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## CANOPY STRUCTURE AND LIGHT CLIMATE IN A YOUNG SCOTS PINE STAND

SEPPO KELLOMÄKI and PAULINE OKER-BLOM

*Seloste*

MÄNNIKÖN LATVUSTON RAKENNE JA LATVUSTON SISÄISET VALAISTUSOLOT

Saapunut toimitukselle 30. 11. 1982

The needle area distribution and crown structure of a young planted Scots pine (*Pinus sylvestris* L.) stand are described. The crown structure and crown shape showed apparent regularity in crown structure regardless of stand dynamics. Similarly, the shoot structure and individual needle area showed regularity in the number of needles per branch and shoot length unit, and consequent phytoarea density inside the needle cylinder. Also the shoot area and needle area distributions were found to show a regular distribution of needle biomass throughout the crown, also inside the crown, in the dominant trees. In the suppressed trees the needle biomass was located in the upper crown and on the surface area of the crown. Estimates of the canopy needle area and distributions are given. The results were applied in calculations of the within-stand light regime. These results correlated well with the empirical results.

## INTRODUCTION

The primary synthesis of dry matter in forest ecosystems is accomplished mainly through photosynthesis in the tree stratum. To predict the photosynthesis of foliage requires knowledge of radiation and other environmental factors affecting leaves at a particular level in a canopy and the corresponding physiological responses of leaves. The whole process, however, is controlled in the main by the prevailing light conditions, as has been documented in the ecological literature, but the photosynthetic response of a tree shoot as a complex interaction between sky light geometry and shoot geometry is poorly understood, as Leverenz and Jarvis have emphasised (1979).

The amount of radiation reaching the leaves depends on the radiation above the canopy and the structure of the canopy. Norman and Jarvis (1974) emphasised detailed measurements of leaf, branch and stem dry weight and leaf area in characterising the vertical canopy structure. They also pointed out the importance of the structure of individual shoots in applying the laboratory mea-

surements to the relationship between photosynthesis and irradiation in field conditions and treating the non-random foliage distribution within the canopy. For example, angular distribution of leaves on an individual shoot and shoot distribution in a whorl are of importance in predicting light conditions in any part of the canopy. In particular, the flux density distributions are needed to predict the non-linear photosynthetic rate with the help of the radiation above the canopy and the canopy structure (Norman and Jarvis 1974).

The aim of the present paper is to describe the structure of the Scots pine (*Pinus sylvestris* L.) stand for developing methods to predict the radiation regime in a particular point of the stand canopy with the help of the stand structure parameters.

We express our gratitude to Prof. Juhan Ross, Institute of Astrophysics and Atmospheric Physics, Estonian Academy of Science, U.S.S.R, and Mr. Heikki Smolander, M. Sc. in Forestry, Academy of Finland, for inspiring discussions and their interest in this study.

## 2. INTERACTIONS BETWEEN STAND STRUCTURE AND LIGHT CLIMATE

### 2.1. General

Calculating the light climate inside a canopy is to a high degree a purely geometrical problem. That is, knowing the size, shape, orientation and spatial distribution of all the phytoelements that the stand is composed of, the distribution of light in the canopy can be calculated.

Most theories concerning the light climate of a stand are based on the assumption of a horizontally homogeneous canopy. This reduces the three-dimensional distribution of phytoelements to a one-dimensional (vertical) distribution. The vertical extinction of light can thus be given in terms of the leaf area index at a certain height and an extinction coefficient which depends on the angular orientation of foliage elements. However, if we are concerned with the light conditions of an individual tree and its dependence on stand structure, a more specific theory is needed.

The reduction of light flux density falling on a given foliage element can be divided into two parts. The shading that arises from parts of the same tree may be called within-plant shading and the shading caused by surrounding trees may be called between-plant shading (Thornley 1976). The reason for this division is that, within-plant and between-plant shading are determined by different characteristics of the stand. Within-plant shading is determined by the inner structure of a tree, while between-plant shading is determined essentially by the size, density and spatial distribution of the trees. Between-plant shading will affect the development of tree structure and the interactions between stand structure and individual tree structure can thus be described.

In the following, a model for describing the stand structure in order to calculate the respective light climate is outlined. The description of the structure of an individual tree. The stand structure at "tree-level" is then described for the trees that will be the basic units of the stand.

### 2.2. The inner structure of a tree

The structure of a coniferous tree is determined by the size, shape and spatial distribution of needles and branches within the tree crown, which can be given some simple geometrical shape. Since most of the shading arises from the needles, our main task is to characterise the distribution of needles and find a theoretical distribution which is in good agreement with reality. The distribution of needles seems to be rather heterogeneous since needles are clumped into shoots. A way to avoid the problem of defining a distribution of individual needles is to take the shoots to be the basic units of the tree and define a distribution of shoots (see Fig. 1). One possible distribution may be the commonly used Poisson distribution.

The outer shape of a shoot can be approximated by a cylinder and the tree canopy can be regarded as composed of these cylinders of varying dimensions and orientations. The distributions for the orientation and dimensions of a shoot as well as the transmission coefficients can be approximated using em-

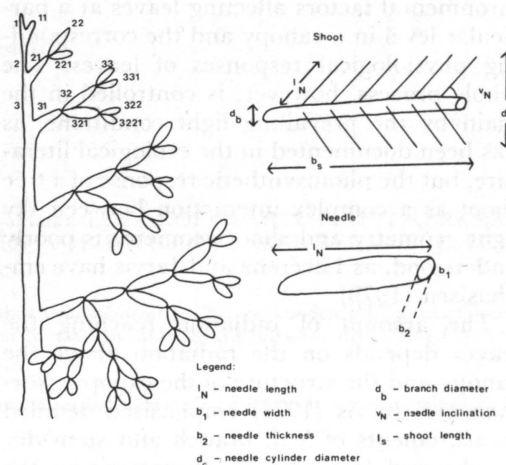


Fig. 1. Schematic presentation of the crown structure parameters and the principles treating needles and the shoot cylinder.

pirical measurements. Given all the above-mentioned parameters, the within-plant shading in any point of the tree canopy can be estimated.

### 2.3. Stand structure at tree-level

Describing the structure of a stand at tree-level is to find the density, spatial distribution and 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 their height. All trees in a given class are then assumed to have a common geometrical shape.

The spatial distribution (at ground level) of trees in each class must be described by some theoretical distribution. Such theoretical distributions are often divided into classes according to three different types (Pohtila 1980):

- Homogeneous distributions for which all trees have an equal growing area,
- Heterogeneous (clumped) distributions with a clear grouping of trees and
- A random (Poisson) distribution.

The development of spatial distribution in a natural even-aged pine stand has been shown to start from a very heterogeneous clustered distribution in the seedling stage which develops into a distribution which is more homogeneous than the Poisson in the mature stand (Pohtila 1980). Mathematically, a Poisson distribution is easiest to handle and may in many cases be justified.

The between-plant shading is determined by the above-mentioned parameters and will,

combined with the within-plant shading, describe the light conditions for a single trees as well as for the whole stand. A detailed description of stand structure makes it possible to estimate the light conditions in any point of the canopy and to calculate the between-plant and within-plant shading separately.

As can be seen, the outlined model requires detailed information of the stand characteristics, many of which are not easily obtained. Many of the parameters involved may, however, prove to be of minor importance for the light climate and one of the aims in applying the model to a well defined stand is to find the essential characteristics of the stand regarding the light climate. A simpler model based on these characteristics can then be constructed and applied more widely. The basic parameters of the outlined model are given in Table 1.

Table 1. The basic parameters of the outlined stand structure model.

Level of hierarchy	Parameters
Tree structure	Crown shape of a tree Density of shoots in crown Spatial distribution of shoots in crown Size of shoots Shape of shoots Orientation of shoots Inclination of shoots Inner structure of shoots
Stand structure	Density of trees Spatial distribution of trees Size distribution of trees

## 3. MATERIAL AND METHODS

### 3.1. Study area

The material comprised a young Scots pine (*Pinus sylvestris* L.) stand located near the Forest Field Station, University of Helsinki (61°24' N, 24°15' E, altitude 150 m). The stand was sown in 1961 to a density of 3200

stems/ha on prescribed burnt morain soil of *Vaccinium* type, i.e., medium fertility. The stand is typical of planted pine stands in the south boreal vegetation zone. The main characteristics of the stand are given in Table 2.

Table 2. Some main characteristics of the stand.

	n	$\bar{x}$	S <sub>x</sub>
Height	32	3.81	0.99
Diameter (D <sub>1.3</sub> )	32	6.28	2.68
Crown width	32	156.31	54.76

### 3.2. Measurements

The diameter distributions at 0,1 m (D<sub>0.10</sub>) and 1,3 m (D<sub>1.3</sub>) 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, 11 sample trees were selected so that each diameter class (D<sub>1.3</sub>) was represented by at least one sample tree. Coordinates and the tree position in relation to points of the compass were recorded before removal of the sample trees to the laboratory for further analysis.

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

The following measurements were made of the sample branches: length, orientation, angle, distance between successive branch whorls, diameter at the middle of successive branch whorls, number of the second order laterals and number of the third order laterals. The current-year shoot of the branch main axis and the second order lateral were then sampled for further analysis.

The following measurements were carried out on the sample representing the branch main axis: 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, 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.

In addition to the above-mentioned measurements, the inner structure of a shoot was studied from photographs of the needle area projected in various directions (inclination and orientations). The photographs were taken from a distance of 1,5 m with a 35 mm camera using a 50 mm lens. The film was Kodak (din 16). The projected needle area of a shoot was expressed as a fraction of the total outline area of the needles based on the measurements from the enlargements of the shoot images. The measuring procedure was that described by Norman and Jarvis (1974).

Finally, the measurements of the light regime within the stand were carried out by the system described by Salminen et al. (1980). The measuring system included 32 sensor units and a data logger (model Veko 771). The sensitivity of the sensors was within the range 400–700 nm, with a peak at 570 nm. The output of the sensor units was logged every two seconds during an eight-minute period. The data were then divided into 32 classes within the light intensity range two to 2000  $\mu E m^{-2} s^{-1}$ . Each class was of equal size in the logarithmic scale. The classified data were stored in a memory, and a new series of measurements started two minutes after the previous measurements had been completed. The measurements represented five height levels in the middle of the study area, including that above the canopy level. The measuring levels were: 4,3; 2,9; 1,6 and 0,3 m above ground level. At each height level the numbers of sensors were 4, 8, 8 and 8, respectively. The light measurements were carried out before the removal of the sample trees.

## 4. TREE STRUCTURE

### 4.1. Crown shape

The crown shape was determined from three sample trees, the biggest, smallest and intermediate. The distribution of branches was similar in all the size classes but the location and the length of the branches were relative to the tree size, as can be seen in Fig. 2 where the crown structure of the tallest, smallest and intermediate sample trees are shown. The crown shape appeared, however, to be similar for the different tree size classes, as shown in Fig. 3. A conical crown shape seemed not to be affected by dominance or suppression in stand dynamics. The result is in accordance with the findings by Kellomäki et al. (1980) and Kellomäki and Tuimala (1981), which show independence of crown

shape of Scots pine on the stand density as well as on the tree position in a stand. Only a severe suppression may change the basic pattern of the Scots pine crown from that presented here (Kellomäki et al. 1980)

### 4.2. Density and spatial distribution of shoots within the crown

The tree crown was assumed to be formed as a system of shoots characterised by the density, distribution and dimensions of the shoots. The number of primary and second

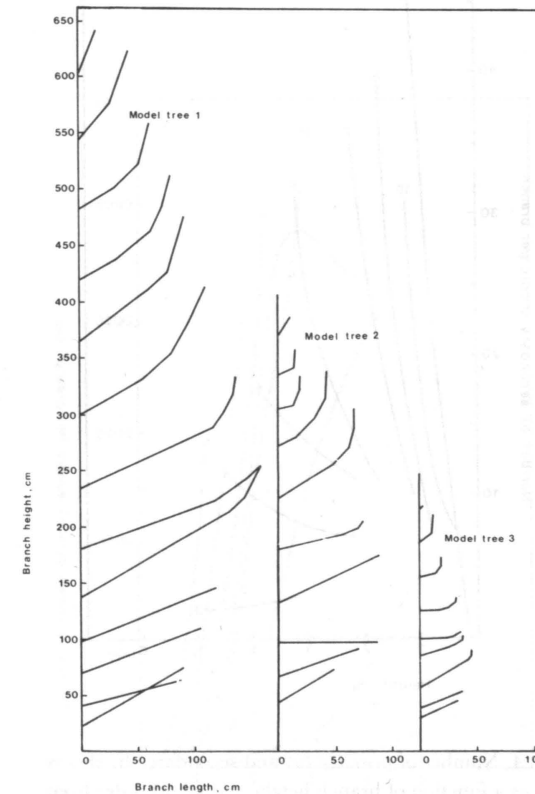


Fig. 2. Crown structure of the model trees.

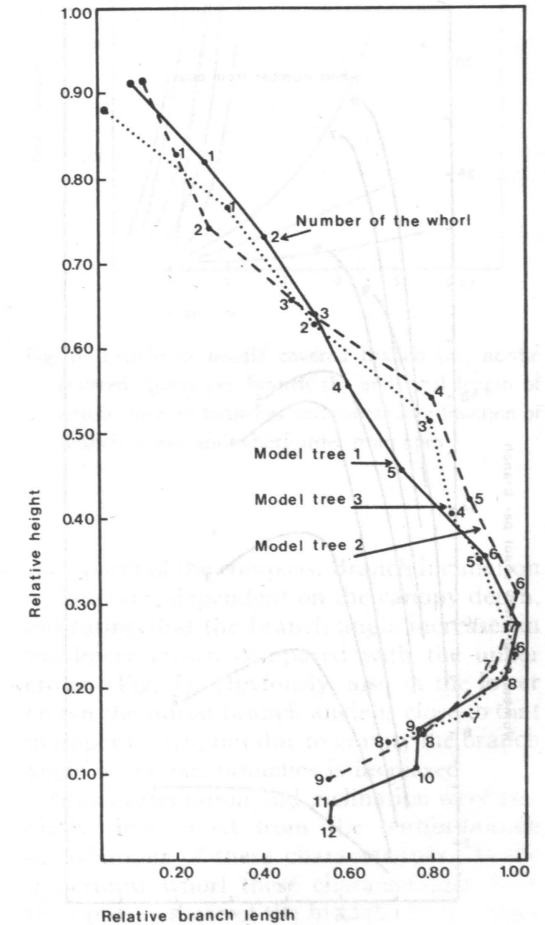


Fig. 3. Crown shape of the model trees.

dary shoots are shown in Figs. 4a and b. The whorl age and location in the crown affect both parameters which have their greatest values at the eighth to ninth whorls at the height one to two metres above soil level. In older branches at lower levels the shoot number decreases, indicating the onset of natural pruning due to shaded branch position. As presented by Flower-Ellis et al. (1976), the loss of shoots seems to be very sensitive to suppression and thus indicates competition from light resources.

The shoot number only partially indicates, however, the length of the needle covered shoots which is maximised earlier than the shoot number (cf. Figs. 5a, b and c). In the branches, too, the needle covered part is maximised at the fifth to sixth whorls at a height

of about three metres above soil level. The same is also apparent for the total length of needle covered shoots and branches in the canopy. On the other hand, the emphasis of the photosynthetically active crown is higher above soil level than is indicated by the branch biomass. The mean shoot density, i.e., number of shoots of mean size, was about 620 shoots per  $m^3$ .

#### 4.3. Shoot orientation and inclination

Shoot orientation and inclination are primarily determined by branch orientation and branch angle. It appears from Fig. 6 that branch orientation is random, representing an equal proportion of branches directed to

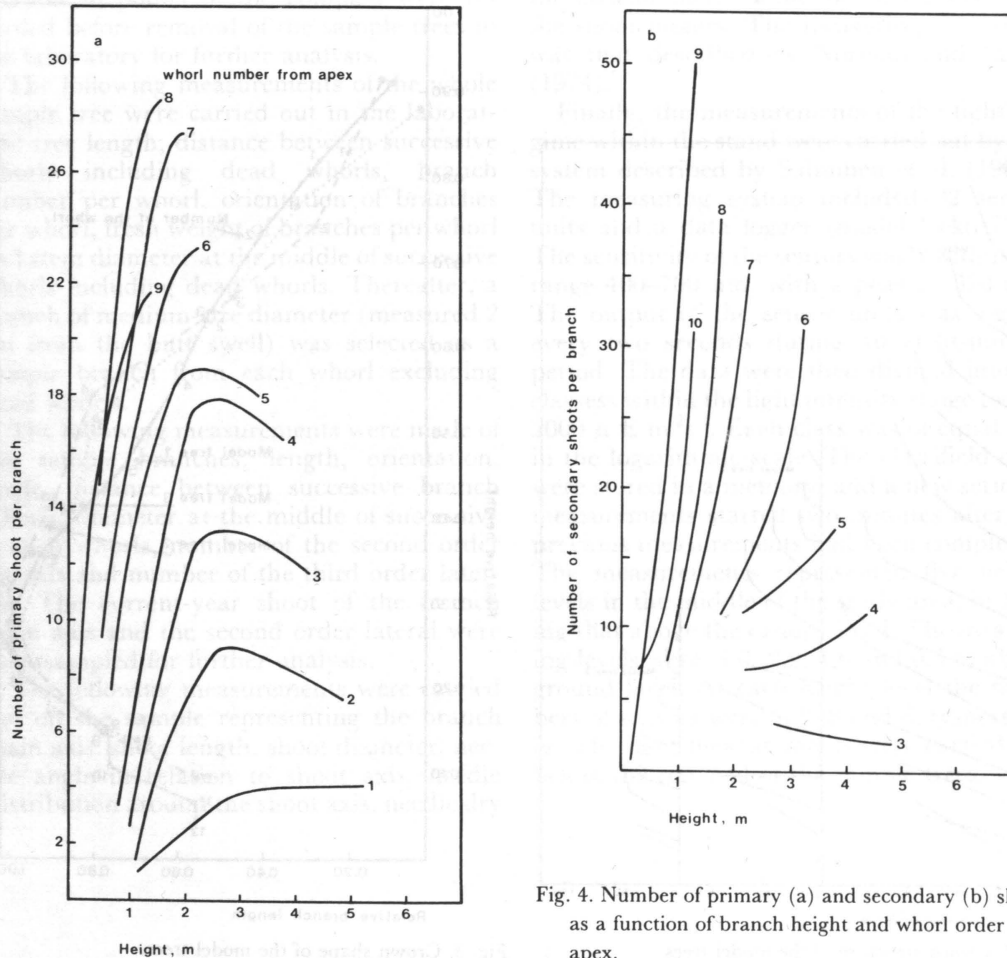


Fig. 4. Number of primary (a) and secondary (b) shoots as a function of branch height and whorl order from apex.

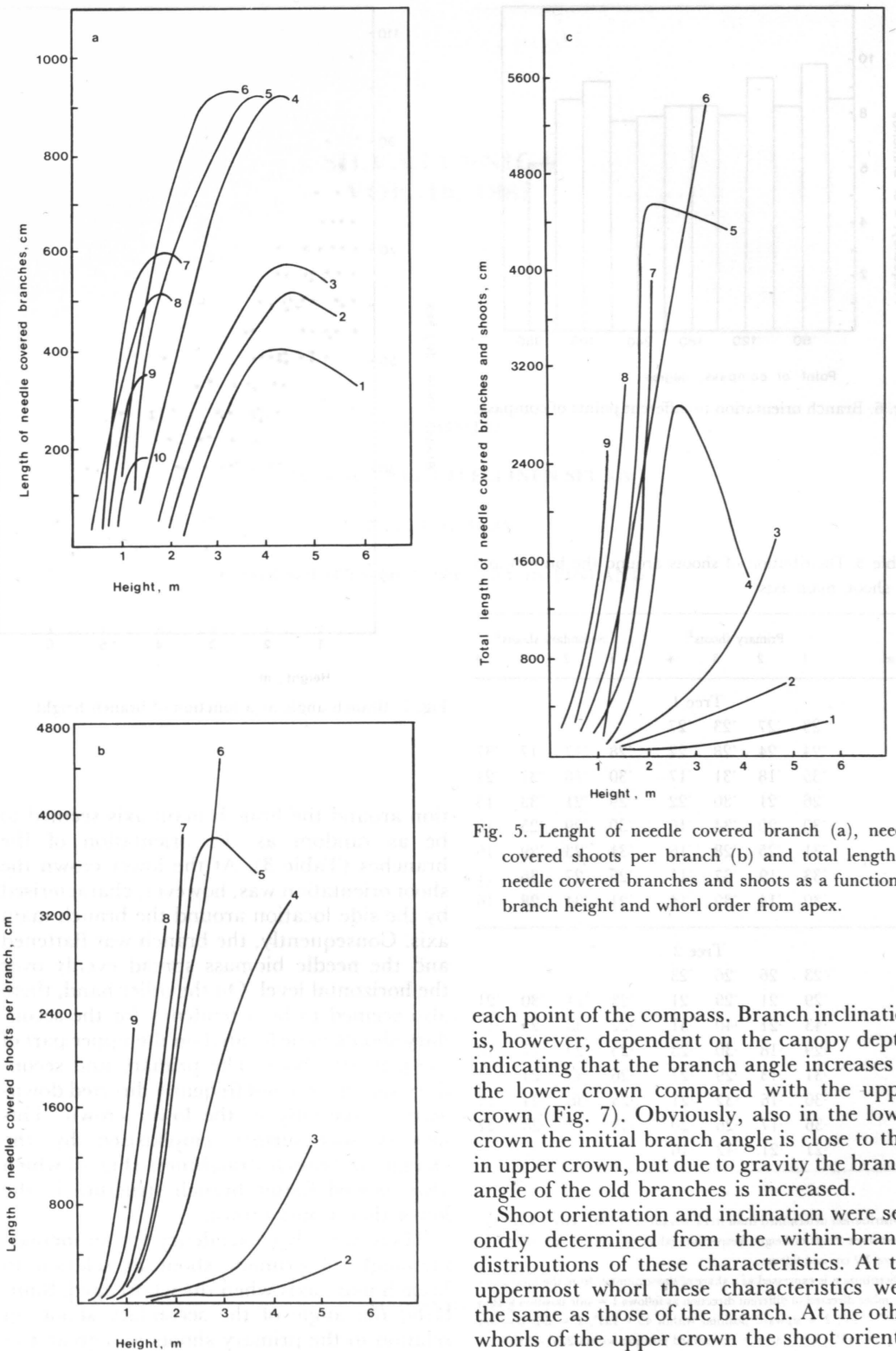


Fig. 5. Length of needle covered branch (a), needle covered shoots per branch (b) and total length of needle covered branches and shoots as a function of branch height and whorl order from apex.

each point of the compass. Branch inclination is, however, dependent on the canopy depth, indicating that the branch angle increases in the lower crown compared with the upper crown (Fig. 7). Obviously, also in the lower crown the initial branch angle is close to that in upper crown, but due to gravity the branch angle of the old branches is increased.

Shoot orientation and inclination were secondly determined from the within-branch distributions of these characteristics. At the uppermost whorl these characteristics were the same as those of the branch. At the other whorls of the upper crown the shoot orienta-

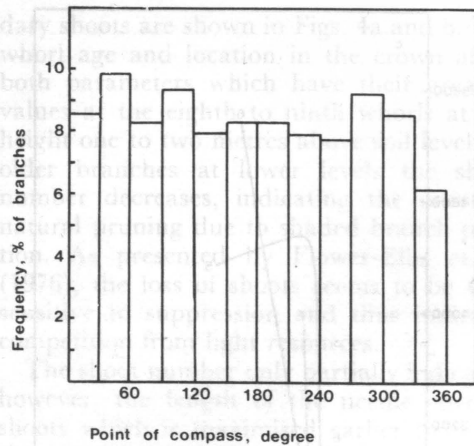


Fig. 6. Branch orientation to different points of compass.

Table 3. Distribution of shoots around the branch and shoot: main axis<sup>1)</sup>

Whorl	Primary shoots <sup>2)</sup>				Secondary shoots <sup>2)</sup>			
	1	2	3	4	1	2	3	4
Tree 1								
2	.23	.27	.23	.27				
3	.24	.24	.28	.22	.28	.17	.17	.37
4	.35	.18	.31	.17	.30	.18	.31	.21
5	.26	.21	.30	.22	.29	.21	.33	.15
6	.30	.20	.34	.16	.30	.29	.25	.16
7	.31	.25	.28	.16	.31	.23	.29	.16
8	.33	.19	.37	.11	.26	.27	.36	.11
9	.30	.14	.39	.14	.21	.34	.28	.16
Tree 2								
2	.23	.26	.26	.23				
3	.29	.21	.29	.21	.23	.24	.30	.21
4	.43	.21	.40	.31	.22	.38	.25	.15
5	.29	.18	.30	.23	.25	.29	.27	.18
6	.31	.13	.29	.27	.26	.33	.24	.17
7	.30	.16	.32	.21	.25	.36	.24	.14
8	.36	.17	.26	.20	.33	.17	.28	.22
9	.21	.21	.42	.16				

1) Distribution determined from trees measured in 1981. Tree 1 was 5.1 m and Tree 2 6.0 m high. Respective values of breast height diameter, were 7.2 cm and 9.0 cm.

2) Distribution is expressed as a share of shoot number from the total shoot number directed to different direction as follows 1 = side position within  $-45^\circ - 45^\circ$ , 2 = upward position within  $45^\circ - 135^\circ$ , 3 = side position within  $135^\circ - 225^\circ$  and 4 = downward position within  $225^\circ - 315^\circ$ .

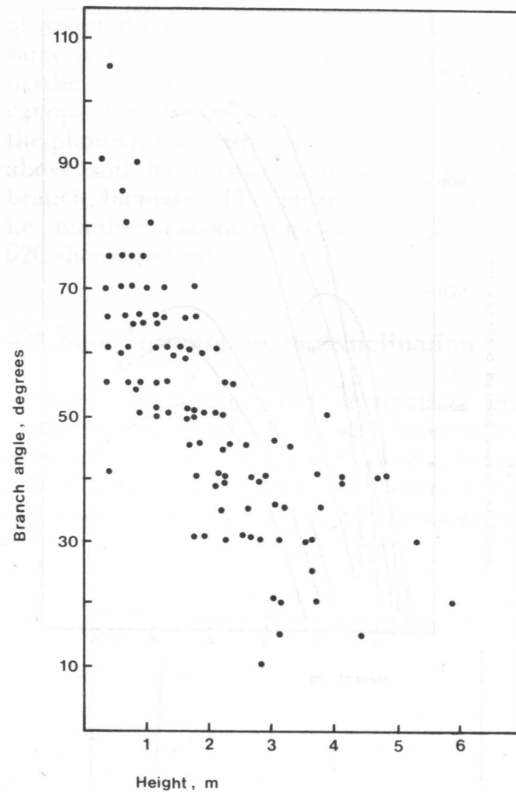


Fig. 7. Branch angle as a function of branch height.

tion around the branch main axis seemed to be as random as the orientation of the branches (Table 3). At the lower crown the shoot orientation was, however, characterised by the side location around the branch main axis. Consequently, the branch was flattened and the needle biomass spread evenly over the horizontal level. On the other hand, there also seemed to be a tendency for the secondary shoots to be located on the upper part of the primary shoot. The primary and secondary shoots were not frequently directed downwards, especially in the lower crown. This process was further emphasised by the changes in branch straightness (Fig. 8) which also showed flatter branch structure in the lower than upper crown.

There was also a tendency for an increasing angle of primary shoot in relation to branch main axis when the whorl aged. Similarly, the angle of the secondary shoots in relation to the primary shoots was greater in

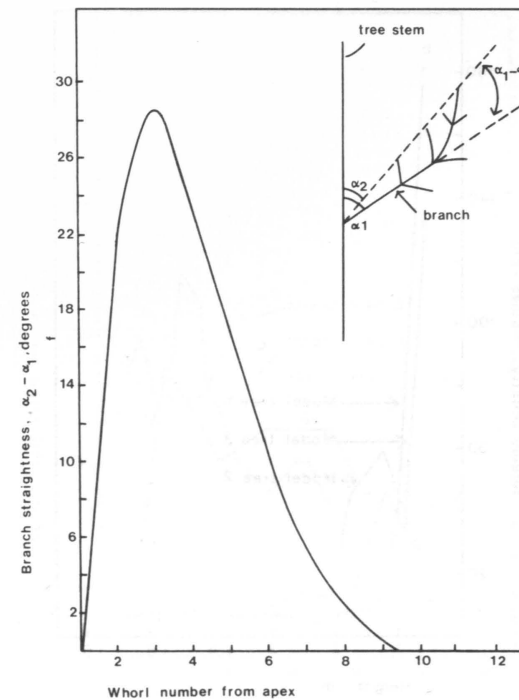


Fig. 8. Branch straightness as a function of whorl order from apex.

the lower than in the upper crown. In other words, the crown structure characterised by the branch inclination and orientation seemed to be repeated at the branch level. In conclusion, random distribution of shoots within the crown space is more likely in the upper than in the lower crown where shoots are apparently randomly located over the level formed by the whorl. It seems, however, that a satisfactory estimate for shoot distribution can be obtained through random distribution.

#### 4.4. Shoot structure

##### 4.4.1. Needle characteristics

The shoot structure was characterised by needle amount, needle dimensions and needle inclination and orientation. The needle number per centimetre of tree stem, branch and shoot according to age classes is pre-

Table 4. Needle number per centimetre in branches and shoots.

Model tree	Needles/cm					
	n	$\bar{x}$	$s_x$	n	$\bar{x}$	$s_x$
1	9	6.49	0.29	9	10.35	3.53
2	7	14.12	2.74	6	24.58	9.17
3	6	10.15	2.32	4	28.22	8.44

Table 5. Mean needle inclination (degree) in branches of model trees 1-3.

Model tree	Needle inclination		
	n	$\bar{x}$	$s_x$
1	10	33	2
2	10	36	3
3	7	47	4

sented in Table 4. In shoots the needle number range was 25-48 per cm and in the branch main axis 11-17 per cm. There was no consistent tendency in relation to tree size as regards the needle number in branches and shoots, but the suppression may increase the needle number. This was especially apparent in the shoots of the lower crown where the needle number per length unit increased sharply (Figs. 9a, b).

The needle inclination in shoots, i.e., at the branch main axis, is presented in Table 5 and Fig. 10. Comparison between model trees shows no clear differences, but a small tendency towards increased needle angle in the suppressed tree. Between needle age classes, however, there seemed to be differences showing a tendency towards increasing needle inclination when the needles aged. There could also be differences between the upper and lower crown indicating greater needle inclination in the latter. This pattern seemed to be associated with the branch angle, i.e., needle inclination increased as a function of increasing branch angle. Similarly, there were more needles in terms of dry weight on the upper part of the branch than on the sides of the branch, as appears from Fig. 11. This was especially evident at the lower crown. Consequently, the needle orientation around shoot axis is not totally random as assumed (cf. Fig. 1).

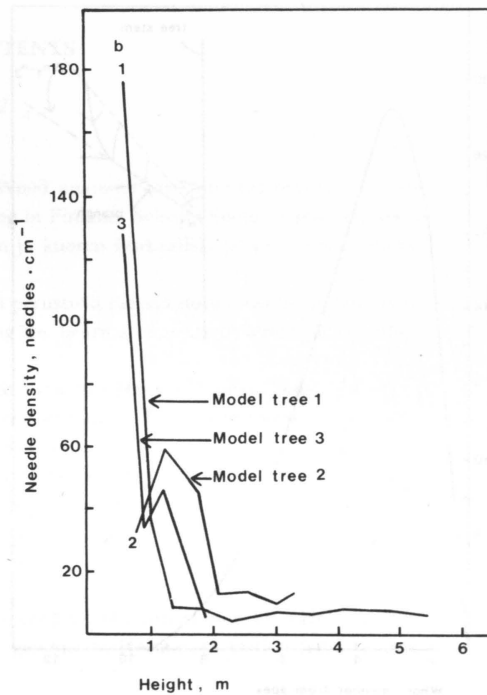
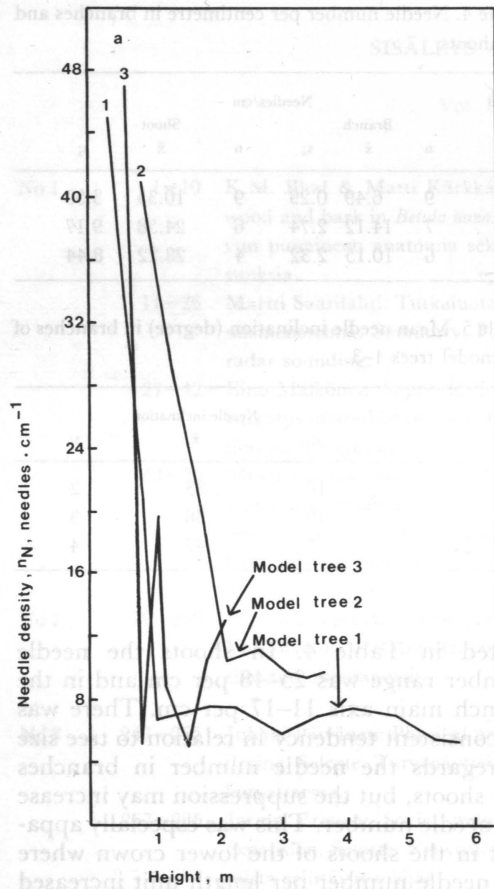


Fig. 9. Needle density for current year shoots of branches (a) and for primary shoots (b) as a function of branch height.

The needle dimensions, i.e., length, thickness and width were closely related to each other (Figs. 12a, b and c). The regression between needle width and needle thickness and that between needle length and needle width was linear. Consequently, the individual needle area is closely related to the above-mentioned needle dimensions and the needle fresh weight (Fig. 12c).

#### 4.4.2. Shoot area characteristics

The needle area of the shoots was determined through the unit area of individual needles with the following equation

$$(1) \quad S_N = l_n (1,785 b_1 + 1,571 b_2)$$

where  $S_N$  is the needle area,  $l_n$  needle length,

$b_1$  needle width and  $b_2$  needle thickness (cf. Tirén 1926). The tree dominance or suppression seemed to have no effect on this relationship. To determine the projected needle area of a shoot, i.e. shoot cylinder surface area, a conversion factor,  $u_c$ , was developed to indicate the phytoarea density inside the needle cylinder in  $\text{cm}^2$  of needle area per  $\text{cm}^3$  of shoot cylinder, i.e.

$$(2) \quad u_c = \frac{S_{FB}}{S_{CB}}$$

where  $S_{FB} = n_N \cdot S_N$ , i.e., phytoarea per branch cm when  $n_N$  refers to the number of needles per branch cm. In Eq(2)  $S_{CB}$  is as follows

$$(3) \quad S_{CB} = S_C - S_B = \frac{\pi d_c^2 - \pi d_B^2}{4}$$

where  $S_C$  is the cross-sectional shoot cylinder

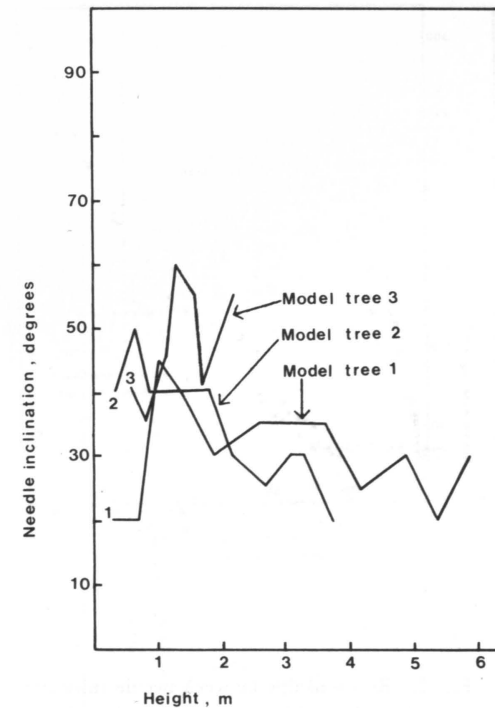


Fig. 10. Needle inclination as a function of branch height.

Table 6. Conversion factor,  $\mu_c$ , for the model trees.

	Conversion factor, $\mu_c$ , $\text{cm}^2/\text{cm}^3$					
	Branch			Shoot		
	n	$\bar{x}$	$s_x$	n	$\bar{x}$	$s_x$
1	9	2.82	0.56	8	3.87	0.74
2	7	5.72	1.10	6	9.27	2.08
3	6	3.23	2.76	4	8.93	10.48

area,  $S_B$  the cross-sectional branch area,  $d_c$  the shoot cylinder diameter and  $d_B$  the branch diameter (cf. Fig. 1). The values of the conversion factor are given in Table 6.

The values of the conversion factor for branch and shoot were affected by tree size and location in the canopy, i.e., suppression. In the lower crown especially the values of the conversion factor increased substantially when suppression increased (Fig. 13). For example, in the smallest tree the value of the conversion factor was six-fold than that in the dominant tree due to increased needle density in the shoots.

The results for shoot structure were utilised in determining shoot area distribution vertically and horizontally. In these calculations the needle area in shoots refers to the area of

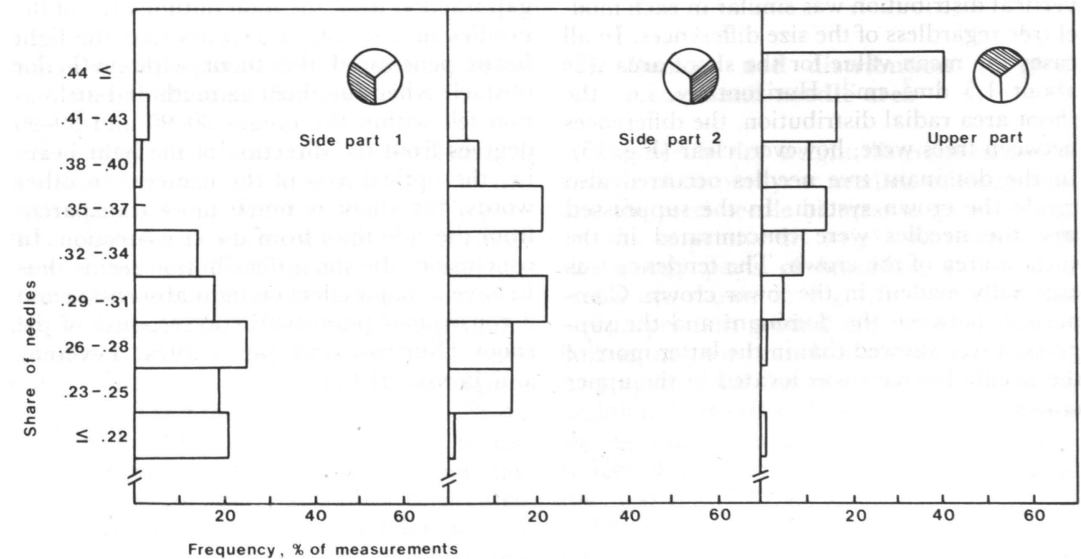


Fig. 11. Distribution of needles around the current year shoot of branch main axis.

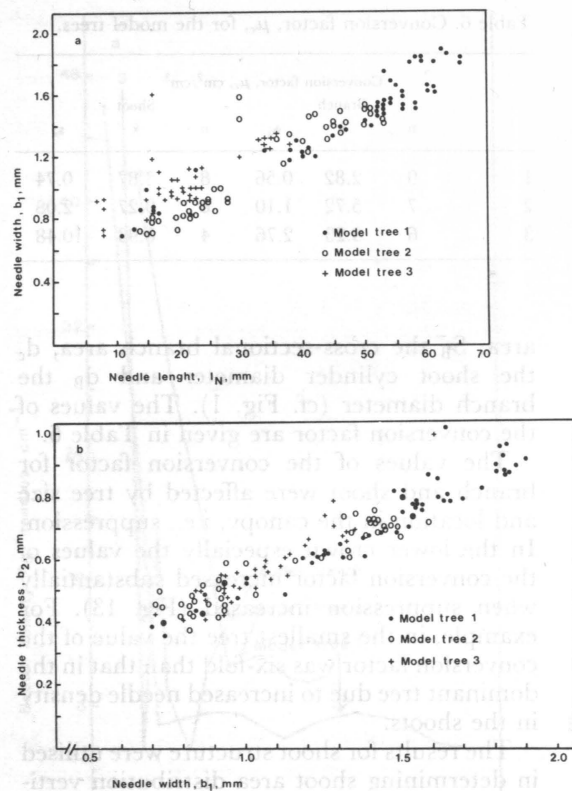


Fig. 12. Relationships between needle thickness and needle width (a), needle length and needle width (b) and needle length, needle fresh weight and needle area (c).

shoot cylinder per length unit of shoot ( $\text{dm}^2 \text{cm}^{-1}$ ). As appears from Fig. 14, the shoot area vertical distribution was similar in each model tree regardless of the size differences. In all cases the mean value for the shoot area was about  $1.5 \text{ dm}^2 \text{cm}^{-1}$ . Horizontally, i.e. the shoot area radial distribution, the differences between trees were, however, clear (Fig. 15). In the dominant tree needles occurred also inside the crown system. In the suppressed tree the needles were concentrated in the surface area of the crown. The tendency was especially evident in the lower crown. Comparison between the dominant and the suppressed tree showed that in the latter more of the needle biomass was located in the upper crown.

The needle area projected in various directions, is presented in Fig. 16 in terms of the gap fraction from the total outline area of the needles in a shoot. It appears that the light beam penetrated the shoot with no major obstacle when the shoot azimuth and inclination fell within the ranges 30–90 and 30–90 degrees from the direction of the light beam i.e. the optical axis of the camera. In other words, the shoot is much more transparent from the side than from the cross-section. In conclusion, the shoot distribution seems thus to have a major effect on light absorption and a consequent photosynthetic response of the shoot (Norman and Jarvis 1974, Leverenz and Jarvis 1979).

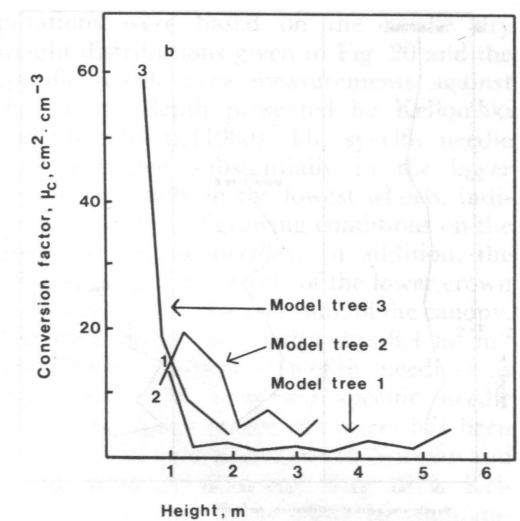
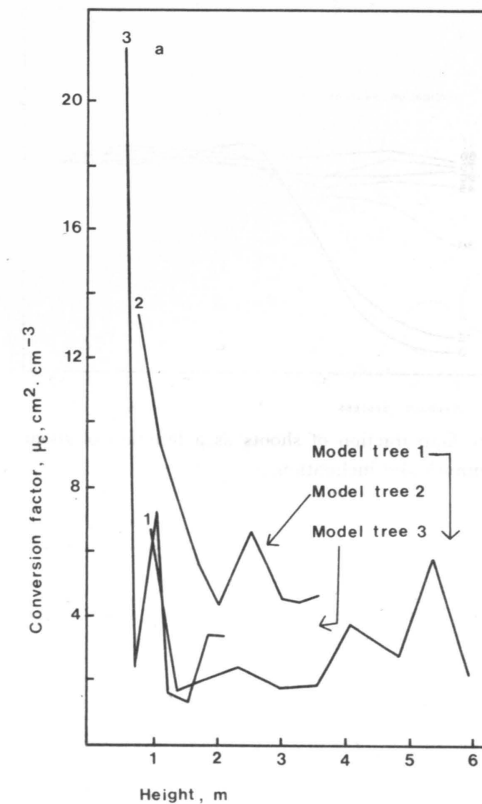


Fig. 13. Conversion factor  $\mu_c$  as a function of branch height for current-year shoots of the branch main axis (a) and for primary shoots (b).

## 5. STAND STRUCTURE

### 5.1. Density, spatial distribution and size distribution of the trees

The total stand density was 3200 stems/ha and the trees were located randomly in the study area, as appears from Fig. 17. No particular pattern was apparent due to the stoniness of the soil even though the east-west orientation of the planting rows was recognizable in the terrain. A clear stratification of the stand was evident as indicated by the frequency distributions of the height and diameter ( $D_{0.1, 1.3}$ ) and the crown width (Fig. 18a, b, c). The height distribution is close to the normal. Comparisons with the corresponding distributions of the naturally regenerated Scots pine stands show marked differences in the natural regenerated stand the distributions are skewed.

### 5.2. Density and distribution of phytomass and needle area

The needle dry weight distribution in the canopy of current-year needles, other needles and the total needle biomass is given in Fig. 19. The respective dry weight distributions of the woody parts of branches, shoots and stems are shown in Fig. 20. The total dry weight per unit ground area for needles was  $0.62 \text{ kg m}^{-2}$ , for branches  $0.72 \text{ kg m}^{-2}$ , shoots  $0.04 \text{ kg m}^{-2}$  and for stems  $13.80 \text{ kg m}^{-2}$ . In addition, first-order shoots and second-order shoots were separated, but the total dry-weight of the second-order shoots was negligible, less than  $0.01 \text{ kg m}^{-2}$ .

The needle area distribution for the current-year needles, other needles and the total needle biomass is given in Fig. 21. The com-



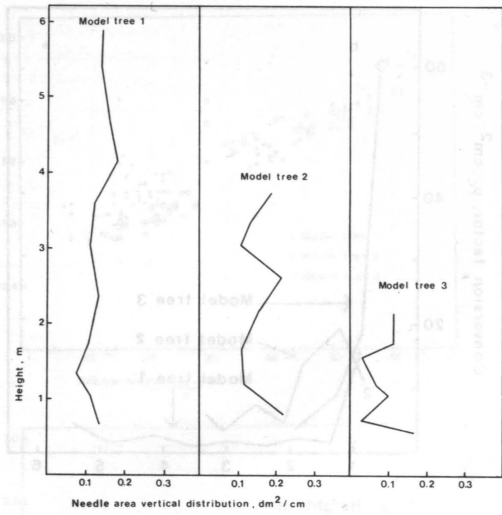


Fig. 14. Shoot area vertical distribution.

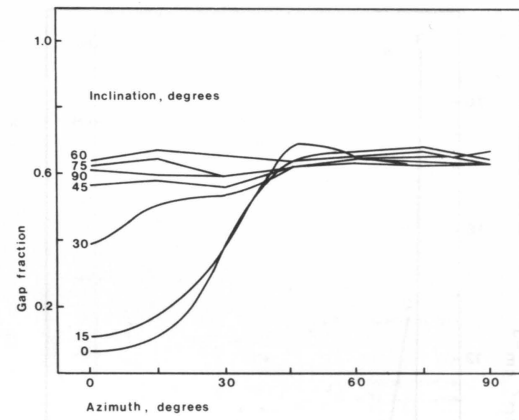


Fig. 16. Gap fraction of shoots as a function of shoot azimuth and inclination.

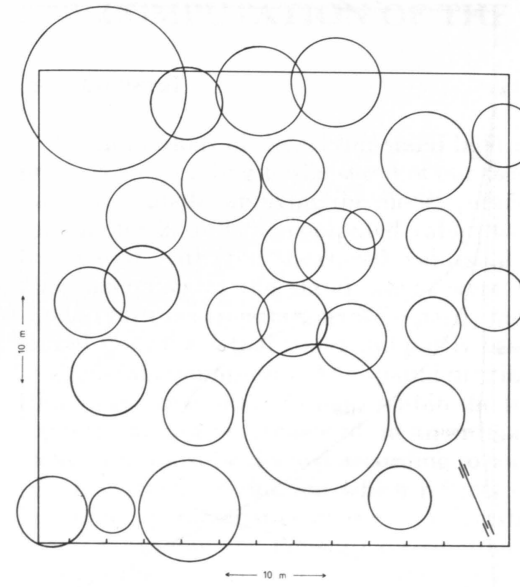


Fig. 17. Location of trees in the sample area.

putations were based on the needle dry weight distributions given in Fig. 20 and the specific needle area measurements against the canopy depth presented by Kellomäki and Oker-Blom (1980). The specific needle area increased substantially in the lower crown, especially in the lowest whorls, indicating the effect of growing conditions on the properties of the needles. In addition, the results emphasise the role of the lower crown in the total needle area account of the canopy. The total needle area index was  $8.4 \text{ m}^2 \text{ m}^{-2}$  when the total surface area of the needles was considered. The increased specific needle area in the lower crown of conifers has been recognised in several studies (cf. Norman and Jarvis 1974, Del Rio and Berg 1979, Kellomäki and Oker-Blom 1980). In computations, the same value of the specific needle area at a particular height are utilised for all the needle biomass components of this level.

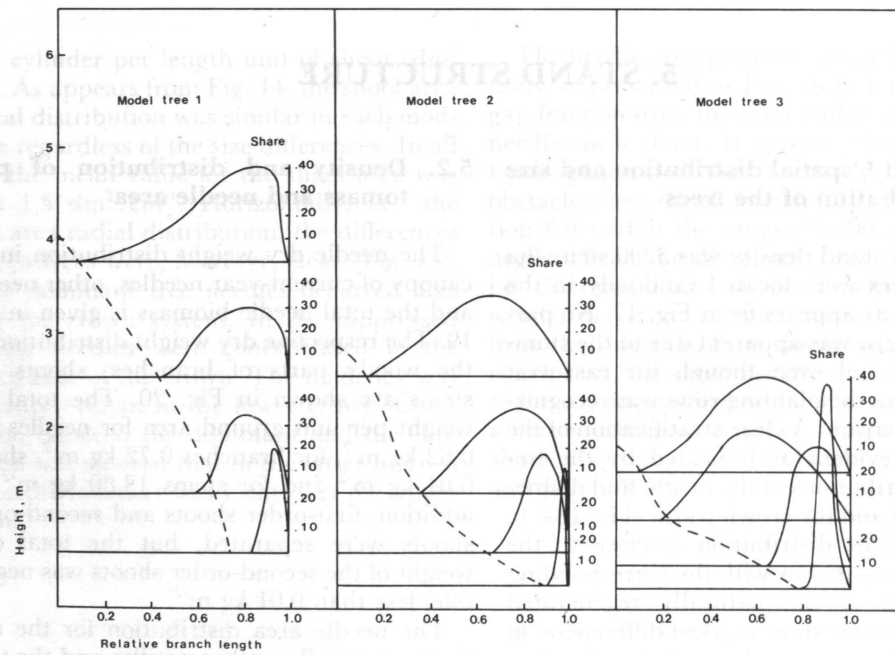


Fig. 15. Shoot area radial distribution.

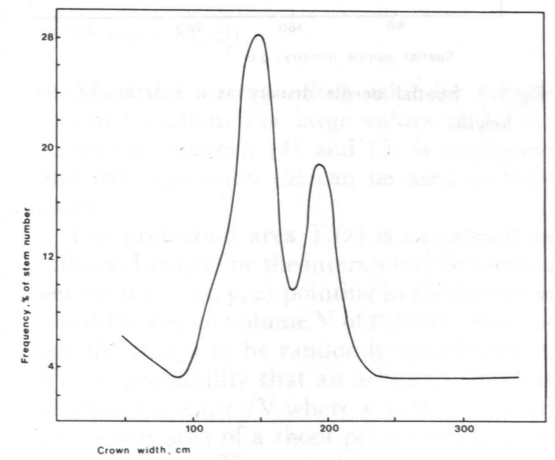
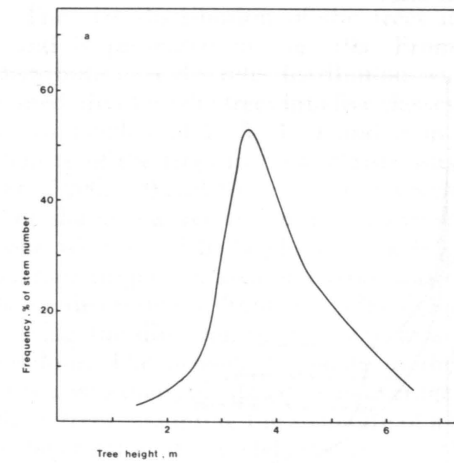
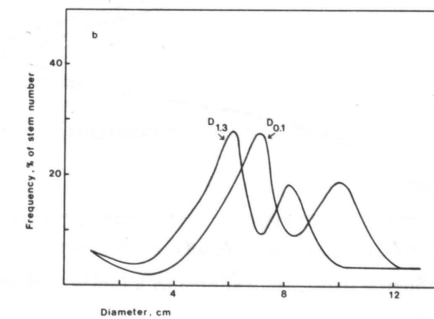


Fig. 18. Frequency distribution of tree height (a), tree diameter (b) and crown width (c).



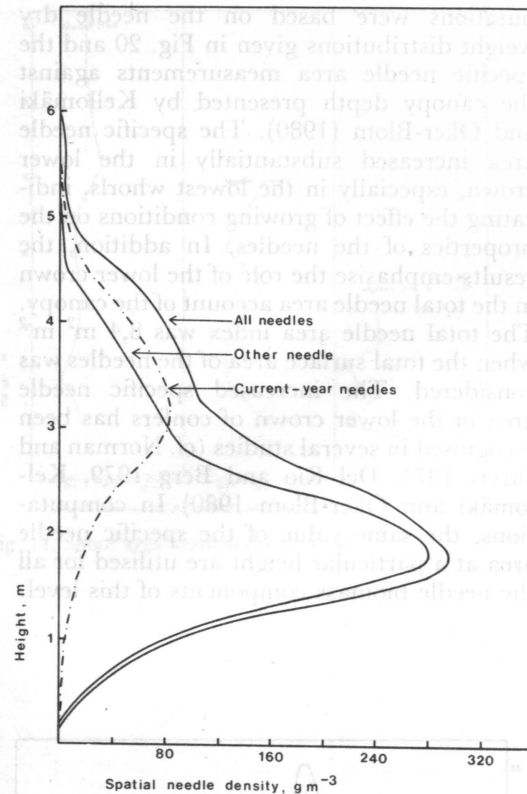


Fig. 19. Spatial needle density as a function of tree height.

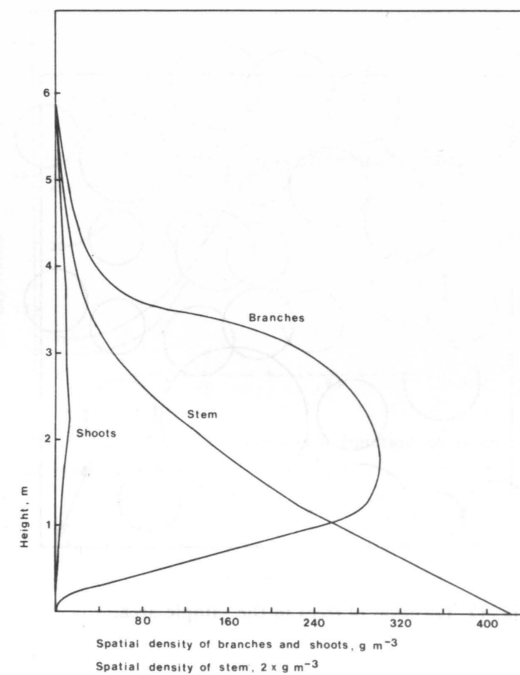


Fig. 20. Spatial density of woody organs as a function of tree height.

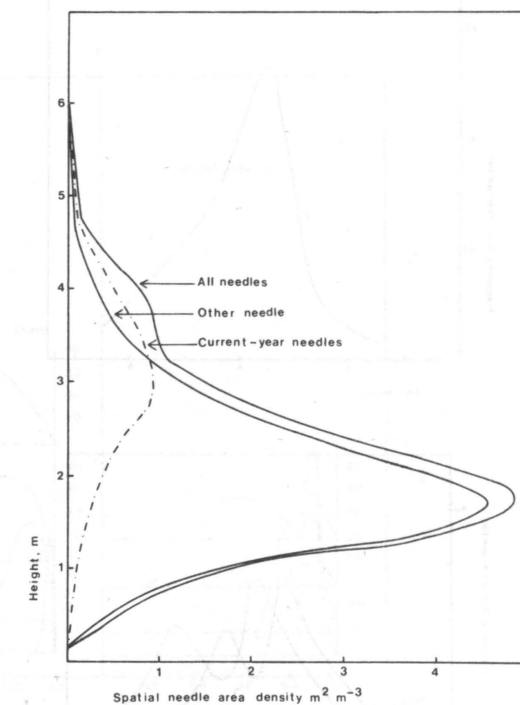


Fig. 21. Spatial density of leaf area as a function of tree height.

## 6. COMPUTATION OF THE WITHIN-STAND LIGHT REGIME

### 6.1. General

Computations of the within-stand light regime corresponding to the stand of our study area were made, applying the model outlined in chapter 2, and the computed values were compared with the measured values. The characteristics of the stand which were required for the computations were partly measured from the actual stand and partly based on general assumptions. The spatial distribution of the trees and of shoots within the tree crowns can not be 'measured' in an ordinary sense, but must be defined according to some mathematical distribution which reflects the essential characteristics of the real distribution. A random (or Poisson) distribution of trees at the ground level and of shoots within the tree crowns was used here, since it represents a reasonable compromise between complete regularity and systematic clumping, neither of which could be observed in the actual stand.

The size distribution of the trees in the stand is presented in Fig. 19a. From this distribution, a discrete distribution was obtained, dividing the trees into five classes with mean heights of 2, 3, 4, 5 and 6 m. The density of the trees in these classes was 200, 800, 1200, 700 and 300 trees ha<sup>-1</sup> respectively. The shape of a tree crown was described as a cone with a width: height ratio of 0.5. The average projection area of a shoot was calculated theoretically from a model shoot, assuming the direction of the shoot axis to be random. The density of shoots in the tree crown was then calculated as an average from three trees, assuming the structure of a shoot to be equal to the model shoot.

### 6.2. Computation principles

Given the distribution of light above the canopy and the above-mentioned stand characteristics, the mean flux density of light in any area within the canopy can be calculated.

Let us take first direct light, from a given direction  $s$ . The relative mean flux density of light at an arbitrary point  $r = (x, y, z)$  in the canopy can be defined as the probability that  $r$  is not shaded in the direction  $s$ , i.e., that  $r$  does not fall within the projection of any tree crown. Since the trees are randomly distributed at ground level the same applies to their projections on any horizontal plane, and the probability that  $r$  is shaded by an arbitrary tree is then  $\bar{T}_s(z)/A$  where  $\bar{T}_s(z)$  is the expected (average) projection area of a tree in direction  $s$  on a horizontal plane at height  $z$  and  $A$  is the ground area of the stand.

Given  $N$  trees, the probability that  $r$  is not shaded by any tree is thus

$$(4) \quad P \{r \text{ not shaded}\} = \left[1 - \frac{\bar{T}_s(z)}{A}\right]^N$$

Keeping the density of trees  $\lambda = N/A$  constant and letting  $N \rightarrow \infty$ , the limiting value of (4) is

$$(5) \quad \exp(-\lambda \bar{T}_s(z))$$

which is the corresponding value for a Poisson distribution. For large values of  $N$ , the difference between (4) and (5) is negligible and the expression (5) can be used in both cases.

The projection area  $T_s(z)$  is calculated as follows. Let  $t_s(r)$  be the intersection between a vector at  $r = (x, y, z)$  pointing in the direction  $s$  and the crown volume  $V$  of the tree. Assuming the shoots to be randomly distributed in  $V$ , the probability that an arbitrary shoot is shading  $r$  is  $a_s t_s(r)/V$  where  $a_s$  is the expected projection area of a shoot perpendicularly to the direction  $s$ . The probability  $P_o(r)$  that  $r$  is not shaded by any of  $n$  shoots is then

$$(6) \quad P_o(r) = \left[1 - \frac{a_s \cdot t_s(r)}{V}\right]^n$$

which can be approximated by the corresponding expression for a Poisson distribution, i.e.

$$(7) \quad \exp(-\varrho a_s t_s(r))$$

where  $\varrho = n/V$  is the density of shoots in the crown.

The projection area of the tree crown is then

$$(8) \quad T_s(z) = \iint_{V_z} 1 - \exp(-\rho a_s t_s(r)) \, dx \, dy$$

where  $V_z$  is the projection of the crown volume  $V$ .

The mean flux density of light from direction  $s$  on a horizontal plane at height  $z$  is then (cf (5))

$$(9) \quad F(s, z) = F(s) \cdot \exp(-\lambda \bar{T}_s(z))$$

where  $F(s)$  denotes the flux density of light on a horizontal plane above a canopy and  $\bar{T}_s(z)$  is the weighted average of the projection areas of trees belonging to the different size classes.

The mean flux density of multidirectional light is similarly found to be

$$(10) \quad F_d(z) = \int I(s) \exp(-\lambda \bar{T}_s(z)) \sin \alpha \, d\omega$$

where  $\omega$  denotes the solid angle  $2\pi$  of the upper hemisphere,  $I(s)$  the initial intensity of light in the direction  $s = (\alpha, \beta)$  ( $\alpha =$  elevation,  $\beta =$  azimuth) and  $d\omega = \cos \alpha \, d\alpha \, d\beta$ .

The flux density of light within a tree can be calculated using the same principles. If  $r$  is a point within the crown of a tree, the probability that  $r$  is not shaded in the direction  $s$  by a surrounding tree is (cf. (4))

$$(11) \quad [1 - \frac{\bar{T}_s(z)}{A}]^{N-1}$$

which has the limiting value of

$$(12) \quad \exp(-\lambda \bar{T}_s(z))$$

and expresses the between-plant shading at  $r$  in the direction  $s$ .

The probability that  $r$  is not shaded by the same tree is (cf. (7))

$$(13) \quad \exp(-\rho a_s t_s(r))$$

where  $t_s(r)$  is defined as before.

This expression is a measure of the within-plant shading at  $r$ , in direction  $s$ .

Combining the between-plant and within-plant shading, the mean flux density of light

from direction  $s$  can be calculated at any point  $r = (x, y, z)$  within the tree crown as

$$(14) \quad F(s, r) = F(s) \exp(-\rho a_s t_s(r)) \cdot \exp(-\lambda \bar{T}_s(z))$$

and the effects of within-plant and between-plant shading can be studied separately.

### 6.3. Computations and results

The mean flux density of radiation and relative radiation sums at different heights in the canopy was computed assuming conditions for which corresponding empirical measurements were available.

In Figs. 22a, b, computed values of the relative mean flux density of direct light with an incoming angle of  $30^\circ$  and  $40^\circ$  are given as functions of depth in the canopy. They represent thus (approximately) conditions during a clear day at solar elevations of  $30^\circ$  and  $40^\circ$ . The respective empirical values are also given in Figs. 22a, b. In Fig. 23 computed values of the relative mean flux density of isotropic light are given as a function of the depth in the canopy. The values are assumed to represent conditions during an overcast day and can be compared with the empirical values given also in Fig. 23. The relative radiation sums on horizontal planes at different heights

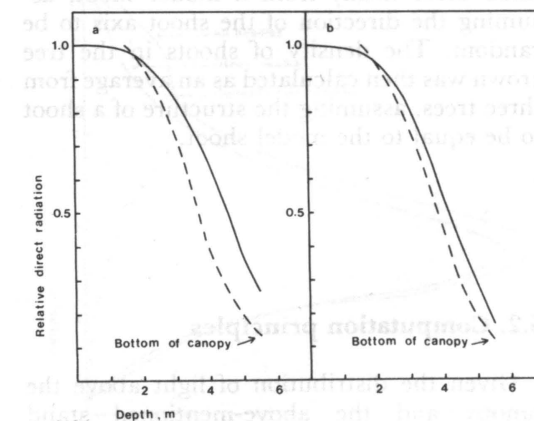


Fig. 22. Computed (solid line) and measured (dotted line) of direct radiation with sun elevation of  $40^\circ$  (a) and  $30^\circ$  (b) as a function canopy depth.

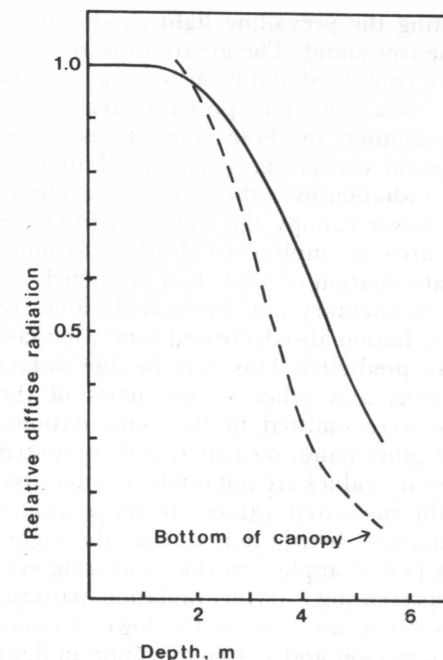


Fig. 23. Computed (solid line) and measured (dotted line) values of diffuse radiation as a function of canopy depth.

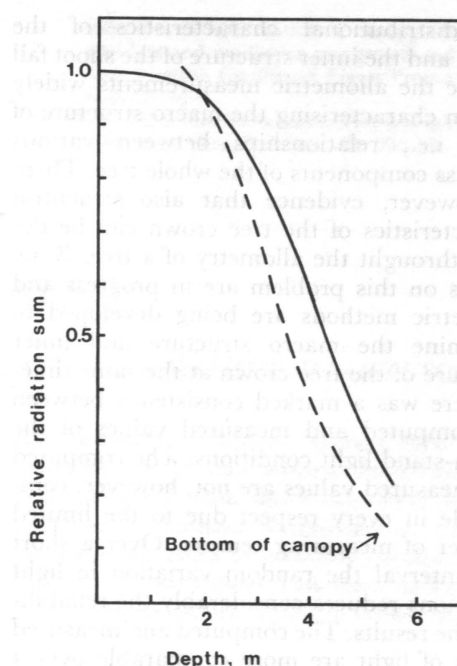


Fig. 24. Computed (solid line) and measured (dotted line) values of radiation sum as a function of canopy depth. The share of diffuse radiation was 10 % in the computations.

during a clear day in August (15. 8.) were computed and are shown in Fig. 24. In the computations the flux density of direct light at a moment  $t$  was given the value of

$$(15) \quad I(t) = k \cdot \exp(-0.23/\sin \alpha) \sin \alpha \, \text{MJ m}^{-2} \, \text{h}^{-1}$$

( $\alpha =$  elevation at time  $t$ )

## 7. CONCLUSIONS

The inner structure of a tree crown and the stand structure at tree level were separated in describing the structure of a young Scots pine (*Pinus sylvestris* L.) stand. The structural characteristics of the tree crown makes it possible to determine the shading due to the tree itself and the resulting light conditions inside the tree crown. The stand structure at tree-level enables estimates of between-tree shading. The combination of between-tree

and within-tree shading can be applied for computation of the within-stand light regime and light conditions in which each tree is growing. Hence, the structure of the tree crown and tree stands is a key for comprehensive studies on the role of light in stand dynamics, and vice versa.

The structural characteristics of the tree crown utilised in our model for the within-stand light regime are not easily obtained.

The distributional characteristics of the shoots and the inner structure of the shoot fall outside the allometric measurements widely used in characterising the macro structure of trees, i.e., relationships between various biomass components of the whole tree. There is, however, evidence that also structural characteristics of the tree crown can be derived through the allometry of a tree. Basic studies on this problem are in progress and allometric methods are being developed to determine the macro structure and inner structure of the tree crown at the same time.

There was a marked consistency between the computed and measured values of the within-stand light conditions. The computed and measured values are not, however, comparable in every respect due to the limited number of measuring sensors. Over a short time interval the random variation in light conditions reduces considerably the reliability of the results. The computed and measured values of light are more comparable over a prolonged time interval, and the theoretical results are then more consistent with the measured values. Hence, the modelling of interaction between canopy structure and light regime seems to have great potentials in

estimating the prevailing light condition inside the tree stand. The greatest discrepancy between computed and measured values is in diffuse radiation. The probable reason for over-estimation in these computations is the assumption concerning even distribution of diffuse radiation over the whole hemisphere. In the lower canopy the radiation from the zenith area is emphasised, leading to more rapid attenuation of light than predicted.

The momentary and integrated values of direct radiation also decreased somewhat faster than predicted. This may be due to fact that stems and other woody parts of the canopy were omitted in the computations. On the other hand, measured and computed momentary values are not totally comparable since the measured values are mean values for radiation distribution during the eight-minute period applied in the measuring system representing varying radiation pattern. This is especially true in the lower canopy where temporal and spatial variation in light regime is pronounced. The consistency between the computed and measured values of direct radiation is, however, satisfactory considering the fact that the computations are totally independent of the measurements.

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## SELOSTE

### MÄNNIKÖN LATVUSTON RAKENNE JA LATVUSTON SISÄISET VALAISTUSOLOJAT

Työssä on tutkittu nuoren männikön latvuston rakennetta ja sen yhteyttä latvuston sisäisiin valaistusolosuhteisiin. Havaittiin, että latvuston yleisrakenne ja latvuksen muoto osoittautui säännönmukaiseksi puun asemasta riippumatta. Myös oksien ja versojen rakenne oli säännönmukaista siten, että esimerkiksi neulasten lukumäärä pituusyksikköä kohti ja verson neulaspinta-ala olivat

säännönmukaisia. Valtapuissa neulaset olivat jakaantuneet tasaisesti yli koko latvuston. Alistetuissa puissa neulasmassa sen sijaan sijaitsi pääosiltaan latvuksen yläoksassa ja latvuksen pintakerroksessa. Latvuksen rakennetietojen avulla on määritelty latvuksen sisäisiä valaistusoloja teoreettisesti. Laskelmien tulokset osoittavat yhdenmukaisuutta empiiristen tulosten kanssa.