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# Silva Fennica

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SEPPO KELLOMÄKI

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**JULKAISIJA:**

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**TOIMISTO:**

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**VASTAAVA TOIMITTAJA**

SEPPO KELLOMÄKI

**TOIMITUSKUNTA:**

KUSTAA SEPPÄLÄ (puheenjohtaja), MATTI KÄRKKÄINEN, (vara-  
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## ECO-PHYSIOLOGICAL STUDIES ON YOUNG SCOTS PINE STANDS: I. TREE CLASS AS INDICATOR OF NEEDLE BIOMASS, ILLUMI- NATION, AND PHOTOSYNTHETIC CAPACITY OF CROWN SYSTEM

SEPPO KELLOMÄKI and PERTTI HARI

SELOSTE:

PUULUOKKA LATVUKSEN NEULASMASSAN, VALAISTUKSEN JA FOTOSYNTHEE-  
SIKAPASITEETIN ILMAISIJANA ERÄISSÄ NUORISSA MÄNNIKÖISSÄ

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The stratification of trees in stands as indicated by dominant, codominant, intermediate, and suppressed trees is analysed using an empirical material representing young Scots pine (*Pinus sylvestris* L.) stands. The relative needle biomass, *i.e.* the needle biomass related to the total maximum needle biomass in the stand, was closely correlated with the relative height of the tree and independent of the stand characteristics. Furthermore, the relative illumination within the crown system was correlated with the relative height of the trees as well as with the relative photosynthetic capacity. When calculated per needle biomass unit it appeared that height growth, radial growth, needle growth, and other growth parameters were the highest in the suppressed trees. The suppressed trees thus appear to be more efficient in utilizing the resources available for growth than trees in other classes. The ecological significance of the results are discussed.

### INTRODUCTION

The concept of tree class, *i.e.* the division of trees into dominant, codominant, intermediate and suppressed trees, is widely used in silviculture to describe the structural and functional characteristics of an even-aged stand. Dominant and codominant trees include the tallest and most vigorous trees in a stand as indicated by the relative height 0,9–1,0 and 0,8–0,9 of the dominant height of a stand. In young stands, dominant and codominant trees are the part of the tree population which will be retained in the future. Intermediate and

suppressed trees, *i.e.* trees representing the relative height 0,7–0,8 and 0,6–0,7, are likely to be eliminated during the course of succession of the stand (cf. ILVESSALO 1929).

Structural differentiation is assumed to be due to competition for environmental resources, mainly light (*e.g.* KUROIWA 1960 a, b). Consequently, the crown system of trees are modified by the existing illumination as demonstrated by FARMER (1976). Therefore the competition status of stand member belonging to any tree class



can be described by the amount of total needle biomass and its illumination, *i.e.* the total amount of photosynthates available for growth as indicated by the concept of photosynthetic capacity (cf. LEDIG 1976). Consequently, differences in structural matter production are to be expected between different tree classes (*e.g.* LÖNNROTH 1925, BORMANN 1965).

The aim of the present study is to investigate the biological validity of the concept of tree class. Three aspects are considered: (1) relationship between tree

class and respective needle biomass, (2) relationship between tree class and respective illumination of needle biomass, and (3) relationship between tree class and the respective values of photosynthetic capacity. Consequently, differences between tree classes are expected in the following growth characteristics: (4) height, and (5) radial growth of the stem, (6) structural matter production by the stem, (7) needle growth, (8) growth of lateral shoots, and (9) bud formation in the crown.

## MATERIAL AND METHODS

### Study areas

The material includes thirteen young even-aged Scots pine (*Pinus sylvestris* L.) stands situated around the Forest Field Station, University of Helsinki, (60° 47' N, 24° 18' E, 150 m a. s. l.). The main characteristics of the stands are given in Table 1. Both naturally regenerated and cultivated stands of ages varying between 3–31 years, as determined at a height of 1.3 m above soil level, were included. All the stands were pure Scots pine stands growing mainly on sites of *Calluna* and *Vaccinium* types. The stand density varied from 1 200 to 20 000 stems per hectare and the stand mean height from two to ten meters. The tending of the stands included both thinnings and elimination of invading deciduous trees. Stands number 9, 12, and 13 were these utilized in the study by ILONEN *et al.* (1979). The stands were measured in 1976–1978. In the analysis, the stand number 1 was, however, omitted due to too large age variation between trees.

### Light measurements

The light measurements needed in the study were carried out with the help of the photosynthetic simulator described by KELLOMÄKI *et al.* (1979). The main emphasis was laid on light available for photosynthesis, *i.e.* a plant specimen's response to light intensity was introduced

into the measuring procedure thus allowing the integration of light available for photosynthesis over the monitoring period (cf. MCCREE 1965). For further details of the measuring system see KELLOMÄKI *et al.* (1979).

A pole of adjustable height was erected at the selected point in the study area. Eight sensors were installed at equal distances along the pole, including one above the canopy. The distances between the sensors were thus stand-specific and proportional to the dominant height of the stand. The outputs of the sensors were read at 08.00 hours and 17.00 hours daily. The measurements were carried out over a period of one week in each stand from July through August 1976–1978.

### Phytometric studies

For the phytometric studies a sample area was chosen around the light measuring tower in each stand. The radius of each sample area was 5.64 m, except for stands number 9, 12, and 13 where twenty trees closest to the light measuring pole were sampled (cf. ILONEN *et al.* 1979). The diameter distribution at a height of 1.3 m above the ground level was determined in the first phase of the sampling, except for stands number 9, 12, and 13 where the sampling was based on the height distribution of the trees. The diameter distribution was determined to the accuracy of

Table 1. Some main characteristics of the study stands.

Stand number	Site type	Stand age yr <sup>1)</sup>	Stand <sup>2)</sup> density stems/ha	Mean diameter cm <sup>3)</sup>	Mean height m <sup>3)</sup>	Number of sample trees	Additional information
1	<i>Calluna</i> Type	15	1 200	3.6	5.1	8	Naturally regenerated
2	»	31	11 500	7.0	9.1	12	»
3	<i>Vaccinium</i> Type	4	12 500	1.8	2.3	8	»
4	»	15	17 500	5.5	6.3	13	»
5	<i>Calluna</i> Type	10	5 300	4.3	4.6	8	»
6	<i>Vaccinium</i> Type	21	5 500	8.0	7.7	15	»
7	»	3	13 800	2.2	2.3	14	Planted
8	»	4	4 500	3.5	3.4	14	Planted
9	»	20	6 300	6.7	6.8	12	Sown
10	<i>Oxalis-Myrtillus</i> Type	9	20 000	5.3	6.7	5	Planted, abandoned field
11	<i>Vaccinium</i> Type	5	7 000	4.3	3.5	13	Planted
12	<i>Myrtillus</i> Type	23	4 500	10.9	9.9	5	Planted
13	»	23	7 000	6.8	7.5	5	Planted

<sup>1)</sup> Measured at 1.3 m above ground level and calculated as a mean of sample trees.

<sup>2)</sup> Mean of density values measured around each sample tree.

<sup>3)</sup> Weighted by diameter distribution.

one centimeter and the height distribution to the accuracy of one decimeter. The minimum number of sample trees was one for each diameter or height class. In stands number 9, 12, and 13 the tallest and shortest trees were also included in the material. Trees with two leaders or other abnormalities were omitted in the sampling.

The sample trees in stands number 1...6 were cut 5 cm above the soil level and moved to the laboratory for further analysis. In other areas the procedure was the same except the root systems of the sample trees were excavated. Roots down to a diameter of one centimeter were tried to harvest.

Several characteristics were determined from each sample tree, but only the following were utilized in the present study: tree height, diameter at 1.3 m above soil level, current annual height growth, current annual radial growth at 1.3 m above soil level, bud number of the leader, needle biomass of the lateral shoot of average length in each whorl divided into four needle age classes, bud number in the same lateral shoot, leader growth of the same lateral shoot and the number of lateral shoots per whorl. Length measurements were carried out with an accuracy of 1 cm, apart from the radial growth which was measured with an accuracy of 0.1 mm using a microscope. The biomass measurements were expressed to the nearest gramme after drying for 24 h at 105°C. For a more detailed description of the phytometris studies see also ILONEN *et al.* (1979).

### Computations

For the analysis the following characteristics were determined for each sample tree: (1) relative tree height, (2) total needle biomass, (3) crown illumination, (4) photosynthetic capacity of the crown, (5) height and (6) radial growth, (7) structural matter production by the stem, (8) needle growth, (9) growth of lateral shoots and (10) bud formation in the crown including that by the main leader.

The relative tree height was determined by relating the height of the sample tree

to the maximum height of the sample trees belonging to the same stand. The total needle biomass was determined by multiplying needle biomass in the sample branch by the number of lateral shoots in the whorl that the medium branch represented. Whorl-specific estimates for needle biomass were then integrated over the whole crown system. Each needle age class was treated separately in the calculations.

The illumination of the crown system was described with the help of the position coefficient, PC, which is a measure of the actual total photosynthesis of a tree during the time interval  $[t_0, t_1]$  related to that in conditions where no shading takes place. The position coefficient is defined as follows

$$(1) \text{ PC } [t_0, t_1] = \frac{\int_{t_0}^{t_1} \delta(x) \cdot p(l(x, t)) \, dt \, dV}{\int_{t_0}^{t_1} p(l_0(t)) \, dt \int_V \delta(x) \, dV}$$

where  $\delta(x)$  is the needle density,  $p$  is the dependence of photosynthetic rate on light intensity,  $l(x, t)$  light intensity at a particular point  $x$  in the crown system and moment  $t$  and  $l_0(t)$  light intensity above the canopy in conditions where no shading takes place.

The photosynthetic capacity of the trees in the stand was approximated by determining the total photosynthesis of the trees with the help of the following Equation (2)

$$(2) \text{ PhC } [t_0, t_1] = \text{ PC } [t_0, t_1] \int_V \delta(x) \, dV$$

where PhC  $[t_0, t_1]$  is the photosynthetic capacity of a tree, *i.e.* the total amount of photosynthetic products obtained during the time period  $[t_0, t_1]$ .

The growth characteristics were expressed per needle biomass unit representing one- through four-year-old needles in order to eliminate the effect of tree size on the results. In the case of height growth and radial growth no additional procedure was needed to obtain tree-specific values for these characteristics. For the needle growth the procedure was the same but the growth was expressed per needle biomass unit

representing two- through four-year-old needles. Other calculations concerning the needle biomass are described above.

The structural matter growth of the stem was determined with the help of the equations developed by HAKKILA *et al.* (1977) for determining the volume of young Scots pine stems. The volume growth was converted into dry matter growth by applying the basic density, 0.405 g/cm<sup>3</sup>, to the volume of wood produced (HAKKILA 1966). The dry matter values were expressed per needle biomass unit as described above.

The growth of lateral shoots was ex-

pressed as a mean value per tree. In these calculations, the growth per whorl was weighted with the number of lateral shoots in the whorl in question. The calculated mean value for the whole tree was expressed per needle biomass. Bud formation per sample tree was determined in the same way as needle growth as for an estimation the total bud number per sample tree was concerned and expressed per needle biomass unit. In the latter calculations the needle biomass representing one- through four-year-old needle was, however, utilized.

## RESULTS

### Relationship between tree class and needle biomass

The regression models between relative tree height and the amount of respective needle biomass (g/tree) in each stand are given in Table 2. The values of the explained variance are rather high, independent of a particular stand or a particular needle age class. In the same coordinates each stand forms, however, a separate graph as indicated by the regression coefficients between the relative height and total needle biomass.

The variation in the regression between

Table 2. Regressions for the relationship between relative tree height (m) and respective total needle biomass (g/tree).

Stand number	Constant	Regression coefficient	R <sup>2</sup>
2	-1361.805	37.040	.645
3	-345.574	7.709	.825
4	-1203.703	27.421	.717
5	-1936.286	60.143	.917
6	-3748.638	73.566	.644
7	-322.159	9.420	.505
8	-823.357	25.588	.679
9	-4511.783	73.046	.695
10	-3223.739	40.813	.944
11	-1104.165	33.723	.784
12	-7733.131	117.980	.828
13	-6639.949	114.623	.703

relative height and the total needle biomass was best explained by the stand height, as appears from Fig. 1. In other words, interpretation of the tree class in terms of the needle biomass is influenced by the stage of development which the stand has achieved. In a young stand the change in relative height means a smaller change in the amount of needle biomass than in a more mature stand. In relative terms, *i.e.* relating the needle biomass per tree to the maximum needle biomass of a tree found in a stand, the standwise grouping in the regression between relative height and needle biomass is eliminated as appears from Fig. 2. The relationship between relative height and relative needle biomass is nonlinear and best described by an exponential function. The proportion of explained variance for a zero-forced function was 0.700.

The limits for the tree classes fall within the steepest part of the fitted function. Consequently, the division of trees into tree classes is nonlinear in terms of relative needle biomass. The following limits for the tree classes in terms of relative needle biomass were obtained:

Tree class	Share of needle biomass % of maximum
Dominant .....	50 - 100
Codominant .....	30 - 50
Intermediate .....	20 - 30
Suppressed .....	- 20



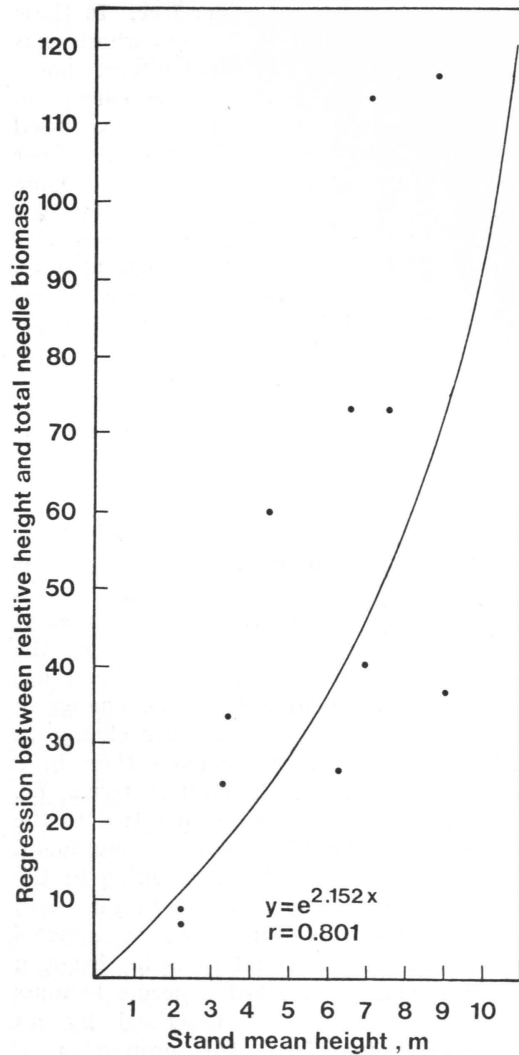


Fig. 1. Relationship between stand height and regression for the regression between relative tree height and respective needle biomass.

There are also sample trees which fall below the lower limit of the suppressed trees. These trees are the most likely to be eliminated during succession of the stand. Hence they are comparable with the suppressed trees and are treated as suppressed trees in silvicultural thinnings.

The mean values for relative needle biomass per tree class are given below:

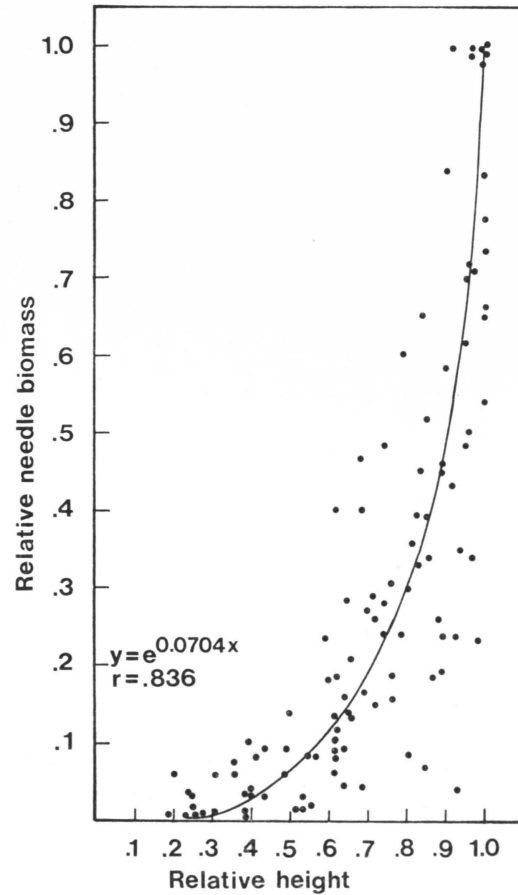


Fig. 2. Relationship between relative tree height and respective values of relative needle biomass.

Tree class	Mean values		Relative values of averages	
	n	$\bar{x}$		
Dominant .....	32	.704	.277	1.00
Codominant ..	17	.339	.150	.49
Intermediate .	12	.285	.131	.40
Suppressed ...	52	.165	.150	.23

The relative needle biomass of the codominants trees is about half that of dominants. In intermediates the needle biomass is comparable with that of codominants, and the difference between these tree classes is meaningless in terms of relative needle biomass. In suppressed trees, including those below the lower

limit of this tree class, the relative needle biomass is about 20 % that of dominant trees and half that of codominant and intermediate trees.

### Relationship between tree class and illumination inside the crown system

The regressions between the relative tree height and position coefficients per stand are given in Table 3. The regressions are stand-specific as are those between relative tree height and needle biomass. The values of the explained variance are, however, rather high independent of any particular stand. The result was expected on the basis of the relationship between the relative height and needle biomass.

The variation in the regression between relative height and the position coefficient was rather closely correlated with the stand height at a mean height greater than 3 m (Fig. 3). The change in relative height in a young pine stand appears to indicate a greater change in the position coefficient than in a more mature stand. Therefore the stage of development of the stand should be considered in interpreting the relative tree height in terms of crown illumination.

Relating the position coefficient of any tree to the maximum value of the position

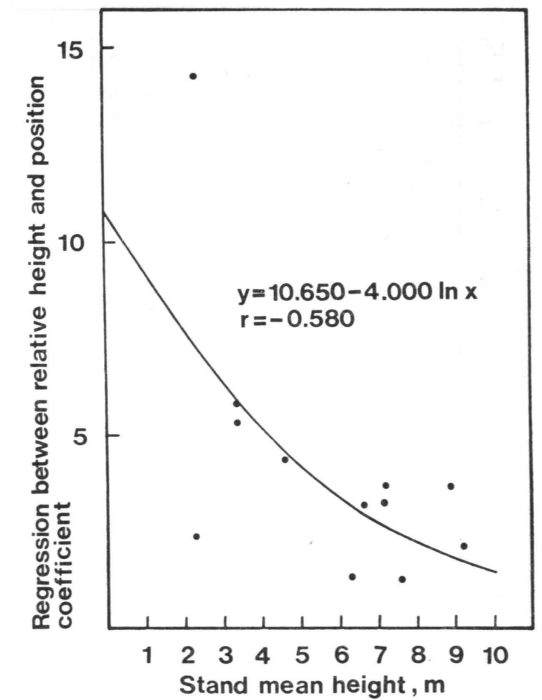


Fig. 3. Relationship between stand height and regression for the regression between relative tree height and respective position coefficient.

coefficient found in a stand eliminates the stand-to-stand differences in the regression between the relative height and position coefficient as appears from Fig. 4. The regression was characterized by pronounced variation. The regression was, however, a linear one. Therefore the relative tree height or tree class gives a direct measure which can be used for evaluating the light conditions of a particular tree in a stand and the survival potential of that tree.

The mean values for the relative position coefficient per tree class are given below.

Tree class	Mean values		Relative values of averages	
	n	$\bar{x}$		
Dominant .....	32	.950	.051	1.00
Codominant ..	17	.855	.090	.90
Intermediate .	12	.751	.121	.80
Suppressed ...	45	.659	.159	.69

Table 3. Regressions for the relationship between relative tree height and position coefficient.

Stand number	Constant	Regression coefficient	R <sup>2</sup>
2	- 18.599	2.015	0.916
3	-1110.493	14.375	0.757
4	0.274	1.317	0.935
5	- 284.063	4.350	0.971
6	27.967	1.243	0.821
7	- 17.618	2.209	0.736
8	- 116.407	5.357	0.568
9	- 13.659	3.233	0.938
10	- 4.266	3.226	0.971
11	- 92.489	5.920	0.741
12	- 14.248	3.620	0.901
13	- 20.313	3.762	0.993

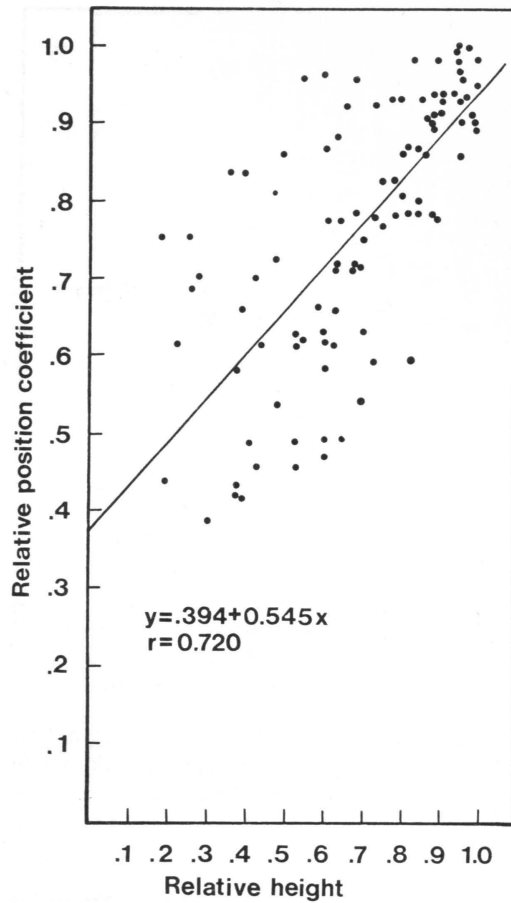


Fig. 4. Relationship between relative tree height and respective values of position coefficient.

The relative illumination received by dominated trees decreases by about ten per cent per tree class. For suppressed trees the relative position coefficient is about 70 per cent of that in dominant trees. Trees seem to fall below the limit of survival when the illumination conditions in the crown system fall lower than 60 per cent of that in dominant trees. The respective limits for all tree classes are as follows.

Tree class	Share of position coefficient % of maximum
Dominant .....	88 - 100
Codominant .....	83 - 98
Intermediate .....	78 - 83
Suppressed .....	- 78

It appears that the relatively small decline in crown illumination is due to the great change in the position of a tree in a stand as indicated by tree class.

#### Relationship between relative tree height and photosynthetic capacity

Regressions between relative tree height and respective estimates for the photosynthetic capacity are given in Table 4. The regressions are stand-specific as are those between needle biomass and position coefficients. The values of the correlation coefficients between relative tree height and total photosynthesis are, however, rather high in all stands. The result was as expected on the basis of the relationship between needle biomass, position coefficient, and relative tree height. Needle biomass, position coefficient and total photosynthesis all seem to be comparable in interpreting the functional meaning of the relative height of a stand member.

The variation in regression between relative height and total photosynthesis was fairly well correlated with the stand height as appears from Fig. 5. The change in relative height in a sapling stand seems to indicate a smaller change in total photosynthesis than in a more mature stand. As in

Table 4. Regressions for the relationship between relative tree height and respective estimate for the photosynthetic capacity.

Stand number	Constant	Regression coefficient	R <sup>2</sup>
2	- 85450.51	2194.450	.617
3	- 29441.18	648.877	.828
4	- 90185.61	1982.635	.704
5	- 178506.90	5308.967	.895
6	- 219729.00	3963.8385	.713
7	- 15505.07	400.585	.683
8	- 24303.22	864.964	.566
9	-1599465.00	2526.392	.702
10	-1084133.00	1357.890	.945
11	- 257957.50	939.162	.621
12	-2464821.00	3698.778	.829
13	-2151569.00	3676.458	.691

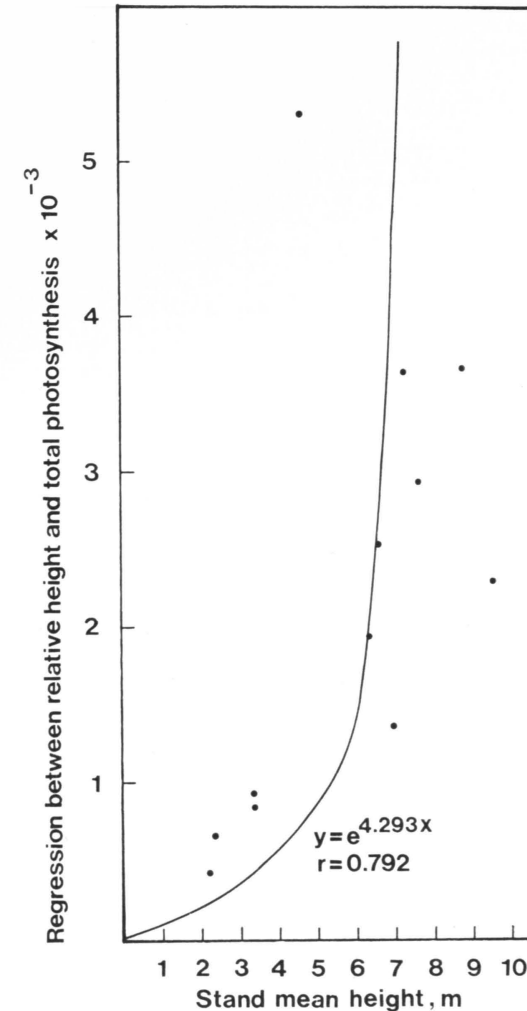


Fig. 5. Relationship between stand height and regression for the regression between relative tree height and respective values of photosynthesis.

the case of needle biomass and crown illumination, the stage of development should also be taken into account as regards the interpretation of relative tree height in terms of total photosynthesis.

The relative total photosynthesis, i.e. the values for total photosynthesis of any stand member divided by the maximum value for total photosynthesis in the same stand, was comparable with the respective relative height (Fig. 6). The relationship is best described with an exponential function.

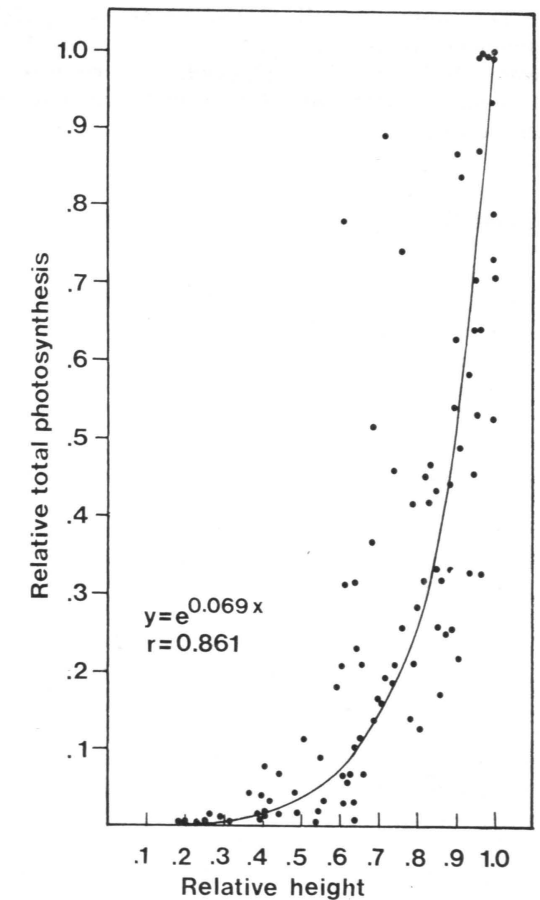


Fig. 6. Relationship between relative tree height and respective values of relative photosynthesis.

Between the values 0.6 - 1.0 the linear function would give, however, nearly the same result. Therefore the relative height of a stand member seems to give a fairly good estimate of the amount of photosynthetes available for growth as compared with the maximum indicated by dominant trees. Each tree class thus represents the following share of the maximum total photosynthesis.

Tree class	Share of photosynthesis % of maximum
Dominant .....	75 - 100
Codominant .....	50 - 75
Intermediate .....	25 - 50
Suppressed .....	- 25



The above stratification seems to be independent of the stage of development which the stand has achieved. The respective mean values for relative photosynthesis are given below.

Tree class	Mean value		Relative value of averages
	n	$\bar{x}$	
Dominant .....	32	.762	1.00
Codominant ..	17	.313	.41
Intermediate .	12	.336	.45
Suppressed ...	45	.100	.13

The mean relative photosynthesis of codominant and intermediate trees is 40–50 per cent of that of dominant trees. The respective value for suppressed trees is 13. The differences in photosynthesis between tree classes are of the same magnitude as those in needle biomass.

Comparison of the relationships between the relative needle biomass and the relative tree height and, on the other hand, the relative photosynthesis and the relative tree height shows that both functions indicate the same functional feature in stand dynamics. In other words, relative needle biomass and relative photosynthesis are closely correlated as appears from Fig. 7. The correlation coefficient for the existing linear relationship was .991.

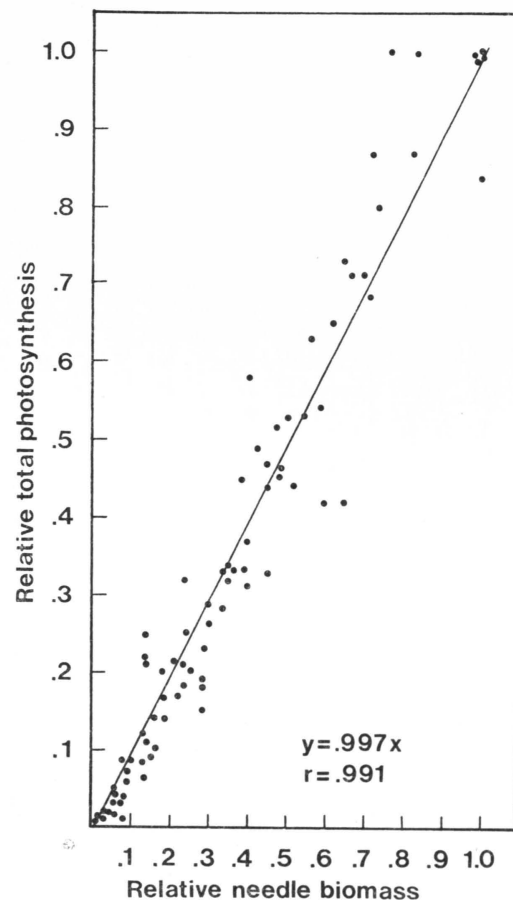


Fig. 7. Relationship between relative needle biomass and relative photosynthesis.

### Stem growth

The analysis of the growth material was done on the basis of mean values representing growth per needle biomass unit. In addition, the material was grouped into young (mean height < 6.5 m) and mature (mean height > 6.5 m) stands in order to eliminate the effect of the stage of development on the analysis. Student's test was also employed in comparing group means.

The height growth per needle biomass unit in different tree classes is presented in Table 5. The height growth of suppressed trees was superior to that in other tree classes. The differences between suppressed trees and trees belonging to other classes were statistically significant ( $p < 0.10$ ). The height growth of suppressed trees was

nearly tenfold that of other trees. This relationship was ever more predominant in young stands. The height growth in other tree classes was, on the other hand, of the same magnitude in each tree class, and no statistical differences were found between them.

The radial growth of stem per needle biomass unit in different tree classes is presented in Table 6. It appears, as in the case of height growth, that the suppressed trees were more efficient than other tree classes. In young stands the difference for suppressed trees is nearly tenfold. Also in more older stands the same trend is recognizable. The differences between the suppressed and the trees belonging to

Table 5. Annual height growth of trees (cm) per needle biomass unit (g) in different tree classes.

Tree class	Stand mean height, m					
	n	< 6.5 $\bar{x}$	s	n	> 6.5 $\bar{x}$	s
Dominant .....	17	.061	.052	15	.018	.009
Codominant .....	4	.088	.061	8	.030	.014
Intermediate .....	6	.064	.027	5	.047	.022
Suppressed .....	35	.417	.481	15	.213	.223
Total .....	62	.264	.401	43	.092	.158

Table 6. Annual radial growth of trees ( $\text{mm } 10^{-1}$ ) per needle biomass unit (g) in different tree classes.

Tree class	Stand mean height, m					
	n	< 6.5 $\bar{x}$	s	n	> 6.5 $\bar{x}$	s
Dominant .....	14	.070	.056	12	.012	.007
Codominant .....	4	.083	.076	8	.017	.008
Intermediate .....	6	.068	.033	5	.033	.016
Suppressed .....	27	.444	.523	12	.255	.513
Total .....	51	.269	.423	37	.095	.305

Table 7. Dry matter production of tree stem (g) per needle biomass unit (g) in different tree classes.

Tree class	Stand mean height, m					
	n	< 6.5 $\bar{x}$	s	n	> 6.5 $\bar{x}$	s
Dominant .....	14	.836	.463	12	.515	.142
Codominant .....	4	.771	.463	8	.593	.127
Intermediate .....	6	.565	.159	5	.516	.128
Suppressed .....	27	.819	.703	12	1.078	1.434
Total .....	51	.790	.579	37	.715	.840

other classes were statistically significant ( $p < 0.10$ ) in young and more mature stands.

The structural dry matter production in the stem, per needle biomass unit, is presented in Table 7. The structural matter production appears to be of equal magnitude in the young stands and independent of the tree class except for suppressed trees taller than 6.5 m. Owing to the pronounced variation the differences between the mean values are not statistically significant.

### Growth of crown

The weight of current-year needles per needle biomass unit per tree class in the young and in the older stands are presented in Table 8. The weight of current-year needles appears to be of equal magnitude in all tree classes. Only a slight trend in favour to the suppressed trees is detectable. Differences between tree classes are not statistically significant.

The number of buds in the leader per

Table 8. Mass of current-year needles (g) per needle unit (g) of previous-year needles in trees belonging to different tree classes.

Trees class	Stand mean height, m					
	n	< 6.5 $\bar{x}$	s	n	> 6.5 $\bar{x}$	s
Dominant .....	17	.435	.168	15	.321	.114
Codominant .....	7	.399	.170	8	.368	.163
Intermediate .....	6	.473	.182	5	.351	.130
Suppressed .....	37	.616	.404	15	.383	.151
Total .....	64	.541	.336	43	.355	.137

Table 9. Number of buds in the leader per needle biomass unit (g) in trees belonging to different tree classes.

Tree class	Stand mean height, m					
	n	< 6.5 $\bar{x}$	s	n	> 6.5 $\bar{x}$	s
Dominant .....	9	1.532	.476	9	1.294	.153
Codominant .....	3	1.753	.521	4	1.499	.604
Intermediate .....	1	1.281		3	1.493	.477
Suppressed .....	16	2.093	.983	8	1.639	.521
Total .....	29	1.856	.825	24	1.468	.425

Table 10. Apical growth of lateral shoots (cm) per needle biomass unit (g) in trees belonging to different tree classes.

Tree class	Stand mean height, m					
	n	< 6.5 $\bar{x}$	s	n	> 6.5 $\bar{x}$	s
Dominant .....	13	.204	.180	15	.052	.024
Codominant .....	4	.274	.227	8	.075	.036
Intermediate .....	3	.120	.062	5	.128	.035
Suppressed .....	21	1.403	.905	15	.696	.918
Total .....	41	.634	.804	43	.290	.610

needle biomass unit per tree class is presented in Table 9. There is a tendency towards increasing the relative bud number as the tree's position deteriorates in a stand. The trend for the suppressed trees seems to be especially clear in the young stands. However, the differences between the tree classes are not statistically significant.

The mean apical growth of average

lateral shoots per needle biomass unit in each tree class is presented in Table 10. The relative growth of lateral shoot is the highest in the suppressed trees, both in the young stands and in the more developed ones. The difference is on the average six-to sevenfold. The differences between suppressed trees and other trees are statistically significant ( $p < 0,10$ ).

## DISCUSSION

Stratification of a tree stand into tree classes as a consequence of intraspecific competition has been widely documented in silvicultural literature since the late nineteenth century (for example BURCKHARDT 1856, KRAFT 1884). In Finland, the use of four tree class in silviculture was standardized by ILVESSALO (1926). The importance of tree class in growth and yield studies has been emphasized for example by LÖNNROTH (1925). The characterization of the stratification of an even-aged tree stand into tree classes is thus a good basis for ecological and silvicultural research and their applications (cf. also NEWBOULD 1966).

The stratification of the tree stands into different tree classes indicated pronounced differences in needle biomass, crown illumination and photosynthetic capacity of Scots pine (*Pinus sylvestris* L.). Especially, the decrease in needle biomass was pronounced and was due to the respective decrease in the photosynthetic capacity. The deteriorated illumination of the crown system is, however, the apparent cause of the decrease in needle biomass and the respective photosynthetic capacity. For example, ILONEN *et al.* (1979) have demonstrated the close correlation between needle growth and crown illumination in one part of the material. Therefore the crown system and its interaction with available light resources seem to play a key role in stratification of a tree stand (cf. WIERMAN and OLIVER 1979).

The relative needle biomass was rather well correlated with the respective values of the photosynthetic capacity. Thus, the relative needle biomass seems to give a direct and reliable measure for estimating the differences in available photosynthates existing between population members. In other words, the crown system of Scots pine can be interpreted as an intergrator of prevailing light expressed in terms of response to light (cf. MCCREE 1965). HORN (1972), for example, has suggested a similar approach for evaluating the ecological significance of the light regime of a successional stand. More comprehensive studies are, however, needed to evaluate the

application of this approach to the measuring of light conditions inside a stand. In particular, the differences between plants in adaptational processes may give rise to biased interpretations.

Stratification of trees into different tree classes also indicated pronounced differences in growth. Shoot growth, radial growth, and structural matter growth of the stems, as well as the mean lateral shoot growth per needle biomass unit were highest in the suppressed trees. The mass of the current-year needles and the number of buds also followed the same pattern but this was not as pronounced as that of the stem growth characteristics. Each growth parameter seemed to emphasize the efficiency of suppressed trees in utilizing the scarce resources available owing to their suppressed position.

The efficiency of the suppressed trees indicates that each tree is profoundly adapted to the prevailing conditions and can maintain its position in the stand. For example, KUKKONEN (1979) found that the response of suppressed Norway spruce (*Picea abies* L. Karst) trees to nitrogen fertilization was superior to that of the respective dominant trees. These results suggest that the suppressed trees are well adapted to the prevailing conditions and are hence capable of efficiently utilizing their actual environment. Thus the stratification of a stand may be an apt response of a population to competition as regards decreasing intraspecific competition. In absolute terms, growth is apparently higher in dominant trees than in suppressed trees as demonstrated in numerous studies since LÖNNROTH (1925) (for example VUOKILA 1977, KUKKONEN 1979).

The basic factors causing the stratification of a tree stand cannot be analyzed on the basis of the present material. Genetical differences in the growth rate of seedlings and microvariation in site properties may primarily initiate stratification. The minute differences in growth rate in the initial stages of a seedling stand seem to result in stand development processes with only positive feed-back loops, *i.e.* a low growth



rate is the driving force for a further deterioration in the availability of resources for growth. Later, these processes are strengthened by pronounced size differences between trees. Elimination of suppressed trees seems to be unavoidable during the course of succession of a Scots pine stand (cf. for example ILVESSALO 1926, FLOWER-ELLIS *et al.* 1976).

The elimination of suppressed trees is, however, a more complicated process than described above since there are several physiological differences between tree classes enabling survival in severely shaded or in other respects deteriorated conditions. For example, there are several physiological changes in the photosynthetic apparatus which are apparently associated with stand stratification. In particular, the differences in photosynthetic response of the crown system to light is of importance as regards the survival of stratified trees. For example, KUROIWA (1960 a, b) found that the photosynthetic rate of dominant *Abies veitchii* and *Abies mariesii* was higher than that in suppressed trees over the whole range of light intensities used in the study. The light compensation and saturation points of photosynthesis in dominant trees, in particular, were higher than those in suppressed trees. This kind of differentiation was characteristic for each needle age class in dominant trees but not in suppressed trees. KUROIWA (1960 a, b) concludes that such differences between tree classes are due to the differences in light environment between them, *i.e.* in the suppressed trees all needles are shaded by the canopies of the larger and dominating trees. Consequently, all the needles of suppressed trees were characterized by shade-leaves of lower compensation and saturation point than those in dominant trees thus enabling efficient utilization of low light intensities below the canopy. In suppressed *Abies* there was, however, no corresponding decrease in photosynthetic rate in aging needles as in dominant trees (cf. also WOODMAN 1971). Therefore the photosynthetic capacity of suppressed trees was considerably higher than one would expect on the basis of the position of a tree in a stand. Similar modification may also be characteristic of Scots pine.

Physiological modifications of the photosynthetic apparatus are also associated with modifications in leaf and needle characteristics. For example, BJÖRKMAN and HOLMGREN (1963) have demonstrated the increase in specific leaf area, *i.e.* unit area per biomass unit, due to shading as an adaptation to the prevailing light intensities. (cf. also BJÖRKMAN 1970). DELRIO and BERG (1979) have also emphasized the sensitivity of leaf morphology of Douglas-fir (*Pseudotsuga menziesii*) to the light regime in which the trees are growing. The light induced changes in specific leaf area may prove to be of great strategic value for survival in a changing environment. It is also worth noticing that the renewal rate of needle biomass in suppressed trees was higher than in trees belonging to other classes. Suppression thus seems to increase the share of efficient current needles at the expense of older non-efficient needles.

LOACH (1973) has paid attention to the differences in respiration rate and compensation point between shade tolerant and intolerant plant species. In shade tolerant species the respiration rate and the CO<sub>2</sub> compensation point were considerable lower than those in intolerant species, *i.e.* the net photosynthesis was comparable in both groups. KUROIWA (1960 a, b) has documented the same phenomena in *Abies* stands. Needle respiration expressed on a needle area basis was considerable higher in dominant trees than in suppressed trees. In tree trunks and root systems the differences between tree classes also followed the same pattern. The differences in respiration rate were associated with similar differences in the nitrogen content of needles and branchlets between tree classes. Such differences have high ecological importance and may be due to the differences in the successional status of different plant species. In a stand consisting of the same species, the lower respiration rate and CO<sub>2</sub> compensation point at decreased light intensities enables a plant to maintain its position in the plant community.

Physiological and morphological changes due to suppression are emphasized as consequences of stand stratification. The efficiency of growth of suppressed trees

may, however, be associated with modification or allocation of photosynthates for growth in the root, trunk and crown systems. These modifications may also explain the process of stratification. It is also worth noticing that the growth characteristics of the stem were especially sensitive to suppression. Furthermore, the growth characteristics of the crown were modified by suppression but not to the same extent as those of the stem. These differences may indicate the hierarchy in the allocation of photosynthates for different growth components. The interaction between tree and environment through photosynthesis takes place in the needles. Therefore needle growth is preferable under any conditions in order to ensure the survival of the plant specimen. On the other hand, accelerated height growth in suppressed

conditions would enable a tree specimen to maintain its position in competition for light. There is, however, a need for further studies to verify this hypothesis.

In conclusion, the present study demonstrates that physiological information is applicable to verify the biological meaning of silvicultural practices. In this respect the concept of tree class seems to be useful since it includes a great variety of adaptational processes in a single parameter. On the other hand, the physiological implications of silvicultural measures are evident and hence the adaptation of trees to the prevailing condition should be taken into consideration in such planning. In thinning and forest fertilization this is of primary importance when trying to maximize the forest productivity.

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#### SELOSTE:

### PUULUOKKA LATVUKASEN NEULASMASSAN, VALAISTUKSEN, JA FOTOSYNTeesin ILMAISIJANA SEKÄ PUULUOKKIEN VÄLISET TUOTOSEROT ERÄISSÄ NUORISSA MÄNNIKÖISSÄ

Tutkimuksessa on tarkasteltu biologisen puuluokituksen merkitystä puiden neulasmassan, latvuksen valaistuksen ja fotosynteesikapasiteetin ilmaisimena. Kolmeentoista nuorehkoon männikköön perustuvan aineiston tarkastelu osoitti että puuluokan sekä puiden suhteellisen neulasmassan välillä vallitsi kiinteä riippuvuus. Puuluokka korreloi kiinteästi myös ao. luokan puiden latvusten saaman valaistuksen ja puiden fotosyn-

teesikapasiteetin kanssa. Puiden pituus- ja paksuuskasvu sekä rungon kuiva-ainetuotos neulasmassan yksikköä kohti saivat kukin suurimmat arvonsa alimpaan latvuskerrokseen kuuluvissa puissa. Myös neulasten ja oksien suhteellinen kasvu sekä silmujen lukumäärä neulasmassan yksikköä kohti lisääntyivät puiden aseman heiketessä metsikössä.