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EFFECT OF THE WITHIN-STAND LIGHT CONDITIONS ON THE SHARE OF STEM, BRANCH AND NEEDLE GROWTH IN A TWENTY-YEAR-OLD SCOTS PINE STAND

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SELOSTE:

METSIKÖN VALAISTUSOLOJEN VAIKUTUS RUNGON, OKSIEN JA NEULASTEN KASVUN OSUUKSIIN ERÄÄSSÄ KAKSIKYMMENVUOTIAASSA MÄNNIKÖSSÄ

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The share of stem, branch and needle growth was dependent on the within-stand light regime in a young Scots pine *(Pinus sylvestris* L.) stand. The share of needle growth increased at the expense of stem and branch growth in poor light conditions. In good light conditions the share of branch wood increased substantially. The share of stem wood growth was maximal in moderate shading, emphasizing the role of sufficient stand density for growing high-quality timber. The basic density of the stem wood was considerably greater in suppressed trees than in dominating trees. These differences were related to the illumination of the crown system.

INTRODUCTION

The role of the within-stand light regime in the development of a tree stand has been recognized in several studies (FORWARD and NOLAN 1961, FARRAR 1961, LOGAN 1965, HORN 1971, LOGAN 1973). The within-stand light regime seems to have a dual role in stand development, *i.e.,* it is the driving force for total growth through photosynthesis and it determines the allocation of photosynthates for crown and stem growth (cf. MONSI and MURATA 1970, HORN 1971, FARMER 1976, ILONEN *et al.* 1979).

The aim of this study was to investigate the relationship between the within-stand light regime and growth and its allocation for stem, branch and needle growth in a young Scots pine *(Pinus sylvestris* L.) stand. Special emphasis was given to determining the dependence of the allocation of growth on the within-stand light regime.

MATERIAL AND METHODS

Description of the study area

The study area was located in Central Finland (61°47'N, 24°18'E, 150 m, a.s.l.) near the Forest Field Station, University of Helsinki. The area belongs to the south boreal vegetation zone with a mean annual temperature of – 3,0 –+ 3,5°C and mean annual precipitation of 600 mm. The mean annual temperature sum with 5 degree's threshold is 1100–1200 d.d.

The study area was a part of a larger young Scots pine stand on site of *Vaccinium* type, *i.e.,* a medium-fertile site with dwarf shurbs (for example *Vaccinium vitis-idae, Calluna vulgaris),* mosses (for example *Pleurozium schreberi, Dicranum* spp.) and scatted herbs and grasses (for example, *Melanpyrum* spp.). The soil of the study area was sand morain. The area faced slightly to south-west.

The stand was sown in 1961 on prescribed burnt ground. It had undergone the thinning and clearing of invading decidious trees, e.g. *Betula* species. Scattered undergrowth of deciduous trees and Norway spruce *(Picea abies),* however, were still in the study area. Their role in stand dynamics is negligible due to suppression by the dominating pines.

The main characteristics of the pine-dominated tree stratum are given in Table 1. The stand density of 3200 stems per hectare exceeds to the some extent the recommended density for managed forests. The mean height of the stand was 3,8 m. The pattern of the stand is notifully regular due to the stoniness of the soil, but east-west orientation of the sowing rows is discernible.

Sampling of the study area

A sample area of 10 x 10 m in size was chosen as the first step of the phytometric measurements. The diameter distribution of the trees at a height of 1,3 m above ground level was determined in the first phase of the sampling. The distribution was determined to an accuracy of one centimeter. In the sampling the minimum number of sample trees was one for each diameter class. Trees with two leaders or other abnormalities were ommitted in the sampling.

Light measurements

A branch of medium diameter was chosen for a detailed analysis from each whorl of the sample trees. The prevailing light conditions around the sample branch were measured in the first phase. This was done by taking hemispherical photographs at the middle of the current-year shoot of the branch main axis. The measuring system consisted of a Canon Fish-eye lens (7,5 m, F 5,6), a 35 mm camera and a special tripod which enabled operation also at the upper part of the canopy. The recommendations by ANDERSON (1964, 1971) and McCREE (1968) were followed in the different phases of the light measurements.

Phytometric measurements

The sample trees were cut 5 cm above ground level and sent to the laboratory for further analysis. Several characteristics were determined from each sample tree. The following were utilized in the present analysis: tree height, distance between successive whorls, diameter at 10 cm from the butt and at 1,3 m above ground level, diameter at the relative heights 0,1, 0,5 and 0,75, diameter at the middle of the successive whorls, location of the whorl from the butt and number of branches in each whorl. In addition, 5 cm thick discs were cut for further analysis at the following heights of the stem: 10 cm from the

Table 1. Some main characteristics of the study area.
Taulukko 1. Eräitä tutkimusalueen puuston tunnuksia.

Characteristic *Tunnus*	Value *Arvo*
Density – *Tiheys*	3200 stem/ha
Mean height – *Keskipituus*	3,81 ± 0,99 m
Mean diameter at 1,3 m above ground level – *Keskim. rinnankorkeusläpimitta*	6,28 ± 2,68 cm
Mean diameter of the crown of pines – *Latvusten keskiläpimitta*	156,31 ± 54,76 cm

butt, 1,3 m above ground level, 0,1 h, 0,5 h, 0,75 h, and in the middle of the successive whorls. Thus, 6–16 discs were cut per sample tree, depending on its size.

The analysis of the above-mentioned sample branch was as follows. In the first phase the needle biomass divided into four age classes was determined to an accuracy of one gram. In the second phase, the current length and radial increment were measured. The latter measurements were carried out with a microscope to an accuracy of 10^{-2} mm at the middle of the branch and at the end of the branch 5 cm from the butt. The measurements were carried out on two lines perpendicular to one another.

The discs of the tree stems were treated as follows. First, the radial growth throughout the discs was measured with the two measuring lines perpendicular to one another. Second, the basic density of wood in one to five of the latest formed annual rings was determined by the water displacement method. The measurements were made from samples taken from the measuring lines for the radial growth measurements.

Computations

The amount of total radiation and its division into direct and diffuse radiation in MJ m^{-2} was computed from the hemispheral photographs as follows

$$(1) \qquad I(t, x_i) = I_s(t, x_i) + I_d(t, x_i),$$

where $I(t, x_i)$ denote the total solar radiation at point x_i and moment t, $I_s(t, x_i)$ direct radiation and $I_d(t, x_i)$ diffuse radiation, respectively. The value of i varies within the range i = 0,1, . . . , n, where i = 0 denotes the point above the canopy. A detailed description to approximate the values of Eq. (1) is given by KELLOMÄKI *et al.* (1979) (see also ANDERSON 1964, 1971).

The light measuremants were used in determining tree position, p_{tr}, in the stand. First, the whorl position, p_w, vas determined through Eq. (2)

$$(2) \qquad P_{wij} = \frac{\int_{t_1}^{t_2} I(x_{ij},t)\,dt}{\int_{t_1}^{t_2} I(x_{oj}t)\,dt},$$

where I is light intensity in MJ m^{-2}, t a moment of time, x_{ij} the place of the i:th whorl of the j:th tree (i = 0,1, . . . , n, where i = 0 represent the place above the canopy) and t_1 and t_2 the beginning and the end of the integration period. In this study it was one day, June 15.

The concept of tree position is defined as follows on the basis of the whorl position

$$(3) \qquad p_{trj} = \frac{\sum_{i=1}^{n} \varrho_{ij} \cdot p_{wij}}{\sum_{i=1}^{n} \varrho_{ij}}$$

where ϱ_{ij} is the needle density in the i:th whorl of the j:th tree.

The light measurements were also used in determining the photosynthetic production of each sample tree

$$(4) \qquad p_{tot}(t_1, t_2) = \sum_{i=1}^{n} \varrho_{ij} \int_{t_1}^{t_2} p\,(I\,(x_{ij}, t)\,)\,dt,$$

where p is the dependence of the photosynthetic rate on light intentisy. The procedure has been described in detail in an earlier paper by KELLOMÄKI *et al.* (1979).

The phytometric material was treated as follows. The needle biomass of a sample branch of a particular whorl was converted into the value of the whorl multiplying the needle biomass of the different age classes by the branch number in a particular whorl. The sum of the whorl-specific estimates yielded the estimate per sample tree. The computations were done separately for different age classes of the needles.

The production of branch wood was determined as follows. First, the volume of the current annual growth of the main axis of the sample branch was determined by the measurements described. The mean of the four radial growth measurements was utilized in the computations. The basis density of the branch wood was assumed to be 0,405 g cm^{-3} when the volume growth was converted into dry matter. Second, the dry matter production of the sample branch was multiplied by the number of branches in the whorls to obtain the whorl-specific estimate of the dry matter production. The branch wood production per sample tree was obtained as a sum of the whorl-specific values of the dry matter production.

The dry matter production of the sample tree stems was determined as follows. First, the volume of the current growth of the part of stem between the successive whorls was determined. The mean of the four radial growth measurements was utilized in the computations. The form of a particular stem part was assumed to be cylindrical. Thereafter, the volume growth was converted into dry matter production by utilizing the values of the basic density of wood obtained in the measuring. The sum of growth in the stem parts yielded the estimate for the total growth of a sample tree stem.

The following model was applied when coupling the light measurements and the phytometric measurements

$$(5) \qquad \frac{dy_{ij}}{dt} = a_i\,(x\,(\,(t)\,)^{b_i} \cdot (P_n\,(t) \cdot L_j\,(t)\,)^{c_i}$$

where dy_{ij}/dt is the growth rate of the i:th growing area (stem, branches, needles) in the j:th tree, t a moment of time, x (t) a matrix of environmental variables, P_n (t) the net assimilation rate per unit of needle dry weight, L_j the total needle dry weight of the j:th tree, and a_i, b_i and c_i parameters characteristic for each growth area. In other words, the growth of a particular growth area was assumed to be dependent on the total amounts of photosynthates available for growth and the share of photosynthates directed to a particular growth area. The latter was assumed to be dependent on the proporties of the growing environment, and it is appoximated by the values of the tree position, p_{tr}. The value of the total net photosynthetic supply is approximated throught the values of p_{tot} as described in Eq. (4).

RESULTS

Basic density of stem wood

The effect of tree position and photosynthetic supply on the basic density of stem wood in given below, applying model (5).

a	b	c	R
0,418	– 0,261	– 0,038	0,830

The tree position and the photosynthetic supply are both negatively correlated with the basic density of the wood representing the surface of the stem. In the former case the correlation coefficient was – 0,775 and in the latter case – 0,798. In both cases the correlation coefficients are statistically significant ($p < 0,100$), as is the total correlation of the model based on these factors. The interpretation of the model, however, is problematic since the correlation between tree position and photosynthetic supply was 0,798. But it is evident that in dominating trees the basic density of wood is considerably lower than in suppressed trees. This is demonstrated in Fig. 1, where the basic density is plotted against tree position and the photosynthetic supply.

Growth of stem and crown

The effect of tree position and photosynthetic supply on stem growth, branch growth, needle growth and the whole above-ground shoot system is given below applying model (5).

	a	b	c	R
Stem	1,807	0,765	0,778	0,989
Branches	0,058	2,156	1,081	0,990
Needles	491,174	5,387	0,020	0,923
Total	8,864	1,723	0,660	0,985

The tree position and the photosynthetic supply both correlate positively with the growth characteristics of the stem and crown (cf. Table 2). In each case the correlation coefficients are statistically significant ($p < 0,01$). The models for the growth of the stem and crown are also statistically significant with a low risk ($p < 0,01$), as indicated by the high values of the explained variance. The interpretation of the models is complicated by the fairly close correlation between the tree position and the photosynthetic supply. Therefore, the contribution of tree position

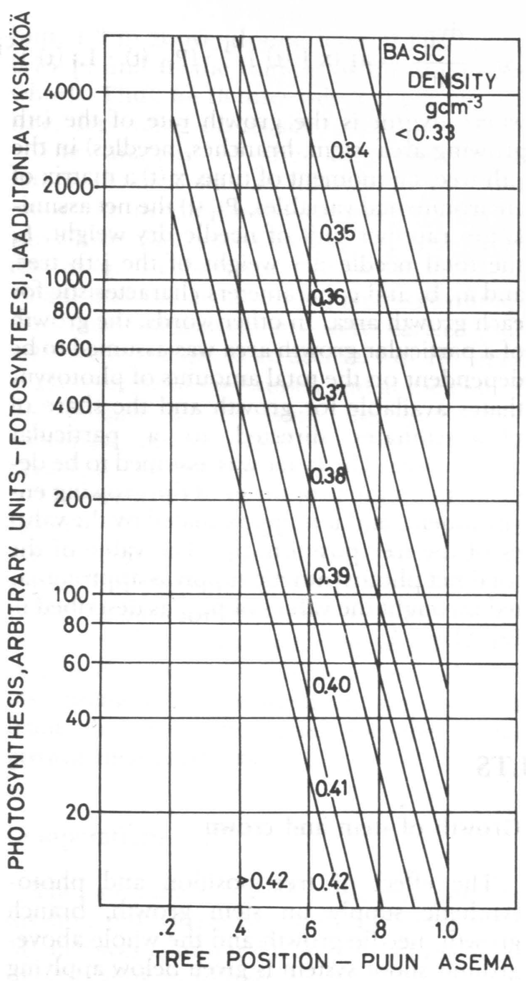

Fig. 1. Basic density of wood plotted against tree position and total photosynthesis.

Kuva 1. Puuaineen tiheys suhteutettuna puun asemaan ja kokonaisfotosynteesiin.

and the photosynthetic supply cannot be evaluated from model (5). It seems evident, however, that an abundant supply of photosynthates is a basic requirement for hight productivity. This is demonstrated in Fig. 2 where the above-mentioned growth characteristics are plotted against the tree position and the photosynthetic supply.

Allocation of growth for stem and crown

Model (5) gave no possibility of determining the dependence of the allocation of growth on the within-stand light regime, as discussed above. Therefore, an attempt was made to eliminate the effect of the photosynthetic supply on the growth characteristics by computing the growth characteristics per photosynthetic unit and relating the results to the tree position, applying model (5). The result of the computations are:

	a'	b'	r
Stem	0,236	– 0,816	0,444
Branches	0,124	2,741	0,847
Needles	0,061	– 1,611	0,268
Total	0,393	– 0,700	0,298

Table 2. Intercorrelations of the studied variables.

Taulukko 2. Tutkittujen muuttujien väliset korrelaatiot.

Variable – *Muuttuja*		1	2	3	4	5	6	7
Stem *Runko*	(1)	1,000						
Branches *Oksat*	(2)	,983	1,000					
Needles *Neulaset*	(3)	,786	,843	1,000				
Tree position *Puun asema*	(4)	,824	,852	,923	1,000			
Photosynthesis *Fotosynteesi*	(5)	,987	,983	,748	,798	1,000		
Wood density *Puuaineen tiheys*	(6)	– ,786	– ,856	– ,832	– ,801	– ,798	1,000	
Total growth *Koko puun kasvu*	(7)	,989	,992	,861	,862	,975	– ,828	1,000

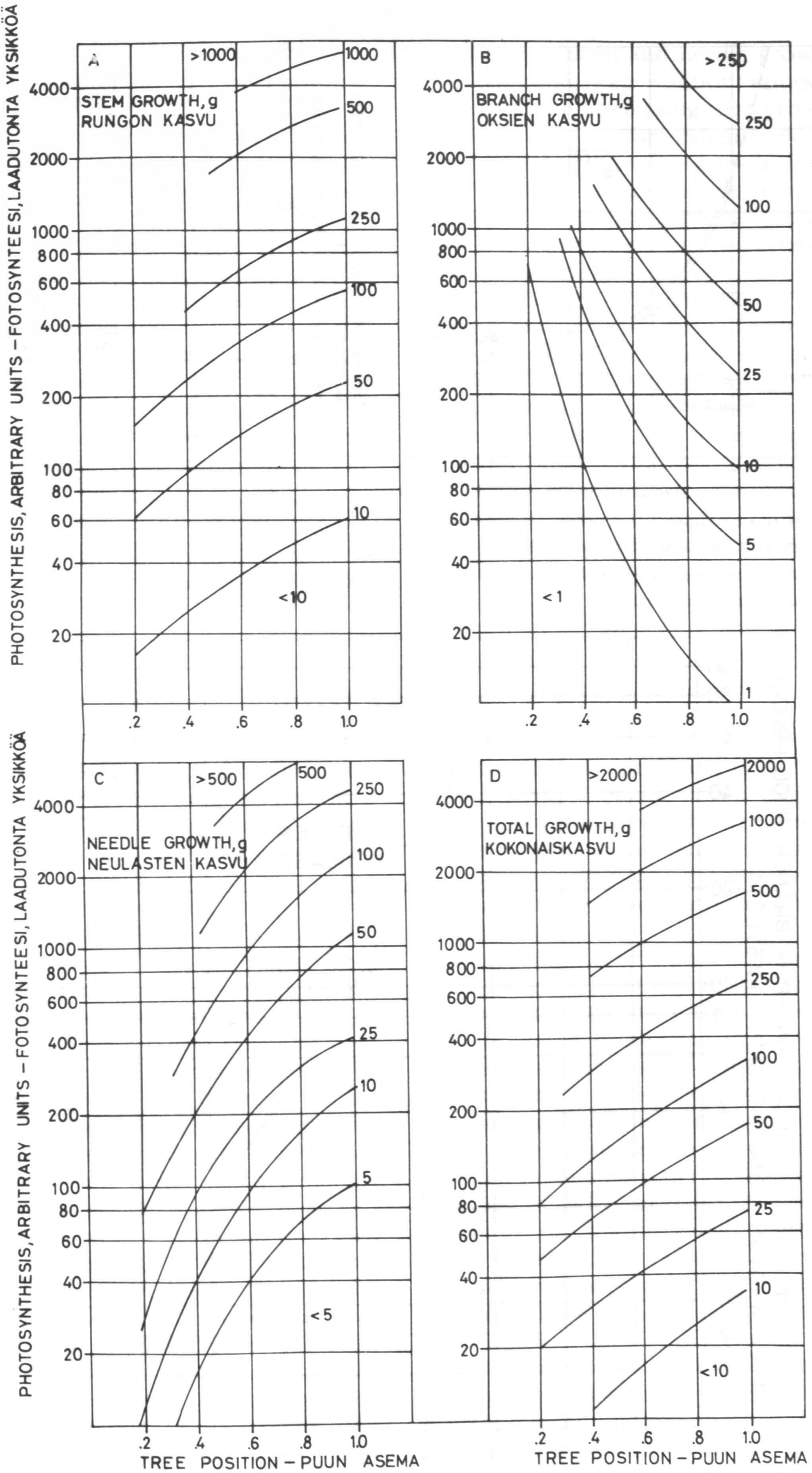

Fig. 2. Growth of different components plotted against tree position and total photosynthesis.

Kuva 2. Puun eri osien kasvu suhteutettuna puun asemaan ja kokonaisfotosynteesiin.

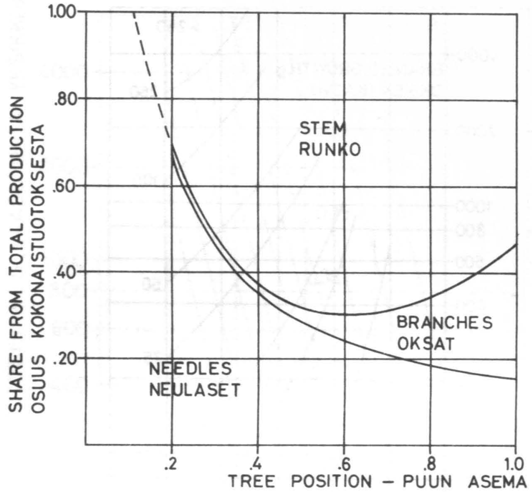

Fig. 3. Share of stem, branch and needle growth from the total growth as a function of tree position.

Kuva 3. Rungon, oksien ja neulasten kasvun osuus kokonaiskasvusta puun aseman funktiona.

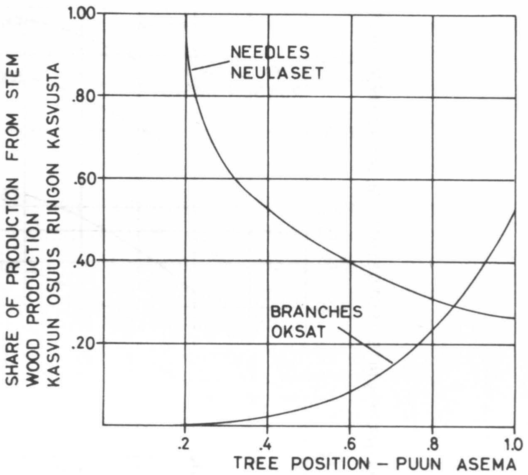

Fig. 4. Ratio between stem growth and branch and needle growth as a function of tree position.

Kuva 4. Rungon kasvun sekä oksien ja neulasten kasvun välinen suhde puun aseman functiona.

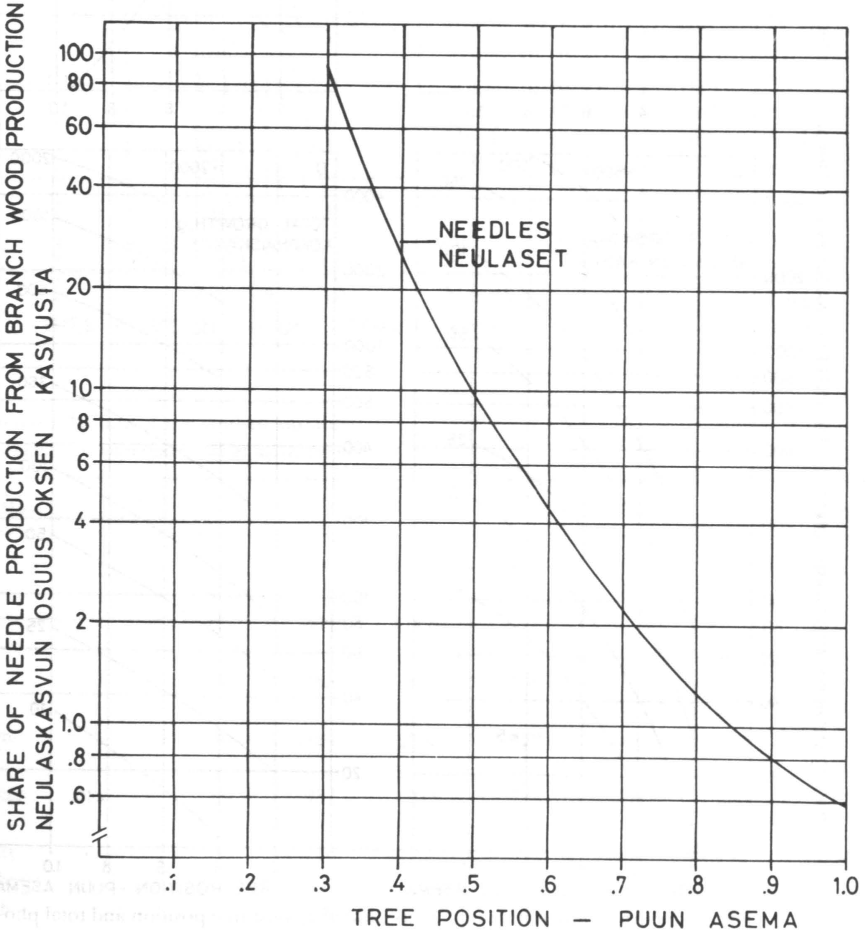

Fig. 5. Ratio between needle growth and branch growth as a function of tree position.

Kuva 5. Neulasten kasvun ja oksien kasvun suhde puun aseman funktiona.

It appears that the growth characteristics are negatively related to the tree position except for branch growth which shows a positive correlation with tree position. Branch growth is also the only growth characteristic which is statistically significantly correlated with tree position ($p < 0,010$). The effect of tree position also on the other growth characteristics is evident, but considerably smaller than that of the photosynthetic supply.

The functions given above describe directly the dependence of growth on the tree position. Therefore, they were utilized in determining the share of the growth of a particular growth characteristic in the total growth as a function of the tree position. The results are given Fig. 3.

The share of stem growth is highest when the tree position lies between 0,5 and 0,7. The increase in tree position values indicates, especially, the increase in branch growth at the expense of stem and needle growth. On the other hand, tree position values lower than 0,5 indicate decreasing stem growth and branch growth at the expense of needle growth. In fact, needle growth increased throughout the range of decreasing tree position, indicating that needle growth was favoured over other growth characteristics in poor light conditions.

The allocation of growth is further demonstrated in Figs. 4 and 5. The priority of needle crowth is emphasized in poor light conditions. In crown growth especially, needle growth is overwhelming compared with that of branches. The results suggest that the growth strategy of the Scots pine favours needle growth in the photosynthetic allocation for growth. Consequently, the growth of the other components can be best understood in this context.

CONCLUSIONS

The growth of Scots pine and its allocation to the stem and crown were studied in a limited material. Two factors affecting growth and its allocation are emphasized: the total photosynthates available for growth and the position of the tree in a stand. In the former case the photosynthetic production per needle biomass unit was computed from hemispherical photographs representing the direct and diffuse radiation at various parts of the sample tree crown. These estimates were converted into the total photosynthates of the sample trees throught the estimates of the total needle biomass of the sample trees. The procedures of approximating the total photosynthesis have been described in detail by KELLOMÄKI, *et al.* (1979, 1980).

The tree position in a stand was described on the basis of the mean crown illumination. This was related to conditions in which no shading occurs to obtain a proper index for the computations. Application of the same light measurements in approximating the total photosynthesis and the tree position confuses interpretation of the results. The relative tree height, for example, is applicable to the tree position index, but it also results in interpretational difficulties. As demonstrated by KELLOMÄKI and HARI (1980), relative height, needle biomass, crown illumination and total photosynthesis of a tree describe the different aspects of the resources available for tree survival and hence the interpretational diffuculties seem to be unavoidable in statistical analyses.

As expected, the total growth of the trees as well as the growth of the stem and crown were closely related to the total photosynthesis. The dry matter production in the stem was also affected by the basic density of the wood. This was related to the photosynthetic supply and tree position: in dominating trees the values of the basic density were 0,32–0,34 g cm^{-3} and in suppressed trees 0,42–0,44 g cm^{-3}. This kind of differentiation may also be evievident in the branch wood. In the upper crown especially, it may be of importance. In this study the basic density value 0,405 g cm^{-3} was used for the branch wood of each sample tree.

The relationships between stem and crown growth were studied by computing the growth observations per photosynthetic unit in order to eliminate the effect of the between-tree differences on the results. Following this, the growth observations were related to the tree position. Except for branch growth, the effect of the tree position on growth was negligible. But it was evident that a suppressed tree position favours needle growth over the growth of the other components. In unsuppressed conditions branch growth increased substantially. The share of the stem in the total growth was greatest in moderate shade conditions. The computations are, however, based on a limited material. Especially the computation for poor light conditions lies outside the range of the original material, where the values of the tree position varied between 0,5 and 0,9. The share of root growth was not studied in this paper, but its decreasing proportion in Scots pine in poor light conditions is very likely (cf. LOGAN 1965, 1973).

The priority of needle growth in poor light conditions is evidently one of the characteristics of the growth strategy of Scots pine. In stand stratification this kind of strategy enables a sufficient supply of photosynthates also in a suppressed tree position. In addition to the priority of needle growth in shading, the resource capture in shading is also improved by the increase in specific leaf or needle area, as reported for example by JARVIS (1964) as well as DEL RIO and BERG (1979). The results suggest that there are several processes compensating for poor light conditions in a stratified stand throught structural and functional modifications in the photosynthetic appratus, as documented by GRIME (1978).

The results of the present study imply that individual stand members attain maximal growth when the interaction between them throught shading is minimized. Consequently, a low stand density is to be preferred. A low stand density implies, however, a substantial branch growth and low basic density of wood. Even in seedling stands these are characteristics to be avoided since the thick branches of the future timber will considerably lower the quality of the wood. Therefore, an adequate initial stand density is one of the most important preconditions for growing high-quality timber for industrial purposes. Later, too, stand density plays a key role in tree stand management as regards the quality of the timber.

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SELOSTE:

METSIKÖN VALAISTUSOLOJEN VAIKUTUS RUNGON, OKSIEN JA NEULASTEN KASVUN OSUUKSIIN ERÄÄSSÄ KAKSIKYMMENVUOTIAASSA MÄNNIKÖSSÄ.

Rungon, oksien ja neulasten osuutta kokonaiskasvusta tutkittiin suhteessa metsikön sisäiseen valaistukseen eräästä kaksikymmenvuotiaasta männiköstä kerätyn aineiston perusteella. Neulasten kasvun osuus kokonaiskasvusta lisääntyi, kun puu joutui lisääntyvän varjostuksen kohteeksi. Hyvissä valaistusolosuhteissa sen sijaan oksien kasvun osuus lisääntyi voimakkaasti. Rungon kasvun osuus oli suurimmillaan, kun latvuksen valaistus oli 60–70 % vastaavasta aukean alueen valaistuksesta. Runkopuun puuaineen tiheys oli dominoivissa puissa selvästi pienempi kuin metsikön alimpiin latvuskerroksiin kuuluvissa puissa.