

## ECO-PHYSIOLOGICAL STUDIES ON YOUNG SCOTS PINE STANDS: II. DISTRIBUTION OF NEEDLE BIOMASS AND ITS APPLICATION IN APPROXIMATING LIGHT CONDITIONS INSIDE THE CANOPY

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### SELOSTE:

NEULASMASSAN JAKAUTUMINEN NUOREN MÄNNIKÖN LATVUKSESSA JA  
TÄMÄN KÄYTTÖ METSIKÖN SISÄISTEN VALAISTUSOLOJEN ARVIONNISSA

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The technique of double normalizing, *i.e.* normalizing the relative needle biomass and the length of the living crown system, is applied to the modelling of the distribution of needle biomass in the canopy of young Scots pine (*Pinus sylvestris* L.) stands. The study based on the parameters of  $\beta$ -function showed that at the individual-tree level, the variance in needle distribution was not closely associated with any tree characteristics. A shift in the point of maximum needle biomass upwards in suppressed trees was, however, evident. This was associated with an increase in the height of the trees. At the stand level, the stand mean height and stand density had an equal and a rather high potential for explaining the variance in the needle distribution. The normalized crowns are utilized in models for determining light extinction in the crown. A special technique for determining the amount of photosynthates available for growth in a particular tree is presented.

### INTRODUCTION

The extinction of light in the canopy system is determined by the vertical distribution and optical properties of the foliage (for example, MONSI & SAEKI 1953). On the other hand, the prevailing illumination shapes the crown system of the stand members by limiting the amount of photosynthates available for branching and growth of the foliage and lateral shoots. Therefore knowledge of the vertical distribution of the foliage is of importance in assessing the survival potential of a stand member,

*i.e.* the amount of light received by foliage and resulting rate of total photosynthesis (cf. WERHAGEN *et al.* 1963). In forestry, especially in tree spacing and thinning problems, information concerning the amount of photosynthetic products is valuable, and there is a need to draw a distinction between the contribution of foliage biomass and light conditions to the photosynthetic capacity of a tree growing in a stand (cf. LEDIG 1976).

This paper presents a model for the

distribution of needles in the canopy of young Scots pine (*Pinus sylvestris* L.) stands. Emphasis is also given to the study of tree-to-tree and stand-to-stand variation in needle distribution. The re-

sulting models have been applied in assessing the mutual shading of stand members and the amount of total photosynthates available for growth by means of calculations based on stand structure.

## MATERIAL

The material is the same utilized by KELLOMÄKI and HARI (1980). It consists of thirteen young Scots pine stands situated near the Forest Field Station, University of Helsinki (60° 47' N, 24° 18' E, 150 m a.s.l.) The characteristics of these stands and the monitoring of the environment, sampling the study area and the whole-tree analysis of the sample trees are described in detail by KELLOMÄKI and HARI (1980). The following stand and sample tree characteristics were utilized in the present analysis: stand mean height, stand

mean density, height of sample tree, total needle biomass of the sample tree, length of living crown of the sample tree, position of whorl within the living crown, and needle biomass of whorl divided into needle age classes.

In addition, photosynthetic light ratio for each whorl as well as position coefficient and photosynthetic capacity for each sample tree were utilized in the analysis. These concepts are described by IONEN *et al.* (1979) and KELLOMÄKI and HARI (1980).

## METHODS AND RESULTS

Data analysis was carried out in the five following phases: (A) construction of a model for needle distribution, (B) estimation of model parameters for each individual tree, (C) estimation of model parameters for each study stand and needle age class, (D) application of the model for assessing the within-stand light conditions, and (E) development of a method for estimating the photosynthetic production in the crown.

### Distribution of needle biomass

A model for needle distribution was developed by normalizing needle biomass per whorl position with respect to the maximum needle biomass and the length of the living crown, as suggested by KINERSON and FRITSCHEN (1971). At this stage all the material was considered as a whole. The normalized needle biomass per whorl in each needle age class is presented in Fig. 1. In addition the distribution of the total needle biomass is presented.

The distribution of current-year needles is mainly determined by the light conditions in the environment through the branching of lateral shoots and the growth of needles and shoots (cf. IONEN *et al.* 1979). Environmental factors other than light become more dominant as the age of the needle classes increases, resulting in variation which is not predictable with the help of light measurements. Especially the effect of water supply and related factors may prove to be of importance. Additional variation is also caused by insect and fungal damage, which appears on branches growing in low light intensity. In the lower part of the crown the variation originating from such factors is pronounced.

The following values were obtained for the location of maximum needle biomass per needle age class within the living crown:

	$\bar{x}$	s
Current-year needles .....	.553	.110
One-year-old needles .....	.482	.134
Two-year-old needles .....	.346	.182
Total needle biomass .....	.432	.128

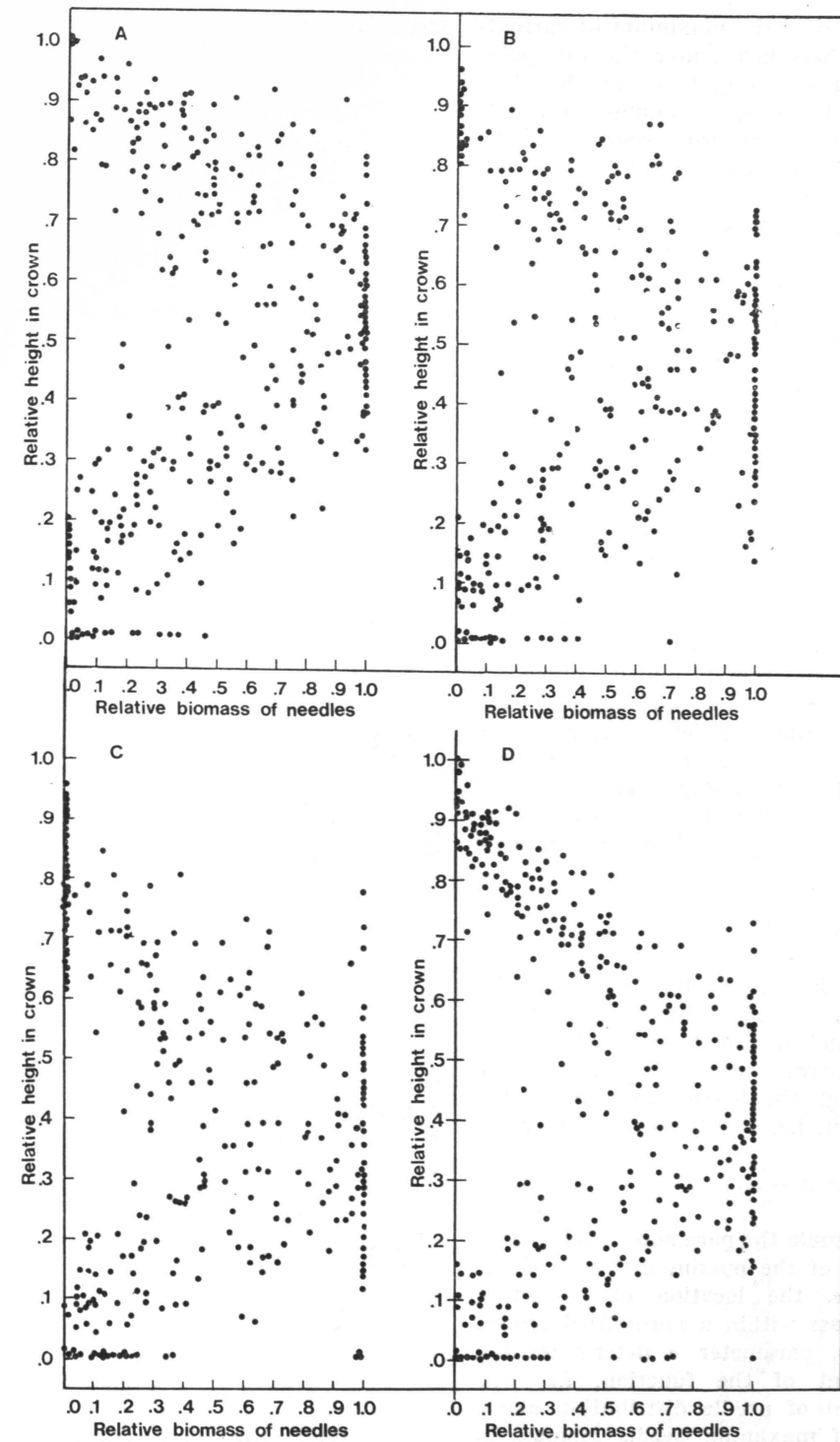


Fig. 1. Distribution of needle biomass within the living crown: A: Current-year needles, B: One-year-old needles, C: Two-year-old needles, D: Total needle biomass.

The location of the maximum of current-year needles was just above the mid-point of the living crown system. In the older age classes the point of maximum needle biomass moves downwards according to the increasing age of the needles, as can be expected due to the development of the growing crown system. The maximum point for the total needle biomass lies just below the mid-point of the living crown system.

Several alternatives are available for describing the distribution of needle biomass. For example, STEPHENS (1969) recommends the application of the normal distribution (cf. also KINERSON and FRITSCHEN 1971). The needle biomass is, however, characterized by a skewed distribution rather than a normal distribution. It appears from Fig. 1 that the amount of needles first increases slowly in the upper part of the crown. However, after a particular point is reached, the amount of needle biomass increases rapidly and it culminates somewhere near to the mid-point of the crown, as described earlier. Thereafter the needle biomass decreases rapidly towards the area of self-pruning. This kind of distribution is satisfactorily described by  $\beta$ -distribution as expressed by the following notation

$$(1) \delta(x) = (x - a)^\alpha \cdot (b - x)^\gamma,$$

where  $\delta(x)$  is the density of the needles at height  $x$ ,  $a$  and  $\gamma$  parameters to be estimated, and  $a$  and  $b$  constants. In a normalized crown system the  $\beta$ -function is forced through the bottom and top of the crown system, i.e.  $a = 0$  and  $b = 1$ , when

$$(2) \delta(x) = x^\alpha (1 - x)^\gamma.$$

In this formula the parameter  $\gamma$  determines the location of the maximum value of the function, i.e. the location of maximum needle biomass within a normalized crown. Respectively, parameter  $\alpha$  determines the turning point of the function, i.e. the turning point of needle distribution above the point of maximum needle biomass in a normalized crown (cf. Fig. 1).

The minimum square sum techniques yielded the following values for the para-

meter  $\alpha$  and  $\gamma$  in each needle age class:

	$\alpha$	$\gamma$	$R^2$
Current-year needles	3.638	4.458	.72
One-year-old needles	3.126	5.832	.77
Two-year-old needles	3.075	6.832	.83
Three-year-old needles	2.977	7.543	.85
Total needle biomass	2.703	3.831	.69

The curve fit for each needle age class is satisfactory in every case as indicated by the correlation coefficient between the observed and calculated values of needle distribution. The values of the proportion of explained variance were between 0,69 and 0,83. The curve fit is more precise in older needle age classes than in current-

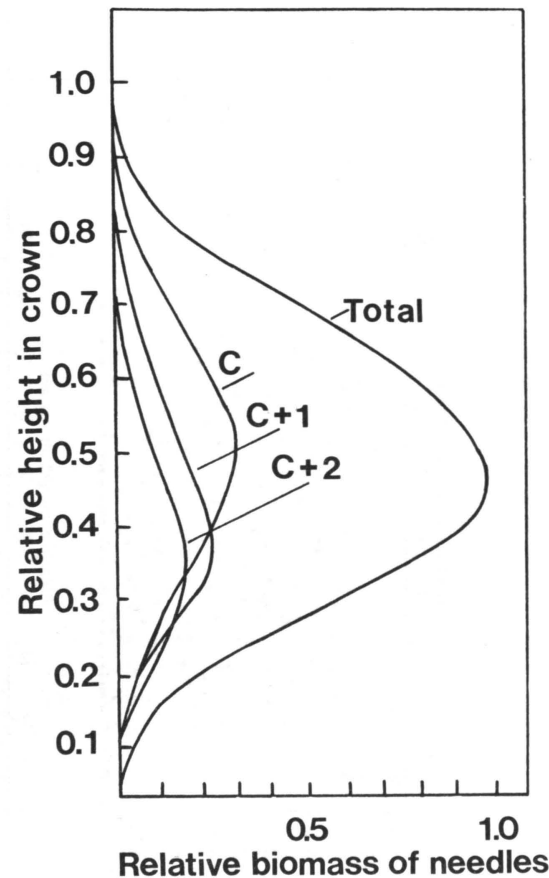


Fig. 2. Distribution of needle biomass per age class based on  $\beta$ -distribution.

year needles. The normalized crown system for each needle age class, as described by the  $\beta$ -function is presented in Fig. 2.

### Effect of tree characteristics on needle distribution

The estimated values of parameters  $\alpha$  and  $\gamma$  were explained by variables describing the characteristics of the trees and stands in order to relate the needle distribution to the dynamics of the stand. The relative needle biomass, relative position coefficient and relative total photosynthesis were employed as explaining variables.

No regular relationships were found between parameters  $\alpha$  and  $\gamma$  and different tree characteristics. The correlation coefficients for the different needle age classes varied from near zero to almost 1,0 as regards the relative tree height, relative needle biomass, relative position coefficient, or relative total photosynthesis depending on the particular stand. However, no explaining variable gave the same results in each stand. The tree-to-tree variation in the values of parameters  $\alpha$  and  $\gamma$  was not related to the properties of the whole stand, either, although high or low correlation between explaining variables and parameters  $\alpha$  and  $\gamma$  occurred in young stands as well as in

Table 1. Values of  $\beta$ -function parameters  $\alpha$  and  $\gamma$  (Eq. 2) for each stand and needle age class and the percentage of explained variance.

Stand number	$\alpha$	$\gamma$	$R^2$	$\alpha$	$\gamma$	$R^2$
	Current-year needles			One-year-old needles		
1	.329	2.067	.407	.275	2.260	.468
2	.259	1.896	.565	.251	1.971	.549
3	.277	2.588	.552	.154	2.764	.592
4	.269	2.563	.610	.212	2.484	.631
5	.422	1.773	.582	.295	1.929	.606
6	.337	1.759	.509	.312	1.882	.544
7	.265	3.211	.629	.197	3.340	.622
8	.232	2.997	.601	.171	2.923	.580
9	.608	2.029	.641	.444	2.076	.601
10	.219	3.531	.665	.221	3.629	.691
11	.592	2.725	.637	.431	2.807	.655
12	.174	2.078	.639	.169	2.143	.662
13	.259	2.131	.595	.285	2.159	.650
	Two-year-old needles			Three-year-old needles		
1	.241	3.235	.588	.235	1.270	.705
2	.266	2.258	.683	.248	2.779	.752
3	.140	4.312	.740	.117	5.432	.822
4	.239	3.355	.744	.159	4.127	.792
5	.249	2.945	.707	.254	3.749	.782
6	.299	2.816	.668	.262	3.550	.746
7	.204	4.734	.761	.396	5.602	.754
8	.202	4.592	.748	.303	5.762	.777
9	.322	3.326	.710	.352	4.419	.784
10	.035	5.503	.864	.042	6.839	.831
11	.320	4.401	.751	.262	5.497	.808
12	.124	3.312	.800	.079	4.192	.863
13	.243	3.226	.731	.466	4.271	.836

more developed stands. Thus, the position of a tree in a stand or other tree characteristic could not explain the tree-to-tree variation in the distribution of needle biomass.

### Distribution of needle biomass inside the canopy of a stand

Table 1 and 2 present the values of parameters  $\alpha$  and  $\gamma$  for each stand and needle age class. The explaining power of the  $\beta$ -function seems to increase as the age of the needle class increases. In the current-year needles and one-year-old needles the percentage of explained variance remains under 70. In two-year-old and three-year-old needles the average degree of determination falls between 70–80 per cent of the total variance. Especially in stands where the mean height is near 10 m, the percentage of explained variance is high. This may indicate that in such stands conditions for tree growth have been stabilized (cf. KINERSON and FRITSCHEN 1971). The percentage of explained variance in the total needle biomass is of the same magnitude as in an individual needle age class (Table 2).

Table 2. Values of  $\beta$ -function parameters  $\alpha$  and  $\gamma$  (Eq. 2) for each stand and the respective percentage of explained variance.

Stand number	Parameters		R <sup>2</sup>
	$\alpha$	$\gamma$	
1	.281	.266	.439
2	.220	1.847	.633
3	.128	2.822	.610
4	.177	2.373	.675
5	.236	1.962	.648
6	.290	1.894	.565
7	.118	2.964	.681
8	.164	2.982	.593
9	.309	2.094	.645
10	.070	3.679	.748
11	.252	2.823	.669
12	.110	2.238	.693
13	.124	2.213	.656

The standwise variance of parameters  $\alpha$  and  $\gamma$  was related to the stand height and stand density (Table 3). The variance in parameter  $\alpha$  was not very well correlated with either variable. The stand height explained less than 10 per cent of the observed variance.

Table 3. Regression models for parameter  $\gamma$  in each needle age class based on stand mean height and density.

Regression model	Constant for whole combination	Regression coefficient	R	P
Current-year needles	2.491		.773	< 0.05
Height		-0.106		
Density		0.000059		
One-year-old needles	2.636		.881	< 0.01
Height		-0.113		
Density		0.000057		
Two-year-old needles	4.276		.713	< 0.05
Height		-0.206		
Density		0.000067		
Three-year-old needles	5.426		.668	< 0.10
Height		-0.241		
Density		0.000069		
Total needle biomass	2.622		.712	< 0.05
Height		-0.101		
Density		0.000048		

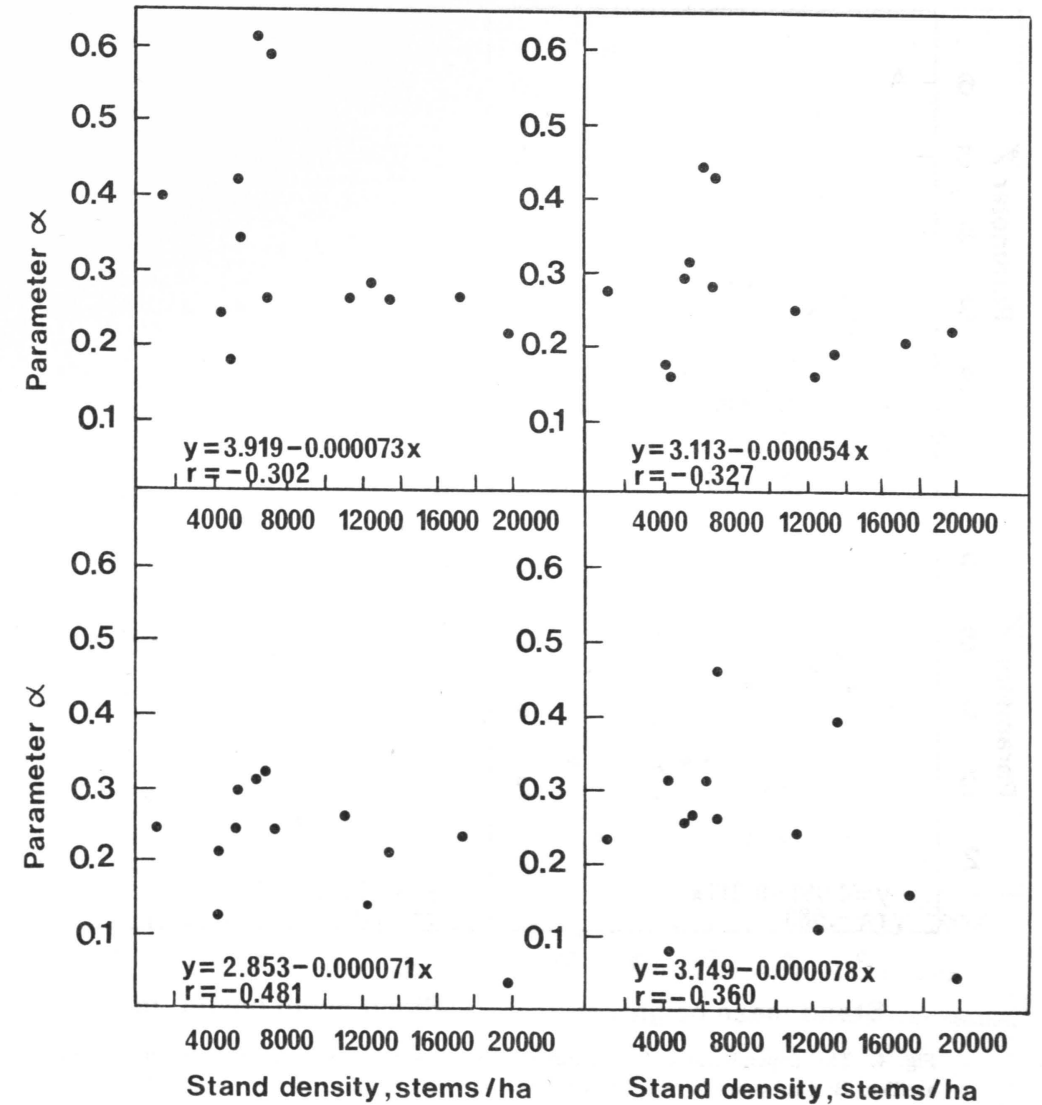


Fig. 3. The dependence of the parameter  $\alpha$  on stand density, A: Current-year needles, B: One-year-old needles, C: Two-year-old needles, D: Three-year-old needles.

The explained variance remained also low as regards the stand density, especially in the case of the current-year needles (Fig. 3). In other needle age classes the explained variance was 10–24 per cent and in the total needle biomass 32 per cent. However, the regressions between the stand density and the parameter  $\alpha$  were statistically significant ( $p < 0.10$ ) only for two-year-

old needles and the total needle biomass as given by

$$(3) \alpha = 2.616 - 0.000079x, r = 0.564$$

where  $x$  is the stand density. It seems evident that only a very high stand density shapes to a greater extent the needle distribution as indicated by parameter  $\alpha$ .

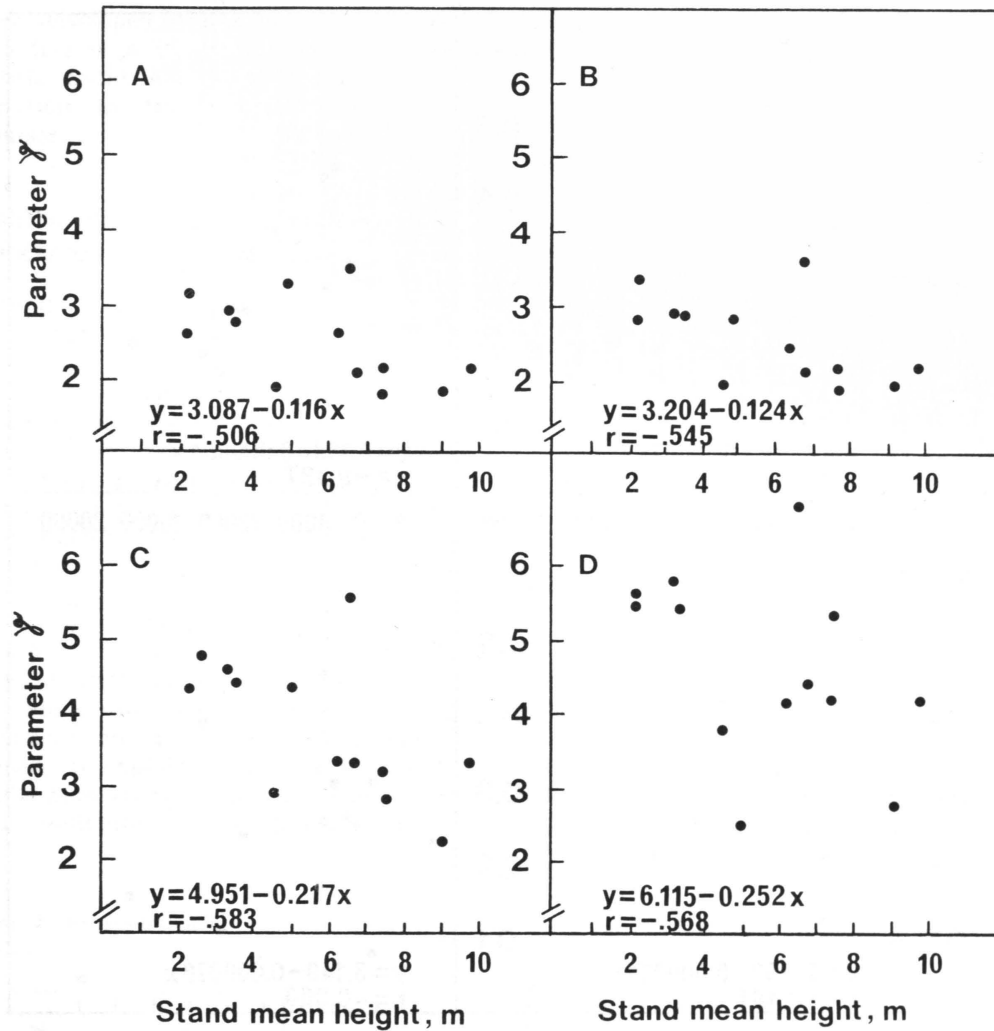


Fig. 4. The dependence of the parameter  $\gamma$  on stand mean height, A: Current-year needles, B: One-year-old needles, C: Two-year-old needles, D: Three-year-old needles.

Therefore any value for parameter  $a$  of between 2.700–3.600 should yield a satisfactory result in estimating the needle distribution in stands of mean height between two and ten meter. Additional studies are, however, needed to substantiate the minor role of parameter  $a$  in describing the needle biomass by the  $\beta$ -function.

The dependence of parameter  $\gamma$  on the stand height and stand density is presented in Figs. 4 and 5. The regression between the stand height and parameter  $\gamma$  seems to be a logarithmic one. The linear model gave,

however, nearly the same degree of determination for the regression, *i.e.* 25–35 per cent depending on the needle age class. The curvilinear dependence of parameter  $\gamma$  on the stand height is interpreted as depicting the stabilization of growth conditions as stand development proceeds. In other words, the growth and development of the crown system follows the particular pattern which is set by the prevailing environment. Especially, the role of the prevailing light conditions is evident but other environmental factors, for example, water supply,

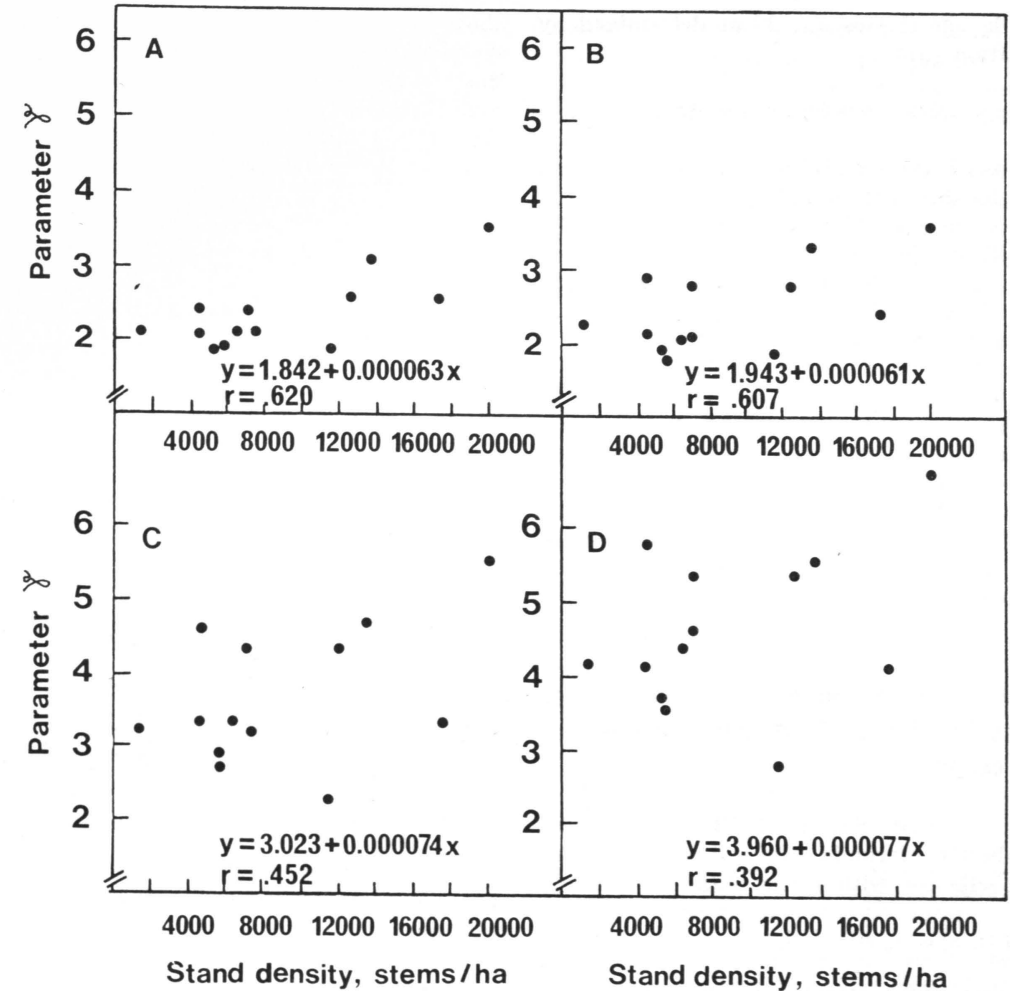


Fig. 5. The dependence of the parameter  $\gamma$  on stand density, A: Current-year needles, B: One-year-old needles, C: Two-year-old needles, D: Three-year-old needles.

may also play an important role. The percentage of explained variance for the total needle biomass was 25 as given by

$$(4) \quad \gamma = 3.111 - 0.110x, \quad r = 0.505$$

where  $x$  is the stand mean height. The regressions for the different needle age classes and the total needle biomass were all statistically significant ( $p < 0.10$ ).

The use of stand density in determining the needle distribution through parameter  $\gamma$  gave better results than when stand mean height was used (Fig. 5). It is worth

noting that the explanatory power of the stand density decreased according to the needle age, *i.e.* quite opposite to the effect of the stand height on the values of parameter  $\gamma$ . The degree of determination remained, however, in each case lower than 40 per cent of the total variance in parameter  $\gamma$ . Thus in the present material, the effect of the stand density on the needle distribution characteristics seems to be of similar magnitude to that of the stand height. The percentage of explained variance in the total needle biomass was of the same magnitude as that in the individual

needle age classes, *i.e.* 29 as determined by equation (5)

$$(5) \gamma = 2,008 - 0,000052 x, r = 0,538$$

where  $x$  is the stand density. The regressions for the different needle age classes and the whole needle biomass were statistically significant ( $p < 0,10$ ).

In the models based on the stand height and density, these variables explain equal parts of the variance in parameter  $\gamma$  (Table 3, p. 248). The contribution of the stand height and the stand density is of significance ( $p < 0,10$ ) in each needle age class including the total needle biomass. The degree of determination of the two-variable model was 40–60 per cent depending on the needle age class. The degree of determination for the total needle biomass was 50 per cent.

#### Application of needle distribution for approximation of light conditions within the canopy.

MONSI and SAEKI (1953) used Beer-Lambert's formula for describing the light climate within the stand as follows

$$(6) 1(t, x) = 1_0(t)e^{-kL(x)},$$

where  $1_0(t)$  is light intensity above the canopy at the moment  $t$ ,  $1(t, x)$  light intensity in the canopy at a particular point  $x$  at moment  $t$ ,  $L(x)$  cumulative leaf area

above the point  $x$ , and  $k$  a coefficient specific for each plant species. In applying this formula for approximation of the light conditions in different parts of the canopy the cumulative leaf area plays a key role and should be determined for the calculation.

In model construction the stem diameter distribution of the stand has been used to obtain the basic compartments of the stand structure model (cf. Fig. 6): (1) height of the trees, (2) needle biomass of the trees and (3) length of the living crown. The following equations were applied in estimating the values of the model compartments:

$$(7) \text{Height of tree} = 3,831 \cdot \ln D_{1,3}, r = 0,97$$

$$(8) \text{Needle biomass} = e^{0,35} \cdot 1,3D, r = 0,94$$

$$(9) \text{Length of crown} = 2,321 \cdot \ln D_{1,3}, r = 0,97$$

Tree height, crown length, and needle biomass were used to estimate the needle distribution within the crown. The needle biomass,  $m_i(x)$ , above the point  $x$  and in the age class  $i$  ( $i = 1, 2, 3, 4$ ) is now obtained by integrating the  $\beta$ -function.

$$(10) m_i(x) = M_i \cdot \int_x^1 x^{a_i} (1-x)^{b_i} dx,$$

where  $M_i$  is the needle biomass of the  $i$ :th age class in the stand.

The needle biomass  $m_i(x)$  can be converted into leaf area as needed in the equation (6).

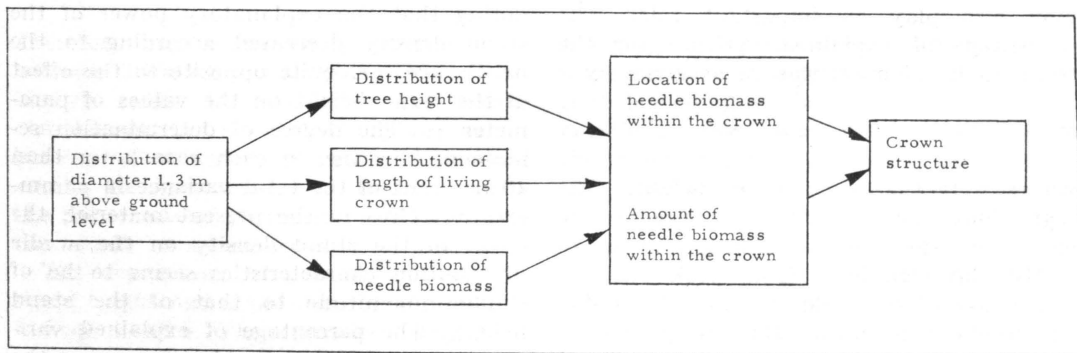


Fig. 6. Principles of crown structure models.

However, we preferred to use the total needle biomass instead of the leaf area. In addition, light climate during a prolonged period has proved to be more applicable in growth studies than momentary values of light intensity. Therefore the concept of photosynthetic light ratio (PLR) was employed in the model construction as determined by the following equation:

$$(11) \text{PLR} [x, t_0, t_1] = \frac{\int_{t_0}^{t_1} p(1(x, t)) dt}{\int_{t_0}^{t_1} p(1_0(t)) dt}$$

where  $p$  is the dependence of photosynthetic rate on light intensity,  $1(x, t)$  light intensity at a particular point  $x$  within the canopy at moment  $t$ ,  $1_0(t)$  the same but above the canopy and  $t_0$  and  $t_1$ , the beginning and end of a particular time interval  $[t_0, t_1]$  (cf. KELLOMÄKI 1977). Photosynthetic light ratio is a measure of the actual amount of photosynthates available for growth related to the conditions above the canopy.

The values of PLR in any point of a crown system are determined by the cumulative needle biomass above the point. MÄKELÄ (1979) has developed the following model for the relationship between cumulative needle biomass  $m(x)$  above a chosen point  $x$  and the amount of light available for growth during a growing season.

$$(12) \text{PLR} [x, t_0, t_1] = \frac{c}{1 + \text{Exp}(-2(\lg m(x) - a)/b)} + 1 - c,$$

where  $t_0$  and  $t_1$ , respectively, indicate the beginning and cessation of the growing season and  $a = 2.3$ ,  $b = -1.2$ , and  $c = 0.8$ . The needle biomass,  $m(x)$ , above the point  $x$  is given by

$$(13) m(x) = \sum_{i=1}^4 m_i(x).$$

In model construction it is assumed that the light extinction is logistic as regards

cumulative needle biomass, *i.e.* its upper asymptote is the unshaded illumination and lower asymptote a value of the shaded illumination determined by the total needle biomass above.

Fig. 7 presents the relationship between PLR and the cumulative needle biomass. Examples of light profiles based on the developed models and expressed in terms of PLR for some model stands are presented in Fig. 8.

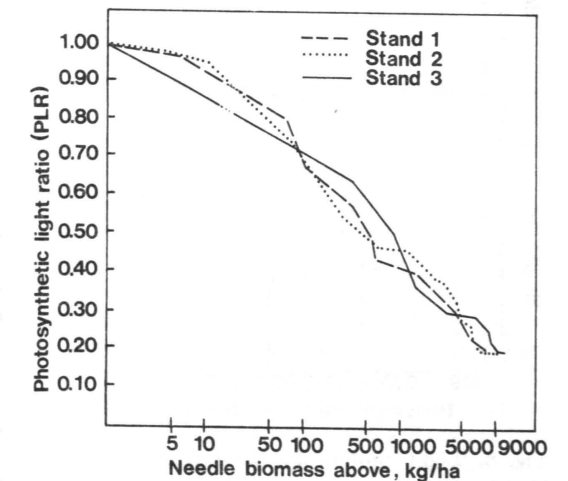


Fig. 7. Relationship between cumulative needle biomass and photosynthetic light ratio (PLR) in three selected stands.

#### Application of needle distribution for approximation of the amount of photosynthates available for growth.

The concept of photosynthetic capacity is frequently used in describing the amount of photosynthates available for growth in the whole tree (LEDIG 1976). This concept describes the total  $\text{CO}_2$ -exchange capacity per tree or whole stand, and is determined by the size of the assimilative surface and rate of photosynthesis. The

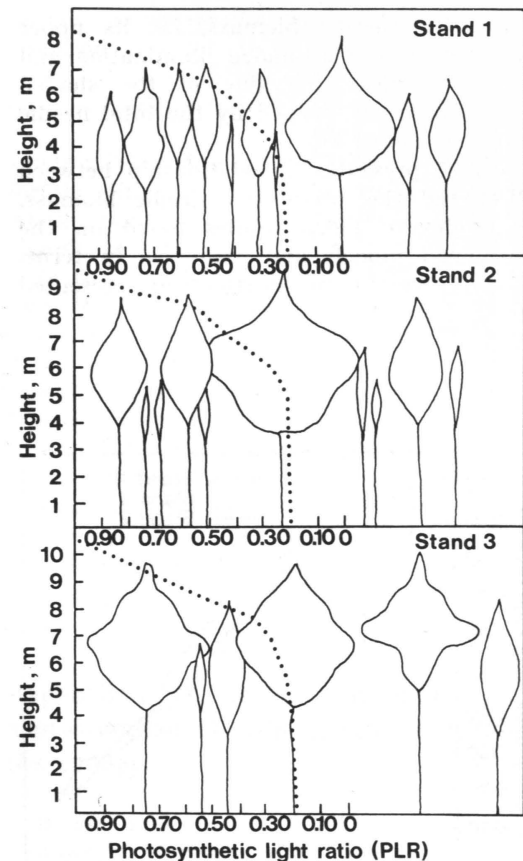


Fig. 8. Light profiles in three selected stands. Width of tree crowns equals to the biomass of the needles.

## CONCLUSIONS AND FURTHER ELABORATION

Analysis of the material showed that the techniques of double normalizing may have great potential in modelling the distribution of the needle biomass in a canopy. However, the applicability of the presented models are limited due to the restricted nature of the material. Especially in open or very dense stands, inaccurate approximations may be obtained. The material consists of young Scots pine stands and therefore further studies should be carried out to test the applicability of the method in older stands. In principle, the variation in needle distribution in mature and stabilized, even-aged stands should be smaller than that in the type of young and fast-

developing stands which consisted the material of this study. There is also evidence that the distribution of needle biomass in such stands may be modified by stand density thus producing a need for density corrections (cf. KINERSON and FRITSCHEN 1971).

$$(14) \quad PC [t, t_0] = \int_V \delta(x) \cdot PLR [x, t_0, t_1] dV,$$

where  $\delta(x)$  is the needle density and PLR the photosynthetic light ratio in a crown layer. The elements needed in these calculation can be obtained by the models described above (see Equations 10, 12, and 13). Thus no further information apart from certain stand characteristics are needed in estimating the photosynthetic capacity of any tree growing in any particular stand.

Even though the analysis of the material gave satisfactory results, it was not possible to explain the distribution characteristics of the needle biomass in an individual tree by means of the position of the tree in the stand or the characteristics of the tree. This indicates the poor fitness of the  $\beta$ -function for describing the needle biomass characteristics of an individual tree or the

low potential of the selected variables to explain the distributional characteristics of the needle biomass in an individual tree. Earlier studies suggest, however, that the light conditions inside the stand may have a dominant role in determining the properties of the needle distribution. For example, KELLOMÄKI and HARI (1980) have demonstrated that the relative needle biomass in young Scots pine stands is fairly well comparable with the total photosynthesis for a prolonged period in the same conditions. Thus, it is reasonable to assume that the light climate also has a role of importance in determining the distribution of needle biomass (cf. also ILONEN *et al.* 1979). Further studies are, however, needed to confirm this hypothesis.

The used light measuring system may also have an effect on the results. Each horizontal layer represents a large amount of vertical variance which remains unspecified when the present method is used. Therefore there are problems in synchronizing the needle density and the respective light intensity. On the other hand, the mean number for each layer omits the role of variance between sun-flecks and shaded areas in the growth and development of the crown system. For example, MORGAN and SMITH (1978) showed that in sun-flecks the growth of lateral shoots may be much greater than would have been expected on the basis of the mean light intensity of the layer. In addition to the light intensity, the changes in photosynthesis also seem to be induced by spectral changes in light. Therefore exceptional care should be paid to the monitoring of light inside the stand when carrying out growth studies of the crown system.

The relationship between parameters  $\alpha$  and  $\gamma$  and the characteristics of needle biomass and tree position suggest that there is a shift in the point of maximum needle biomass upwards in suppressed trees. There is, however, a pronounced variance in this relationship which is independent of the stand. The same phenomenon is more easily recognized in stand-level calculations where the negative regression between stand height and parameter  $\gamma$  and stand density and parameter  $\alpha$  are evident (Figs 3 and 4). The positive regression between

stand density and parameter  $\gamma$  indicates the same phenomenon. The increasing stand height and suppression seem, thus, to have the same effect on the needle distribution of young Scots pine. Evidently, both phenomena are caused by the deteriorating light conditions inside the canopy as regards to the stand member's position in the stand. This interpretation is, however, not completely clear, since the contribution of the stand density is unexpectedly small. A possible explanation for this phenomenon is a low sun elevation in Finland even at Midsummer which emphasizes the role of stand depth in the extinction of light in a stand. A possible explanation may also be found in the limited material and its specific properties.

As expected the current-year needles were situated higher in the stand than the older ones (Fig. 1). Within stand heights of five to ten meter the distribution characteristics of the current-year needles were the same with only a small further shift upwards. Also in the one-year-old needles the levelling off of parameter  $\gamma$  between the height range five to ten meter is evident. In two-year- and three-year-old needles the levelling off is negligible and a continuous shift in the point of maximum needle biomass upwards is evident throughout the whole range of the tree height variance. Apparently this is associated with increasing self-pruning induced by increasing stand height and the decreased amount of light available for photosynthesis. Further studies are, however, needed to test this hypothesis. On the other hand, the turn-over time for Scots pine needles is three to five years, which is clearly associated with the linear regression between stand height and the parameter  $\gamma$  for two- and three-year-old needles.

At the stand level, it seems to be possible to estimate the needle distribution characteristics satisfactorily through the  $\beta$ -function. Especially, the values of parameter  $\gamma$  are closely associated with stand height and density, and the values of parameter  $\alpha$  with the density of the stand, thus enabling the modelling of the needle distribution in a crown as part of the stand dynamics (cf. KELLOMÄKI *et al.* 1979). The contribution of parameter  $\alpha$  is, however, important

only in very high densities. Therefore the same values of this parameter seem to be widely applicable in calculations. Further studies are, however, needed to validate this assumption and to develop better models for describing the crown dynamics in a »pole-stage» stand. Especially the direct relationship between the crown characteristics and the prevailing light climate within the stand would facilitate the modelling of the stand dynamics in many essential respects.

Normalized crown models facilitate the determination of the light conditions in any point of the crown system by means of the relationship between light extinction

and needle biomass. In silviculture this information can be applied in approximating the total amount of photosynthates available for growth, and also used to evaluate the survival potential of a particular tree in an even-aged stand where pronounced differentiation in diameter and height between trees has occurred. This enables one to use an eco-physiological approach to thinning problems through the concept of photosynthetic capacity. However, further studies are needed to determine the relationship between photosynthetic capacity and stand growth and structure in order to evaluate its applicability in practical forestry.

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## SELOSTE:

### NEULASMASSAN JAKAUTUMINEN NUOREN MÄNNIKÖN LATVUKSESSA JA TÄMÄN KÄYTTÖ METSIKÖN SISÄISTEN VALAISTUSOLOJEN ARVIOINNISSA

Neulasten jakautumista nuoren männikön latvuksessa on tarkasteltu normalisoimalla sen määrä

eri latvuserroksissa suhteessa neulasten maksimimäärään ja sen sijaintiin latvuksessa.  $\beta$ -funktion

parametreihin perustuva tarkastelu osoitti, että neulasmassan jakautuminen ei korreloinut selvästi yhdenkään tutkitun puun asemaa kuvaavan tunnuksen kanssa. Neulasmassan maksimikohdan havaittiin kuitenkin nousevan puun jouduttua muiden varjostamaksi. Samoin oli laita puuston pituuden ja tiheyden kasvaessa tai yksittäisen puun varjostuksen lisääntyessä. Metsikkötasolla

puuston keskipituus ja tiheys osoittautuivat molemmat tärkeiksi neulasmassan jakaantumisen selittäjiksi. Normalisoituja latvuksia hyväksi käyttäen on esitetty menetelmä latvuksen sisäisten valaistusolojen määrittämiseksi. Latvuksen valaistusoloja ja neulasjakautumaa hyväksi käyttäen on edelleen esitetty menetelmä yksittäisen puun fotosynteesikapasiteetin määrittämiseksi.