

ECO-PHYSIOLOGICAL STUDIES ON YOUNG SCOTS PINE STANDS: IV. ALLOCATION OF PHOTOSYNTHATES FOR CROWN AND STEM GROWTH

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SELOSTE:

NUORTEN MÄNTYJEN LATVUSTEN JA RUNKOJEN KASVUN SUHDE FOTOSYNTESIIN JA METSIKÖN VALAISTUSSUHTEISIIN

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Crown and stem growth of young Scots pines (*Pinus sylvestris* L.) were studied in relation to photosynthate supply and light conditions in a stand. The magnitude of needle and bud formation, and radial and height growth were to a great extent dependent on the photosynthate supply. However, in shaded conditions the growth of each characteristic was greater than expected on the basis of photosynthate supply. In the stem system this was especially apparent for height growth. Consequently, height growth was favoured at the expense of radial growth in shaded conditions. It also appeared that the basic density of wood was negatively related to both tree position and photosynthate supply.

INTRODUCTION

The availability of photosynthates for growth determines the basic level of the productivity of a tree. It also has a considerable influence on the structure of a stand. In stand stratification, the basic processes take place, however, in each community member. Hence the allocation of photosynthates for different growth components, *i.e.*, stem growth, crown growth and root growth, determines the actual growth and structure of an individual community member and subsequently the whole community, as demonstrated by PROMNITZ (1975).

In stand development, the allocation of photosynthates is apparently associated with changes in the environment. Especially, the change in light climate seems to be of importance as suggested by MONSI and MURATA

(1970). Therefore the succession of light climate in stand development may control the allocation of photosynthates for the growth components since it determines the total amount of photosynthates available for growth. The within-stand light climate seems, thus, to have a dual role in stand development, *i.e.*, it is the driving force for total growth by determining the overall supply of photosynthates and it affects their allocation for the different growth components (cf. HARRIRI and PRIOUL 1978).

The object of the present study was to investigate the role of the prevailing light climate in the allocation of photosynthates for growth in Scots pine (*Pinus sylvestris* L.) stands over a period of one year. The problem was considered in relation to (1) crown growth

and (2) stem growth, the former component being divided into needle and bud formation and the latter component into radial and height growth. The basic density of wood and

the relationship between early and late wood was also studied in relation to the prevailing light climate and photosynthetic supply.

MATERIAL AND METHODS

Phytometric studies

The material consisted of stands number 3, 4, 6, 7, 8, 9 and 11, *i.e.* the stands of *Vaccinium* site type utilized earlier by KELLOMÄKI and HARI (1980). The stands are located near the Forest Field Station, University of Helsinki (60° 47'N, 24° 18'E, 150 m a.s.l.). The stand characteristics, environmental measurements, the sampling in the study areas and the whole tree analysis of the sample trees were described in detail by KELLOMÄKI and HARI (1980).

The following sample tree characteristics were used in the present study: total height, diameter at a height of 1,3 m above ground level, needle biomass per tree divided into four age classes, current height growth, number of buds per tree, and total current radial growth and its division into early wood and late wood at the heights 0,1, 1,3, 2,0, 3,0, 4,0, 5,0, 6,0 and 7,0 m above ground level and at the relative heights 10, 50 and 75 per cent of the tree height. The basic density of the five outermost growth rings was also determined at the same heights. The radial growth was measured with a microscope to an accuracy of 0,1 mm. The biomass measurements were expressed to the nearest gram after drying for 24 h at 105°C. The basic density was determined as gcm^{-3} by the water displacement method. The basic density measurements and determination of bud formation were made only for stands 3, 4 and 6.

Computations

The crown and stem biomass of the sample trees was determined for each sample tree with the help of the above tree characteristics. Stem growth 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 values obtained in the above-mentioned measurements. The mean value of the basic density of the whole material was $0,396 \text{ gcm}^{-3}$.

It is assumed in the analysis of the material that the growth at any growing area within a tree depends on the supply of photosynthates and the tree position which, in turn, determines the share of photosynthates directed to a particular growing area, *i.e.*

$$(1) \frac{dy_{ij}}{dt} = a_i(x(t))^{b_i} \cdot (P_G(t)L_j(t) - R_i(t))^{c_i},$$

where dy_{ij}/dt is the growth rate of the i :th growing area in the j :th tree, t a moment of time, x a matrix of environmental variables, $P_G(t)$ the gross assimilation rate per unit of leaf dry weight, $L_j(t)$, $R_i(t)$ the respiration rate and a_i , b_i and c_i parameters characteristic for each growth area.

Furthermore, it is assumed that the respiration rate of each growing area is the same. Hence, Eq. (1) can be written in terms of the net assimilation rate as follows

$$(2) \frac{dy_{ij}}{dt} = a_i(x(t))^{b_i} \cdot (P_n(t)L_j(t))^{c_i},$$

where P_n is the net assimilation rate per unit of leaf dry weight.

In this study, model (2) covered a period of one year, *i.e.*, t is one year and $x(t)$ the annual light regime in a stand. It is approximated through the position coefficient as determined by KELLOMÄKI and HARI (1980). The net annual supply of photosynthates, $P_n(t)L_j(t)$, is approximated through the photosynthetic capacity as defined by KELLOMÄKI and HARI (1980).

In both Equations the parameter a_i indica-

ted the specific growth rate at a particular growing area, *i.e.*, growth per photosynthetic unit, and it can be calculated through Eq. (2) by eliminating the effect of photosynthesis on growth. Values of a_i for different

growing areas can be employed in comparisons of the growth of different growing areas. Special emphasis is laid on the dependence of this parameter on the environment, *i.e.*, on light conditions.

RESULTS

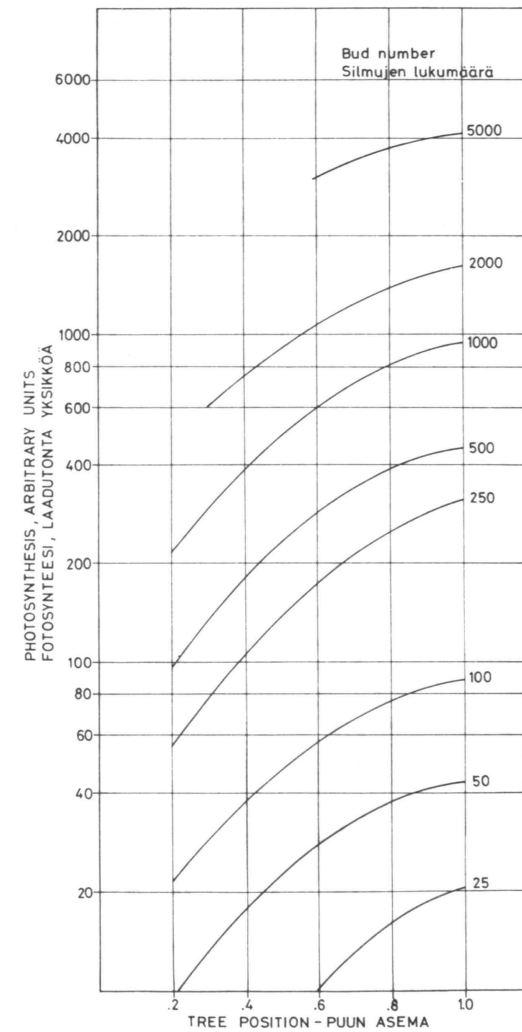


Fig. 1. Number of buds in tree crown as a function of tree position and total photosynthesis.

Kuva 1. Latvuksen silmujen lukumäärä puun aseman ja kokonaisfotosynteesin funktiona.

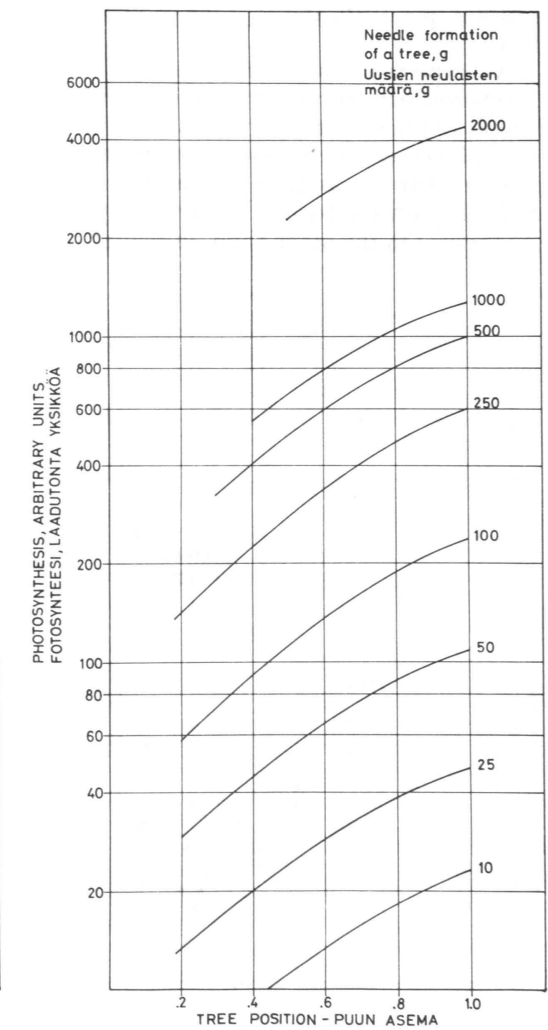


Fig. 2. Needle growth as a function of tree position and total photosynthesis.

Kuva 2. Uusien neulasten määrä puun aseman ja fotosynteesin funktiona.

Crown growth

Owing to the limited nature of the material, only bud formation and needle formation in the whole crown were considered. The values of the parameter for model (2) are given in Table 1 as estimated by the minimum square sum technique. The suggested model gave satisfactory results in both cases as indicated by the total correlation and the respective share of explained variance. The effect of tree position and photosynthesis on bud formation and needle formation are statistically significant ($p < 0,10$), and so is the combined effect.

As expected, bud formation and needle formation are correlated positively with the supply of photosynthates. In unshaded conditions, however bud formation and needle formation were not as great as would be expected solely on the basis of the level of photosynthesis. On the other hand, in shaded con-

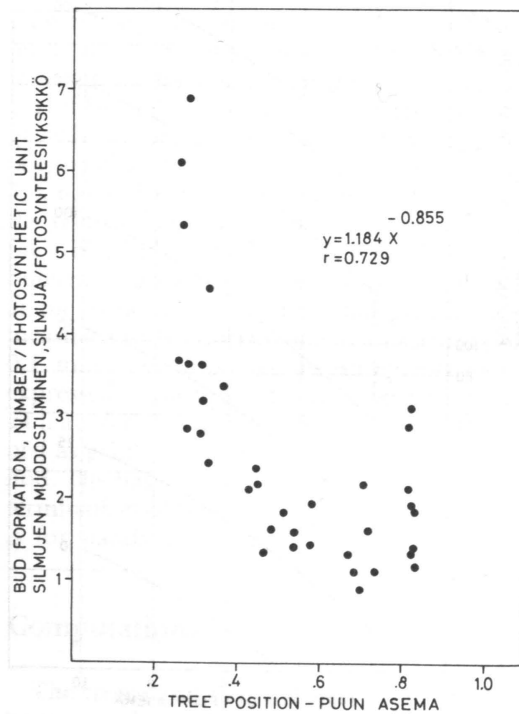


Fig. 3. Number of buds per photosynthetic unit as a function of tree position.

Kuva 3. Latvuksen silmujen lukumäärä fotosynteesiyksikköä kohti puun aseman funktiona.

Table 1. Models for bud formation and needle growth. Taulukko 1. Silmujen ja neulasten muodostumisen malleja.

Dependent variable Selitettävä muuttuja	Parameters — Parametrit			R
	a ¹⁾	b	c ²⁾	
Bud formation, buds Silmujen muodostuminen	6.814	-0.620	0.883	.951
Needle growth, g Neulasten kasvu	0.787	-0.820	0.989	.991

1) a: bud number per photosynthetic unit for bud formation or g per tree and photosynthetic unit for needle formation

a:n arvo on silmujen lukumäärä fotosynteesiyksikköä kohti tai neulasten määrä grammoina fotosynteesiyksikköä kohti.

2) c: photosynthesis in arbitrary units
fotosynteesi laaduttomina yksikköinä

ditions bud formation and needle formation were greater than the supply of photosynthates presupposes. This is illustrated in Figs 1

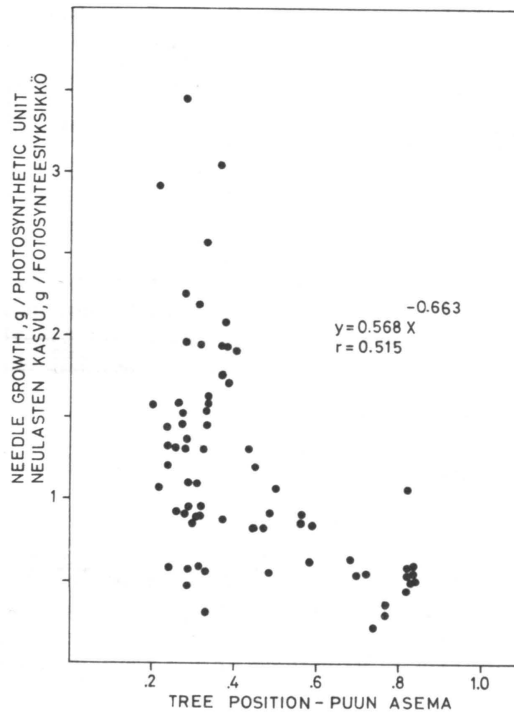


Fig. 4. Needle growth per photosynthetic unit as a function of tree position.

Kuva 4. Uusien neulasten määrä fotosynteesiyksikköä kohti puun aseman funktiona.

and 2, where bud formation and needle formation are presented as a function of tree position and supply of photosynthates.

However, bud formation was more sensitive to shading than needle formation when the effect of photosynthesis was eliminated, as appears from Figs 3 and 4. This difference is interpreted as indicating the crucial role of bud formation also in needle formation, since needles are formed from buds and thus it has a great influence on needle growth.

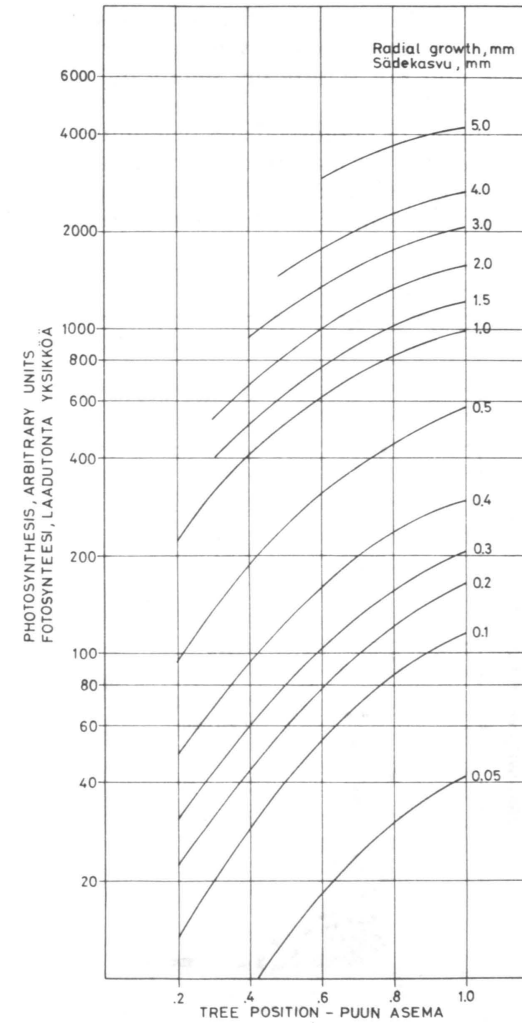


Fig. 5. Radial growth as a function of tree position and photosynthesis computed from the total material.

Kuva 5. Sädekasvu puun aseman ja kokonaisfotosynteesin funktiona laskettuna kokonaisaineistosta.

Stem growth

Height growth and radial growth

Models for height growth and radial growth are given in Table 2. Two models are given for radial growth where only the radial growth at 1,3 m above the ground and the mean radial growth in different parts of the stem were used as dependent variables. In the latter case, radial growth represents the mean

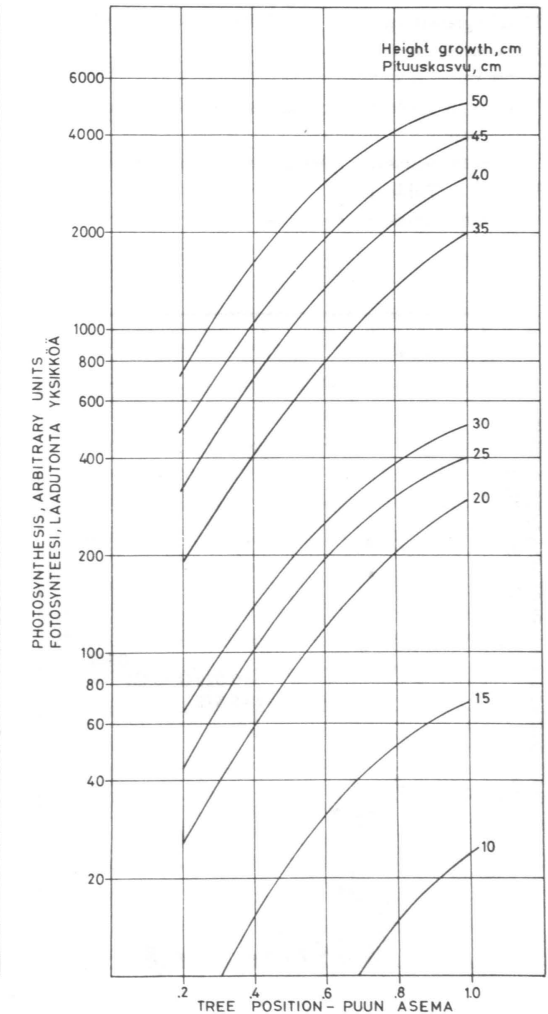


Fig. 6. Height growth as a function of tree position and photosynthesis.

Kuva 6. Pituuskasvu puun aseman ja kokonaisfotosynteesin funktiona.

Table 2. Models for radial growth and height growth.
Taulukko 2. Sädekasvun ja pituuskasvun malleja.

Dependent variable Selitettävä muuttuja	Parameters — Parametrit			
	a ¹⁾	b	c ²⁾	R
Radial growth mm, total material Sädekasvu mm, koko aineisto	12.206	-0.038	0.142	0.424
Radial growth mm in stands 3, 4 and 6 Sädekasvu metsiköissä 3, 4 ja 6	21.434	-0.082	0.335	0.963
Height growth cm Pituuskasvu, cm	5.864	-0.349	0.241	0.764

1) a: as in Table 1 concerning separately each characteristic
kuten taulukossa 1 koskien erikseen kutakin suuretta

2) c: as in Table 1
kuten taulukossa 1

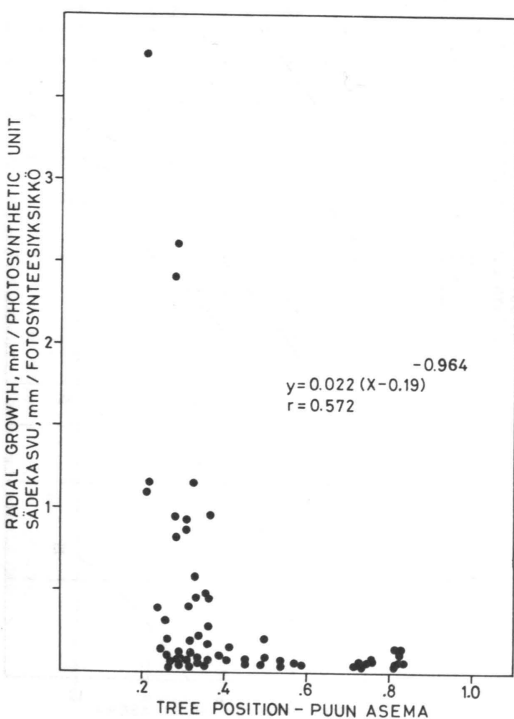


Fig. 7. Radial growth per photosynthetic unit as a function of tree position computed from the total material.
Kuva 7. Sädekasvu fotosynteesiyksikköä kohti puun aseman funktiona kokonaisaineistosta laskettuna.

thickness of xylem layer formed annually round the stem. These measurements concern stands 3, 4 and 6.

Model (2) gave satisfactory results for height growth as well as for the radial growth as indicated by the mean thickness of the xylem layer. In the latter case, the share of the explained variance was much greater than in the model where the radial growth at 1,3 m above ground level was studied. The models were statistically significant ($p < 0,10$) in all cases. In the model for height growth the effects of tree position and supply of photosynthates were both statistically significant ($p < 0,10$). In the models for radial growth the influence of tree position was, however, negligible and not statistically significant within the ordinary limits ($p > 0,10$). In other words, the supply of photosynthates determines to a great extent the magnitude of radial growth. Height growth and radial growth are presented in Figs 5 and 6 as a function of tree position and the level of photosynthesis.

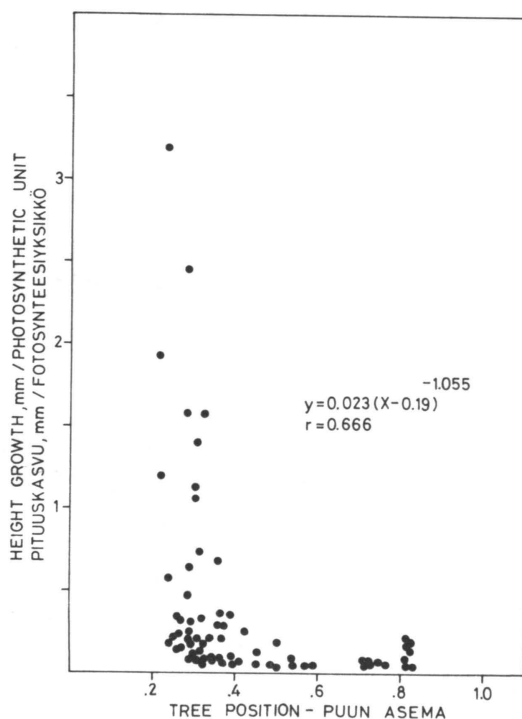


Fig. 8. Height growth per photosynthetic unit as a function of tree position.

Kuva 8. Pituuskasvu fotosynteesiyksikköä kohti puun aseman funktiona.

tion and the level of photosynthesis.

Height growth was a little more sensitive to tree position than radial growth, as appears from Figs 7 and 8. In both cases, the dependence of growth on photosynthesis was almost linear within the values 0,4–1,0 of tree position. Within smaller values of tree position, a considerably accelerated growth seemed to be characteristic. Height growth seemed however, to be preferable under these conditions.

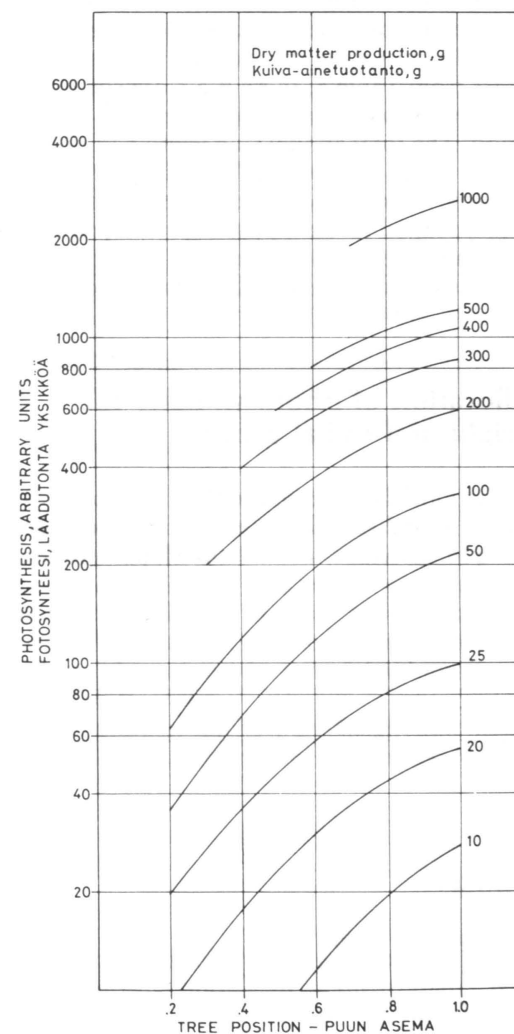


Fig. 9. Dry matter production of stem as a function of tree position and photosynthesis.

Kuva 9. Rungon kuiva-ainetuotanto puun aseman ja kokonaisfotosynteesin funktiona.

Dry matter production

Models for dry matter production of the stem, basic density and other wood characteristics are presented in Table 3. Model (2) gave a satisfactory result as regards the total dry matter production, width of early wood and width of late wood. Variations in basic density and in the share of late wood were only partially explained by position coefficient and supply of photosynthates. In each case the

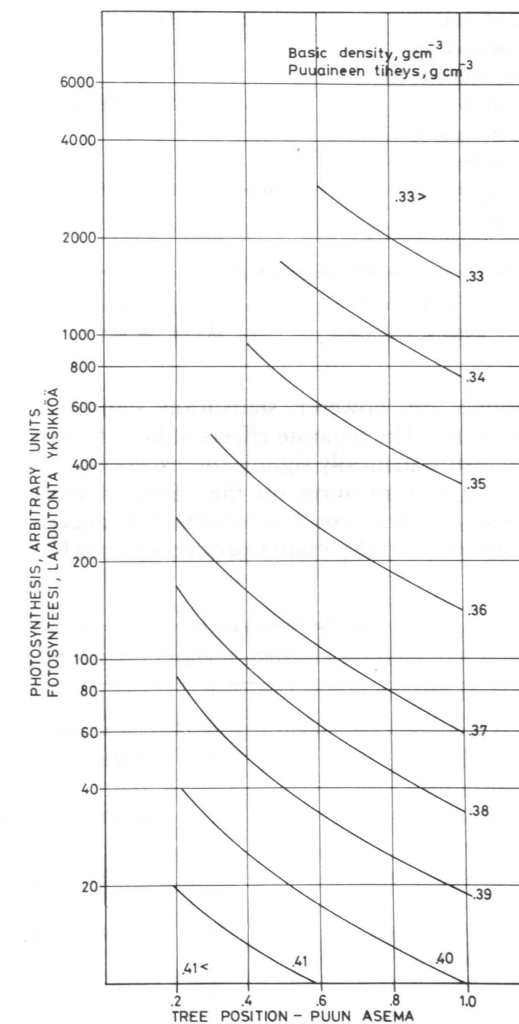


Fig. 10. Basic density of wood as a function of tree position and photosynthesis.

Kuva 10. Puuaineen tiheys puun aseman ja fotosynteesin funktiona.

Table 3. Models for basic density, early wood, late wood and total dry matter production of stem.

Taulukko 3. Puuaineen tiheyden sekä kevät- ja kesäpuun ja rungon kuiva-ainetuotannon malleja.

Dependent variable Selittävä muuttuja	Parametres - Parametrit			
	a ¹⁾	b	c ²⁾	R
Basic density, gcm ⁻³ Puuaineen tiheys	445.991	-0.022	-0.039	0.498
Width of early wood, mm Kevätpuun leveys	15.317	-0.865	0.350	0.950
Width of late wood, mm Kesäpuun leveys	6.012	-0.106	0.284	0.951
Proportion of late wood, % Kesäpuun osuus	31.519	-0.033	-0.061	0.456
Total dry matter production, g Rungon kuiva-ainetuotanto	0.189	-1.450	0.988	0.913

1) a: as in Table 2
kuten taulukossa 2

2) c: as in Table 2
kuten taulukossa 2

models are, however, statistically significant ($p < 0,10$). The separate effects of both factors are also statistically significant, except the effect of tree position on the width of early wood and late wood ($p > 0,10$). The dependence of total dry matter production and ba-

sic density on tree position and supply of photosynthates is demonstrated in Figs 9 and 10.

The total dry matter production was slightly more sensitive to shading than radial growth and height growth, as appears from Fig. 11. In other words, the dry matter production per photosynthetic unit was accelerated in shaded conditions. This is also emphasized by the increased values of basic density, which is negatively related to both tree position and supply of photosynthates. The same phenomenon is indicated also by the dependence of the share of late wood on tree position and photosynthesis and the dependence of basic density on the share of late wood. As appears from Table 4, there is a close correlation between basic density and the share of late wood. The total annual ring width had only a minor effect on the basic density. The width of early wood and late wood were almost linearly related to the supply of photosynthates and only a negligible increase in these characteristics could be detected in shaded conditions.

Allocation of photosynthates for height and radial growth

The models describe the flow of photosynthates to individual growth components. In the tree, however, the relationships between

Table 4. Correlations between variables used in the analysis.
Taulukko 4. Analyysissä käytettyjen muuttujien välisiä korrelaatioita.

Muuttuja Variable	1	2	3	4	5	6	7	
Basic density Puuaineen tiheys	(1)	1,000						
Width of ring Luston leveys	(2)	-0,547	1,000					
Width of early wood Kevätpuun leveys	(3)	-0,592	0,997	1,000				
Width of late wood Kesäpuun leveys	(4)	-0,294	0,935	0,905	1,000			
Proportion of late wood Kesäpuun osuus	(5)	0,791	-0,576	-0,633	-0,265	1,000		
Photosynthesis Fotosynteesi	(6)	-0,471	0,962	0,949	0,948	-0,453	1,000	
Tree position Puun asema	(7)	-0,326	0,299	0,295	0,267	0,215	0,365	1,000

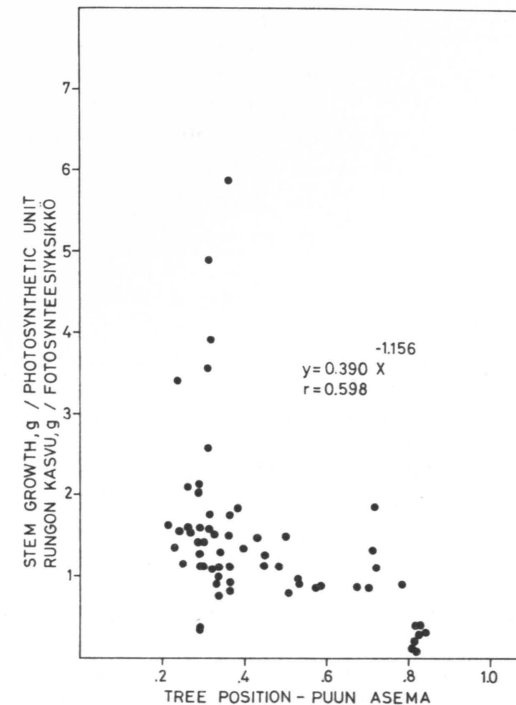


Fig. 11. Dry matter production of stem per photosynthetic unit as a function of tree position.

Kuva 11. Rungon kuiva-ainetuotanto fotosynteesiyksikköä kohti puun aseman funktiona.

partition models are of importance since they indicate the share of the total amount of photosynthates directed to a certain growth component in relation to other growth components. Conclusions can be drawn from these relationships about the future development of the tree structure.

The relationship between height and radial growth calculated with the help of the respec-

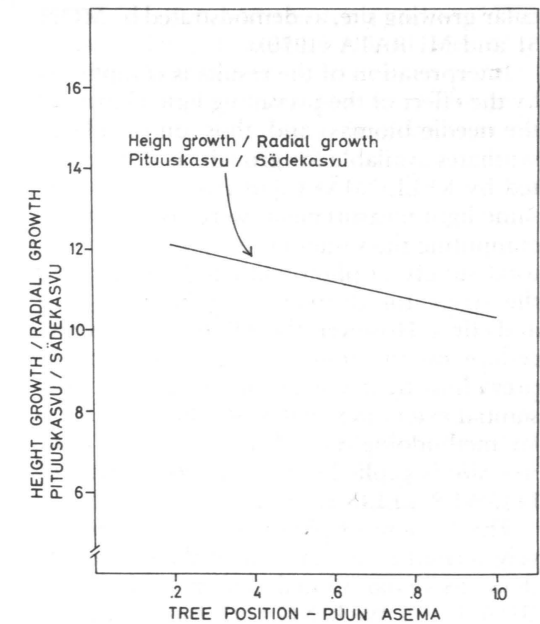


Fig. 12. Ratio between height growth and radial growth as a function of tree position.

Fig. 12. Pituuskasvun ja sädekasvun suhde puun aseman funktiona.

tive partition models is presented in Fig. 12. Height growth appeared to be favoured at the expense of radial growth when illumination of the crown system deteriorated. The increase in height growth in relation to radial growth is, however, only 1.2-fold in deep shade compared with unshaded conditions. However, even a small increase in height growth at the expense of radial growth may in long run yield considerable changes in stem form and the consequent quality of timber.

DISCUSSION

A model based on tree position in a stand and the total supply of photosynthates was developed assuming that the effects of these factors on the crown and stem growth of Scots pine (*Pinus sylvestris* L.) are multiplicative. In other words, the growth depends on the total supply of photosynthates and the amount of photosynthates received by a particular gro-

wing site, as argued by LEDIG (1969) and PROMNITZ (1975). The latter factor is assumed to be dependent on the environment and thus dynamically connected with the succession of the tree stand. In this study, the within-stand light climate was assumed to be the most important factor affecting the share of the total photosynthates received by a parti-

cular growing site, as demonstrated by MONSI and MURATA (1970).

Interpretation of the results is complicated by the effect of the prevailing light climate on the needle biomass and, thus, on the photosynthates available for growth, as demonstrated by KELLOMÄKI and HARI (1980). The same light measurements were also utilized in computing the values of tree position and the total supply of photosynthates, thus limiting the scope for distinguishing between cause and effect. However, the influence of this procedure on the result is negligible since the prevailing light conditions shape to a substantial extent the total needle biomass. Similar methodological difficulties are met when tree size is applied to explain tree growth (cf. FLOWER-ELLIS *et al.* 1976).

The amount of photosynthates was positively related to the growth of the crown and stem, as demonstrated earlier by EMMINGHAM and WARING (1977) and KELLOMÄKI *et al.* (1979). This seems to hold in moderate shading especially. In heavily shaded conditions, however, crown and stem growth was greater than expected on the basis of the supply of photosynthates. In unshaded conditions the situation was reversed. This is interpreted as indicating the functional and structural changes in the growth system due to shading. For example, the increased needle area per unit of dry weight associated with prevailing light conditions was reported by DEL RIO and BERG (1979). They suggested that this modification improves the capture of the scarce light resources of shaded conditions. The possible physiological and structural changes in the photosynthetic apparatus and growth have been discussed earlier by KELLOMÄKI and HARI (1980).

The relationship between mean radial growth over the whole stem and tree position and photosynthesis was calculated in stands 3, 4 and 6. In these calculations the share of explained variance was considerably higher than in the calculations where only the radial growth at 1.3 m above ground level was studied. The result emphasizes the fact that wood formation takes place simultaneously throughout the stem and should be taken into account when studying the relationship between photosynthetic production and structural matter production. In growth studies this requirement may, however, result in consider-

able measuring difficulties.

The basic density of wood was negatively related to tree position and the supply of photosynthates. The share of explained variance, however, was relatively small, indicating that also factors other than those included in the analysis may have an effect on the basic density. In fact, the formation of xylem tissue seems to be to a great extent a temperature controlled process, which may, however, be limited also by the supply of photosynthates and hence by the light intensity (cf. FORD *et al.* 1978, DENNE 1971, 1979). This assumption is supported by the relationship between the share of late wood and basic density found in this study. For example, MIKOLA (1950), LARSON (1957), RICHARDSON (1964), LEDIG *et al.* (1975), and SAIKKU (1975) have demonstrated the role of temperature in late wood formation. The width of early wood and late wood was, however, almost linearly related to the amount of photosynthates. It is evident that further studies are needed before distinctions can be drawn between the role of genotype and different environmental factors in determining the values of basic density (eg. VELLING 1974, KELLOMÄKI 1979 a, b).

Height growth was favoured at the expense of radial growth within the whole range of values of tree position. This growth strategy seems to be characteristic for a variety of light-demanding tree species like Scots pine (cf. BORMANN and LIKENS 1979). The favouring of height growth at the expense of radial growth is typical of light-demanding tree species which possess a high potential for maintaining dominance in the stand. Apparently, the favouring of height growth against radial growth in shaded conditions may lower the physical strength of the stem. This may, however, be compensated by increased basic density of wood. Thus, the proper physical strength of stem may be maintained even in poor light conditions. Further studies are needed to verify these assumptions.

All the growth characteristics emphasize the role of light conditions in the growth and development of individual trees and stands and its importance in silvicultural practice. The great magnitude of growth requires unobscured illumination of the crown. Poor stem form, increased crown growth and low basic density seem, however, to be unavoidable

consequences of maximised production of dry matter (cf. UUSVAARA 1974). These drawbacks appear to be avoidable by increasing shadig through preferring sufficiently dense stands, but only at the expense of the growth of individual trees. Similar results can also be obtained by favouring considerable

height variation between trees and avoiding too early elimination of deciduous trees. More comprehensive studies are needed to develop proper management procedures for growing high quality timber to the maximum extent.

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SELOSTE:

NUORTEN MÄNTYJEN LATVUSTEN JA RUNKOJEN KASVUN SUHDE FOTOSYNTeesiin JA METSIKÖN VALAISTUSSUHTEISIIN.

Taimikko- ja tiheikkövaiheen metsiköistä kerättyä aineistoa hyväksi käyttäen on tutkittu männyn latvusten ja rungon kasvun suhdetta puun kokonaisfotosynteesiin ja latvusten valaistukseen. Silmujen ja neulasten muodostuminen latvuksessa sekä rungon sädekasvu, pituuskasvu ja kuiva-ainetuotanto riippuvat selvästi puun kokonaisfotosynteesistä. Latvusten valaistuksen heiketessä nämä

kasvutunnukset saivat suurempia arvoja kuin kokonaisfotosynteesin perusteella oli odotettavissa. Ilmiö oli erityisen selvä pituuskasvussa. Osoittautuikin, että sädekasvu taantuu pituuskasvu nopeammin latvusten valaistuksen heiketessä. Rungon pintapuun tiheys oli sitä alhaisempi mitä parempi latvusten valaistus ja mitä suurempi puun kokonaisfotosynteesi olivat.