

Trees as a water transport system

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TIIVISTELMÄ: PUUN RAKENNE VEDENKULJETUSSYSTEEMINÄ

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The structure of 20 Scots pine (*Pinus sylvestris* L.) trees was analyzed as a water transport system. There is a tight linear regression between the cross-sectional area of the stem at the height of its lowest living branch and the cross-sectional area of its roots, between the cross-sectional area of the stem at the height of its lowest living branch and the total cross-sectional area of its branches, and between the cross-sectional area at the base of a main branch and the total cross-sectional area of its subsidiary branches. The capacity of successive organs, measured as cross-sectional areas, to transport water was thus found to be regular within a tree.

Työn lähtökohtana on hypoteesi, että veden kuljetus on määräävä tekijä puun rakenteen muodostumisessa. Tällöin puun peräkkäisten vedenkuljetussysteemien (paksut juuret, runko, oksat ja sivuoksat) vedenkuljetuskapasiteetin tulisi vastata toisiaan.

Työssä havaittiin, että paksujen juurten ja elävän latvuksen alarajan kohdalta mitatun rungon poikkileikkauspinta-alojen välillä on voimakas lineaarinen regressio. Samoin elävän latvuksen alarajan kohdalta mitatun rungon ja oksien yhteenlaskettujen poikkileikkauspinta-alojen välillä sekä oksan tyven ja oksan sivuoksien yhteenlaskettujen poikkileikkauspinta-alojen välillä on voimakas lineaarinen regressio. Lisäksi puun ja oksan sisällä on voimakas regressio rungon poikkileikkauspinta-alan ja yläpuolella olevien oksien yhteenlasketun poikkileikkauspinta-alojen sekä oksan poikkileikkauspinta-alan ja sivuoksien poikkileikkauspinta-alojen välillä. Saadut kokeelliset tulokset tukevat selvästi lähtökohtana olevaa hypoteesiä.

Keywords: cross-sectional area, stem, coarse roots, branches, water transport system, *Pinus sylvestris*
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Introduction

Establishing whether or not regularities exist in the structure of trees represents a valuable tool for estimating the current state and growth of tree stands. Such relationships have often been derived on a purely empirical basis, for example the allometric power laws (Ledig 1969). It seems reasonable to assume, however, that if structural regularities exist, they should be associated with functional systems that are dependent upon such structures. A balance between structure and function makes the system more efficient from the point of view of energy and material consumption, and can hence be expected to have increased in proportion during the course of evolution. If this is true, then it would appear that structural regularities are derived from the requirements of metabolic function.

There is a lot of empirical evidence to indicate that the cross-sectional area of tree

stems is correlated with the leaf area, i.e. the transpiring tissue (e.g. Rogers & Hinckley 1979, Waring et al. 1980, Kaufman & Troendle 1981, Waring et al. 1982). A theoretical basis for this relationship has been suggested in the pipe model theory presented by Shinozaki et al. (1964a, 1964b).

Both empirical and theoretical considerations emphasize that trees have a balanced structure in which the size of the transporting tissue is related to that of the consuming tissue. The present paper is a further development of the idea. We examine the relationship between the size of different transporting tissues. The cross-sectional areas of the coarse roots, the branches and the stem of Scots pine (*Pinus sylvestris* L.) are considered within the framework of a physical analogy model.

Theory and model

The water transporting tissue in the stem and branches of coniferous trees is formed of elongated tracheid cells. Water movement between tracheids is facilitated by numerous pits in the tracheid walls. The water transporting part of the tracheids, as well as the water transporting capacity of the pits, is smaller in latewood than in earlywood (Bauch et al. 1972). Compared with the vertical water flow, the horizontal flows between growth rings are negligible. The velocity of the water flow in conifers is less than 1 m/h (Huber 1956). This means that the flow of water is non-turbulent.

A physical model of water flow in the stem and branches can be derived by forming hydrodynamical equations describing the flow through the tracheids and pits between the tracheids. The macroscopical properties of the water flow can then be derived from the microscopical model. Many difficulties will, however, arise because of the complicated structure of the conducting system. A different approach to modelling the physical situ-

ation is adopted in this paper. The main physical properties of the water flow are described by means of an approximate model.

Compared with the outside dimensions of pine, the tracheids are so small that fluctuations in the flow between single tracheids can be neglected. The process is approximated by a steady, laminar flow, i.e. there are no oscillations in the flow over time. The water is running in sheaths arranged inside one another. A sheath thus describes a growth ring. It is assumed that there is no movement of water between the sheaths.

The essence of the above assumptions is that the storage of water in the stem remains constant and that the dimensions of the growth rings do not change. It is therefore a question of an analogy model which is applicable to long-term considerations only. The velocity of the steady flow could be interpreted as the mean annual velocity of water flow through the growth rings, but the analysis below is not confined to any particular interpretation.

Let dA be an infinitesimal area in a sheath. Let v be the velocity of the water moving along the sheath. The water volume dQ flowing through the area dA in unit time is

$$dQ = v dA. \quad (1)$$

The mean velocity of the flow over the cross section of a sheath is defined as

$$v' = \frac{Q}{A} = \frac{1}{A} \int_A v dA, \quad (2)$$

where A is the cross-sectional area of the sheath.

Consider the flow of water at two heights h_a and h_b . Denote the cross-sectional areas with A_a and A_b , velocities with v_a , v_b and mean velocities v'_a , v'_b correspondingly. It follows from the conservation of mass that

$$\int_{A_a} v_a dA_a = \int_{A_b} v_b dA_b. \quad (3)$$

Eqs. (2) and (3) yield, when combined,

$$v' A = \text{constant}. \quad (4)$$

Let A_s be the cross-sectional area of a growth ring in the stem and v'_s the corresponding mean velocity of flow. Let A_i , where $i = 1, \dots, n$, be the cross-sectional areas of the same growth ring in the main branches above the point in the stem where A_s is measured. Let v'_i be the corresponding mean velocities in the branches.

Using the conservation of mass, the amount of water flowing through the stem and through the branches, are obtained

$$A_s = \frac{1}{v'_s} \sum_{i=1}^n v'_i A_i. \quad (5)$$

This equation can be generalized to a set of sheaths one inside the other, i.e. to the whole cross-sectional areas of the stem and main branches.

If it is assumed that the mean velocity of the water flow is the same in all the main branches, then the model predicts that there is a linear regression between the cross-sectional area of the stem and the sum of the cross-sectional areas of the main branches above this part of the stem, i.e.

$$A_s = \frac{v'_b}{v'_s} \sum_{i=1}^n A_i. \quad (6)$$

v'_b is the mean velocity of water in the branches.

The present article analyses the structure of a number of Scots pine trees within the framework of Eq. (6). The objective is to examine whether or not such a correlation exists, whereas the interpretation of the correlation coefficients in terms of real water flow velocities is not attempted. The relationship between the stem and the branches is analysed as indicated above, and the analysis is further extended to the analogous case of the stem and the coarse roots.

Methods and material

The study was carried out in a 40-year-old Scots pine (*Pinus sylvestris*) stand situated near the field station of the Forest Institute of the Karelian branch of the Akademia of Science, USSR, 50 kilometres from Petroszawodsk. The stand had regenerated naturally after a forest fire. The soil at the site consisted of sand, and the site was of the Calluna site type according to the classification of Cajander (1946). The variation in the size, age and density of the stand was rather large. The mean diameter was 4.5 cm, the mean height

was 5.7 m, and the volume was 75 m³ ha⁻¹.

The diameters of the large roots, stem, main branches and intermediate branches were measured under bark to an accuracy of 0.2 mm. The stems and branches were measured near to the mid-point between successive whorls. The diameter of the roots was measured at the point where the rapid tapering of the roots ceased and the root attained a stable diameter. The location of each measuring point was determined subjectively.

Results

As the large roots supply water to the stem, the cross-sectional area of the water transporting tissues in the stem and in the large roots should follow Eq. (6). The regression between the total cross-sectional area of the roots and the cross-sectional area of the stem at the height of the lowest living branch is shown in Fig. (1). The amount of water flowing in the stem is the same as that flowing through the branches. Thus Eq. (6) should also hold for the cross-sectional area of the stem and the sum of the cross-sectional area of the branches. The regression between the cross-sectional area of the stem at the height of the lowest living branch and the total cross-sectional area of the branches in a tree is shown in Fig. (2). A pine branch and a whole pine tree have the same geometrical structure: the leading shoot of a branch corresponding to the stem and the subsidiary branches of a branch corresponding to the main branches extending from the stem. The regression between the cross-sectional area at the base of a main branch and the total cross-sectional area of its subsidiary branches is close (Fig. (3)).

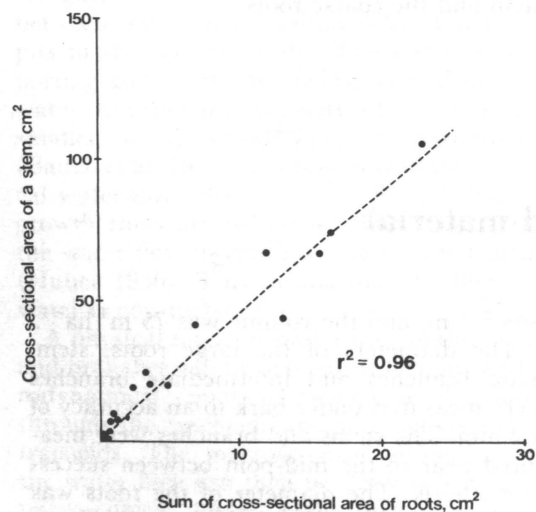


Fig. 1. The regression between the cross-sectional area of a stem at the height of its lowest living branch and the sum of the cross-sectional area of its roots.

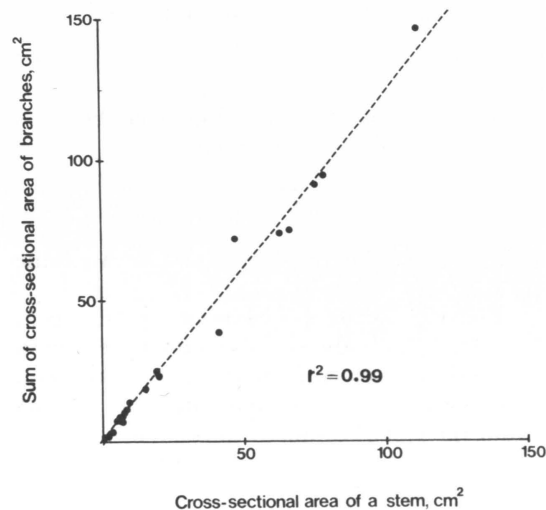


Fig. 2. The regression between the cross-sectional area of a stem at the height of its lowest living branch and the sum of the cross-sectional area of its branches.

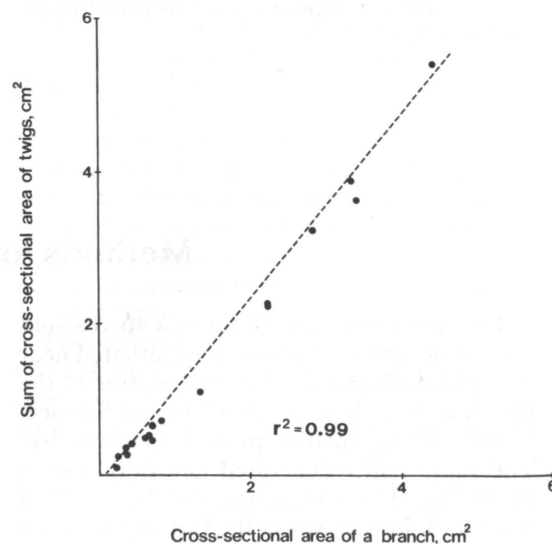


Fig. 3. The regression between the cross-sectional area at the base of a branch and the sum of the cross-sectional area of its subsidiary branches.

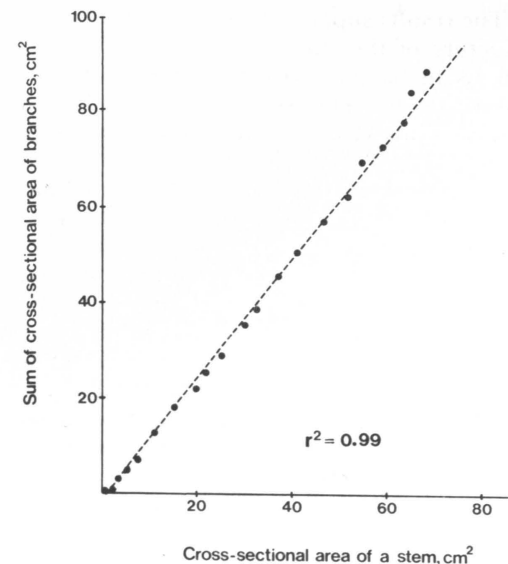


Fig. 4. The regression between the cross-sectional area of a stem at the mid-point of successive whorls and the cross-sectional area of the branches above the measuring point.

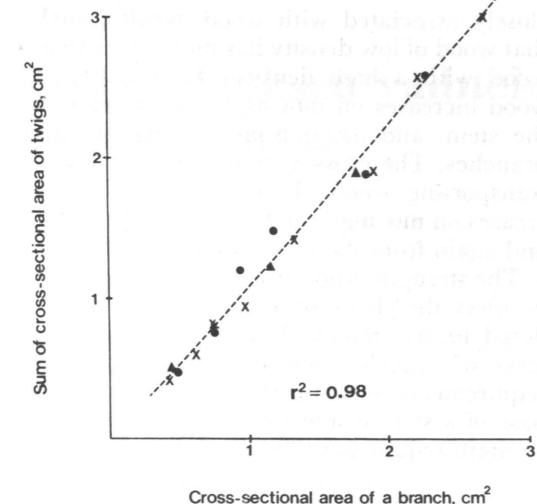


Fig. 5. The regression between the cross-sectional area of three branches at the mid-point of successive subsidiary branches and the sum of the cross-sectional area of its subsidiary branches "above" the measuring point on the branch. Each branch is marked with its own symbol.

The cross-sectional area of a stem and the total cross-sectional area of the main branches above a point can also be analyzed within a tree. As the observations are no longer independent of each other, a high degree of inter correlation can be expected. For this reason, the main interest should be focused on the form of the regression. The regression for an example tree is presented in

Fig. (4). Laasasenaho (1982) has reported the cross-sectional area of the stem and the sum of the cross-sectional area of the branches as a function of height in three trees. The results are in agreement with the close linear regression found in this study between the cross-sectional areas. The same type of regression can also be determined for a main branch and its subsidiary branches (Fig. (5)).

Discussion

It is clearly apparent from Figs. (1) – (5) that the relationships between the cross-sectional areas tend to be linear. The lower measuring accuracy of the roots is reflected as a greater degree of variance in Fig. (1) than in Figs. (2) and (3), which are based on more exact measurements. There are two points in Fig. (2) which lie outside the general regression lines. The general shape of these trees

differed from the norm for the stand: one had very short and the other very long branches. The regressions within a tree also seem to be linear in Figs. (4) and (5).

According to the hypothesis, the slopes of the straight lines in Figs. (1) – (5) are determined by the mean velocity of the water flow. The water transport capacity of the wood in the different parts of a tree is determined to a

great extent by the cross-sectional area of the pores of the tracheids. The area of pores is closely associated with wood density, such that wood of low density has more pores than wood with a high density. The density of wood increases on moving from the roots to the stem, and again from the stem to the branches. The cross-sectional area of water-transporting wood (Figs. (1) and (2)) increases on moving from the roots to the stem, and again from the stem to the branches.

The strength properties, which undoubtedly affect the shape of a tree, are not considered in this model. It is evident that the forks of branches are affected by strength requirements and also that the shape of the base of a stem is affected by the mechanical strength requirement (Ylinen 1952).

The results support the hypothesis that the structure of the transporting tissue of Scots pine is in balance with the water transport requirements. The systematically collected empirical material is so far limited only to a single stand. The results should be confirmed by measuring additional stands representative of stands growing on different site types and of different origin. The correlations between the cross-sectional area of the stem and the amount of leaves or needles could be generated by a balanced system of water transport and transpirative demand. Thus the observations of Kaufman and Troendle (1981), Waring et al. (1982) and Albrektsen (1984) suggest that the result can be extended to cover several tree species.

References

- Albrektsen, A. 1984. Sapwood basal area and needle mass of Scots pine (*Pinus sylvestris*) trees in central Sweden. *Forestry* 57: 35–43.
- Cajander, A. 1949. Forest types and their significance. *Acta Forestalia Fennica* 56 (5): 1–71.
- Bauch, J., Liese, W. & Schulz, R. 1972. Morphological variability of the bordered pit membranes in gymnosperms. *Wood Sci. Technol.* VI: 165–184.
- Huber, B. 1956. Die Gefäßleitung. In Ruhland, W. (ed.) *Handbuch der Pflanzen Physiologie* 3: 541–582.
- Kaufman, M. R. & Troendle, C. A. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *Forest Sci.* 27 (3).
- Laasasenaho, J. 1982. Taper curve and volume functions for pine, spruce and birch. *Communications Instituti Forestalis Fenniae* 108.
- Ledig, F. T. 1969. A growth model for tree seedlings based on the rate of photosynthesis and the distribution of photosynthate. *Photosynthetica* 3 (3): 263–275.
- Rogers, R. & Hinkley, T. M. 1979. Foliar weight and area related to current sapwood area in oak. *For. Sci.* 25 (2): 298–303.
- Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964. A quantitative analysis of plant form – the pipe model theory. I Basic analysis. *Jpn. J. Ecol.* 14: 97–105.
- , Yoda, K., Hozumi, K. & Kira, T. 1964. A quantitative analysis of plant form – the pipe model theory. II Further evidence of the theory and its application in forest ecology. *Jpn. J. Ecol.* 14: 133–139.
- Waring, R. H., Thies, W. G. & Muscato, D. 1980. Stem growth per unit of leaf area: A measure of tree vigour. *For. Sci.* 25 (1): 112–117.
- Ylinen, A. 1952. Über die Mechanische Shaftformtheorie der Bäume. *Silva Fennica* 76.

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