Silva Fennica 1986, vol. 20 n:o 2: 91–105

Architecture of Scots pine crown: phytometrical characteristics of needles and shoots

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TIIVISTELMÄ: MÄNNYN NEULASTEN JA VERSOJEN FYTOMETRINEN RAKENNE

Ross, J., Kellomäki, S., Oker-Blom, P., Ross, V. & Vilikainen, L. 1986. Architecture of Scots pine crown: phytometrical characteristics of needles and shoots. Tiivistelmä: Männyn neulasten ja versojen fytometrinen rakenne. Silva Fennica 20(2): 91–105.

Dimensions (length, width and thickness) of needles in crowns of young Scots pines (*Pinus sylvestris* L.) were found to be related linearly to each other. Similarly, the needle area was linearly correlated with the needle biomass. In the lower crown, needle length was linearly correlated with the length of the shoot, but in the upper crown needle length did not vary according to any regular pattern. Needle density was negatively correlated with shoot length. In the lower crown the needle density varied 20–40 cm^{-1} and in the upper crown 15–20 cm^{-1}. The increasing needle angle of aging needles seemed to be characteristic for Scots pine shoots.

Tutkimuksen mukaan männyn (*Pinus sylvestris* L.) neulasten pituuden, leveyden ja paksuuden välillä vallitsee lineaariset regressiot, joiden kulku oli kasvupaikan hyvyydestä riippumaton. Myös neulasten biomassan ja niiden pinta-alan välillä vallitsi lineaarinen riippuvuus. Latvuksen alaosassa neulasten pituus oli lineaarisesti riippuvainen vastaavan verson pituudesta toisin kuin latvuksen yläosassa, jossa ko. riippuvuus vaihteli säännöttömästi. Latvuksen alaosassa oli neulastiheys 20–40 ja yläosassa 15–20 neulasta/cm. Neulaskulma kasvoi verson vanhetessa. Tehtyjen mittausten perusteella on laadittu yleinen menetelmä männyn latvukseen neulaspinta-alan määrittämiseksi.

Key words: *Pinus sylvestris*, needle dimensions, shoot structure, phytometrical regressions

ODC 174.7 *Pinus sylvestris* + 53 +164.5+181.6

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Approved on 16. 4. 1986

1. Introduction

For modelling of forest productivity, detailed information about forest radiation conditions, plant water status and CO_2 exhange is necessary. All these properties are highly dependent on the structure of the stand and on the architecture of the individual trees. For mathematical modelling of radiative transfer in the forest, in particular, the detailed phytometrical characterization of stand structure, crown structure and area distrubution of foliage inside the crown must be known. Seldom are all levels in the hierarchy of canopy structure described satisfactorily, however, because such analysis requires extensive work. The problems are especially great for coniferous forests (cf. Norman and Jarvis 1974, 1975).

The aim of this study was to investigate the structure of Scots pine (*Pinus sylvestris* L.) shoots in the context of stand structure as outlined above. In our approach the organization of the tree is divided into needle, shoot and tree levels, with the tree level representing the basic unit for the description of stand structure. In this report, however, we deal only with needle and shoot levels which will be outlined later.

This study is part of the joint project "Exchange of Energy and Mass in Boreal Coniferous Forests" organized by the Finnish and Soviet Academies of Science. The project is coordinated by Dr. Pertti Hari (Finland) and Professor Juhan Ross (USSR). The authors acknowledge the scientific interest and contructive support expressed towards this project by Dr. Hari, who has also reviewed the manuscript for the Finnish Forestry Society.

2. Outlines of stand structure

Reduction of light flux density on a given foliage element is due to shading by the other part of the same tree (within-tree shading) and to shading by the surrounding trees (Thornley 1976). The within-tree shading is determined by the inner structure of the tree, while between-tree shading is determined mainly by the structure of the stand. Between-tree shading affects the development of the tree structure. Thus, we can describe the interactions between the structure of the stand and the structure of an individual tree.

The structure of the crown of a coniferous tree is determined by the size, shape and spatial distribution of needles and branches within the crown. The needles are located on *shoots,* which can be considered to be the basic units of the branch structure and of the consequent crown structure. The outer shape of the shoots can be approximated by a cylinder, and the tree crown can be regarded as being composed of these cylinders in varying dimensions and orientations (Table 1).

Table 1. Basic parameters of the outlined model of stand structure.

Level of hierarchy	Parameter
Shoot structure	Needle dimensions Needle area Needle angle on the shoot Needle density on the shoot
Tree structure	Inclination of shoots Azimuth of shoots Shape of shoots Size of shoots Spatial distribution of shoots in the crown Density of shoots in the crown Crown shape of a tree
Stand structure	Density of trees Spatial pattern of trees Size distribution of trees

In describing the stand structure, a *tree* is a proper unit, that which aggregates shoots into tree structure. At the tree level density, spatial distribution, orientation, size and shape of individual shoots can be considered to be the basic properties of the tree structure (Table 1).

In describing the structure of a *stand* at tree level we must find density, spatial pattern, size and shape of individual trees, which are taken to be the basic units of a stand. A discrete size distribution of trees can be obtained by dividing the trees into classes according to height. All trees in a given class are then assumed to have the same geometrical shape (Table 1).

3. Methods and material

3.1. Address system for describing the structure of the crown

In this study the description of the crown structure is based on an address, which indicates the age, order and location of shoots inside the tree crown (see Fig. 1).

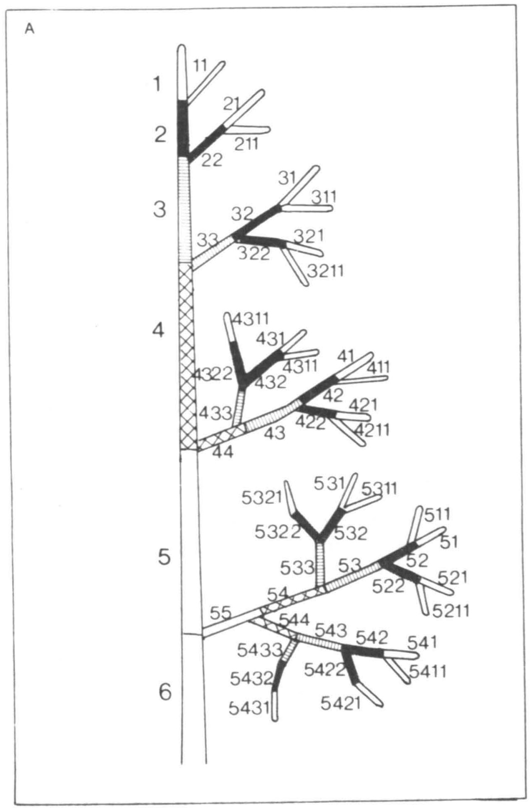


Fig. 1. Address system applied to describe crown structure in the hierarchical system.

The shoots of the main trunk, *i.e.* the annual height increments, are characterized by one-digit numbers. The shoots of a first-order branch are indicated by two-digit numbers, the first digit determining the order of the whorl on the trunk from the apex. The second digit in the address number denotes the order of the whorl on the first order branch from its top. The shoots of the second-order branch are indicated by three-digit numbers, the first digit determining the order of the whorl on the trunk form the stem apex. The second digit in the address number denotes the order of the whorl on the first-order branch, starting from the top of the branch. The last digit in the shoot address indicates the age of the shoots. In the same manner the shoots of the third-order branch are indicated by four-digit numbers, etc.

3.2. Description of crown structure

The crown structure is described in three phases (depicted in Fig. 2). First, the location of the shoot was determined using the orientation and location of the shoots in relation to ground level and to the trunk. Second, the shoot structure was characterized by the length and diameter of the shoot and its axis, the number of needles on the shoot and the needle angle of the shoot. Third, the needle structure was described by the length, thickness, width and dry weight of the needles. Thus, the needle is the basic unit of the shoots, which are described by the distributions of the needle dimensions.

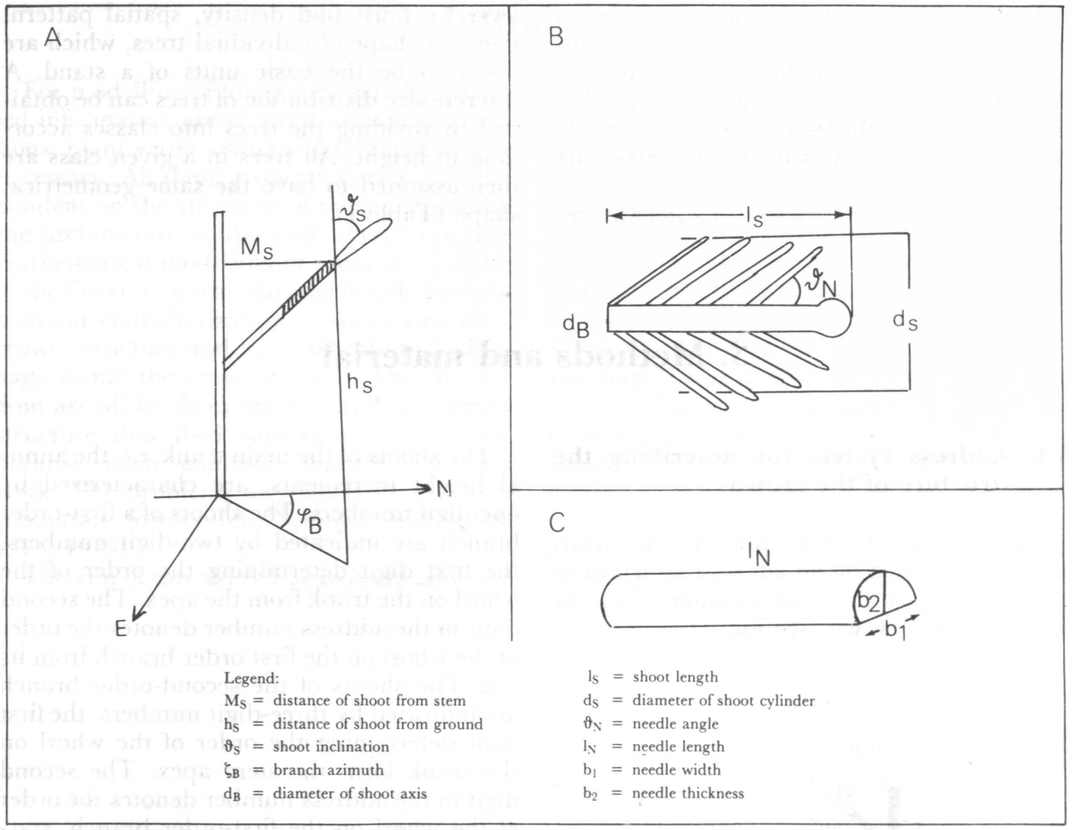


Fig. 2. Schematic presentation for measuring (A) shoot location, (B) shoot structure and (C) needle structure.

3.3. Study areas

The field measurements were carried out in tree young stands of Scots pine (*Pinus sylvestris* L.), two in Finland and one in Karelia, USSR. The study areas were located at approximately the same geographical latitudes (61°–62°), but different in history, age, stand architecture and soil type. The longitudinal difference between the easternmost and the westernmost study area was about 600 kilometers. Thus, the effects of actual site conditions and climatic differences on the crown structure of Scots pine can be compared for these areas.

The Finnish study areas were located near Hyytiälä Forest Field Station (University of Helsinki) and Mekrijärvi Biological Field Station (University of Joensuu). The stands were planted twenty years ago on morain soil of medium fertility, *i.e. Vaccinium* site type in a density of 3200 and 2000 stems per hectare. Both stands were homogeneous regarding tree height and stem diameter.

The study area in the USSR was located near the Forest Field Station of the Forest Institute (Academy of Sciences, USSR, Karelian branch) 50 kilometers north of Petrozawodsk. The site was characterized by sandy soil of the *Calluna* type, *i.e.* of poor fertility. The stand had regenerated naturally after a forest fire. The variation in height and diameter of the trees in the stand was rather large (Figs 3–4). The oldest trees were about 50 years old, the mean age being about 40 years. The spatial pattern of trees in the Finnish and Karelian stands are shown in Fig. 5.

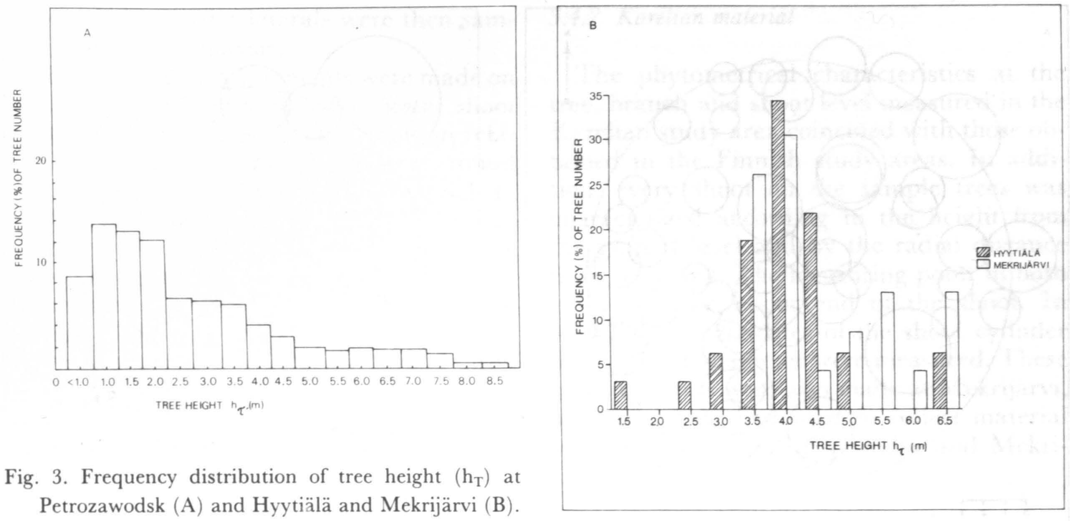


Fig. 3. Frequency distribution of tree height (h_T) at Petrozawodsk (A) and Hyytiälä and Mekrijärvi (B).

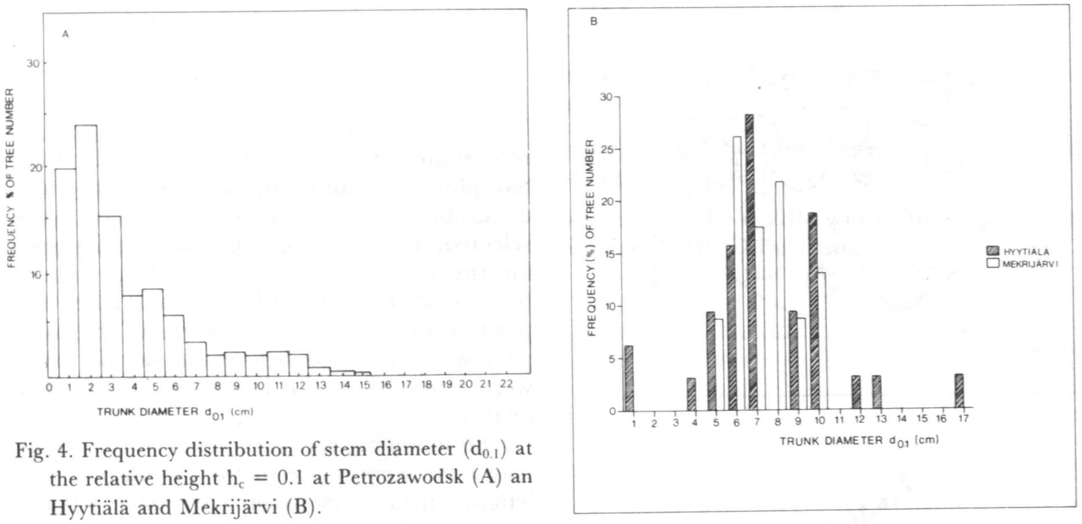
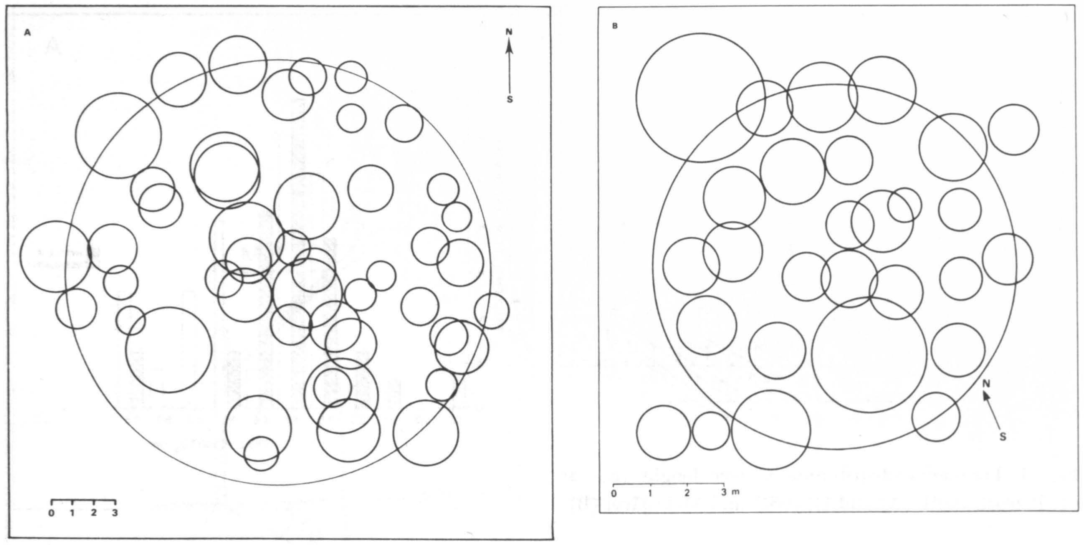


Fig. 4. Frequency distribution of stem diameter ($d_{0.1}$) at the relative height h_c = 0.1 at Petrozawodsk (A) an Hyytiälä and Mekrijärvi (B).

Comparison of the study areas showed that the stand at Mekrijärvi was the most homogeneous (spatial pattern, height distribution). For height distribution there were peaks at heights of 4–5 m and 6–7 m. The same was also true at Hyytiälä, with an additional peak at a height of 1 m. In Petrozawodsk young trees with a height of 1–2 m dominated, but there was a secondary maximum at heights of 3.5 and 7.5 m. Obviously, the natural seeding in Petrozawodsk has yielded a skewed distribution that emphasized the dominance of young trees, unlike the plantings at Hyytiälä and Mekrijärvi, for which the height distribution was close to the normal distribution. Analysis of the diameter distribution indicated similar regularities for diameter.



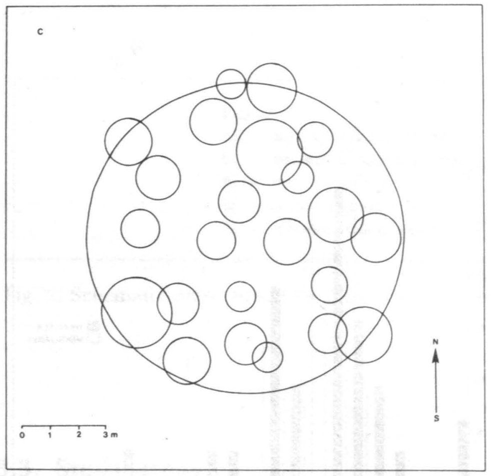


Fig. 5. Spatial pattern of trees in sample areas at Petrozawodsk (A), Hyytiälä (B) and Mekrijärvi (C).

3.4. Measurements

3.4.1. Finnish material

In the Hyytiälä study area the stem diameter distributions at 0.1 of relative height ($d_{0.10}$) and 1.3 m ($d_{1.3}$) above the soil level and the height distribution of the trees were determined in the first phase of the measurements over a sample area of 10 m × 10 m chosen from the study area. Thereafter, sample trees were selected so that each diameter class was represented by at least one sample tree. Sampling was similar in the Mekrijärvi study area, but only three sample trees were selected, representing the lower and upper fourths and the middle section of the diameter distribution. Coordinates and the tree position in relation to the points of the compass were recorded before the sample trees were removed to the laboratory for further analysis.

The following measurements of the whole *sample tree* were made in the laboratory: tree length, distance between successive whorls, number of branches per whorl, orientation of branches in each whorl, fresh weight of the branches in each whorl and stem diameter at the middle of the successive whorls (including dead whorls.) Thereafter, a branch of medium diameter (measured 2 cm outside the butt swell) was selected as the sample branch from each whorl (excluding dead whorls).

The following measurements were taken from the *sample branches*: length, orientation, distance between successive branch whorls, and number of second-order and third-order laterals. The current-year shoots of the second- and third-order laterals were then sampled for further analysis.

The following measurements were made on the sample representing *the shoots*: shoot length, shoot diameter, needle angle in relation to shoot axis, needle distribution around the shoot axis, needle dry weight (24 h, 105°C), shoot dry weight and length, thickness, as well as width and dry weight of five needles in the middle of the shoot. Thereafter, the shoot angle of the second-order shoot in relation to the first-order shoot, the distances between successive whorls of second-order shoots, and the dry weight of needles and the shoot axis were determined in the branch. In addition, the number of third-order shoots in the branch was counted.

3.4.2. Karelian material

The phytometrical characteristics at the tree, branch and shoot level measured in the Karelian study area coincided with those obtained in the Finnish study areas. In addition, every shoot on the sample trees was characterized according to the height from the ground level and by the radial distance from the trunk. The measuring point in both cases was the upper end of the shoot. In addition, the diameter of the shoot cylinder and the twig diameter were measured. These measurements were also made at Mekrijärvi, so that the method used to collect material was indentical in Petrozawodsk and Mekrijärvi.

4. Results

4.1. Needle dimensions

4.1.1. Relations between needles dimensions

Needle width and thickness were related linearly with a high proportion of explained variance ($r^2 > 0.9$) due to this regression (Fig. 6). The relationship can be described by Equation (1)

$$\text{Petrozawodsk: } b_2 = 0.62b_1 - 0.23 \quad (1)$$
$$\text{Hyytiälä: } b_2 = 0.43b_1 - 0.09$$

where b_1 is the needle width (mm) and b_2 is the needle thickness (mm).

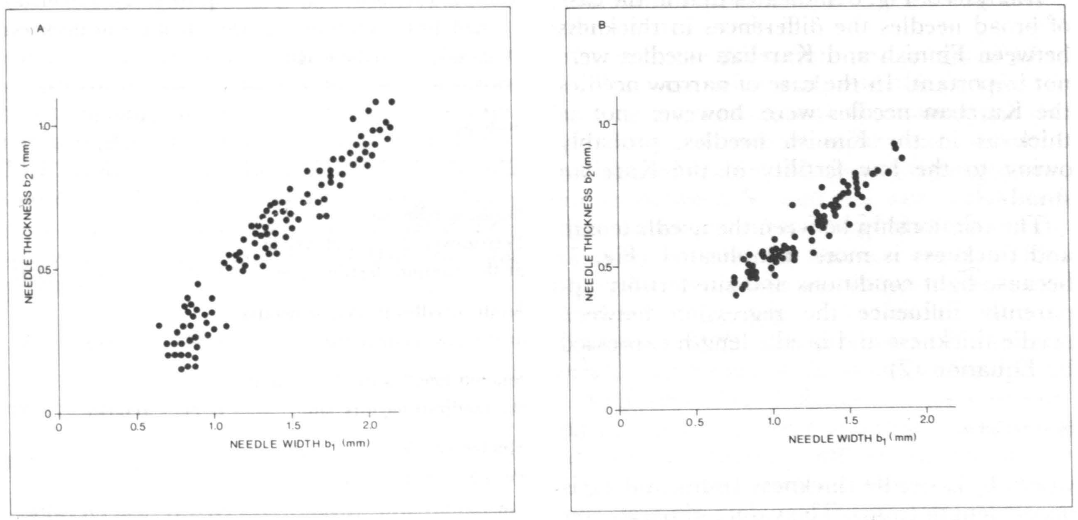


Fig. 6. Relationship between needle width b_1 and needle thickness b_2 at Petrozawodsk (A) and at Hyytiälä (B). Each point represents the mean value for ten needles of the same shoot.

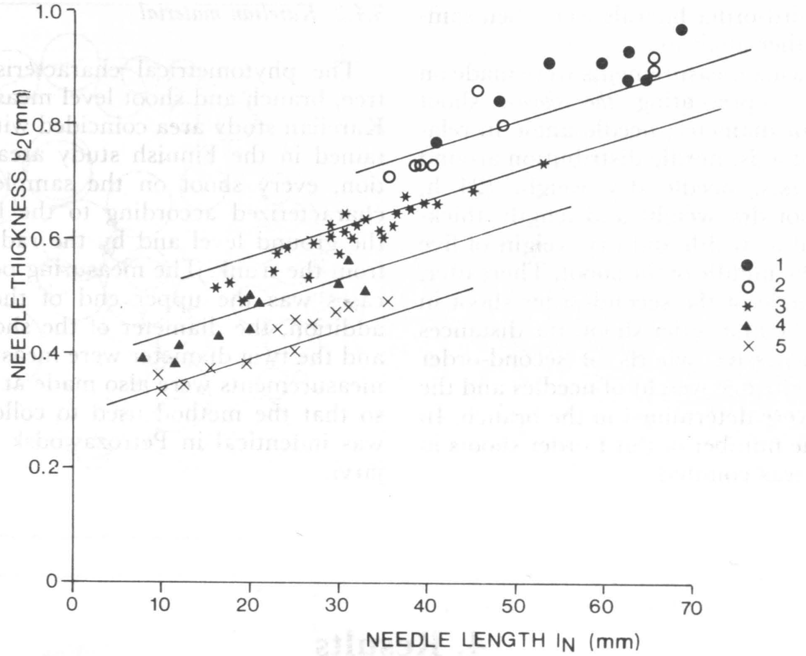


Fig. 7. Relationships between needle length l_N and thickness b_2 with the following legend for the figure:

1. Sunlit needles in Petrozawodsk at the medium fertility site
2. Sunlit needles in Hyytiälä at the medium fertility site
3. Sunlit needles in Petrozawodsk at the low fertility site
4. Shaded needles in Hyytiälä at the medium fertility site
5. Shaded needles in Petrozawodsk at the low fertility site

Analysis of Fig. 6. indicates that in the case of broad needles the differences in thickness between Finnish and Karelian needles were not important. In the case of narrow needles the Karelian needles were, however, not as thick as in the Finnish needles, probably owing to the low fertility of the Karelian stand.

The relationship between the needle length and thickness is more complicated (Fig. 7) because light conditions and site fertility apparently influence the regression between needle thickness and needle length expressed by Equation (2)

$$b_2 = b \cdot l_N + a \quad (2)$$

where b_2 is needle thickness (mm) and l_N is needle length (mm). The values of parameter a in Equation (2), for a constant value of b, in different cases are given in Table 2.

Table 2. Parameters (a, b) for Equation (2). The model had the from $b_2 = a + b\ l_N$, where b_2 is needle thickness and l_N is needle length.

Study areas	Parameters a	b	r²
Sunlit needles in Petrozawodsk[1] and Hyytiälä at the medium fertility site	0.56	0.0045	0.91
Sunlit needles in Petrozawodsk at the low fertility site	0.44	0.0045	0.84
Shaded needles in Hyytiälä at the medium fertility site	0.39	0.0045	0.93
Shaded needles in Petrozawodsk at the low fertility site	0.30	0.0045	0.65

[1] Needles taken from solitary trees

In particular, the value of the interception (parameter a) is dependent on the growing conditions. This means that at the same needle length the sunlit needles are thicker than the shaded ones. Similarly, the needles representing a medium fertility site are thicker than those representing a low fertility site.

4.1.2. Needle area and needle dimensions

The surface area of a needle is *a priori* a function of the needle dimensions, i.e. thickness, width and length, which are dimensions of the needle body. Equation (3) describes fairly well the relationship between the surface area and dimensions of the needle as demonstrated by Tirén (1926)

$$S_N = \frac{\pi}{2}\left(\frac{1}{2}\, b_1 + b_2\right) l_N + b_1 l_N \quad (3)$$

where S_N is the surface area (mm^2), b_1 the width (mm), b_2 the thickness (mm) and l_N the length (mm) of the needle.

Equation (3) can be further elaborated with the help of Equations (1) and (2) into a form in which the surface area of the needle, is given only as a function of its length. This relationship is given by Equation (4)

$$S_N = a_1 l_N + a_2 l_N^2 \quad (4)$$

where S_N is the surface area (mm^2), l_N the length (mm) and a_1 (mm) and a_2 the parameters of the needle. The values of the parameters are given for different cases in Table 3. The application of Equation (4) indicated that the surface area of short needles in Hyytiälä was somewhat smaller than that in Petrozawodsk. The opposite was true for long needles.

4.1.3. Area and dry weight of needles

Obviously, the needle surface area is also a function of the needle dry weight, as can be concluded on the basis of the above analysis.

Table 3. Parameter a_1, and a_2 for regression between needle area (S_N) and needle length (l_N) (Equation) as estimated for the different study areas. The model had the form $S_N = a_1 l_N + a_2 l_N^2$ where l_N is needle length

Study area	a_1	a_2
Sunlit needles in Petrozawodsk[1] at the medium fertility site	2.8	0.035
Sunlit needles in Hyytiälä at the medium fertility site	2.1	0.045
Sunlit needles in Petrozawodsk at the low fertility site	2.4	0.035
Sunlit needles in Hyytiälä at the medium fertility site	1.4	0.045
Shaded needles in Petrozawodsk at the low fertility site	1.8	0.035

[1] Needles taken from solitary trees.

Several methods were used in studying the regression between the surface area (S_N) and the dry weight (m_N) of the needles. First, the dry weight, length, width and thickness of each needle were measured and the needle surface area was calculated using Tirén's model (Equation 3). The results of these calculations are presented in Fig. 8 as the mean values of ten needles.

Second, the dry weight and length of 1000 needles were measured, and the correlation between m_N and l_N was determined for the total material without separating the sunlit and shaded needles. Moreover, the regression curves between S_N and m_N were calculated separately for sunlit and shaded needles using Equation (4) and the function m_N (l_N) (Fig. 8). Third, the needle surface area was calculated with the help of Tselniker's method (Tselniker 1982) on the basis of the dry weight and length of the needles (Fig. 8).

Analysis of Fig. 8 shows that for a certain needle class, *i.e.* sunlit or shaded needles or needles representing different levels of site fertility, the correlation between the surface area and the dry weight of the needle is curvilinear. If the dry mass density (ϱ_N) of the needles is assumed to be constant, the

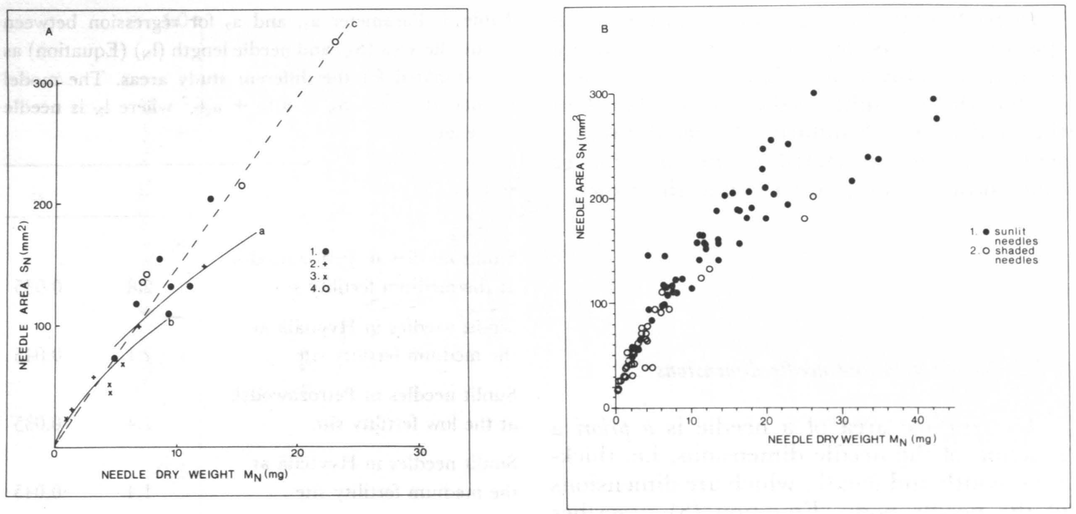


Fig 8. Relationship between needle dry weight m_N and needle area S_N at Petrozawodsk (A) and at Hyytiälä (B).

Legend for Petrozawodsk (section A)

1. Sunlit needle on the medium fertility site
2. Sunlit needle on the poor fertility site
3. Shaded needle on the poor fertility site S_N calculated by means of Tiren's formula.
4. S_N calculated from measurements of needle dry weight m_N and length l_N using Tselniker's method.

a. and b: sunlit and shaded needles correspondingly on poor fertility sites. S_N estimated by means of functions $m_N(l_N)$ and $s_N(m_N)$.
c. ecological relationship between needle area and dry weight m_N.

Legend for Hyytiälä (section B)

1. sunlit needles on medium fertility site
2. shaded nedleson medium fertility site

following relationships can be obtained for surface area and dry weight of the needles.

$$S_N = \text{const.} \times b_l l_N \quad (5)$$

(S_N proportional to $b_l l_N$)

and

$$m_N = \text{const.} \times b_l^2 l_N \varrho_N \quad (6)$$

(m_N proportional to $b_l^2 l_N \varrho_N$)

where S_N is the surface area (mm^2), m_N the dry weight (mg), b_l the width (mm), l_N the length (mm) and ϱ_N the dry mass density (mg mm^{-3}) of the needle. Consequently, the specific needle area can be written as follows

$$S_s = \frac{S_N}{m_N} = \text{const.} \times \frac{1}{b_l \varrho_N} \quad (7)$$

where S_s is the specific area (mm^2 mg^{-1}), S_N the surface area (mm^2), m_N the dry weight (mm), b_l the width (mm) and ϱ_N the dry mass density (mg mm^{-3}) of the needle.

Equation (7) indicates that an increase in the length and width of the needles results in a decrease in the slope of the curve S_N (m_N). The correlation between S_N and m_N is not very close, however, and within a certain needle class the deviation is noticeable. Thus, if we study the needles of different classes simultaneously, the correlation between S_N and m_N can be presented separately for different age classes and ecological conditions (cf. Fig. 8).

The regression curve for the relationship between the needle surface area and the needle dry weight in the total material is more linear than those of the individual needle classes (Fig. 8). In the case of the total material, the surface area is proportional to the dry weight of the needles as given in Equation (8)

$$S_N = 14.3 \, m_N \quad (8)$$

where S_N is the surface area (mm^2) and m_N the dry weight (mg) of the needles. The proportion of explained variance (r^2) was 0.93. Equation (8) should be considered as an ecological relationship between needle area and dry weight.

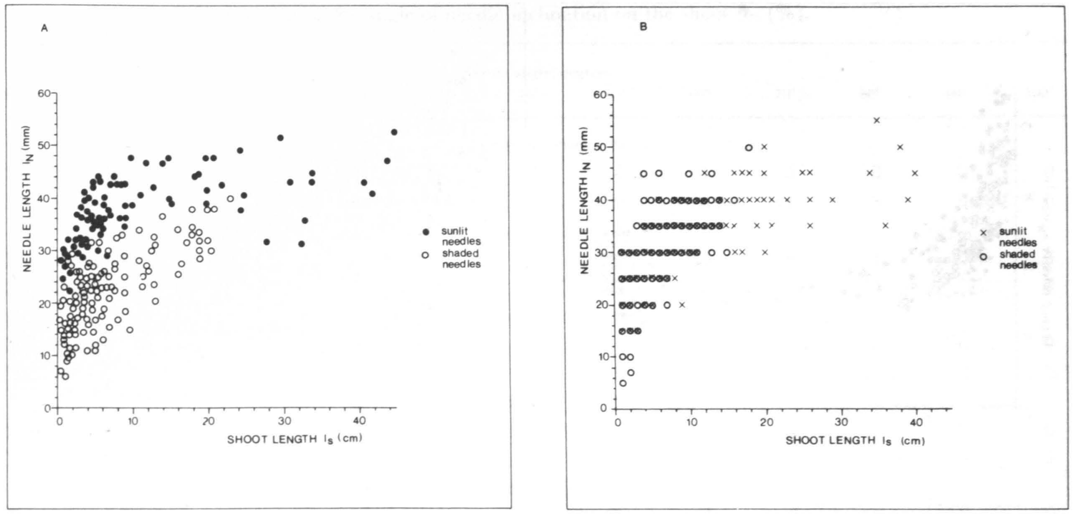


Fig 9. Relationship between shoot length l_s and needle length l_N at Petrozawodsk (A) and Mekrijärvi (B).

4.2. Shoot dimensions

4.2.1. Shoot and needle length

The methods outlined above for estimating the needle surface area of a shoot or of a whole tree are too laborious to be applied in practice. Therefore the relationship between the shoot dimensions and needle dimensions were evaluated in order to find a method that could estimate the needle surface area of a shoot or a whole tree in a simpler way than that based on the needle dimensions. One practical method proved to be that based on the regression between shoot length (l_S) and needle length (l_N), because shoot length is easily measured and interpreted in terms of needle length. The relationship between shoot length and needle length is demonstrated in Fig. 9.

Despite the broad scattering of the measurements, it seems reasonable to present the function $l_N(l_S)$ separately for sunlit and shaded needles, since the function $l_N(l_S)$ has the same shape for both. The functions for these needle categories differ, however, with respect to the interception of the regression curves, *i.e.* needles on sunlit shoots are one centimeter longer than those on shaded shoots. The function $l_N(l_S)$ is nearly the same for the Finnish and Karelian materials (Fig. 9).

4.2.2. Shoot length and needle density

Needle density (n_N) is also an important characteristic of a shoot. The correlation between needle density and shoot length is obvious, but there is an unexpected variation in this relationship (Fig. 10). Therefore shoots in the Karelian material were divided into three parts: (i) the trunk and first-order sunlit branches, (ii) the second-order sunlit branches and (iii) the third-order sunlit and all shaded branches.

Apparently, the needle density of sunlit needles or tree trunk and first-order branches is smaller than that on shaded branches or second-order branches. The needle density in the Finnish material is nearly the same but is more variable than in the Karelian material. In the Finnish material the different categories of shoot do not clearly differ as they do in the Karelian material.

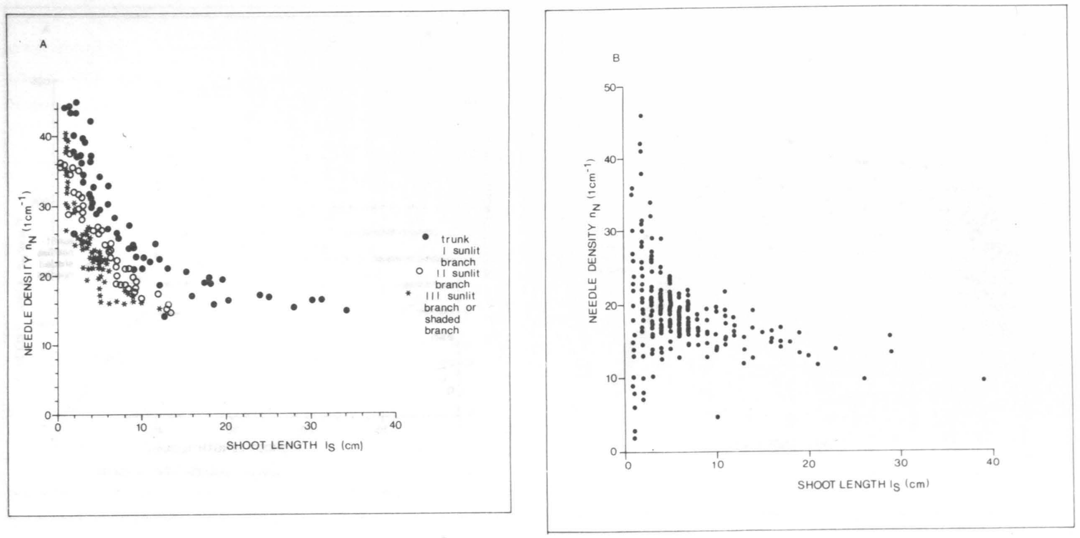


Fig. 10. Relationhip between shoot length l_S and needle density n_N at Petrozawodsk (A) and Hyytiälä (B).

4.2.3. Needle age

The great variability in needle density indicates the limited life span of the needles, *i.e.* over the course of time the needle density (n_N) decreases due to aging of the needles. We shall characterize the decrease in needle density over the course of time by means of the needle age factor (C_A), which is a function of the time in years. The needle age factor indicates the proportion of original needles present in a shoot at a particular time, expressed as value 0.0, . . . ,1.0. From the measurements of C_A made in Mekrijärvi and in Petrozawodsk we obtained the following values:

Needle age factor	Age of needles, years 1	2	3	4	5	6
C_A	1.0	1.0	0.8	0.5	0.1	0.0

During the first two years, the mortality of needles is negligible. Thereafter, the number of needles from a particular year decreases drastically so that we would not expect to find needles older than five years (cf. Tirén 1926).

4.2.4. Needle surface area of the shoot

As one would expect, the needle surface area of a shoot (S_{NS}) can be expressed as a function of the needle age factor, needle density, shoot length and needle surface area. With the help of Equation (9), this function is given as follows

$$S_{NS} = C_A n_N l_S \frac{S_N}{100} \qquad (9)$$

where S_{NS} is the needle surface area of a shoot (cm^2), C_A the age factor, n_N the density (1 cm^{-1}), l_S the shoot length (cm), and S_N the surface area of one needle (mm^2).

The relationship between the needle area of a shoot and the shoot dimensions can also be given in such a form that the shoot length is the only factor that has to be measured in order to determine the needle surface area of a particular shoot. First, needle density will be given as a function of the needle class and shoot length in terms $n_N(l_S)$ given in Table 5. Second, the needle surface area will be expressed as a function of the needle class and needle length in the term $S_N(l_N(l_S))$ given by Equation (4) and Table 2. Consequently, the needle surface area of a shoot calculated according to Equation (10) is as follows

$$S_{NS} = \frac{C_A \cdot l_S}{100} n_N(l_S) S_N(l_N(l_S)) \qquad (10)$$

where S_{NS} is the needle surface area of a shoot (cm^2), C_A the age factor, l_S the shoot length, $n_N(l_S)$ the function for the relationship between needle density and shoot length, and $S_N(l_N(l_S))$ the function between needle surface area and needle length, which is a function of shoot length (cf. Fig. 10). Thus for approximate calculations of the needle area of a shoot (S_{NS}), one only needs to know the site quality, the needle class of the shoot and the length of the shoot.

Table 4. Frequency distribution of the angle of needle inclination on the shoot ϑ_N (%).

Study area	Needle angle, degrees 10°	20°	30°	40°	50°	60°	70°	80°	90°	100°
			1st year needles, %							
Petrozawodsk	2	54	40	3	0	1	0	0	0	0
Mekrijärvi	1	5	16	25	20	18.5	11	3	0.5	0
			2nd year needles, %							
Petrozawodsk	1	2	6	13	42	35	0	1	0	0
Mekrijärvi	0	0	1.5	11.5	22	28	24	11	2.5	0
			3rd year needles, %							
Petrozawodsk	0	0	0	7	40	53	0	0	0	0
Mekrijärvi	0	0	1	8.5	19	23.5	27.5	17.5	2.5	0.5
			4th year needles, %							
Petrozawodsk	0	0	0	0	36	64	0	0	0	0
Mekrijärvi	0	0	2	7	16.5	22	33	15.5	3	1
			All years together, %							
Petrozawodsk	1	29	22	7	20	21	0	0	0	0

4.2.5. Needle angle

The needle angle in relation to the shoot axis together with needle length determines the diameter of the shoot cylinder, *i.e.* the surface area of the needle cylinder. According to Table 4, the needle angle (ϑ_N) apparently increases with the age of the needles. For the Karelian material the mean ϑ_N is about 25° for first-year needles, 50° for second-, 55° for third- and 60° for fourth-year needles.

There are, however, systematic differences between the needle angles of trees at Petrozawodsk and Mekrijärvi. The ϑ_N at Mekrijärvi is 10–20° greater than that in Petrozawodsk. The difference for the first- year needles is especially great. Thereafter, the needle angle distribution at Mekrijärvi is more uniform. Owing to the shape of the distribution function of ϑ_N for different years at Petrozawodsk, the total distribution function of ϑ_N for all needles is biomodal; the first maximum is about 25° and the second is about 55°.

5. Discussion

Coniferous trees are characterized by a complex hierarchy of trunk, branches, shoots and needles. In principle, this system should be described thoroughly, for example, for modelling the radiative transfer of tree stand; otherwise, only approximate estimates of the within-stand light regime can be obtained. The labour involved in such an analysis is nearly overwhelming, as we found during this study. In spite of this, the work is worth doing because it provides a solid basis for developing simpler and handier methods for characterizing the tree structure in order to model productivity of a tree stand.

Our approach to describing tree structure is based on an address system used for determinig the position of a shoot in the tree hierarchy. The system is the same as that suggested by Strachler on the basis of Horton's ordering of stream size hierarchy (Leopold 1971, McMahon and Kronauer 1976). Strachler's system has been useful for describing not only rivers but pulmonary arteries, and branching of coniferous trees. For example, computations of the address system provides a way of dealing with individual shoots in the context of the whole tree structure.

According to our results, the allometry between needle dimensions is clear, as demonstrated by Tirén (1926). Consequently, the area of a single needle can be determined in several ways utilizing, for example, needle length or needle mass. Due to the variation in site fertility and position of the needle in the crown, however, there is variation in the allometric relations between needle dimensions.

Therefore, precise analysis of the needle area of the whole crown demands that the influence of site fertility and light conditions also be considered. It was also apparent, however, that the linear regression between needle mass and area should provide a good approximation of the area of an individual needle (cf. Kellomäki and Oker-Blom 1983).

Needle length was related to shoot length, yielding a logaritmic function between these variables. In shaded conditions the level of the function was lower than that in sunny conditions, but the shape of the curves was similar. The needle biomass and area for the whole crown can thus be approximated through this function, taking into consideration the needle density on the shoot and the relationship between needle length and needle area. For this purpose, a procedure has been presented for finding a simpler method than that actually used in the study.

Needle density declined with increasing shoot length, owing to the fact that for a given year the number of needle primordia per bud is constant for different parts of the crown. On the other hand, shoot elongation at the same time varies dependig on the position of the shoot in the crown. Consequently, needle density in the lower crown is considerably higher than in the upper crown. Variation in needle density is also due to variation in site fertility; this results in lower density values in fertile sites than in poor sites.

One of the main conclusions of the study was the presentation of a formula for approximation of the needle area of a shoot on the basis of site quality, shoot length and density of needles for different age classes (Equation 10). The method, while still tentative, does considerably simplify the problem of how to estimate the needle area of a tree. Therefore, in future studies of the current topic the proposed method will be elaborated further.

The needle angle of aging needles increased consistently at Petrozawodsk and at Mekrijärvi. The needle angle of the first-year needles, however, is greater at Mekrijärvi than at Petrozawodsk. This difference apparently indicates the difference in the season when the measurement were made, because the first-year needles at Mekrijärvi were measured in the spring just after the needles emerged, but the needles at Petrozawodsk were measured during the summer after they emerged. Thus, the difference seems to be due to the measuring procedure and does not indicate a real difference between Mekrijärvi and Petrozawodsk. The increasing needle angle of aging needles seems, however, to be characteristic for Scots pine shoots.

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Apendix: Variables and symbols used in the study.

Symbol	Explanation	Dimension	Symbol	Explanation	Dimension
M_S	Distance of shoot from tree stem	cm	$d_{1.3}$	Stem diameter at breast height	cm
h_S	Distance of shoot from groud level	cm	h_T	Tree height	m
L	Shoot order		a	parameter (Eq. (2))	mm
ϑ_S	Shoot inclination	degree	b	parameter (Eq. (2))	
φ_S	Shoot azimuth	degree	a_1	parameter (Eq. (4))	mm
φ_B	Branch azimuth	degree	a_2	parameter (Eq. (4))	
d_S	Shoot diameter	mm	S_N	Needle surface area	mm^2
d_B	Diameter of shoot axis	mm	S_{NS}	Needle surface area of shoot	cm^2
ϑ_N	Needle angle	degree	m_N	Needle dry weight	mg
l_S	Shoot length	cm	ϱ_N	Needle dry mass density	$mg\ mm^{-3}$
l_N	Needle length	mm	S_S	Specific needle area	$mm^2 mg^{-1}$
b_1	Needle width	mm	n_N	Needle density	cm^{-1}
b_2	Needle thickness	mm	C_A	Needle age factor	cm^{-1}
$d_{0.1}$	Stem diameter of tree at the relative height of 0.1	cm			