will have been completed by the time the wood reaches the age of 40 years, which agrees with Zimmermann & Brown (1971). But here it must be noted that heartwood may be formed earlier as well. Perfusion of dye solutions through xylem segments of Norway spruce (Sellin, 1988) have revealed that the innermost growth ring often loses water permeability already in the 3rd to 6th year after formation. An early formation of heartwood has also been observed in *Pseudotsuga menziesii* (Smith et al., 1966) and *Picea rubens* (Kyker-Snowman & Wilson, 1988). In the rate of heartwood formation, there may be also differences in different regions within the area of distribution. The number of sapwood rings increases with moving from south to north (Trendelenburg, 1939).

The sapwood thickness of middle-aged and old dominant spruce trees was on an average 4 times that of suppressed trees. This observation could easily be explained by a very little radial increment of suppressed trees as the result of the low rates of photosynthesis and net assimilation under a dense canopy. As to the rate of heartwood formation expressed on the basis of the number of growth rings, dominant and suppressed trees did not differ. These results indicate that, regardless of the crown class, the tree age is an important determinant of the number of growth rings in the sapwood zone. Sapwood thickness of dominant trees varied by the aspects of stem, while the thickest band was revealed at the northern aspect. In suppressed trees no statistically significant differences in sapwood thickness between aspects were observed. For these trees their location with respect to higher trees and the distance from them are certainly more substantial factors than the direct solar radiation, dominant winds and other ecological factors connected with definite compass points.

The relative sapwood thickness in spruce trees decreased with the increasing age of the tree, reaching on an average 25% of d.i.b. at the age of 100 years. The age-related decline in relative sapwood thickness was considerably faster in suppressed than in dominant trees. This difference between dominant and suppressed trees could not be caused by the rate of heartwood formation, but rather by differences in the width of the inner and outer annual rings. Little difference was revealed in the widths of sap- and heartwood growth rings in 20- to 50-year-old dominant trees, while in suppressed trees of the same age the width of heartwood rings exceeded 2.5 times that of sapwood.

The relative sapwood area decreased from nearly 100% in seedlings to 48% in dominant trees at the age of 100 years. A similar portion of sapwood was observed at the stem base of healthy spruce trees in Germany (Trendelenburg, 1939). The damaged trees grown in polluted regions had remarkably smaller sapwood portion (Bauch, 1986; Rademacher et al., 1986). The water transport system of spruce trees in Vooremaa region seems to be unaffected by air pollution.

The fact that dominant trees had relatively much more sapwood than the suppressed ones is not surprising. The trees well exposed to solar radiation and open to winds have a high transpiration rate. One can guess that the correspondingly higher need for water of the trees would be satisfied in the case when the conducting system has a relatively larger cross-sectional area and the water storage, greater capacitance. Thus, the relative sapwood area (with a correction for the tree age) could serve as an indicator of the tree condition. The larger the sapwood portion is, the greater is the tree's water storage and the more stable the water transport system. Waring & Running (1978) have observed a considerable decrease in permeability in the stems of *Pseudotsuga menziesii* during summer, owing to a decrease in the relative water content in sapwood. One of the reasons for dying of suppressed trees during drought periods or after abrupt changes of radiation regime due to cutting may be the inability of the water transport system to provide an adequate water supply for the needles. Naturally, this hypothesis needs an experimental proof.

The vigour index decreased asymptotically with the tree age, remaining nearly constant at the age of 40 years. As a close correlation has been found to exist between the transverse sapwood area and the amount of leaves supported by the sapwood in many tree species (Kaufmann & Troendle, 1981; Waring et al., 1982), IOV expresses also the relative efficiency of the stemwood production. The mean IOV was 0.038 for dominant trees in Vooremaa region. This is less than 0.05, the value of IOV measured by Münster-Swendsen (1987) for spruce stands in North Zealand, Denmark. In the present case, IOV was lower due to a larger sapwood basal area, but not on account of the last annual increment width.

The vigour of the trees growing in a stand is to a large extent correlated with their position in the stand, i.e. with the crown class. The values of IOV for dominant trees exceeded the mean value of that for suppressed trees by almost 1.7 times. The reduced substrate availability, primarily the availability of PhAR in the present case, decreases the vigour of trees, consequently also their resistance to unfavourable ecological factors.

Our results suggest that the sapwood thickness of Norway spruce trees increases depending on the crown class with the increasing age of the tree. One can use the characteristic of species-specific thickness of sapwood only within the definite age and crown classes of trees.

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VIII. Trees, 1993, 7(4): 220-226

Trees (1993) 7: 220–226

Structure and Function
Trees

Resistance to water flow in xylem of *Picea abies* (L.) Karst. trees grown under contrasting light conditions

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Received April 30, 1991/December 21, 1992

Summary. The relative hydraulic conductivity (k) of xylem and resistance (R) to water flow through trunk, primary roots and branches in *Picea abies* trees growing under contrasting light conditions were investigated. The xylem permeability to water was measured by forcing 10 m*M* water solution of KCl through excised wood specimens. From the values of k, the sapwood transverse area and the length of conducting segments, R of the whole trunk, branches and roots was calculated. The relative conductivity of xylem in open-grown trees exceeded that of shade-grown trees by 1.4–3.1 times, while k was closely correlated with the hydraulically effective radius (r_e) of the largest tracheids (r^2 was 0.85–0.94 for open- and 0.51–0.79 for shade-grown trees). Because of both a low k and a smaller sapwood area in shade-grown trees the resistance to water movement through their trunk, roots and branches was many times higher. The distribution of R between single segments of the water-conducting pathway differed considerably in trees from different sites. At high water status the largest share of the total resistance in open- as well as shade-grown trees resides in the apical part of the trunk. The contribution of the branches to total xylem resistance is supposed to increase with developing water deficit.

Key words: *Picea abies* – Xylem – Relative hydraulic conductivity – Resistance to water flow – Tracheid radius

Introduction

Water flow in a soil-plant-atmosphere continuum is governed by two fundamental factors: the driving forces and the resistance of the flow path. Water has to move along several links of the transport path, all of which exert resistance to the flow: filtration resistance in soil, resistance of epithelial tissues, bark and endodermis to water entrance to roots, frictional resistance of xylem elements, influence of gravitational field, stomatal resistance, boundary layer resistance etc. In the present study, attention is focused on the resistance of sapwood, by which water and nutrients are transported from roots to leaves. In conifers, unlike other groups of vascular plants, the xylem makes a considerable contribution to the total resistance to water flow (Hellkvist et al. 1974; Jarvis 1975; Tyree et al. 1975; Tyree 1988; Tyree and Sperry 1989). This observation could be explained by morpho-anatomical peculiarities of coniferous trees: water is transported long distances (dozens of metres), and only tracheids participate in axial water flow.

The resistance of the water-conducting pathway is determined by its length, configuration, transverse area and permeability. The water-conducting efficiency of the sapwood depends primarily on the inner properties of the plant, the most important of which are the xylem water status (Edwards and Jarvis 1982; Jones 1989; Pothier et al. 1989a; Tyree and Sperry 1989; Sellin 1991) and the anatomical structure of the wood (Bolton and Petty 1975; Legge 1985; Calkin et al. 1986; Schulte and Gibson 1988; Pothier et al. 1989a). Wood is formed in the process of xylogenesis under simultaneous action of a multitude of environmental factors. Thus, all climatic, edaphic, meterological and biotic factors, on which the course of xylogenesis depends, can affect indirectly the hydraulic resistance of xylem.

The present investigation involves measurements of xylem permeability in order to estimate resistances to water flow through the trunk, primary roots and branches in Norway spruce trees growing under contrasting conditions of light competition. The xylem resistances presented in this paper were calculated for steady-state conditions, assuming water movement directly through the conducting tissue without significant exchange between conduits and storage. This holds true at high water status, when differences in water potential between conducting and storage tissue are negligible. The dependence of the relative conductivity of xylem on the tracheid diameter is also discussed.

Table 1. Characterization of the sample trees

Tree no.	Tree age (years)	Tree height (m)	Number of primary branches	Number of primary roots	Site
1	40	14.84	183	14	Field
2	50	4.29	38	7	Under dense canopy

Materials and methods

Plant material. The measurements were carried out on Norway spruce [*Picea abies* (L.) Karst.] trees at Vooremaa Ecology Station, Estonia, during the summer months of 1986 and 1988. A detailed description of the climate, relief, soil and vegetation of the site has been published earlier (Frey 1977). Two 40- to 50-year-old sample trees (Table 1) growing under contrasting light conditions served as the main study material. The trunk, two to three model roots and three model branches (one branch from the lower, middle and upper third of the crown) taken from each tree were divided into ten sections. From each section one xylem segment was cut for permeability measurements. Additionally, xylem segments were taken from trunks, roots and branches of several younger trees in order to establish the relationship between the relative conductivity and tracheid diameter.

Permeability measurements. Xylem permeability to water was measured on freshly cut trunk, root and branch specimens of 20–30 mm length by the methods of Booker and Kininmonth (1978) and Zimmermann (1978). Disks of 25–30 mm width were cut from thick parts of trunks and roots, from which sapwood cylinders of 15 mm diameter were extracted with a plug cutter attached to a drilling machine. The specimen preparation included a recutting of the faces to remove the torn and clogged tracheid ends, and their saturation with water under vacuum. The permeating fluid was 10 m*M* water solution of KCl deaerated under vacuum immediately prior to the measurements. The pressure difference between the specimen faces was 0.5×10^4–1.5×10^4 Pa.

The relative conductivity of specimens was calculated according to Darcy's law (Nobel 1991):

$$k = q * l * \eta/(\Delta P * A) \tag{1}$$

where k is the relative conductivity (m^2), q the volume flow rate ($m^3 s^{-1}$), l the length of the specimen (m), η the dynamic viscosity of the liquid ($N\ s\ m^{-2}$), ΔP the pressure difference (Pa), and A the transverse area of the conducting xylem (m^2).

Xylem transverse area. Immediately after making the permeability measurements crystal violet or methylene blue (0.5% w/v aqueous solution) was forced through each specimen to demarcate the area of the conducting xylem, i. e. sapwood. In the stem and root disks the sapwood – heartwood border was identified by using a differential translucence method (Waring et al. 1982). In case of need it was checked by a differential absorption method by immersing disks for a moment in a weak water solution of the dyes mentioned above. The conducting portion of xylem could be distinguished by its more intensive colour. Both the specimens and the disks were photocopied and their conducting and total transverse areas were determined from enlarged photographs with a graphics tablet (Hipad Digitizer, Houston Instrument, USA) attached to a personal computer.

The mean k of a disk was calculated as a weighed average:

$$k = \sum_{i=1}^{n} (k_i * A_i) / \sum_{i=1}^{n} A_i \tag{2}$$

where k_i is the relative conductivity and A_i the conducting area of the ith xylem cylinder cut from the disk.

Trunk, root and branch resistance. The resistance R ($Pa\ s\ m^{-3}$) to the water flow through xylem is defined by the following ratio (Jarvis 1975; Fitter and Hay 1987):

$$R = \Delta\Psi/q \tag{3}$$

where $\Delta\Psi$ is a water potential difference (Pa). In permeation experiments $\Delta\Psi$ can be replaced with the applied pressure difference ΔP:

$$R = \Delta P/q \tag{4}$$

Substituting q from Eq. 1 into Eq. 4 gives

$$R = l * \eta/(A * k) \tag{5}$$

It was assumed that the values of A and k measured on a sample segment are characteristic of the whole corresponding section. All resistances were calculated for the permeating fluid temperature of +20°C ($\eta = 10^{-3}\ N\ s\ m^{-2}$). R of single roots, branches and trunks was calculated by adding the resistances of ten sections taken from each plant part in series:

$$R = \sum_{i=1}^{10} R_i \tag{6}$$

where R_i is the resistance of the ith xylem section. The trunk resistance was estimated in four parts: from ground level to the base of the live crown, and the lower, middle and upper third of the crown zone. The total resistance (R_t) of the branch and root system can be calculated by adding reciprocals of the resistances linked in parallel way (Fitter and Hay 1987):

$$R_t = \frac{1}{\sum_{i=1}^{n} \frac{1}{R_i}} \tag{7}$$

where R_i is the resistance of the ith branch or root. We proceeded from mean resistances per sample segment:

$$R_t = \frac{\sum_{i=1}^{n} R_i}{n \cdot m} \tag{8}$$

where n is a number of sample branches or roots, and m the total number of branches or roots.

Tracheid radii. Minor and major inner diameters of the largest tracheids in at least 30 segments of root, stem and branch wood from both sites were measured with an ocular micrometer. For each specimen lumina of the ten largest tracheids of ten outer growth rings were measured. The mean hydraulically effective radius of tracheids (r_e) was computed by using several approximations applied for xylem conduits of diverse species (Ewers and Zimmermann 1984a; Legge 1985; Parker and Pallardy 1985; Buchmüller 1986; Calkin et al. 1986). The calculations were made on the basis of the tracheid diameters measured in (1) the outermost growth ring, (2) the growth ring with the largest tracheids, (3) the three outer growth rings, and (4) in all the observed (up to ten) growth rings. The mean radius of the largest tracheids was treated as an estimation of the maximal radius of water conduits.

To establish the relationship between k and r_e a stepwise regression analysis was applied using a polynomial of the fourth power.

Results

Effect of growth conditions on xylem resistance

The k of xylem showed significant differences between middle-aged trees grown under contrasting light conditions (Tables 2, 3). A comparison of the middle sections of primary roots, branches and trunks revealed that in an open-

Table 2. Hydraulic properties of xylem in trunk and primary roots of middle-aged trees grown under contrasting light conditions: tree number 1 – an open-grown tree; tree number 2 – a suppressed tree grown under a dense canopy layer

Trunk

Tree no.	Trunk length (m)	Relative conductivity (× 10^{-12}), m^2			Resistance (× 10^{14}) Pa s m^{-3}
		Trunk base[a]	Trunk middle part[b] (mean ± SE)	Trunk top[a]	
1	14.84	1.75	3.21 ± 0.08	0.74	0.4
2	4.29	1.33	1.02 ± 0.15	0.02	119.4

Primary roots

Tree no.	Root length (m)	Relative conductivity (× 10^{-12}), m^2			Resistance (× 10^{14}) Pa s m^{-3}
		Root base[a]	Root middle part[b] (mean ± SE)	Root tip[a]	
1	5.43	1.43	11.07 ± 1.06	2.24	0.9
	5.70	0.76	11.16 ± 0.36	2.04	2.6
2	2.40	0.66	6.71 ± 0.32	0.12	14.0
	2.81	0.24	6.75 ± 1.03	1.42	6.9
	3.23	0.89	9.65 ± 0.61	1.35	3.6

[a] Values based on measurements of one xylem segment
[b] Mean values based on measurements of four xylem segments

grown tree *k* of root wood was approximately 1.4, of branch wood, 1.8 and of stem wood, 3.1 times higher than that in a tree from under dense canopy. In the proximal and distal sections of the organs, differences in *k* between the two sites were even greater.

In a shade-grown tree the *R* of single roots exceeded roughly by 5 times, of branches, by 1 order of magnitude and of the trunk, by 3 orders of magnitude the respective values of *R* for an open-grown tree (Tables 2, 3). The trunk resistance of the open-grown tree from ground level to the base of the live crown was 0.3×10^{11} and from the crown base to the upper third of the crown, 2.1×10^{11} Pa s m^{-3}, both parts making up only a small fraction of the trunk's R_t (Fig. 1). The corresponding values for the shade-grown tree were 29.6×10^{11} and 48.4×10^{11} Pa s m^{-3}, respectively. In addition to the absolute values, also the relative distribution of resistances between the segments of the water transport system varied in trees under different light conditions. Thus, *R* of a trunk, of a primary branch and of a root were in the proportions 1 : 18 : 5 in the open- and 1 : 0.57 : 0.07 in the shade-grown tree.

The estimation of the resistance of the whole tree in this way is complicated, since a huge number of segments of lower orders are linked with primary branches and roots. Approximate estimations suggest that the largest part of the R_t under saturated conditions both in open- and shade-grown trees is associated with the trunk. The summed resistance (i.e. primary roots, branches and trunk all together) was 0.5×10^{14} for the open- and 122.4×10^{14} Pa s m^{-3} for the shade-grown tree.

Relationship between k and tracheid radius

In transverse section, the tracheid lumina are intermediate in shape between a polygon and an ellipse. The most suit-

Table 3. Hydraulic properties of xylem in the primary branches of middle-aged trees grown under contrasting light conditions: tree number 1 – an open-grown tree; tree number 2 – a suppressed tree grown under a dense canopy layer

Tree no.	Branch length (m)	Height above the ground (m)	Relative conductivity (× 10^{-12}), m^2			Resistance (× 10^{14}) Pa s m^{-3}
			Branch base[a]	Branch middle part[b] (mean ± SE)	Branch top[a]	
1	3.45	2.38	0.64	1.22 ± 0.03	0.20	10.3
	2.78	6.70	0.49	1.79 ± 0.14	0.18	2.7
	1.25	12.19	0.43	0.86 ± 0.08	0.13	5.9
2	1.52	2.28	0.19	0.63 ± 0.11	0.05	77.2
	1.26	2.83	0.18	0.85 ± 0.11	0.04	64.3
	0.63	3.80	0.13	0.64 ± 0.12	0.03	63.6

[a] Values based on measurements of one xylem segment
[b] Mean values based on measurements of four xylem segments

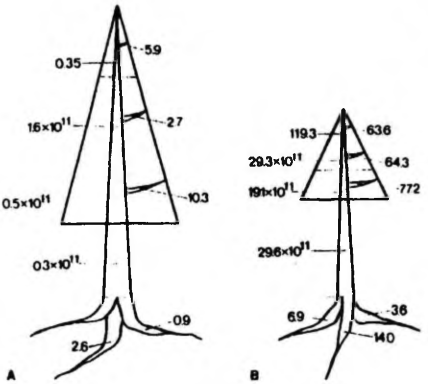

Fig. 1 A, B. Distribution of xylem resistances (Pa s m^{-3}) in an open- (**A**) and shade-grown spruce tree (**B**). The numbers in the diagram have to be multiplied by the factor 10^{14} if not indicated otherwise

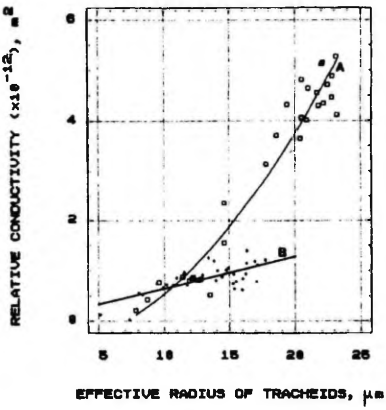

Fig. 2. Relative conductivity (k) of xylem as a function of the hydraulically effective radius (r_e) of the largest tracheids in *P. abies* stemwood. (*A*) Open-grown trees; the regression equation: $k = 1.07 \times 10^{-14} r_e^2 - 5.32 \times 10^{-13}$, $r^2 = 0.94$, $P < 0.001$; (*B*) Shade-grown trees; the regression equation: $k = 6.28 \times 10^{-14} r_e + 9.78 \times 10^{-15}$, $r^2 = 0.51$, $P < 0.001$

able approximation of the hydraulically effective radius (r_e) of tracheids for spruce turned out to be the following expression:

$$r_e = 2 * r_s * r_l/(r_s + r_l) \qquad (9)$$

where r_s is the minor and r_l the major radius of the lumen. A regression analysis revealed a close relationship between k and r_e (Figs. 2–4). The mean r_e of the largest tracheids explained 85–94% of the total variation of k in open- and 51–79% in shade-grown trees. Therefore, one must conclude that k of xylem in a water-saturated state depends to a significant extent on the diameter of the largest xylem conduits.

The best correlation between k and r_e for stem and root wood was found for the case when the estimation of r_e was based on tracheid diameters measured in three outer growth rings, while for branch wood, the best estimate was based only on the outermost ring. For trees grown under favourable light conditions the relationship between k and r_e in root and branch wood was approximated by a cubic parabola, and in stem wood, by a quadratic parabola. In the shade-grown trees the range of the diameters and relative conductivities measured was less, dispersal of the data was relatively high and, therefore, the correlation was weaker. The dependence of k on r_e in the shade-grown trees for root, branch and stem wood was approximated by a linear function.

A comparison of the regression lines indicates that k of both root and branch wood (Figs. 3, 4) in the trees from different sites increased at a similar rate with increasing r_e. However, for stem wood (Fig. 2), there was a remarkable difference between trees growing under contrasting light conditions. In the open-grown trees, the increment of k per unit increment of r_e was several times greater than that for

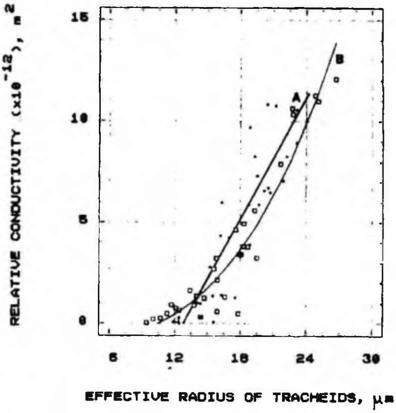

Fig. 3. Relative conductivity (k) of xylem as a function of the hydraulically effective radius (r_e) of the largest tracheids in *P. abies* rootwood. (*A*) Open-grown trees; the regression equation: $k = 7.77 \times 10^{-16} r_e^3 - 8.87 \times 10^{-13}$, $r^2 = 0.91$, $P < 0.001$; (*B*) Shade-grown trees; the regression equation: $k = 9.91 \times 10^{-13} r_e - 1.27 \times 10^{-11}$, $r^2 = 0.77$, $P < 0.001$

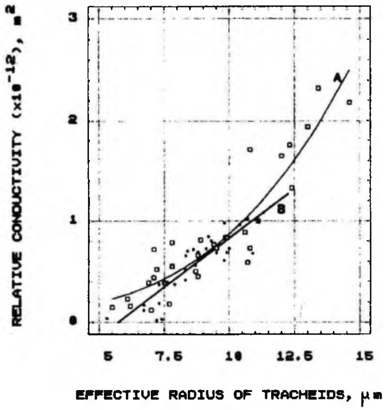

Fig. 4. Relative conductivity (k) of xylem as a function of the hydraulically effective radius (r_e) of the largest tracheids in *P. abies* branchwood. (*A*) Open-grown trees; the regression equation: $k = 7.72 \times 10^{-16} r_e^3 + 1.01 \times 10^{-13}$, $r^2 = 0.85$, $P < 0.001$; (*B*) Shade-grown trees; the regression equation: $k = 1.94 \times 10^{-13} r_e - 1.10 \times 10^{-12}$, $r^2 = 0.79$, $P < 0.001$

shade-grown trees. Presumably, in addition to tracheid diameter, the stem wood of trees differs significantly in other structural variables which influence its hydraulic properties.

Discussion

The aim of this study was to expand our understanding of the internal resistances to water flow through trees. The flow rate of liquid volume through ideal capillaries, as defined by Poiseuille's law, is proportional to the fourth power of the capillary radius (Zimmermann 1983; Nobel 1991). Therefore, from a theoretical standpoint, the flow rate through the xylem should primarily be a function of the tracheid radius. The relative conductivity of xylem in an open-grown spruce tree exceeded that of a shade-grown tree by 1.4–3.1 times. Since k was closely correlated with r_e of the largest tracheids, high R of suppressed trees may be attributed to narrower tracheids. On the other hand, some reports suggest that the lumen is not the main constituent of resistance to fluid flow through a tracheid (Petty 1970; Bolton and Petty 1975; Calkin et al. 1986). Model simulations indicated that only 21.4% of R in tracheids of *Podocarpus nagi* is attributable to lumina (Schulte and Gibson 1988). Petty and Puritch (1970) have shown that 39% of resistance to the flow through tracheids in *Abies grandis* was accounted for by resistance in the lumen, the rest being sited in the margo of the bordered pits. Nevertheless, it was suggested that in the first-formed earlywood, with its relatively large number of large bordered pits, the lumina may cause more than half of R_t.

The strong correlation between k and mean r_e of only the largest tracheids measured in one or three outermost growth rings can be explained as follows. Firstly, a few outer growth rings seem to play a dominant role in the long-distance water transport in Norway spruce (Sellin 1990). Though the permeability of coniferous wood is preserved for many years, the contribution of the inner sapwood to total water transport is considerably less than that of outer annual rings. This is in agreement with heat-pulse velocity measurements (Mark and Crews 1973; Ikeda and Suzaki 1987) demonstrating xylem permeability to increase in the direction of the cambium, except in close proximity to the cambial zone. There are some data (Lassoie et al. 1977) that seem to refute our position. We are of the opinion that heat-pulse velocity cannot be always considered an adequate indicator of xylem conductivity. Under increasing water stress inner sapwood rings contain a greater percentage of cavitated tracheids and aspirated bordered pits, causing faster flow in the remaining functional latewood conduits of small diameter. Moreover, reduction in k with increasing distance from the cambium has been measured in several other conifers (Puritch 1971; Markstrom and Hann 1972; Booker 1984). Reduction of permeability with age in inner growth rings is caused by xylem embolism, aspiration and plugging of pits by extractives (Krahmer and Côte 1963; Mark and Crews 1973; Jones and Peña 1986; Ikeda et al. 1988). Secondly, if there is sufficient water supply (i.e. a saturated xylem), the bulk of the water is probably transported through large-diameter earlywood tracheids. Thirdly, the diameter of xylem elements has been found to be correlated with several other anatomical characteristics of wood (Buchmüller 1986; Calkin et al. 1986; Jinxing 1989; Ewers et al. 1990).

The relationship between k and r_e observed in this study is of a correlative rather than a causative nature, as it is not strictly consistent with Poiseuille's equation. However, the close correlation no doubt indicates a structural-functional basis of the relationship. Regardless of the anatomical complexity of wood structure, tracheid diameter is an important determinant of the hydraulic conductivity of xylem. In empirical studies of xylem permeability, it is preferable to characterize the hydraulic properties of the wood by a maximal radius (i.e. the radius of the largest conduits) as compared to an overall mean radius of xylem elements. In most cases the lumen radius decreases smoothly from a maximum in the first-formed earlywood tracheids to a minimum in latewood cells. Considering the fact that small changes in tracheid diameter are accompanied by substantial changes in conductivity, the maximal tracheid radius is a more meaningful characteristic of wood structure with respect to permeability than the mean radius.

Because of both low k and less sapwood area in shade-grown trees the resistance to water movement through their trunk, roots and branches is many times higher than in open-grown trees. The distribution of resistances (Fig. 1; Tables 2, 3) between single segments of the water transport system indicates that the contribution of the trunk to the overall resistance in shade-grown trees is considerably greater than that in open-grown trees. In middle-aged *Pinus banksiana* trees the trunk resistance was found to increase with decreasing site index. The xylem resistances on the best and poorest sites differed by 2 orders of magnitude (Pothier et al. 1989b), a difference similar to that between open- and shade-grown Norway spruce trees in this study. Sapwood resistance of the trunk in spruce from ground level to the upper third of the crown coincides with the values reported for *P. banksiana* trees of corresponding age and vigour (Pothier et al. 1989b). The summed resistance of an open-grown Norway spruce tree was 5×10^{13} Pa s m^{-3}, a value comparable with those published for *Picea sitchensis* – 1×10^{13} (Hellkvist et al. 1974) and *Malus domestica* – 10×10^{13} Pa s m^{-3} (Landsberg et al. 1976).

The present data and the data reported earlier on the hydraulic architecture of Norway spruce (Sellin 1988) led us to the following conclusion: the major part of the xylem resistance resides in the trunk (in its apical part), but not in primary branches. This position agrees with the findings reported for *Pinus sylvestris* (Roberts 1977). It is true that Roberts (1977) found most of the tree's resistance to reside in the root system. However, his "root resistance" includes the axial resistance of xylem conduits, as well as the radial resistance to the water entrance into the xylem, which is the major component of the plant's R_t (Passioura 1982). Roberts' data show that stem resistance exceeds that of the branches.

Similar dimensions and sapwood hydraulic resistances indicate that a top of the trunk and a primary branch may be considered functional analogues concerning long-distance water transport in spruce trees. Low resistance to water flow in the trunk, except in the topmost part (Fig. 1), creates more equal conditions for water supply for branches situated at different height in the crown. If there is a water deficit, the tree's top is in a preferential situation because of the hydraulic architecture, favouring water flow along the main axis (Sellin 1988). For the tree grown under favourable light conditions R for one branch or root exceeds R of the trunk (Table 2), but the summed resistance of both the roots and branches is less than that of the trunk because of the large number of conducting segments linked in parallel with each other. As a consequence, there are a number of parallel flows within the crown and root system.

At a first glance our results appear to contradict the widespread opinion that the bulk of resistance is localized in branches, particularly in minor twigs. This view follows from a hydraulic hierarchy of different parts of the tree, found in many species (Thompson et al. 1983; Ewers and Zimmermann 1984a, b; Ikeda and Suzaki 1984; Sellin 1988; Tyree and Sperry 1988). Nevertheless, the hydraulic hierarchy resulting from differences in specific or leaf-specific conductivity does not necessarily reflect the distribution of total xylem resistance, which depends on the number and ramification of the conducting segments as well. Furthermore, the relative distribution of xylem resistances cannot be regarded as a static phenomenon. A given spatial pattern of resistances, characteristic of the tree at high water status, will change as soon as water deficits develop. Changes in resistance of a twig influence all the twigs which have at least one section of the conduit in common (Richter 1973). The distribution of resistances described above by us holds true when xylem is water-saturated or near to saturation state (during rainy periods and under low atmospheric evaporative demand). When the xylem water content falls, beginning from twigs close to the sites of water loss, the k of the xylem will decrease steeply (Sellin 1991). Here we suppose that the contribution of the branches to total xylem resistance increases with increasing water deficit. This conforms to Zimmermann's conception of plant segmentation (Zimmermann 1983; Salleo and Lo Gullo 1986; Tyree and Sperry 1988, 1989). Naturally, this hypothesis needs further experimental verification.

Thus, spruce trees grown under contrasting light conditions differ in resistance to water flow in xylem. The greatest differences in R between the open- and shade-grown trees occurred in the trunk. This result was expected because in adverse environments the amount of substrate allocated to the stem depends on the reserves left after the tree has met root, foliage, and reproductive commitments (Waring 1980, 1987). Low levels of the resources available for trunk growth, in turn, result in both a smaller conducting area and narrower tracheids. Consequently, the light conditions of a site exert significant influence on xylem anatomy and, therefore, on the water-conducting capacity of xylem.

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IX. Canadian Journal of Forest Research, 1994

(In press)

SAPWOOD - HEARTWOOD PROPORTION RELATED TO TREE DIAMETER, AGE AND GROWTH RATE IN *PICEA ABIES*

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Sellin, A. 1994. Sapwood - heartwood proportion related to tree diameter, age and growth rate in *Picea abies*. Can. J. For. Res.

The relationships of sapwood radial width and transverse area to tree diameter, age and growth rate were investigated in *Picea abies* (L.) Karst. A total of 125 trees growing with (suppressed trees) and without competition for light (dominant trees) were sampled. Both sap and heartwood amounts showed an increase with diameter at the stem base, while heartwood portion increased more rapidly. In young trees sapwood prevails both in terms of diameter and transverse area. After trees have reached a certain age, the width of the sapwood band remains more or less constant (on an average 7.8 cm for dominant and 2.0 cm for suppressed trees), and heartwood amount exceeds that of sapwood. The percentage of heartwood in suppressed trees is substantially bigger than in dominant trees of the same age. Sapwood amount is closely correlated with the tree diameter, but not age. Tree age controls the number of rings in sapwood, while the sapwood width depends on tree's radial growth rate as well.

Introduction

Participating in life processes of the tree, sapwood differs from heartwood in anatomical and physiological features. The cross-sectional area of sapwood has been found to be related to the amount of foliage distal to the cross-section (Dean et al. 1988; Kyker-Snowman and Wilson 1988; Long and Smith 1988; Bormann 1990; West and Wells 1990; Coyea and Margolis 1992; Robichaud and Methven 1992; Usoltsev 1993), that follows from physiological balance between water demand by the crown and the ability of the stem to conduct water. Sapwood area is a characteristic of stem conductive capacity, while its water storage capacity is dependent on the volume of the sapwood. Thus, sapwood amount is an input variable in modeling of tree water relations (Waring and Running 1976; Jarvis et al. 1981; Čermák et al. 1984; Edwards et al. 1986). There is a growing interest in sapwood amount in respect of its role in carbon balance of trees (Keane and Weetman 1987; Gerrish 1988), as sapwood contains more than 80% of the living cells of the stems. Stem maintenance respiration was found to be linearly correlated with sapwood volume in *Pinus contorta* Dougl. and *Picea engelmannii* Parry (Ryan 1990). Therefore the proportions of sapwood are necessary for good estimates of maintenance respiration of woody tissues (Ryan 1991).

Besides its biological features, sapwood differs from heartwood in density, chemical composition, mechanical and technological properties. In several applied areas the sapwood - heartwood proportion is an important characteristic of the timber (Ruppert and Graham 1974; Nelson 1976; Panshin and de Zeeuw 1980). The preference in pulpwood is for sapwood while a larger portion of heartwood is desirable in lumber. Since sapwood - heartwood transformation is of interest from both academic and economic aspects, it is worthwhile to provide information on the amounts of the two different zones of xylem in Norway spruce [*Picea abies* (L.) Karst.], a common commercial species in Europe.

In our previous paper (Sellin 1991), sapwood thickness of *Picea abies* trees was discussed in relation to the tree age. Sapwood thickness increased in absolute terms, whereas its relative proportion decreased with the age of the tree. Great differences were found in sapwood radial width between dominant and suppressed trees in linear measurements, but not in the number of sapwood rings. The results of the present study expand our understanding of the sapwood - heartwood relationships in spruce with respect to tree diameter and radial growth rate. The equations predicting both sapwood width and transverse area from tree diameter and age, the characteristics closely associated with tree size, have been also derived.

Material and methods

The study was carried out in June and July, 1989 on 4- to 117- year-old *Picea abies* trees growing at Vooremaa Ecology Station, East Estonia. The trees were selected out of uneven-aged stands in *Hepatica* and *Oxalis* forest site types, situated on rich brown forest soil. A detailed description of the climate, relief, soil and vegetation of the study area has been published formerly (Frey 1977). A total of 60 trees growing with (suppressed trees) and 65 trees without competition for light (dominant trees) were studied. The sample trees were chosen from the two extreme crown classes according to their position in stand and crown appearance. Dominant trees have long conical-shaped crowns with branches bearing live needles along most of the branch. In contrast, suppressed trees have short crowns limited to the upper part of the bole. Their needles are often concentrated to the ends of the branches flattened at the top. The visual selection was verified by measuring tree vigour as the ratio of basal area growth to sapwood basal area for the last year (Waring et al. 1980) . The mean value of the index of vigour was 0.038 ± 0.002 (S.E.) for the dominant and 0.023 ± 0.003 for suppressed trees (Sellin 1991). Saplings were taken from forest plantations or from under the dense canopy of higher trees and forest understorey. For simplicity we name them dominant and suppressed trees as well, respectively. Trees were selected so that all age classes would be represented. The distribution of the sample trees by age and diameter is presented in Tables 1 and 2. The significance of selecting dominant and suppressed trees is that they differ dramatically in diameter at a given age, and therefore are suitable for separating age from diameter effects.

Table 1. Distribution of sample trees by age (a)

Age range (years)	Number of trees	
	Dominant class	Suppressed class
$a \leq 20$	16	16
$20 < a \leq 40$	12	18
$40 < a \leq 60$	12	11
$60 < a \leq 80$	10	8
$80 < a \leq 100$	11	7
$100 < a$	4	0

Table 2. Distribution of sample trees by diameter inside bark (**d**)

Dominant class		Suppressed class	
Diameter range (cm)	Number of trees	Diameter range (cm)	Number of trees
$d \le 10$	12	$d \le 1$	14
$10 < d \le 20$	7	$1 < d \le 5$	8
$20 < d \le 30$	14	$5 < d \le 9$	10
$30 < d \le 40$	13	$9 < d \le 13$	9
$40 < d \le 50$	11	$13 < d \le 17$	9
$50 < d$	8	$17 < d$	10

The trees were sampled at the stem base: the saplings were cut off and cross-sectional disks were cut from the stems above the root collar, in older trees 4 increment cores were extracted at the breast height along stem radii at 90° angles. The sapwood - heartwood border both on fresh increment cores and stem disks was identified by simultaneous use of differential translucence and aniline pencil methods (Münster-Swendsen 1987).

The widths of heart and sapwood were measured with the precision of 0.5 mm, the width of the last annual ring, 0.01 mm. To eliminate the variability resulting from bark thickness, the diameter measured inside the bark (d.i.b.) was used. The transverse areas of the two wood zones were calculated approximating the stem cross section to an ellipse. For data processing a correlation analysis, and simple and nonlinear regression procedures based on the least squares method were applied. To approximate sap and heartwood amounts versus tree diameter (**d**) and age (**a**) the functions giving the best fit in terms of determination coefficient (R^2) and standard error of estimate (S.E.E.) were chosen. The derived regressions (Tables 4 and 5) were used for generalized depiction of the sapwood - heartwood proportion in Figures 1 to 4. In order to derive an equation better approximating sapwood width (**W**), also the radial growth rate (I_R) of trees was included in the analysis. We proceeded from the simple relation that trunk radius equals to the product of **a** and I_R, and consequently, thickness of the sapwood band would be a function of the product. As **W** depends curvilinearly on **a**, and the scattering of I_R is big, a multiplicative function of the following type was used

[1] $W = l * a^{m} * I_R^{n}$,

where **l**, **m** and **n** are constants.

Methodological details have been published in our previous paper (Sellin 1991).

Results

The radial width and transverse area of both sap and heartwood showed an increase with diameter at the stem base of Norway spruce trees (Figs. 1 and 2), while the amount of heartwood increased more rapidly. The curves depicted in Figs. 1 and 2 have been obtained as a result of approximation of the pooled data on spruce trees of both dominance class. Addition of the data on suppressed class to those on dominant one

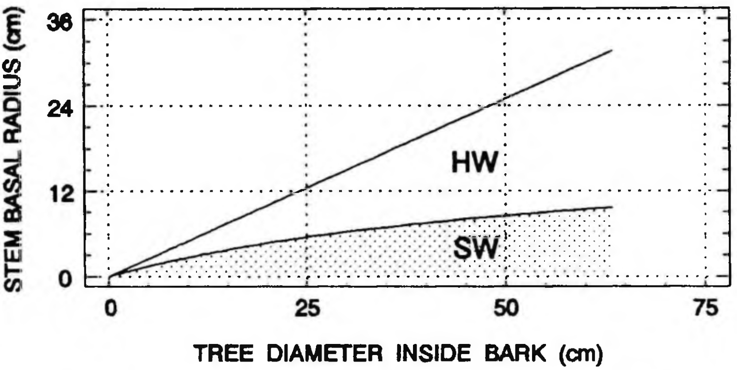

Fig. 1. Sap (SW) and heartwood (HW) width versus tree diameter inside bark for all trees together.

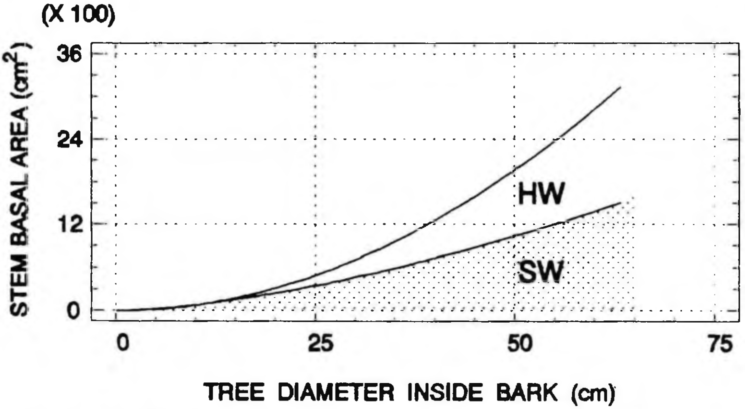

Fig. 2. Sap (SW) and heartwood (HW) transverse area versus tree diameter inside bark for all trees together.

did not substantially influence the shape of the curves because of the little range of diameters in suppressed trees (Table 2).

In young spruce trees sapwood prevails as regards both diameter and basal area. After the d.i.b. grow over 15 cm for dominant and 1.2 cm for suppressed trees, the heartwood thickness exceeds that of sapwood. The transverse area of heartwood in Norway spruce exceeds that of sapwood at the d.i.b. over 57 and 3.3 cm for dominant and suppressed class, respectively.

Analyzing sapwood - heartwood proportion in relation to tree age (a), it was impossible to join the data on all trees because of very different wood radial increments, in trees from different crown classes in particular. For the same reason the approximation of the sapwood - heartwood proportion versus tree age (Figs. 3 and 4) appears to differ from that versus tree diameter (Figs. 1 and 2). In young trees,

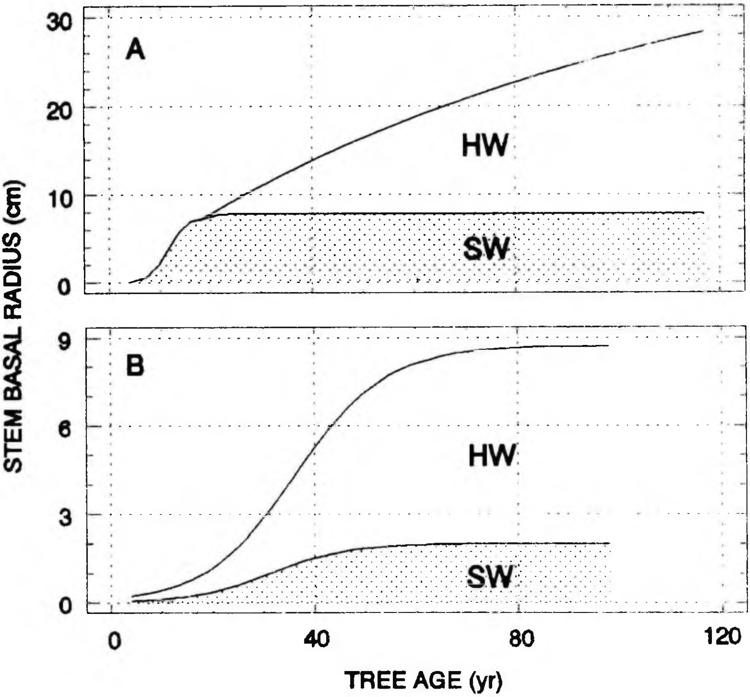

Fig. 3. Sap (SW) and heartwood (HW) width versus tree age. A, dominant trees; B, suppressed trees.

sapwood width (W) increases up to the age of 25 and 65 years, respectively for dominant and suppressed trees (Fig. 3), until wood radial growth rate and heartwood formation rate will be equalized. Further, as trees grow older W seems to remain more or less constant.

In Norway spruce the mean sapwood thickness was 7.8 cm for adult dominant and 2.0 cm for suppressed trees. Heartwood width exceeds that of sapwood on an average at the age over 47 years in dominant and 12 years in suppressed trees. Transverse area of the heartwood exceeds that of the sapwood at the age over 98 in dominant and 43 years in suppressed spruce trees (Fig. 4). It is characteristic for suppressed class that the increase of both total wood and sapwood amount in relation to tree age is describable by a logistic curve (Fig. 3B, 4B). Saplings, growing under dense canopy, sustain severe competition from both older trees and forest understorey resulting in very thin annual increments. From the age of about 20 years the stem radial growth rate increases and after the age of 60 years it decreases again. Mean thickness of the last annual increment was merely 0.33±0.06 (S.E.) mm in 60-year-old and older suppressed trees.

Correlation analysis revealed that the tree diameter (d), age (a) and radial growth

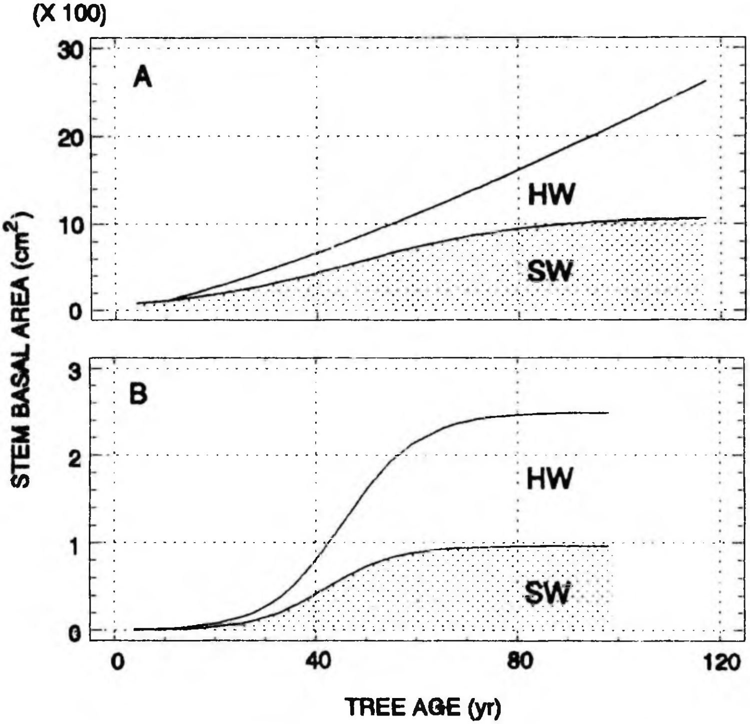

Fig. 4. Sap (SW) and heartwood (HW) transverse area versus tree age. A, dominant trees; B, suppressed trees.

rate (I_R) are the most relevant characteristics concerning sapwood amount (Table 3). Both sapwood width and transverse area are most closely correlated with **d**, the simple correlation coefficient was 0.800 and 0.938, respectively. The thickness of sapwood band at the stem base was predicted from tree diameter to about an equal degree (R^2=0.62-0.68) for separate dominance classes as well as for all trees together (Table 4). Tree diameter describes 68% of the total variation in sapwood width for all trees pooled. The relationship is approximated by the following function:

[2] $W=18.8*d/(d+60.4)$,

where W is the sapwood radial width (cm), **d** - the tree diameter inside bark (cm). However, the determination coefficient is relatively low and the standard error of estimate too big (Table 4) to use this equation for precise estimation of the thickness of sapwood band. Sapwood area as compared with sapwood width was considerably better correlated (R^2=0.88-0.91) with tree diameter. The general regression for all trees combined is

[3] $g_{sw}=2.19*d^{1.575}$,

where g_{sw} is the sapwood transverse area (cm^2). The comparison of actual and predicted values of g_{sw} is presented in Fig. 5.

Table 3. Correlation matrix of the variables sapwood radial width (W), number of sapwood rings (N), sapwood basal area (g_{sw}), tree diameter (d) and age (a), mean radial growth rate (I_R), radial growth rate based on sapwood rings (I_{Rsw}) and index of vigour (IOV). The upper number indicates a simple correlation coefficient (r), the lower one, a significance level (P). ns, not significant at 0.05 level of probability

	W	N	g_{sw}	d	a	I_R	I_{Rsw}	IOV
W	1.000	0.547 <0.001	0.845 <0.001	0.800 <0.001	0.454 <0.001	0.799 <0.001	0.764 <0.001	-0.372 <0.001
N		1.000	0.599 <0.001	0.722 <0.001	0.925 <0.001	0.233 0.009	0.056 ns	-0.692 <0.001
g_{sw}			1.000	0.938 <0.001	0.631 <0.001	0.596 <0.001	0.461 <0.001	-0.341 <0.001
d				1.000	0.779 <0.001	0.631 <0.001	0.432 <0.001	-0.488 <0.001
a					1.000	0.183 0.042	-0.014 ns	-0.642 <0.001
I_R						1.000	0.931 <0.001	-0.232 0.009
I_{Rsw}							1.000	-0.067 ns
IOV								1.000

The general regressions of sapwood amount from tree age for all trees combined had R^2 values much lower than those for the separate dominance classes (Table 5). Tree age cannot be used as a predictor either of W or g_{sw}, because of great differences in width of growth rings between single trees, especially between the trees from different sites or dominance classes. In addition to the variability of g_{sw}, also the variability of the total basal area resulting from great differences in tree's growth rate is added. Thus, it is expedient to take into consideration the radial growth rate (I_R) of trees as well. There is a statistically significant ($P<0.001$) positive correlation between sapwood amount and I_R (Table 3): sapwood is thicker in spruce trees having more rapid diameter growth (Fig. 6).

The application of the equation [1] gives an empiric model, that relates W to both the age and radial growth rate. Better fit resulted from using the tree growth rate during the last life period corresponding to the sapwood zone:

[4] $W=0.195*a^{0.656}*I_{Rsw}^{1.04}$, $R^2=0.93$, $P<0.001$, S.E.E. $=0.94$,

where I_{Rsw} is the mean radial growth rate calculated on the base of sapwood rings (mm yr^{-1}).

Table 4. Equations relating sapwood radial width (**W**) and transverse area (**g_{sw}**) to the tree diameter inside bark (**d**). Sapwood width and tree diameter are in cm, sapwood area in cm^2. For all equations $P<0.001$

Sapwood characteristic	Sampled trees	Regression equation	R^2	S.E.E.
radial width	dominant	$W=10.1*d/(d+10.4)$	0.62	2.03
	suppressed	$W=4.96*d/(d+24.6)$	0.63	0.60
	all together	$W=18.8*d/(d+60.4)$	0.68	2.05
transverse area	dominant	$g_{sw}=5.05*d^{1.36}$	0.88	148.7
	suppressed	$g_{sw}=0.454*d^{1.88}$	0.81	21.3
	all together	$g_{sw}=2.19*d^{1.575}$	0.91	119.5

Table 5. Equations relating sapwood radial width (**W**) and transverse area (**g_{sw}**) to the tree age (**a**). Sapwood width is in cm, sapwood area in cm^2 and tree age in years. For all equations $P<0.001$

Sapwood characteristic	Sampled trees	Regression equation	R^2	S.E.E.
radial width	dominant	$W=7.82/(1+e^{5.98-0.505*a})$	0.63	2.00
	suppressed	$W=2.02/(1+e^{4.13-0.132*a})$	0.60	0.63
	all together	$W=0.550*a^{0.539}$	0.23	3.19
transverse area	dominant	$g_{sw}=1088/(1+e^{2.70-0.0578*a})$	0.72	229.6
	suppressed	$g_{sw}=96.6/(1+e^{5.95-0.142*a})$	0.65	29.4
	all together	$g_{sw}=8.47*a-73.7$	0.40	312.5

Discussion

Both sapwood width (**W**) and transverse area (**g_{sw}**) increased with diameter of the tree (**d**) in *Picea abies* (Figs. 1 and 2). There is a variation from this pattern observed in different species. Lassen and Okkonen (1969) reported that **W** increases with increasing **d** in *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus contorta* Dougl., *Pinus ponderosa* Laws., *Picea engelmannii* Parry and *Thuja plicata* Donn, whereas in *Larix occidentalis* Nutt., it keeps more or less the same regardless of **d**. Yang and Murchison (1992) found **W** for *Pinus contorta* var. *latifolia* Engelm. to be independent of tree diameter. In even-aged stand of *Pinus taeda* L., **W** has been found to be linearly correlated with **d** (Blanche et al. 1984).

In young spruce trees sapwood prevails both in terms of diameter and area. After trees have reached a certain diameter, the heartwood thickness exceeds that of sapwood. Analysing the variation in sapwood - heartwood proportion depending on both tree diameter and age disclosed differences between the effects of **d** and **a** on

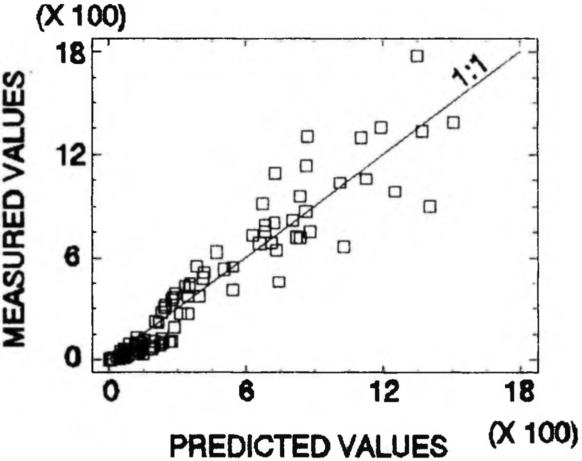

Fig. 5. Comparison between predicted (by Eq. 3) and measured values of sapwood transverse area (cm^2). $R^2=0.91$, $P<0.001$.

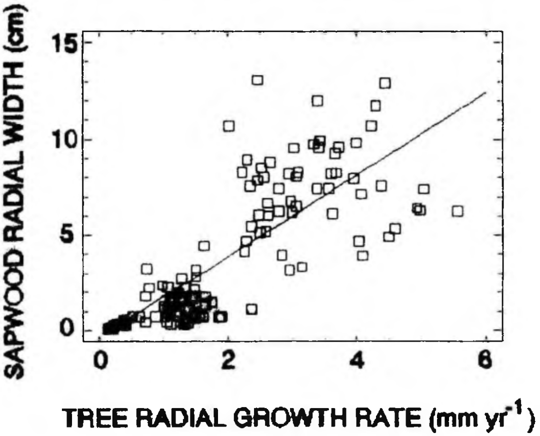

Fig. 6. Sapwood width (W) versus mean radial growth rate (I_R). The regression equation: **$W=2.13 * I_R - 0.38$**, $R^2=0.64$, $P<0.001$, S.E.E. $=2.18$.

sapwood amount. In young trees W and g_{sw} increase with a up to certain age, and further they remain nearly constant, on the contrary to those depending on **d** (Figs. 1 to 4). There are similar data on some other conifers (Lassen and Okkonen 1969), sapwood thickness of which increases fast during the first 15 to 20 years of growth, after that it increases only slightly. In *Picea mariana* (Mill.) B.S.P., W culminates at age 60, after which it seems to lessen again (Hazenberg and Yang 1991).

Smith et al. (1966), Yang et al. (1985), Bormann (1990), and Yang and Murchison (1992) have reported concerning various conifers, sapwood radial thickness to be independent of the tree age. In *Picea abies*, however, W is in correlation with a up to certain age, after which W reaches a plateau depending on crown class (Fig. 3). Weak correlation or its total lack between tree age and sapwood thickness is characteristic if sapwood linear measurements are considered. At the same time, tree age is one of the main factors determining the number of sapwood rings in *Picea abies* (Table 3; Sellin 1991), *Picea mariana* (Hazenberg and Yang 1991), *Pinus banksiana* Lamb. (Yang and Hazenberg 1991) and *Pinus contorta* (Yang and Murchison 1992). Moreover, the number of annual rings contributing to sapwood at a given age is independent of the site quality (Pothier et al. 1989a), tree vigour (Kaufmann and Watkins 1990) and crown class (Sellin 1991).

Our data confirm that the share of heartwood in suppressed spruce trees is substantially bigger than in dominant trees of the same age. Bauch et al. (1988) found the mean relative area of sapwood to diminish from 37.5% in dominant trees to 34.0% in suppressed ones. Similar results have been published concerning sapwood volume in high and low-vigour *Pinus contorta* trees as well (Kaufmann and Watkins 1990). The radial growth rate of suppressed spruce trees decreases remarkably after the age of 60 years (Figs. 3B and 4B). For the age 80 their growth has been practically completed, and further they will die in case of extreme meteorological or edaphic conditions (severe drought, lasting frost in late winter, abrupt change in soil water conditions). Dominant trees, on the contrary, continue intensive growth at this age (Figs.3A and 4A).

Sapwood - heartwood proportion is formed as a result of balance between two critical functions of tree boles, mechanical support of the crown and water supply to the foliage (Long et al. 1981). Our results demonstrate a difference in this proportion between trees of the two extreme crown classes. As a tree grows, the number of branches as well as the leaf area are increasing. At the same time, sapwood volume enlarges exponentially with leaf area growing, accompanied by proportionate increase of maintenance respiration (Ryan 1989). From certain tree's size onwards, the growing respiration costs begin to limit further increase of sapwood. It causes a sapwood enlargement to cease, and some time later the growth of the whole tree will be stagnated. This happens substantially earlier in suppressed trees, because carbohydrate reserves are always lower in trees growing under stress conditions (Waring 1987). This process explains decrease in sapwood relative portion with the age of the trees growing (Sellin 1991). The cost of maintenance respiration to support the living parenchyma cells in sapwood balances the benefits of water conduction, sapwood storage and mechanical support (Ryan 1989).

The sapwood basal area is closely correlated with tree diameter in Norway spruce: d.i.b. describes 91% of the total variation in sapwood transverse area and might serve as the means of accurately predicting sapwood amount. It can be seen from Fig. 5 that there is a high degree of correspondence between predicted and observed sapwood area. As the data on the two extreme crown classes have been included in the analysis, one can suppose that the equation [3] fits the trees of the whole range of dominance.

The radial growth rate (I_R) of trees is relatively weakly related to sapwood amount in Norway spruce (Table 3; Fig. 6), because it is highly variable from tree to tree as well as in one tree during its life-time. The result will agree with those reported for *Thuja plicata* (Wellwood and Jurazs 1968) and *Pseudotsuga menziesii* (Lassen and Okkonen

1969), but sapwood width in *Pinus contorta* has been found to be independent of I_R (Yang and Murchison 1992). It is interesting to note here, that Pazdrowski (1988) established opposite relationship between relative sapwood width and diameter increment for *Pinus sylvestris* L.

Tree age and radial growth rate combined gave more precise estimate of W (Eq. 4) as compared to the age, diameter or growth rate taken alone (Tables 3, 4, 5). Inclusion of the growth rate calculated on the base of sapwood rings (I_{Rsw}) substantially improved the regression due to the lack of correlation ($r=-0.014$) between **a** and I_{Rsw} (Table 3). Of course, the equation [4] does not have practical importance as a tool for predicting sapwood width, but it is of certain theoretical significance. Such a model helps us better understand factors which control the sapwood - heartwood proportion in Norway spruce. Tree age determines a general pattern of increase of the sapwood thickness according to the addition of new sapwood rings (Sellin 1991), but the actual value of W in adult trees is determined by the growth rate (i.e. by the width of annual increments). The influence of ecological factors (resulting from either dominance relations or site quality) on sapwood - heartwood proportion is mediated by the radial growth rate. The index of vigour (IOV), a handy tool for assessment of tree vitality (Waring et al. 1980; Münster-Swendsen 1987), does not serve this purpose. Besides, inclusion of IOV in the equation cannot materially improve the approximation, as it is an age-related characteristic (Table 3).

Our results suggest that the sapwood - heartwood proportion differs greatly in trees depending on their diameter, age and dominance class. In suppressed trees the share of heartwood is substantially bigger than that in dominant trees of the same age. Tree age is a poor predictor of sapwood width and basal area, both better determined by the tree diameter.

Acknowledgments

I am grateful to Prof. T.Frey, Tartu University, and Dr. A.Koppel, Institute of Zoology and Botany, Estonian Academy of Sciences, for critical remarks and helpful comments on the manuscript.

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X. Manuscript submitted for publication in Tree Physiology

RESISTANCE TO WATER FLOW IN XYLEM OF *PICEA ABIES* TREES GROWN IN CONTRASTING EDAPHIC CONDITIONS

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Summary

The hydraulic architecture of *Picea abies* (L.) Karst. trees growing in contrasting edaphic conditions was investigated. The trees grown in a well-drained brown forest soil and a waterlogged highbog soil differed significantly in the hydraulic properties of the xylem. The relative conductivity of the xylem (**k**) for the trees in favorable soil conditions was 1.1-2.2 times as large as the **k** measured in bog-grown trees. The mean tracheid radius explained 73%, diameter of xylem segment 8% and tree age 5% of the total variation in **k**.

The mean leaf-specific conductivity (LSC) for the stems of the trees in favorable soil conditions was about 1.8 times as large as that for bog-grown trees, i.e. the potential water transport capacity of the stem per unit amount of foliage for the trees in a forest soil is significantly higher. The trees in a well-drained soil, growing at a greater risk of water stress, have a conducting system with a larger margin of safety.

At a high water status the largest share of xylem resistance for the trees grown under waterlogged conditions resides in the root system, and for the trees grown in a well-drained soil, in the trunk. Most of the stem resistance in the trees at both sites is localized in the top.

Keywords: Huber value, leaf-specific conductivity, *Picea abies*, relative conductivity, resistance to water flow, xylem.

Introduction

The primary driving force of the water movement against the gravitational field and plant's inner obstacles is the tension resulting from the evaporation of water in the leaf. The water movement in vascular plants occurs mainly through the elongate conduits of the xylem - vessels and tracheids, because at maturity they provide a pathway of maximum hydraulic conductance. Although there is a continuity of liquid water between the leaf and the soil via the xylem, no rapid equalization of water potential throughout the plant can occur because of various resistances in the soil-plant-atmosphere continuum.

In the present study, attention is focused on the resistance of the xylem by which water and nutrients are transported from roots to leaves. The anatomical structure formed under the influence of a multitude of ecological factors determines both the efficiency (i.e. hydraulic conductivity) and stability (i.e. resistance to embolism) of the xylem as a transport pathway (Tyree and Dixon 1986, Tyree and Sperry 1989, Sperry and Tyree 1990, Sperry and Sullivan 1992).

In coniferous trees, due to their morpho-anatomical peculiarities, the frictional resistance of xylem elements makes a considerable contribution to the total resistance to water flow (Hellkvist et al. 1974, Tyree et al. 1975, Tyree and Sperry 1989). It is the hydraulic resistance of the xylem that is responsible for differences in leaf water potential within the tree crown, as the flux of water in the stem and branches lags behind the water losses from the foliage. Therefore the conductance of the stem in conifers is supposed to be an important factor limiting the shoot function and development (Pothier et al. 1989). This holds true for broad-leaved species as well. The hydraulic limitations imposed by roots, shoots and petioles in *Acer saccharum* Marsh. do not allow trees to attain maximum stomatal conductance at midday even without soil water stress (Yang and Tyree 1993). The xylem resistance growth with water deficit has been observed to cause a drop of the leaf water potential in *Vitis vinifera* L. to the level sufficient to completely inhibit the shoot growth (Schultz and Matthews 1988). In *Populus* L. species, the plant survival is related to the hydraulic properties of the xylem rather than to the dehydration tolerance of leaf tissues (Braatne et al. 1992).

The resistance of the water-conducting pathway is determined by its length, configuration, transverse area and permeability. In our previous paper (Sellin 1993), the resistance to water flow in the xylem of Norway spruce [*Picea abies* (L.) Karst.] trees growing under contrasting light conditions was discussed. At a high water status the largest share of the xylem resistance in open- as well as shade-grown trees resides in the trunk. This appears to contradict the widespread opinion that the bulk of resistance is localized in branches, particularly in minor twigs (Tyree 1988, Yang and Tyree 1993). Such distribution of xylem resistance is considered a common feature for different tree species regardless of the variation of ecological conditions. This standpoint has mainly been derived from a comparison of the values of leaf-specific conductivity in different parts of the tree (Zimmermann 1978, Thompson et al. 1983, Tyree et al. 1983, Ewers and Zimmermann 1984) by presuming that the drop in xylem pressure is inversely proportional to the leaf-specific conductivity and that the transpiration rate is even throughout the crown .

Yet, there are some more experimental data calling in question the idea of the unique distribution pattern of xylem resistance within plants. In *Pinus sylvestris* L. stem resistance has been reported to exceed 3.4-fold that of branches (Roberts 1977). As a matter of fact, Roberts (1977) has found the bulk of the tree's resistance residing in the root system. However, his "root resistance" includes both the axial resistance of xylem conduits and the radial resistance to the water entrance to the xylem, being the major component of the plant's total resistance (Passioura 1982). The stem's contribution to the resistance to the water flow is also the largest in some desert species, such as *Encelia farinosa* Gray and *Hilaria rigida* (Thurb.) Benth ex Scribn., the ratio of root:stem:leaf resistance averaging 0.2:1:0.1 (Nobel and Jordan 1983).

The present investigation involves measurements of xylem permeability in order to compare the hydraulic architecture of Norway spruce trees growing in contrasting edaphic conditions: in a rich well-drained brown forest soil and a poor waterlogged highbog soil. The xylem resistances presented in this paper were calculated for steady-state conditions by assuming the water movement directly through the vascular tissue without significant exchange between conduits and storage. This holds true at a high water status when the difference in water potential between the conducting and the storage tissue is negligible.

The dependence of the relative conductivity on tree and xylem characteristics will also be discussed.

Materials and methods

Plant material. The measurements were performed on *Picea abies* trees at Vooremaa Ecology Station, East Estonia, during the summer months of 1986 and 1989. A detailed description of the climate, relief, soil and vegetation of the study area has been published formerly (Frey 1977). Two middle-aged trees growing in contrasting edaphic conditions served as the main study material (Table 1). Tree 1 grew in the edge of a nemoral spruce forest in a rich well-drained brown forest soil, pH_{H2O} of the rooted zone was 5.2. Tree 2 grew in the border of a boggy pine forest and an open raised bog in a waterlogged highbog soil, pH_{H2O} was 4.5. Both sample trees were exposed to sunlight.

Table 1. Characterization of the sample trees.

Tree no.	Tree age, years	Tree height, m	Number of primary branches	Number of primary roots	Soil type	Forest site type
1	40	14.84	183	14	brown forest soil	*Hepatica*
2	78	7.65	119	13	highbog soil	raised bog

The trunk, 2 sample roots and 3 sample branches (one branch from each, the lower, the middle and the upper third of the crown) taken from each tree were divided into 10 sections. From each section 1 xylem specimen was cut for permeability measurements. Additionally, xylem specimens were taken from trunks, roots and branches of 6 younger trees in order to establish the relationship between the relative conductivity and the tracheid diameter.

Permeability measurements. Xylem permeability to water was measured on freshly cut trunk, root and branch specimens of 20-30 mm length by the methods of Booker and Kininmonth (1978) and Zimmermann (1978). Disks of 25-30 mm width were cut from thick parts of trunks and roots, from which sapwood cylinders of 15 mm diameter were extracted with a plug cutter attached to a drilling machine. The specimen preparation included a recutting of the faces to remove the torn and clogged tracheid ends, and their saturation with water under vacuum. The permeating fluid was a 10 mM water solution of KCl deaerated under vacuum immediately prior to the measurements. The difference of the hydrostatic pressure between the specimen faces was 0.5×10^4-1.5×10^4 Pa.

The relative conductivity of the specimens was calculated according to Darcy's law (Jarvis et al. 1981, Nobel 1991):

$$k = \frac{q \times l \times \eta}{\Delta P \times A}, \qquad (1)$$

where **k** is the relative conductivity (m^2); **q**, the volume flow rate ($m^3 s^{-1}$); **l**, the length of the specimen (m); η, the dynamic viscosity of the liquid (N s m^{-2}), **ΔP**, the pressure difference (Pa), and **A**, the transverse area of the conductive xylem (m^2). In order to characterize the xylem conductive area relative to the leaf amount supplied, the Huber value was used (Ewers and Zimmermann 1984):

$$HV = \frac{A}{m} \ , \tag{2}$$

where **HV** is the Huber value (m^2g^{-1}), and **m**, the dry weight of the needles situated apically relative to the xylem segment (g). Leaf-specific conductivity, **LSC** (m^4g^{-1}), was calculated as:

$$LSC = k \times HV \ . \tag{3}$$

Xylem transverse area. Immediately after making the permeability measurements crystal violet or methylene blue (0.5% w/v aqueous solution) was forced through each specimen to demarcate the area of the conductive xylem, i.e. sapwood. In stem and root disks the sapwood - heartwood border was identified by using a differential translucence method (Waring et al. 1982). In case of need it was doubled by a differential absorption method by immersing disks for a moment in weak water solutions of the dyes mentioned above. The conductive portion of the xylem could be distinguished by its more intensive color. Both the specimens and the disks were photocopied and their conductive and total transverse areas were determined from enlarged photographs with a graphics tablet (HIPAD DIGITIZER, Houston Instrument, USA) attached to a personal computer.

The mean **k** of a disk was calculated as a weighed average:

$$k = \frac{\sum_{i=1}^{n} (k_i \times A_i)}{\sum_{i=1}^{n} A_i} \ , \tag{4}$$

where k_i is the relative conductivity and A_i, the conductive area of the *i*th xylem cylinder cut from the disk.

Trunk, root and branch resistance. The resistance **R** (Pa s m^{-3}) to the water flow through the xylem is defined by the following ratio (Jarvis et al. 1981, Fitter and Hay 1987):

$$R = \frac{\Delta\Psi}{q} \ , \tag{5}$$

where $\Delta\Psi$ is the water potential difference (Pa). In permeation experiments $\Delta\Psi$ can be replaced with the applied pressure difference ΔP (Pa):

$$R = \frac{\Delta P}{q} \ . \tag{6}$$

A substitution of **q** from Eq. 1 into Eq. 6 gives

$$R = \frac{l \times \eta}{k \times A} \ . \tag{7}$$

It was assumed that the values of **A** and **k** measured on a specimen are characteristic of the whole corresponding section. All resistances were calculated for the permeating fluid temperature of +20°C ($\eta = 10^{-3}$ N s m^{-2}). The resistance (**R**) of single roots, branches and trunks was calculated by adding the resistances of 10 sections taken from each plant part in series:

$$R = \sum_{i=1}^{10} R_i \, , \tag{8}$$

where R_i is the resistance of the *i*th xylem section. The total resistance (R_t) of the branch and root system can be calculated by adding reciprocals of the resistances linked in a parallel way (Fitter and Hay 1987):

$$R_t = \frac{1}{\sum_{i=1}^{n} \frac{1}{R_i}} \, , \tag{9}$$

where R_i is the resistance of the *i*th branch or root. We proceeded from mean resistances per sample segment:

$$R_t = \frac{\sum_{i=1}^{n} R_i}{n \times t} \, , \tag{10}$$

where **n** is the number of sample branches or roots and **t**, the total number of branches or roots.

Tracheid radii. Minor and major inner diameters of the largest tracheids in at least 30 sample segments of root, stem and branchwood from each habitat were measured with an ocular micrometer under 400-fold magnification. For each specimen lumina of the 10 largest tracheids of 3 outer growth rings were measured. As an approximation of the hydraulic radius (r) the minor and major radii of the elliptic lumen of each tracheid were averaged (Ewers and Zimmermann 1984).

Relative conductivity depending on tree and xylem characteristics. The contribution of tree and xylem characteristics to the variation in **k** was estimated by an analysis of variance by using the SAS statistical package (SAS/STAT 1988). Because of unbalanced data, a random model analysis of variance was applied. The mean lumen radius of the largest tracheids, diameter and location (i.e. standardized distance from branch, root or stem base) of the sample segment, habitat, xylem type (i.e. branch-, root- or stemwood), tree height and age as nonmetric or discrete variables were included in the analysis. The effect of the same characteristics on **r** was analyzed as well. In final analyses only the characteristics having a statistically significant influence on the response variable were included.

The pooled data on both habitats were subjected to a stepwise regression analysis (forward-selection procedure) to select the metric variables to be entered (F-ratio > 4) into an empiric equation relating **k** to tree and xylem characteristics. The stepwise variable selection procedure was applied also to the data on three xylem types separately for each habitat to establish the relationship between **k** and **r**. In the last case we proceeded from a polynomial of the fourth power:

$$k = a_1 \times r^4 + a_2 \times r^3 + a_3 \times r^2 + a_4 \times r + a_5 \, , \tag{11}$$

where a_1, a_2, a_3, a_4 and a_5 are constants.

Results

Effect of growth conditions on hydraulic architecture. The transverse area (A) of the conducting xylem declined steadily in the direction of tree's top (Fig. 1). In the basal part of the stem the sapwood area of the tree grown in a brown forest soil was by an order of magnitude larger than that of the tree in highbog soil. Also, the relative conductivity (**k**) of the xylem showed a difference between the trees grown in contrasting edaphic conditions (Tables 2 and 3). A comparison of the middle sections of primary roots, branches and trunks revealed that in the tree grown in a forest soil, **k** of rootwood was approximately 2.2-fold ($P < 0.01$), of branchwood, 1.2-fold (n.s.*), and of stemwood, 1.1-fold (n.s.) higher than that in the tree grown in a bog soil. The same trend holds true about the proximal and distal sections of the organs. The analysis of variance applied to the pooled data revealed no statistically significant effect of the habitat on **k**.

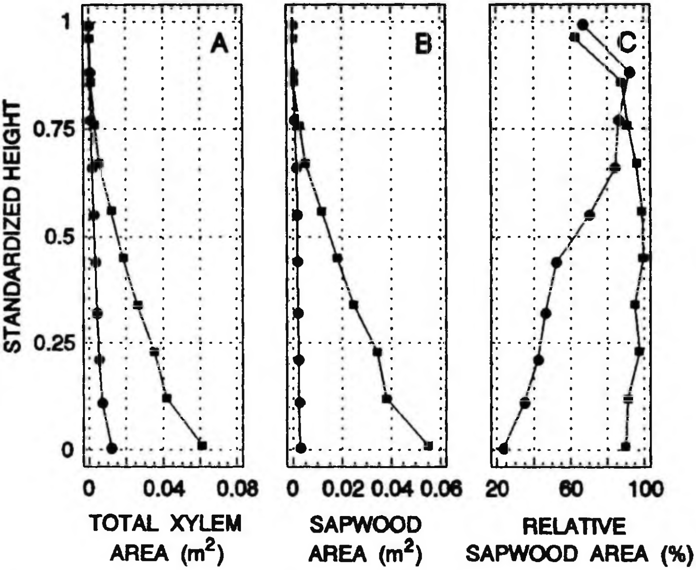

Fig. 1. Vertical variation of the trunk transverse area in the trees grown in a brown forest soil (*squares*) and a highbog soil (*circles*). **A**, total xylem area; **B**, sapwood area in absolute terms; **C**, relative sapwood area.

Spatial variation of **k** along the stem (Fig. 2A) as well as branches (Fig. 3A) holds a common pattern irrespective of the habitat type: **k** was maximal in the middle of the

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*not statistically significant at the level of probability 0.05

Table 2. Hydraulic properties of the xylem in the trunks and primary roots of the trees grown in contrasting edaphic conditions: 1 - a tree grown in a rich well-drained soil; 2 - a tree grown in a poor waterlogged soil.

TRUNK

Tree no.	Trunk length, m	Relative conductivity ($\times 10^{-12}$), m^2			Resistance ($\times 10^{14}$), Pa s m^{-3}
		Trunk base[a]	Trunk middle part[b] (mean ± S.E.)	Trunk top[a]	
1	14.84	1.75	3.21±0.08	0.75	0.4
2	7.65	1.66	2.80±0.34	0.21	7.2

PRIMARY ROOTS

Tree no.	Root length, m	Relative conductivity ($\times 10^{-12}$), m^2			Resistance ($\times 10^{14}$), Pa s m^{-3}
		Root base[a]	Root middle part[b] (mean ± S.E.)	Root tip[a]	
1	5.43	1.43	11.07±1.06	2.24	0.9
	5.70	0.76	11.16±0.36	2.04	2.6
2	10.40	1.59	7.04±1.78	0.35	52.3
	3.61	0.30	3.15±0.59	0.03	221.5

[a] Values based on measurements on one xylem segment

[b] Mean values based on measurements on four xylem segments

organ and declined in both basipetal and acropetal directions. Also the vertical variation of the Huber value (HV) in the stems of the sample trees was similar. HV was more or less constant in most part of the stem, averaging 0.70×10^{-6} $m^2 g^{-1}$ for the forest- and 0.43×10^{-6} $m^2 g^{-1}$ for the bog-grown tree, and increased sharply in the topmost part (Fig. 2B). The differences in the mean HV between the trees was highly significant ($P<0.001$). The vertical distribution of leaf-specific conductivity (LSC), contrary to that of k and HV, differed qualitatively in trees from different sites (Fig. 2C). In the forest-grown tree LSC was relatively constant in the most part of the stem (mean value 1.99×10^{-18} $m^4 g^{-1}$), except the top with its high value (3.54×10^{-18} $m^4 g^{-1}$). In the bog-grown tree LSC declined evenly in acropetal direction. The mean LSC for tree 1 exceeded 2-fold ($P<0.001$) that in tree 2. There were no salient differences in the spatial variation of the hydraulic characteristics of primary branches in the trees from contrasting sites (Fig. 3).

Distribution of xylem resistance. In the bog-grown tree the resistance (R) of the trunk exceeded by 1 order, and of single roots, nearly by 2 orders of magnitude the respective values of the tree grown in a forest soil (Table 2). It was impossible to compare the primary branches from this aspect, because of high variability of R for branches of the

Table 3. Hydraulic properties of the xylem in the primary branches of the trees grown in contrasting edaphic conditions: 1 - a tree grown in a rich well-drained soil; 2 - a tree grown in a poor waterlogged soil.

Tree no.	Branch length, m	Height above the ground, m	Relative conductivity ($x10^{-12}$), m^2			Resistance ($x10^{14}$), Pa s m^{-3}
			Branch base[a]	Branch middle part[b] (mean ± S.E.)	Branch top[a]	
1	3.45	2.38	0.64	1.22 ± 0.03	0.20	10.3
	2.78	6.70	0.49	1.79 ± 0.14	0.18	2.7
	1.25	12.19	0.43	0.86 ± 0.08	0.13	5.9
2	1.74	0.95	0.09	1.13 ± 0.07	0.74[c]	6.8
	1.91	3.44	0.59	1.37 ± 0.09	0.06	110.5
	0.58	6.86	0.20	0.65 ± 0.15	0.13	8.4

[a] Values based on measurement on one xylem segment

[b] Mean values based on measurements on four xylem segments

[c] The very top of the branch was died

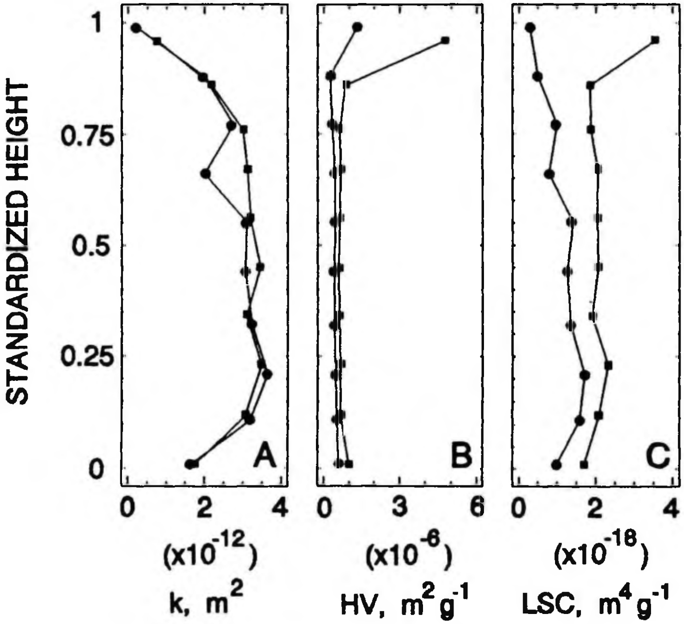

Fig. 2. Vertical variation of xylem hydraulic characteristics in the trunks of the trees grown in a brown forest soil (*squares*) and a highbog soil (*circles*). A, relative conductivity; B, Huber value; C, leaf-specific conductivity.

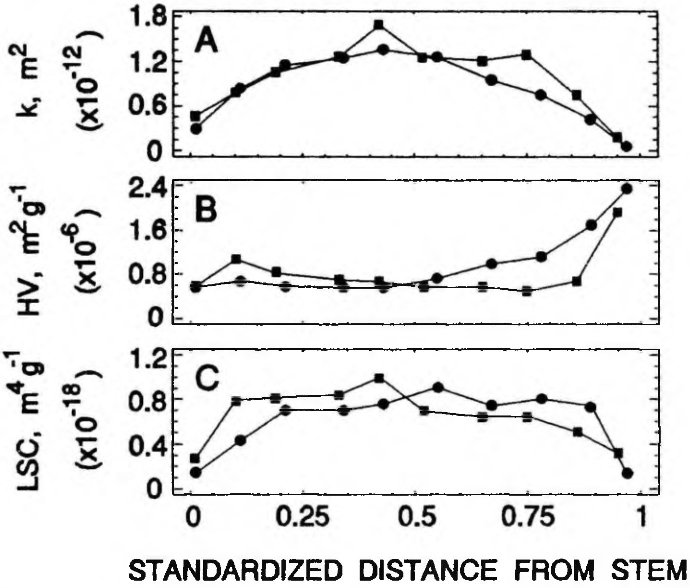

Fig. 3. Variation of xylem hydraulic characteristics in primary branches of the trees grown in a brown forest soil (*squares*) and a highbog soil (*circles*). **A**, relative conductivity; **B**, Huber value; **C**, leaf-specific conductivity.

bog-grown tree (Table 3). Spatial distribution of **R** within the stem holds a common pattern for both trees: **R** was the lowest in basal sections and increased with the growing of distance from the ground (Fig. 4). Most of the stem resistance is localized in the topmost part, while the nine lower sections make up only a small fraction of the trunk's total resistance. The same spatial pattern of xylem resistance holds also true for primary branches and roots.

The distribution of resistance between single segments of the water transport system varied in trees from different habitats (Tables 2 and 3). **R** for a trunk, a primary root and a branch were in the proportions 1:5:18 in tree 1 and 1:19:6 in tree 2. Our estimates suggest that the largest part of the summed resistance (i.e. primary roots, branches and trunk all together) in saturated conditions lies in trunk for the tree grown in a well-drained soil, and in the root system for the tree grown in a waterlogged conditions. The summed resistance was 0.5x10^{14} and 18.1x10^{14} Pa s m^{-3}, respectively.

Relative conductivity related to tree and xylem characteristics. The results of the analysis of variance are presented in Tables 4 and 5. The location of the sample segment, habitat, tree height and xylem type have no statistically significant effect on relative conductivity of the xylem. The estimations of variance for **k** related to relevant factors were obtained from the following system of equations:

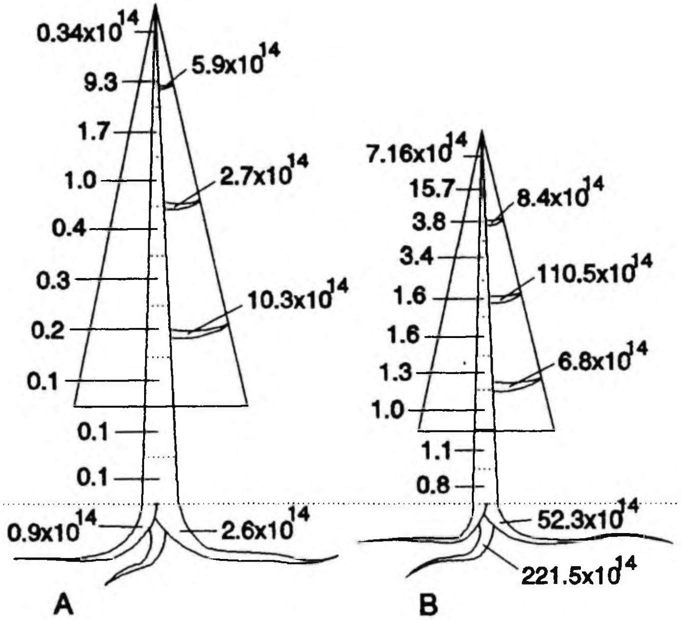

Fig. 4. Distribution of xylem resistances (Pa s m^{-3}) for the trees grown in a brown forest soil (A) and a highbog soil (B). The numbers in the diagram are to be multiplied by the factor of 10^{11} if not indicated otherwise.

$$\begin{cases} 87.96 = \sigma_e^2 + 15.56\sigma_r^2 \\ 9.04 = \sigma_e^2 + 20.33\sigma_a^2 \\ 9.58 = \sigma_e^2 + 13.68\sigma_d^2 \\ 1.05 = \sigma_e^2\,, \end{cases} \tag{12}$$

where σ_r^2, σ_a^2 and σ_d^2 are variances for **k** caused respectively by the tracheid radius, tree age and the diameter of the xylem segment, and σ_e^2 is a residual dispersion. The tracheid radius explained 73%, the diameter of the xylem segment 8% and tree age 5% of the total variation in **k**. For the tracheid radius the random model analysis of variance resulted in the following system of equations:

$$
\begin{cases}
1119.93 = \sigma_e^2 + 33.44\sigma_x^2 \\
227.69 = \sigma_e^2 + 12.59\sigma_h^2 \\
27.88 = \sigma_e^2 + 2.91\sigma_s^2 \\
59.01 = \sigma_e^2 + 13.11\sigma_l^2 \\
4.92 = \sigma_e^2 ,
\end{cases}
\qquad (13)
$$

where σ_x^2, σ_h^2, σ_s^2 and σ_l^2 are variances for **r** related to the xylem type, tree height, site type and location of the sample segment, respectively. The lumen radius of the tracheids depended significantly on the xylem type, tree height, habitat and location of the specimen, which described respectively 49, 26, 12 and 6% of the variability.

The stepwise regression analysis applied to the pooled data resulted in an empiric model relating **k** to the tracheid radius, diameter of the xylem segment and tree height.

$$
\mathbf{k} = 5.12\times10^{-16}\mathbf{r}^3 - 1.74\times10^{-13}\mathbf{d} + 5.92\times10^{-14}\mathrm{H} - 1.64\times10^{-13}, \qquad (14)
$$
$$
R^2=0.89 \;,\; S.E.E.=0.83\times10^{-12} \;,\; P<0.001 \;,
$$

where **r** is the mean lumen radius of the largest tracheids (μm); **d**, the diameter of the xylem segment (cm), and H, the tree height (m). All constants of the equation, except the free term, were highly significant ($P<0.001$). It can be seen from Figure 5 that there is a fair correspondence between the predicted and the observed values of conductivity.

Table 4. Results of the analysis of variance for relative conductivity (**k**).

Source of variation	Sum of squares	D.F.	Mean square	F-ratio	Sig. level
Tracheid radius	527.79	6	87.96	83.49	.0001
Segment diameter	67.05	7	9.58	9.09	.0001
Tree age	36.17	4	9.04	8.58	.0001
Residual	130.64	124	1.05		
Total (corr.)	868.57				

Table 5. Results of the analysis of variance for the tracheid inner radius (**r**).

Source of variation	Sum of squares	D.F.	Mean square	F-ratio	Sig. level
Xylem origin	2239.87	2	1119.93	227.44	.0001
Habitat	27.88	1	27.88	5.66	.0189
Tree height	910.78	4	227.69	46.24	.0001
Sample location	531.12	9	59.01	11.98	.0001
Residual	581.04	118	4.92		
Total (corr.)	4229.45				

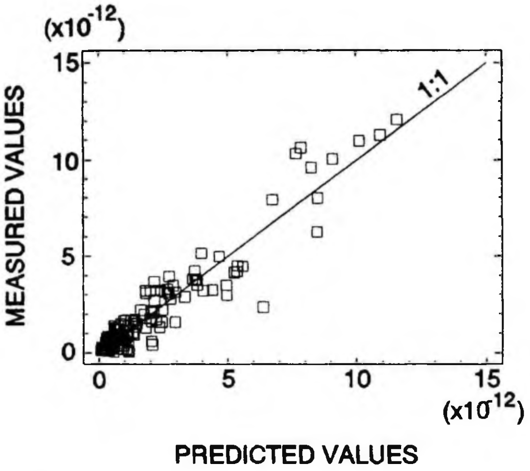

Fig. 5. Comparison between the predicted (by Eq. 14) and the measured values of xylem relative conductivity (cm^2). $R^2 = 0.89$, $P < 0.001$.

The variation of **k** depending on **r**, the most relevant characteristic, was analyzed in more detail. The data on three xylem types were treated separately for both habitats and the corresponding regressions were developed (Table 6). 79-95% of the total variation of **k** for tree 1, and 55-76% for tree 2 can be accounted for by **r** of the largest tracheids. One may conclude that xylem hydraulic conductivity in a water-saturated state depends to a significant extent on the diameter of conduits. The mean radii of the tracheids measured for the trees grown in a bog soil tended to be smaller as compared to those for the trees in a forest soil (Table 7).

Table 6. Regression equations relating relative conductivity of the xylem (**k**) to the mean lumen radius of the largest tracheids (**r**). **k** is in m^2 and **r** in μm. For all equations $P < 0.001$.

Forest site type	Xylem origin	Regression equation	R^2	S.E.E. $(x10^{-12})$
Hepatica	root	$k = 6.46x10^{-16}r^3 - 7.69x10^{-13}$	0.93	1.03
	stem	$k = 1.03x10^{-14}r^2 - 6.49x10^{-13}$	0.94	0.47
	branch	$k = 1.12x10^{-14}r^2 - 2.85x10^{-13}$	0.79	0.29
raised bog	root	$k = 1.82x10^{-17}r^4 - 7.56x10^{-14}$	0.76	1.36
	stem	$k = 3.96x10^{-16}r^3 + 2.81x10^{-13}$	0.55	0.75
	branch	$k = 1.06x10^{-15}r^3 - 1.33x10^{-13}$	0.69	0.28

Table 7. Lumen radius of the largest tracheids in the trees grown in contrasting site types.

Forest site type	Xylem origin	Lumen radius, µm	
		Range	Mean ± S.E.
Hepatica	root	6.9-30.2	$18.9^{a} \pm 0.43$
	stem	8.0-25.0	$18.7^{b} \pm 0.44$
	branch	4.5-17.3	$10.3^{c} \pm 0.23$
raised bog	root	9.9-27.7	$18.3^{a} \pm 0.50$
	stem	6.9-21.2	$17.4^{b} \pm 0.30$
	branch	3.4-12.9	$9.4^{c} \pm 0.18$

[a] The difference between the means is statistically not significant
[b] The difference is significant at 0.02 level of probability
[c] The difference is significant at 0.01 level of probability

Discussion

The aim of this study was to expand our understanding of the factors determining the resistance to the water flow through trees. The studying of the hydraulic architecture of the spruce trees grown in contrasting sites should provide information on the reaction norm of the tree's water-conducting pathway. The relative conductivity of the xylem in a tree grown in favourable soil conditions was 1.1-2.2 times as large as the **k** measured in a bog-grown tree (Tables 2 and 3). Lower **k** in the trees grown in a poor waterlogged soil can be attributed to smaller tracheids (Table 7), because there is a close relationship between **k** and **r** (Table 6). According to Poiseuille's equation the flow rate of a liquid volume through ideal capillaries is proportional to the fourth power of the capillary radius (Zimmermann 1983, Nobel 1991). Therefore, little differences in **r** are accompanied by substantial differences in **k**.

Waterlogged soil conditions have a complex consequence on physiological processes in plants. Generation of ATP in anaerobic glycolysis leads to a rapid and inefficient exhaustion of plant reserves (Fitter and Hay 1987). The wasteful use of energy resources is accompanied by the accumulation of potentially toxic end-products of fermentation, changes in the amounts of growth substances, disturbance of nitrogen metabolism, decline in contents of plant pigments, slowing down of the rate of ion and water uptake and transport in roots (Grossnickle 1987, Smit and Stachowiak 1988, Birner and Steudle 1993). A hypoxia and low nutrient availability, the factors combined in bog soils, result in low productivity of trees which is expressed in lower photosynthetic rate, depression of the extension as well as the radial growth, and high root mortality (Levan and Riha 1986, Veretennikov 1989, Dang et al. 1991). The effect of edaphic conditions on productivity for the spruce trees appears in drastically different basal areas (Fig. 1).

In spruce trees, **k** was proportional to the 2nd to 4th power of the tracheid radius, varying with the habitat and the xylem origin (Table 6). Although there is a causal relationship between **k** and **r**, it cannot be strictly consistent with Poiseuille's law in the present case, because only the largest tracheids of 3 outer growth rings have been taken into account. Besides, coniferous tracheids are sufficiently different from ideal capillaries by their structure, which presents various physical constraints to the water flow. There are reports suggesting that a lumen is not the main constituent of resistance to the fluid flow through a tracheid (Calkin et al. 1986, Schulte and Gibson 1988). Most of the resistance to the water flow in coniferous wood is accounted for by the margo of the bordered pits. Close correlation between **k** and **r** for spruce xylem can be explained by the fact that the tracheid diameter is related to its length, pit diameter, area of pit membranes, number of pits, and the dimensions of the pit cavity and canal (Calkin et al. 1986, Schulte and Gibson 1988, Jinxing 1989), the anatomical characteristics all having impact on xylem permeability.

The mean **r** of the largest tracheids described 73% of the total variation in **k** for all spruce trees taken together. The diameter of the xylem segment and the tree age explained only a small part of the variation, although their impact on **k** was highly significant (Table 4). Applying the stepwise regression analysis to metric variables, the tree height instead of its age was incorporated into the model (Eq. 14). Pothier et al. (1989) have also reported for *Pinus banksiana* Lamb. that sapwood permeability is well correlated with the tree height within younger age classes. Tracheid radius in turn depended on the xylem origin, tree height, habitat and location of the specimen (Table 5). The habitat type has no essential effect on **k** for pooled data, however, there was a statistically significant ($P < 0.01$) difference for rootwood between the sites. Thus, we can draw a conclusion that waterlogged conditions have impact primarily on the formation of rootwood - the part of the tree which is under immediate influence of unfavourable environmental conditions. In *Abies balsamea* (L.) Mill., for comparison, **k** of sapwood was correlated with tracheid radius, tree age, diameter and height, while the linear regression of sapwood conductivity from tracheid length, site quality or basal area increment was not statistically significant (Coyea and Margolis 1992).

The mean HV for the stem of a tree grown in well-drained soil is about 1.6 times as large as that for a bog-grown tree. Consequently, there are more needles supported by the unit area of sapwood for a tree growing under waterlogged conditions. The difference in LSC for the stem was even greater in the sample trees: the potential water transport capacity of the stem per unit amount of foliage for a tree in a forest soil is at an average 1.8 times higher as compared to the tree under waterlogged conditions. The differences in HV and LSC in trees are explicable with the degree of the risk of water deficit, which could lead to a catastrophic xylem dysfunction due to embolism and a consequent desiccation-induced leaf loss (Tyree and Sperry 1988, 1989). The trees in a well-drained soil growing at a higher risk of water stress have a water transport system with a larger margin of safety, i.e. a larger conducting area of the xylem per unit amount of foliage and a higher transport capacity helping to avoid critical xylem tensions. The trees growing in a waterlogged soil, on the contrary, do not face the unavailability of water, and neither a redundant sapwood area nor high relative conductivity are required. Similar results have been obtained in experiments with *Fraxinus pennsylvanica* Marsh.: LSC was significantly larger in drought-stressed versus well-drained seedlings (Shumway et al. 1991). As for the hydraulic characteristics of branches, there were no significant differences between the spruce trees at the two habitats.

The resistance to water movement through the trunk and roots in a bog-grown tree exceeds by 1 to 2 orders of magnitude that of a forest-grown tree (Table 2). The distribution of the resistance between single segments of the vascular system indicates that the contribution of roots to the overall resistance for the trees grown in a waterlogged soil is considerably greater than that for the trees under well-drained conditions. The summed xylem resistance of the spruce tree grown in favourable edaphic conditions was 5×10^{13} Pa s m^{-3}, a value comparable with the total resistance published for *Picea sitchensis* (Bong.) Carr. - 1×10^{13} (Hellkvist et al. 1974) and *Malus domestica* Borkh. - 10×10^{13} Pa s m^{-3} (Landsberg et al. 1976). The resistance for the spruce tree grown in a poor waterlogged soil was much higher - 181×10^{13} Pa s m^{-3}. The contrasting difference arises primarily from a small sapwood area (Fig. 1), but also from lower **k** (Tables 2 and 3) as well as smaller number of branches (Table 1) in the bog-grown tree. Our results agree with those reported for other conifers in literature. Flooded seedlings of *Picea mariana* (Mill.) B.S.P. and *Picea glauca* (Moench) Voss have a greater resistance to the water flow compared with nonflooded seedlings (Grossnickle 1987). Sapwood resistance in *Pinus banksiana* Lamb. increases with the decreasing of site index (Pothier et al. 1989).

The estimations suggest that the largest share of the summed resistance of the trunk, primary branches and roots in Norway spruce resides in the root system for the trees grown in a waterlogged soil, and in the trunk for the trees grown in a well-drained soil. Our results show that there is no universal distribution of xylem resistance among the stem, primary roots and branches for the trees in whatever ecological situation, but it seems to be affected by growth conditions. Furthermore, the relative distribution of xylem resistance should be considered a dynamic rather than a static phenomenon. A spatial pattern of hydraulic resistances, being highly dependent on the xylem water status, will likely change as soon as water deficit develops. However, our results do not rule out the occurrence of the largest resistance in minor branches of higher orders.

The distribution of resistance within the stem is of common regularity for the trees from both sites: most of the stem resistance is localized in the top. The resistance of the topmost section of the trunk in Norway spruce is of the same magnitude as **R** for primary branches (Fig. 4). Low resistance to water flow throughout most of the trunk, except the top, creates more equal prerequisites for water supply for the branches situated at different heights in the crown. Without this, the branches near the base of the tree would be hydraulically favoured over the branches at the apex and the shoots at tree's top would be subjected to a chronic water deficit due to the long distance and the gravitational forces.

To summarize, the spruce trees grown in contrasting edaphic conditions differ significantly in resistance to water flow in the xylem. This difference is explainable more by a smaller conductive area of the xylem than by lower xylem permeability in bog-grown trees.

Acknowledgments

I am grateful to Dr. Olevi Kull, Institute of Ecology, Estonian Academy of Sciences, for critical remarks and helpful comments on the manuscript. Special thanks are due to Dr. Tõnu Möls, Tartu University, for helping with statistical data processing and to Mrs. Evi Vaik for improving the English text.

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