SILVA FENNICA VOL. 15, 1981, N:o 3:306–322

CROWN STRUCTURE AND STEM GROWTH OF NORWAY SPRUCE UNDERGROWTH UNDER VARYING SHADING

ILPPO GREIS and SEPPO KELLOMÄKI

SELOSTE:

VARJOSTUKSEN VAIKUTUS ALIKASVOSKUUSIEN LATVUKSEN RAKENTEESEEN JA RANGAN KASVUUN

Saapunut toimitukselle 1980-12-20

The crown structure and stem growth of Norway spruce (*Picea abies* (L.) Karst.) undergrowth was studied in relation to the prevailing light conditions and potential photosynthesis. Shading decreased the stem height growth more than the length increment of laterals, producing a plate-shaped crown in deep shade. Needles responsed to shading by adapting a horizontal inclination in deep shade. The needles were wide and thin respectively in shade. In the open the needle cross-section was almost square. Stem radial growth and height growth were both effected by shading exhibiting a linear response to the prevailing light conditions and the potential photosynthesis. Light conditions under dominating trees were closely correlated with the basal area of the dominating trees.

INTRODUCTION

In Finland, Norway spruce (*Picea abies* (L.) Karst.) undergrowth is common in mature tree stand growing on fertile and medium fertile sites. They most frequently occur in Scots pine and deciduous tree stands (MIKOLA 1966), since spruce seedlings are capable of adapting to the prevailing growing conditions.

Such undergrowth is also common in mature spruce stands but not to the same extent as in pine and deciduous tree stands. Heavy suppression of dominating spruces seems to be responsible for the low frequency of undergrowth in spruce stands (PÖNTYNEN 1929).

Suppression and consequent adapatation are evident in the growth of spruce undergrowth. For example, the umbrella-shaped crown is a result, especially under heavy suppression, of increased growth of the laterls compared with that of the main axis. In addition, needle inclination is horizontal under suppression. On the other hand, the spruce undergrowth responds to release by increasing growth of the main axis and vertical needle inclination. Consequently, the crown morphology and growth of spruce undergrowth seem to be associated with light conditions, especially. Other crown characteristics apparently associated with the prevailing light conditions are also described (cf. for example SIREN 1949).

It is assumed in this study that the prevailing light conditions maily control the growth of the spruce undergrowth. This hypothesis is applied in the study of the crown morphology and stem growth system. In crown morphology, the relationship between the prevailing light conditions and the branch growth and subsequent crown shape, the needle inclination and needle dimensions are detemined. In stem growth, the radial and height growth of the stemsystem is related to the prevailing light conditions. In addition, the relationship between dominating trees and the prevailing light conditions underneath is considered.

MATERIAL AND METHODS

Study area

The study material was gathered in Central Finland near to the Forest Field Station, University of Helsinki (61°47′ N, 24°18′ E, 150 m a.s.l.). It represents the spruce undergrowth in a mature 105-years-old spruce stand growing on a *Myrtillus* site on morain soil. The varying density of the tree stand was utilized in the experimental layout. The characteristics of the separate sample plots in the tree stand are given in Table 1.

Sample plots

Two series of sample plots representing varying stand density and light conditions were selected in the study area. There were six sample plots, 200 m² in size, in both series. They represent a basal area of 5–37 m² ha^{-1}, a height of 18–27 m, a diameter of 22–36 cm and a volume of 35–472 m³ ha^{-1}. The sample plots were dominated by spruce apart from plot number one where pine was dominant. In addition, one sample plot was selected from an open area representing an eight-year-old spruce stand. In Table 1 the sample plots are listed in order of increasing shading of the dominant trees.

Sample trees

Two typical trees were selected from among the undergrowth for the study. An attempt was made to include trees with well-formed crowns in the study so as to avoid measuring difficulties due to abnormalities in the growth of branches. In addition, the variation in tree size and age was minimized. The tallest sample tree was 156 cm and the smallest 65

Table 1. Main characteristics of the tree stands in the sample plots.
Taulukko 1. Koealojen puustotunnukset.

Sample plot *Koeala*	Basel area *Pohja-pinta-ala* m²/ha	Mean height *Keski-pituus,* m	Mean diameter *Keski-läpimitta* cm	Volume *Kuutio* *m³/ha*	Proportion of tree species *Puulajisuhteet*		
					Pine *mä*	Spruce *ku*	Birch *ko*
III	–	1	2	–		1.0	
I.1	5	18	25	35	.6	.4	
I.2	9	20	23	87	.1	.9	
I.3	20	25	28	238		1.0	
I.4	32	26	35	394		1.0	
I.5	37	27	30	472		1.0	
I.6	33	27	29	420		1.0	
II.1	9	22	32	95		.9	.1
II.2	17	22	30	159		1.0	
II.3	20	26	31	246		1.0	
II.4	22	24	36	252		1.0	
II.5	31	23	27	341		1.0	
II.6	27	20	22	261		1.0	

cm, the mean height being 109 cm. The oldest sample tree was 40 years and the youngest 8 years, the mean age being 22 year. The youngest sample trees represent those growing in the open area.

Phytometric measurements

The sample trees were transferred to the laboratory where several measurements were carried out. The following measurements were made on the main axis: retprospective height growth to an accuracy of one centimeter, radial growth to an accuracy of 10^{-2} mm at the base of the stem and age of the sample tree. The two latter measurements were carried out by means of a microscope.

The measurements concerning the sample tree crowns are presented in Fig. 1. The measurements of the first-order branch concerned the longest laterial of the third whorl counting from the apex, if the particular branch had developed normally, *i.e.* there were no insect or fungus damages etc. The second-order branch measured represented the third laterial of the same free as those for the selection of the first-order whorl. The retprospective length increment of the first- and the second-order sample branches were measured to an accuracy of one centimeter.

Characterisation of the structure of the needle biomass of the current-year shoot of the main axis of the first-order sample branch included measurements of needle inclination and dimensions of the needles as presented in Fig. 2. The vertical inclination was measured to an accuracy of five degrees. In order to detemine the orientation of the needles the shoot cross-section was assumed to be 180°. This zone was divided into three sectors of 60°. The needles belonging to a particular sector were removed and weighted to an accuracy of 10^{-3} g after drying for 24 h at 105°C. Thus, the orientation of the needles represents the biomass weighted share of a particular sector as described above.

Measurements of the needle dimensions included the determination of the needle width, length and thickness as well as their dry weight. The length measurements were carried out on ten separate needles. The dry weight represents the collective weight of the above needles after drying for 24 h at 105°C, divided by the number of sample needles. The length measurements were carried out to an accuracy of 10^{-2} mm and the weight measurements to an accuracy of 10^{-3} g.

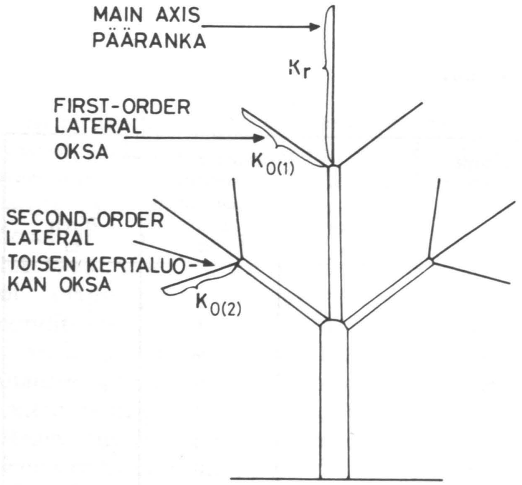

Fig. 1. A schematic presentation of a sample tree where Kr denotes the height growth of the stem, $K_{O(1)}$ the length increment of the first-order lateral and $K_{O(2)}$ the length increment of the second-order laterial.

Kuva 1. Kaavakuva koepuusta. Kr = päärangan pituuskasvu, $K_{O(1)}$ = ensimmäisen kertaluokan oksan pituuskasvu, $K_{O(2)}$ = toisen kertaluokan oksan pituuskasvu.

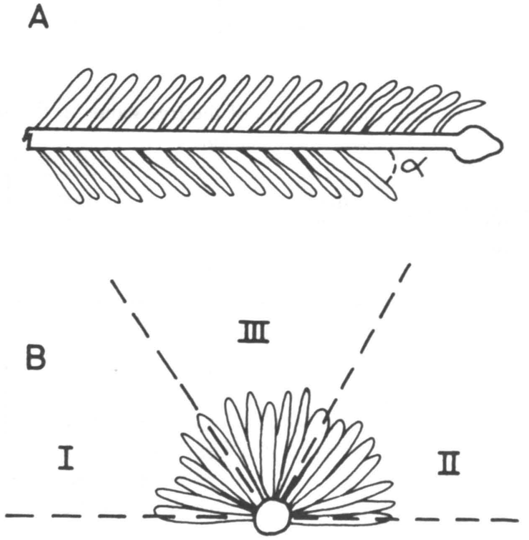

Fig. 2. A schematic presentation of the measuring of needle inclination in branches. A: vertical inclination; B: orientation.

Kuva 2. Neulasten asennon mittaaminen. A: neulaskulman määritys kasvaimen pituussuunnassa; B: neulasten sijoittuminen kasvimen poikkileikkauksessa.

Light measurements

The light conditions in the environment around each sample tree were measured by means of hemispherical photographs. The photographs were taken with a camera having a negative size of 24 mm x 35 mm. The lens was a Canon Fish-eye lens (7,5 mm, F 5,6). A special tripod was needed for operations above the sample tree crown in order to facilitate automatical levelling of the camera and its azimuthal orientation. The film was Kodak Panatomic – X having a sensitivity of DIN 16. The exposure time was measured in relation to the zenith. The diaphragm aperture was adjusted to be three degrees greater than the measured value in order to emphasize the contrast between sky and the canopy image of the over-lying trees. Standard methods were used in developing the films. A proof was taken on Agfa Orto H -paper from each negative. The proof had a mat surface and the hemispheral disc had a diameter of 100 mm on the proof.

Computations

In the computations, the characteristics of the crown structure and growth of the sample tree were related to the characteristics of the prevailing light conditions. In addition, estimates of potential photosynthesis were also computed and used as light measurements in the computations.

The computed energy units for the hemisphere above a particular sample tree are given in Table 2. The hemispheral photographs were digitalised for this purpose in the Laboratory of Physics and Computation, Helsinki University of Technology.

The digitalization procedure is described in detal by HOLM (1979 a, b). An example of a hemispherical photograph and a respective digitalised image is given in Fig. 3.

A computer programme written in FORTRAN IV was available for numerical computations of light and photosynthesis (HOLM 1979 a, b, c). In the light

Table 2. Energy units computed for the hemisphere above a particular sample tree.

Taulukko 2. Alikasvoskuusten yläpuolista puoliavaruutta kuvaavilta valokuvilta lasketut energiatunnukset.

Unit and weather type *Suure ja säätyyppi*		Dimension *Dimensio*	Explanation *Selitys*
$\bar{E}_d$	cloudy *pilvinen*	MJ/m²/day	Diffuse radiation for overcast sky *Päällyspuuston varjostaman hajasäteilyn energia pilvisellä säällä*
$\bar{E}_d$	sunny *aurinkoinen*	MJ/m²/day	Diffuse radiation for clear sky *Päällyspuuston varjostaman hajasäteilyn energia aurinkoisella säällä*
$\bar{E}_b + d$		MJ/m²/day	Total radiation for clear sky *Päällyspuuston varjostaman kokonaissäteilyn energia*
$\bar{E}_d/E_d$	cloudy *pilvinen*		Ratio between diffuse radiation below and above canopy for overcast sky *Päällyspuuston varjostaman ja varjostamattoman hajasäteilyn energian suhde pilvisellä säällä*
E_d/E_d	sunny *aurinkoinen*		Ratio between diffuse radiation below and above canopy for clear sky *Päällyspuuston varjostaman ja varjostamattoman hajasäteilyn energian suhde aurinkoisella säällä*

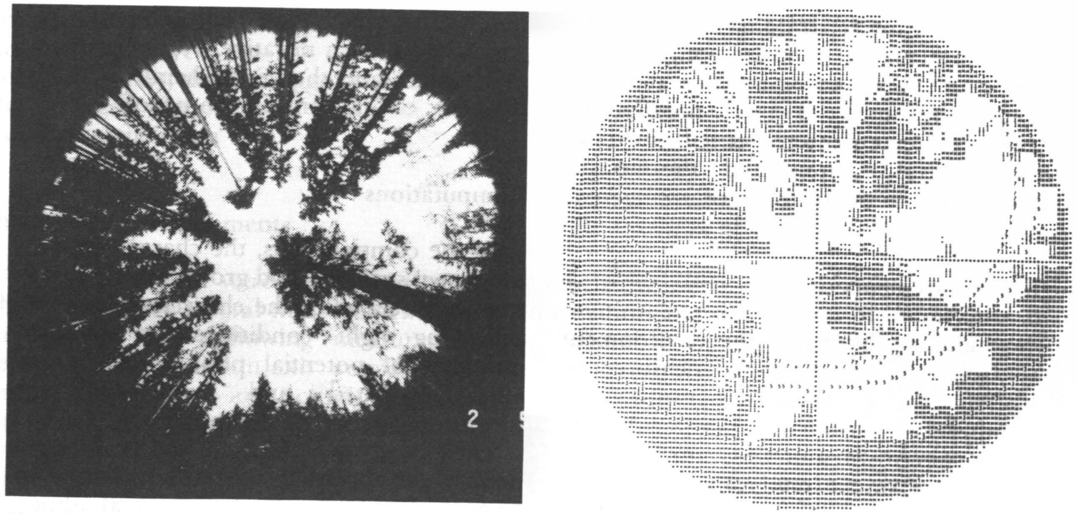

Fig. 3. An example of a hemispheral photograph (left) and the respective digitalized image (right).
Kuva 3. Esimerkki valon mittaukseen käytetystä valokuvasta (vasemmalla) ja vastaavasta digitalisoidusta kuvasta (oikealla).

computations, the light intensity was assumed to be formed of direct ($\bar{E}_b$) and diffuse ($\bar{E}_d$) light intensities, *i.e.*

$$(1)\quad \bar{E}_T = \bar{E}_b + \bar{E}_d,$$

where $\bar{E}_T$ is the total radiation. The computational procedure is described in detail by HOLM (1979 a, b, c) based on the works by ANDERSON (1964), MADGWICK and BRUMFIELD (1969), D.I.E. (1973) and DUCREY (1975 a).

The computed photosynthetic units are given in Table 3. Eq. (2) was employed in the computation

$$(2)\quad p(\bar{E}) = p_{max} \tan h \left(\frac{\bar{E}}{E_p}\right),\ gm^{-2}s^{-1},$$

Table 3. Photosyntethetic units computed from the radiation obtained from the hemispheral photographs.
Taulukko 3. Valokuvien säteilyarvoista lasketut fotosynteesitunnukset.

Unit and weather type *Suure ja säätyyppi*		Explanation *Selitys*
$P(\bar{E}_d)/P(E_d)$	cloudy *pilvinen*	Ratio between photosynthesis below and above canopy for on overcast sky based on diffuse radiation *Päällyspuuston varjostaman ja varjostamattoman pilvisen sään hajasäteilyenergiaa vastaavien fotosynteesiarvojen suhde*
$P(\bar{E}_d)/P(E_d)$	sunny *aurinkoinen*	Ratio between photosynthesis below and above canopy for a clear sky based on diffuse radiation *Päällyspuuston varjostaman ja varjostamattoman aurinkoisen sään hajasäteilyenergiaa vastaavien fotosynteesiarvojen suhde*
$\frac{P(\bar{E}_{b+d})}{P(E_{b+d})}$		Ratio between photosynthesis below and above canopy for a clear sky based on total radiation *Päällyspuuston varjostaman ja varjostamattoman kokonaissäteilyn energiaa vastaavien fotosynteesiarvojen suhde*

Table 4. Independent and dependent variables used in the final analysis. See also Tables 2 and 3.
Taulukko 4. Aineiston analysoinnissa käytetyt selittävät säteily- ja fotosynteesitunnukset ja selitettävät koepuutunnukset. Katso myös taulukko 2 ja 3.

Units of radiation and photosynthesis *Säteily- ja fotosynteesitunnukset*		Units of crown structure and growth of spruce undergrowth *Alikasvoskuusten morfologiaa ja kasvua kuvaavat tunnukset*
– $\bar{E}_d$	cloudy *pilvinen*	– Ratio between height growth of stem and length increment of the first-order lateral, $K_r/K_{o(1)}$ (see Fig. 1) – *Päärangan päätekasvaimen ja oksan päätekasvaimen pituuskasvujen suhde, K_r-/$K_{o(1)}$ (kts. kuva 1)*
– $\bar{E}_d$	sunny *aurinkoinen*	– Ratio between length increment of the first-order and second-order laterials, $K_{o(1)}/K_{o(2)}$ – *Oksan päätekasvaimen ja toisen kertaluokan oksan päätekasvaimen pituuskasvujen suhde $K_{o(1)}/K_{o(2)}$*
– $\bar{E}_{b+d}$	sunny *aurinkoinen*	
– $\bar{E}_d/E_d$	cloudy *pilvinen*	– Vertical inclination of needles – *Neulaskulma kasvaimen pituussuunnassa (kuva 2 A)*
– $\bar{E}_d/E_d$	sunny *aurinkoinen*	– Orientation of needles in shoot cross-section – *Neulasten sijoittuminen kasvaimen poikkileikkauksessa (kuva 2 B)*
– $P(\bar{E}_d)/P(E_d)$	cloudy *pilvinen*	
– $P(\bar{E}_d)/P(E_d)$	sunny *aurinkoinen*	– Ratio between thickness and width of needles – *Neulasten paksuuden ja leveyden suhde*
– $\frac{P(E_{b+d})}{P(E_{b+d})}$	sunny *aurinkoinen*	– Ratio between needle surface and needle biomass – *Neulasten pinta-alan ja massan suhde*
		– Ratio between shoot needle biomass in current-year shoot – *Näyteoksan rangan ja neulasten massan suhde*
		– Radial and height growth of the stem – *Koepuiden säde- ja pituuskasvu*

where p is photosynthesis, $\bar{E}$ a chosen component of the radiation or the total radiation ($\bar{E}_b$, $\bar{E}_d$ or $\bar{E}_T$) above the canopy of a particular sample tree, tan h equal to 0.762, p_{max} the maximum value of photosynthesis and E_p a parameter having a particular value. The values 0.3, 0.6 and 0.9 $MJm^{-2}\ h^{-1}$ were applied of photosynthesis, were carried out every 30 minutes. Thereafter the momentary values were integrated over a period of one day in order to obtain the light and photosynthesis estimates related to the characteristics of the crown structure and growth. The computations were carried out for June 3rd and normalized on the basis of the radiation observations made at Tampere meteorological station (61°28′N, 23°44′E, 92 m a.s.l.), 50 km south of the experimantal area.

In the final analysis, the characteristics of the crown structure and growth were related to the estimates of light and photosynthesis as discussed above. Several combinations of the dependent and the independent variables given in Table 4 were computed. The best results were given by the diffuse radiation for the overcast sky ($\bar{E}_d$ cloudy) and the respective photosynthetic estimate (P ($\bar{E}_d$)/(E_d) cloudy). In the latter case, the computations were carried out by applying the value 0,9 MJ m^{-2} h^{-1} of parameter Ep. The results based on the characteristics of the radiation and the phtotosynthesis only are presented later.

RESULTS

Effect of shading on crown shape

The ratio between the height growth of the stem and the length increment of the first order lateral, $K_r/K_{o(1)}$, were used as an indicator of the development of the crown in relation to the estimates of the prevailing linght conditions and the potential photosynthesis. The ratio was comparable with both factors as appears from Figs 4 and 5. In the sample area representing the open area the value of the ratio was more than 13 times greater than the respective values obtained under heavy shading. Consequently, in the long run a plate-shaped crown is likely to be formed in spruces under heavy shading due to the higher growth rate in the branches than in the main leader of the stem. In an open area or under moderate shading, a reverse pattern of the ratio indicates that in those conditions a cone-like crown is expected to be formed in a long run. The degree of shading should be less than 70 percent before a cone-shaped crown is likely to be formed. The regression between the ratio and the estimates of light and photosynthesis was statistically significant in both cases ($p < 0.100$).

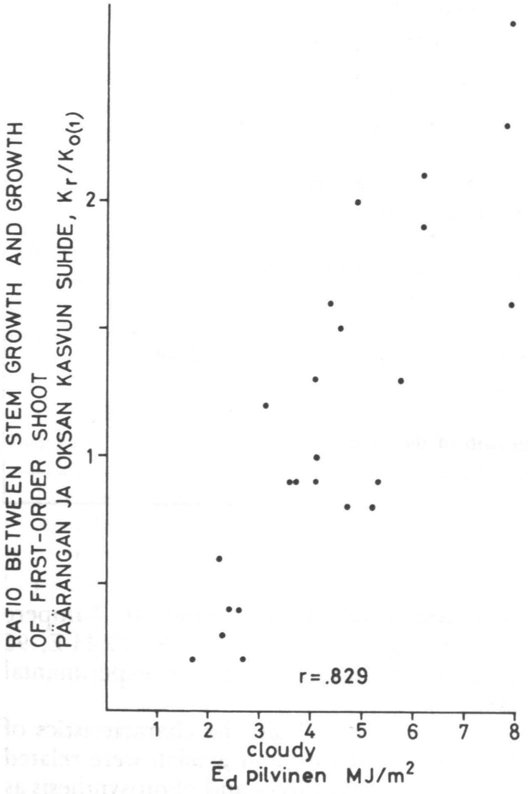

Fig. 4. Ratio between the height growth of the stem and the length increment of the first order laterial, $K_r/K_{o(1)}$, as a function of the estimate of diffuse radiation under the canopy during a cloudy day, $\bar{E}_d$ cloudy.

Kuva 4. Rangan kasvun ja ensimmäisen kertaluokan oksan kasvun suhde, $K_r/K_{o(1)}$*, suhteutettuna päällyspuuston alla vallitsevaan säteilyyn pilvisenä päivänä,* $\bar{E}_d$ *pilvinen.*

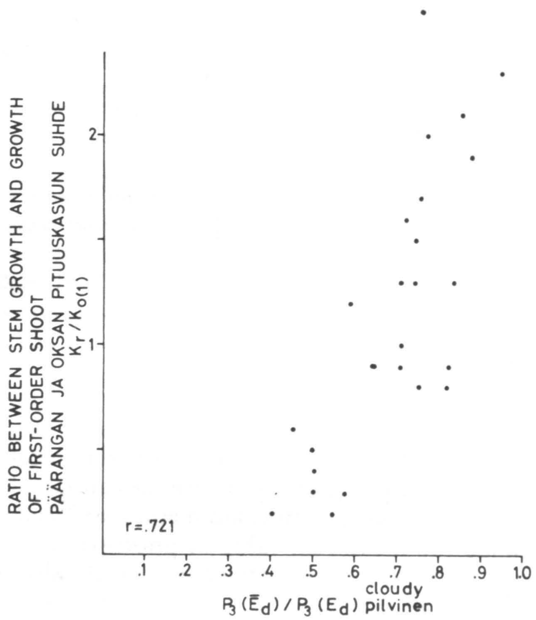

Fig. 5. The same as in Fig. 4 but as a function of the estimate of photosynthesis under the canopy during a cloudy day, $P(\bar{E}_d)/(E_d)$ cloudy.

Kuva 5. Kuten kuvassa 4 mutta suhteutettuna päällyspuuston latvuksen alla vallitsevaan potentiaalisen fotosynteesin tasoon pilvisenä päivänä, $P(\bar{E}_d)/P(E_d)$ *pilvinen.*

Effect of shading on branch shape

The ratio between the length increment of the first- and second-order laterlas, $K_{o(1)}/K_{o(2)}$, was used as an indicator of the expected shape of the branches. This ratio also seems to be dependent on the estimates for radiation and photosynthesis prevailing above the undergrowth, as appears from Figs 6 and 7. The growth pattern is similar to that between the stem and the first-order laterial. In other words, in heavy shading, the growth rate of the second-order laterial is greater than that of the first-order laterial. Consequently, in heavy shading the branches of spruce undergrowth are likely to be wider than those formed in moderate shading. This process is, however, not very clear since the maximum values of the length increment of the first-order laterials were their greatest, only twice the respective values of the second-order laterial. Only in one case was the length increment of the first-order laterial smaller than that of the second-order one. The dependence of the ratio between the growth of the first- and second-order laterials on estimates of light and photosynthesis was also not as close as that between stem growth and growth of the first-order laterial. The regressions between the ratio and the estimates were statistically significant ($p < 0,100$) in bots cases.

Effect of shading on the characteristics of the needles

Distribution of the current dry matter production in the laterals into needle growth and wood formation was described by means of the ratio between these two characteristics. There was no clear dependence between the ratio and the prevailing light conditions and potential photosynthesis ($p > 0,100$). Values for the ratio varied between 0,38–0,83. The ratio between needle growth and wood formation lay between the above limits within

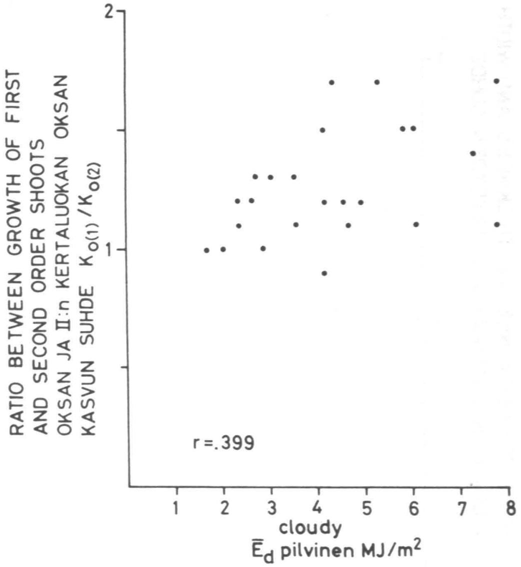

Fig. 6. Ratio between the length increment of the first order laterial and the second order laterial, $K_{o(1)}/K_{o(2)}$, as function of the estimate of diffuse radiation under the canopy during a cloudy day, $\bar{E}_d$ cloudy.

Kuva 6. Ensimmäisen kertaluokan oksan ja toisen kertaluokan oksan pituuskasvun suhde, $K_{o(1)}/K_{o(2)}$*, suhteutettuna päällyspuuston alla vallitsevaan säteilyyn pilvisenä päivänä,* $\bar{E}_d$ *pilvinen.*

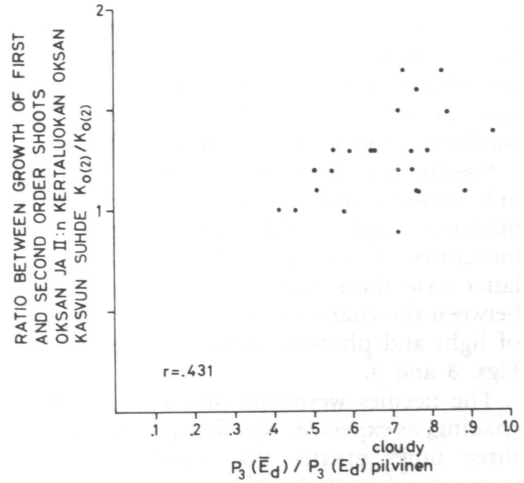

Fig. 7. The same as in Fig. 6 but as a function of the estimate of photosynthesis under the canopy during a cloudy day, $P(\bar{E}_d/P(E_d)$ cloudy.

Kuva 7. Kuten kuvassa 6 mutta suhteutettuna päällyspuuston alla vallitsevan potentiaalisen fotosynteesin tasoon pilvisenä päivänä, $P(\bar{E}_d)/P(E_d)$ *pilvinen.*

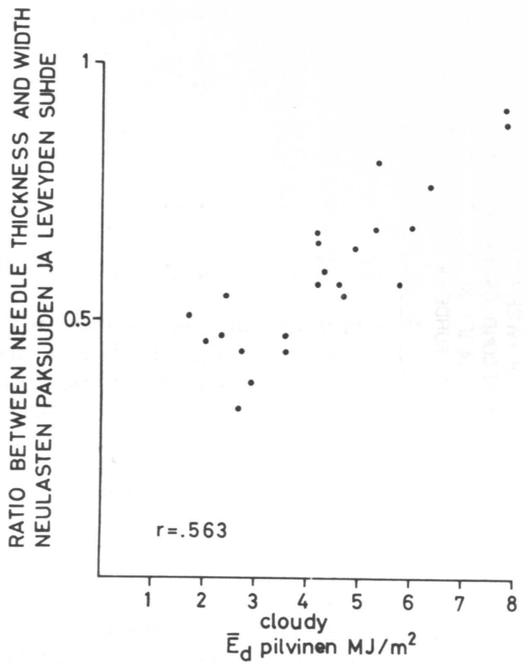

Fig. 8. Ratio between needle thickness and width as a function of the estimate of diffuse radiation under the canopy during a cloudy day, $\overline{E}_d$ cloudy.

Kuva 8. Neulasen paksuuden ja leveyden välinen suhde suhteutettuna päällyspuuston alla vallitsevaan säteilyyn pilvisenä päivänä, $\overline{E}_d$ pilvinen.

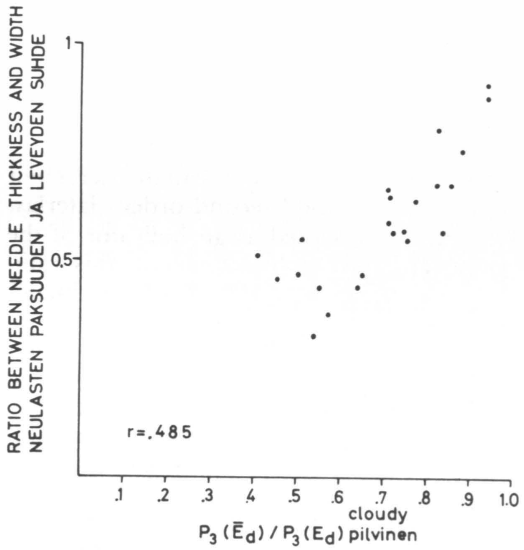

Fig. 9. The same as in Fig. 8 but as a function of the estimate of photosynthesis under the canopy during a cloudy day, P($\overline{E}_d$)/PE$_d$ cloudy.

Kuva 9. Kuten kuvassa 8 mutta suhteutettuna päällyspuuston alla vallitsevan potentiaalisen fotosynteesin tasoon pilvisenä päivänä P($\overline{E}_d$)/P(E_d) pilvinen.

the whole range of light and photosynthesis. In other words, needle growth and respective wood formation behaved in exactly the same way in relation to the prevailing light conditions and potential photosynthesis.

Specific needle area i.e. needle area per unit biomass, and the ratio between needle thickness and width, were applied as indicators of needle structure. Only in the latter case there was any clear relationship between the characteristics and the estimates of light and photosynthesis, as presented in Figs. 8 and 9.

The needles were thin and wide in heavy shading, as expected. Needle width was nearly three times greater than needle thickness occured when the light intensity was 25 percent of that in the open area. In the open area, the ratio between needle thickness and width was almost one, indicating a square cross-section of the needles. The regressions for the ralationship between the ratio and the estimates for light and photosynthesis were statistically significant in both cases ($p < 0{,}100$).

The vertical inclination of the needles was dependent on the prevailing light conditions and the potential photosynthesis, as appears from Figs 10 ja 11. In heavy shading the needle inclination was about five degrees and in the open area the respective value was about 45 degrees. There is, of course, considerable variation in the dependence. However, the results seem to support the observation that in suppressed spruces or in the lower crown of unshaded spruces the needles are nearly horizontal on the lateral shoots. In the open area the needles are inclined more towards the vertical than when growing in the shade. The regressions for the ralationships between needle inclination and the estimates of light and photosynthesis were statistically significant ($p < 0{,}100$).

The orientation of needles in relation to light and photosynthesis remained unclear. These regressions were not statistically

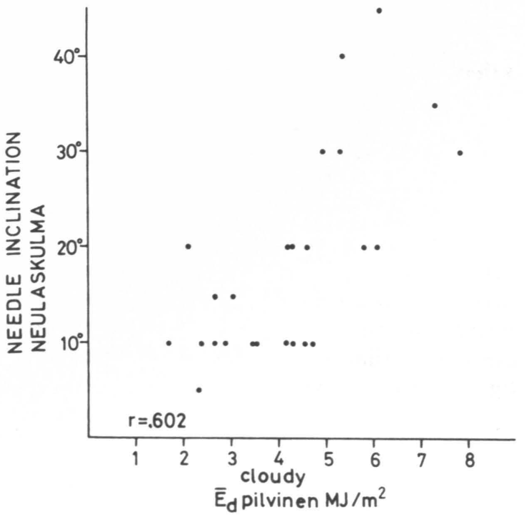

Fig. 10. Needle inclination as a function of the estimate of diffuse radiation under the canopy during a cloudy day, $\overline{E}_d$ cloudy.

Kuva 10. Neulasten kulma suhteutettuna päällyspuuston alla vallitsevaan säteilyyn pilvisenä päivänä, $\overline{E}_d$ pilvinen.

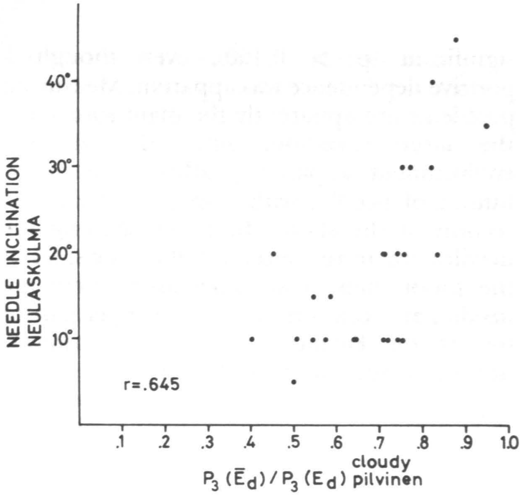

Fig. 11. The same as in Fig. 10 but as a function of the estimate of photosynthesis under the canopy during a cloudy day, P($\overline{E}_d$)/P(E_d) cloudy.

Kuva 11. Kuten kuvassa 10 mutta suhteutettuna päällyspuuston alla vallitsevaan potentiaaliseen fotosynteesin tasoon pilvisenä päivänä, P($\overline{E}_d$)/P(E_d) pilvinen.

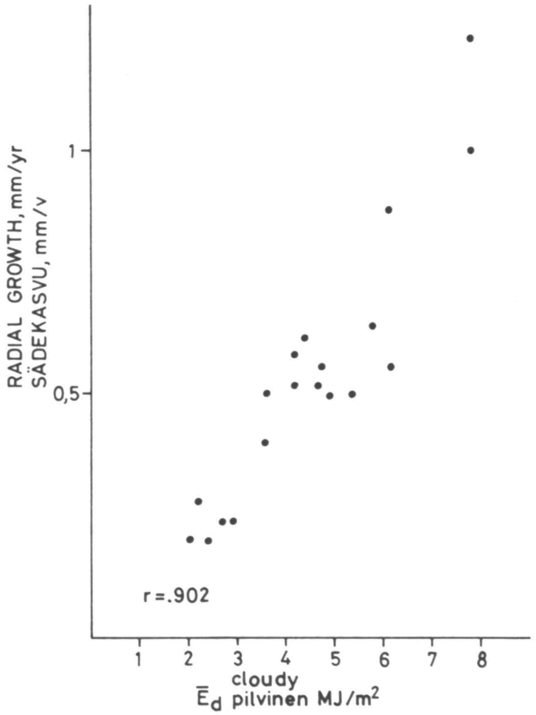

Fig. 12. Radial growth as a function of the estimate of diffuse radiation under the canopy during a cloudy day, $\overline{E}_d$ cloudy.

Kuva 12. Sädekasvu suhteutettuna päällyspuuston alla vallitsevaan säteilyyn pilvisenä päivänä, $\overline{E}_d$ pilvinen.

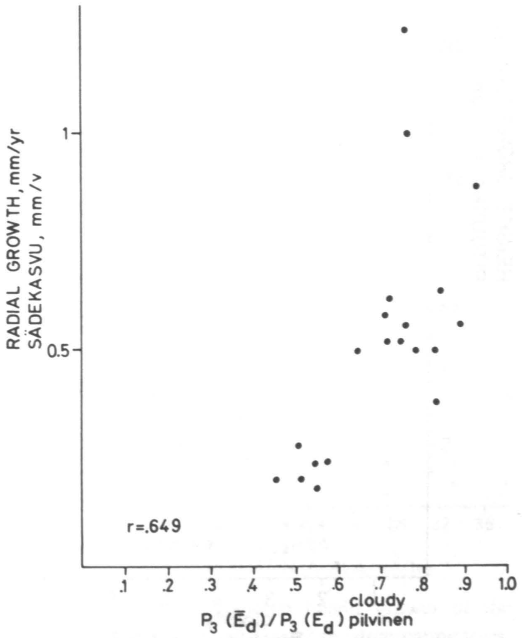

Fig. 13. The same as in Fig. 12 but as a function of the estimate of photosynthesis under the canopy during a cloudy day, P($\overline{E}_d$)/P(E_d) cloudy.

Kuva 13. Kuten kuvassa 12 mutta suhteutettuna päällyspuuston alla vallitsevan potentiaalisen fotosynteesin tasoon pilvisenä päivänä, P($\overline{E}_d$)/P(E_d) pilvinen.

significant ($p > 0,100$), even though a positive dependence was apparent. Measuring problems are apparently the main source for the large variation, since the growing environment apparently affects the distribution of needles with respect to the cross-section of the shoot. In heavy shading the needles are more concentrated on the sides of the shoot than in an open area where the needles are concentrated on the upper part of the shoot. Further studies are, however, needed to support this observation.

Effect of shading on stem growth

The dependence of the radial growth of the sample trees on the prevailing light conditions and the potential photosynthesis is presented in Figs 12 and 13. The dependence is clear and statistically significant ($p < 0,100$). The radial growth in heavy shading was about 0,2 mm yr^{-1} and in an open area nearly six-times greater. The regressions between radial growth and the estimates of light and photosynthesis are almost linear.

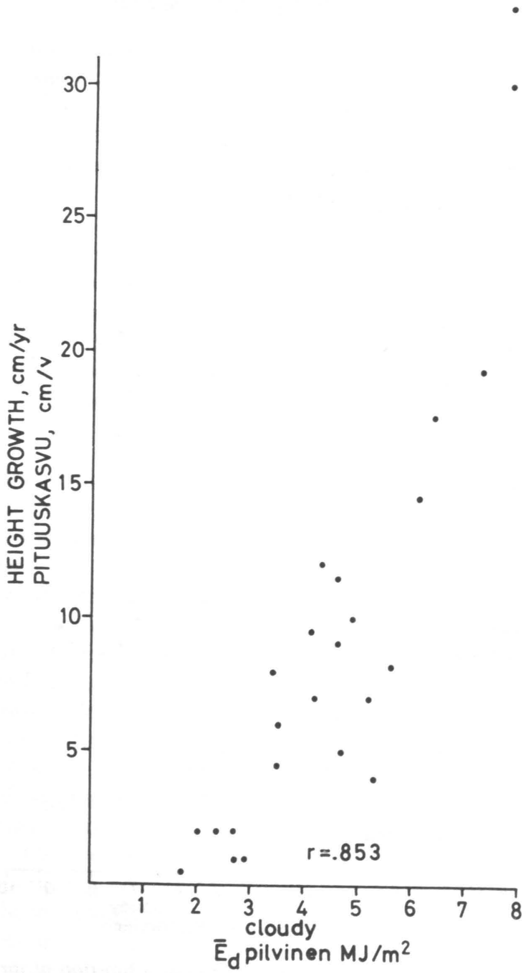

Fig. 14. Height growth as a function of the estimate of diffuse radiation under the canopy during a cloudy day, $\bar{E}_d$ cloudy.

Kuva 14. Pituuskasvu suhteutettuna päällyspuuston alla vallitsevaan säteilyyn pilvisenä päivänä, $\bar{E}_d$ pilvinen.

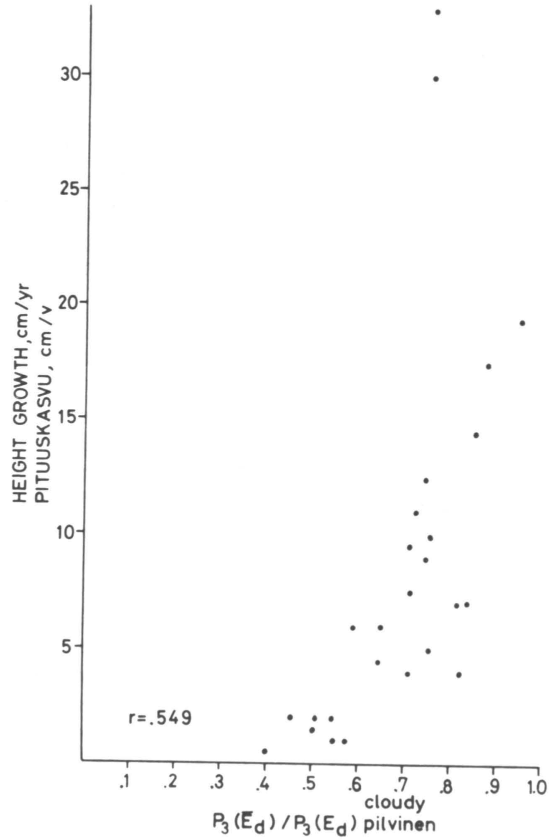

Fig. 15. The same as in Fig. 14 but as a function of the estimate of photosynthesis under the canopy during a cloudy day, $P(\bar{E}_d)/P(E_d)$ cloudy.

Kuva 15. Kuten kuvassa 14 mutta suhteutettuna päällyspuuston alla vallitsevan potentiaalisen fotosynteesin tasoon pilvisenä päivänä, $P(\bar{E}_d)/P(E_d)$ pilvinen.

The response of the stem height growth was also apparent as that of radial growth, as appears from Figs. 14 and 15. The height growth in the open area was almost 60-times greater compared with that in a heavy shade. In absolute terms the height growth varied within the range, 0,5–33 cm, depending on the prevailing light conditions and the potential photosynthesis. The role of other environmental factors associated with suppression may also be evident in growth responses, as discussed later. The regressions between height growth and the prevailing light conditions and the potential photosynthesis were statistically significant at a low risk level ($p < 0,100$).

Relationship between dominating trees and prevailing light conditions.

The relationship between several characteristics of the dominating trees and the prevailing light conditions was studied in order to develop a method for predicting the light conditions through tree characteristics. The most promising result was given by the basal area of the dominating trees, as appears from Fig. 16 ($p < 0,001$). The dependence is especially close when the basal area is less than 20 m^2 ha $^{-1}$. It appears that a 15-fold increase in the basal area reduces the diffuse radiation on a cloudy day, $\bar{E}_d$ cloudy, to a third of that in the open area.

The regression between the basal area and the light conditions can be applied in studing the relationship between the basal area of the dominating trees and the growth of the spruce undergrowth. In addition, the regression between the height growth and the prevailing light conditions was utilized in calculating the relationship between the basal

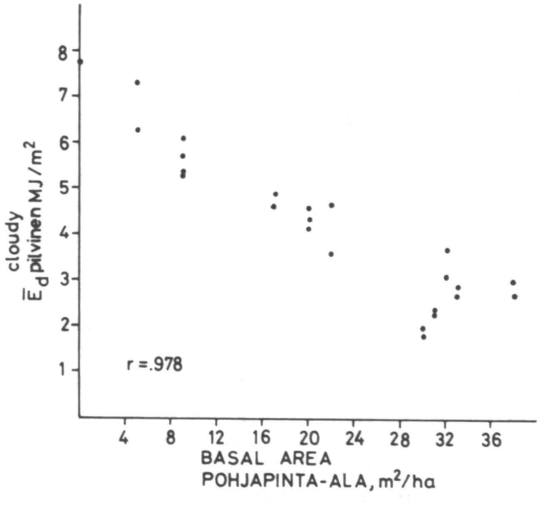

Fig. 16. Effect of the basal area of dominating trees on the estimate of diffuse radiation under the canopy during cloudy day, $\bar{E}_d$ cloudy. Correlation coefficient computed after logaritmic transformation of basal area values.

Kuva 16. Päällyspuuston pohjapinta-alan suhde latvuston alla vallitsevaan säteilyyn pilvisenä päivänä, $\bar{E}_d$ pilvinen. Korrelaatiokerroin laskettu logaritmisesti muunnetuista pohjapinta-ala-arvoista.

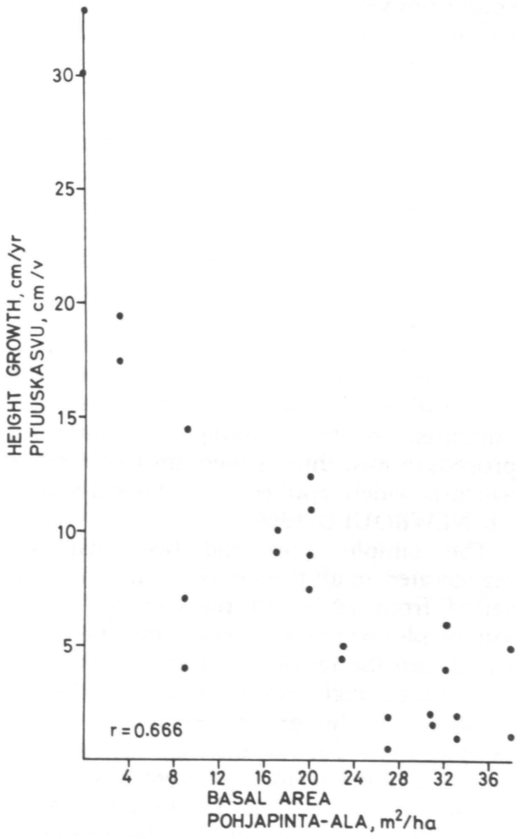

Fig. 17. Relationship between height growth of the undergrowth and the basal area of the dominating trees. Correlation coefficient computed after logaritmic transformation of basal area and height growth values.

Kuva 17. Alikasvoskuusten pituuskasvun ja päällyspuuston pohjapinta-alan välinen suhde. Korrelaatiokerroin laskettu logaritmisesti muunnetuista pohjapinta-ala- ja pituuskasvaimista.

area and height growth, as presented in Fig. 17. As expected, close negative correlation exists between these variables. It appears that values of basal area of less than 10 m^2 ha^{-1} indicates a height growth of between 15–30 cm. Respective values for the basal area of 19–20 m^2 ha^{-1} are 10–15 cm, for the basal area of 20–30 m^2 ha^{-1} 5–10 cm, and for the basal area greater than 30 m^2 ha^{-1} less than 5 cm.

DISCUSSION

The crown structure and the stem growth of undergrowth Norway spruce were studied in relation to the prevailing light conditions and the respective photosynthetic production. Only 26 sample trees representing different conditions were measured. Due to the limited nature of the material, the results are considered to have only an approximative value. In other words, they may well describe the general pattern of the process but not the absolute values of the crown and the stem characteristics investigated in this study. For the latter purpose a more comprehensive material is needed than that available now.

Two criteria were applied in selecting the sample trees, i.e. the sampled trees should be measurable in every aspect and they should be representive of the other trees in a particular sample area. Therefore trees with two leaders or other abnormalities were ommitted in the sampling. The sampling procedure was, thus, a medium tree method which is widely applied in ecological studies (cf. NEWBOULD 1966).

The sample trees had been naturally regenerated in all the sample plot. Their age varied from 20 to 40 years except in the sample plot which represented the open area. In this case the age of the sample trees was, on the average, eight years. Apparently there is variation in the growth responses of the sample trees due to internal factors. The influence of this factor on the crown structure and the stem growth has not been studied in detail, but it is assumed to be negligible compared with that of light conditions. However, the order of the sample plots as regards the response of the sample trees to the light conditions is apparently valid (cf. SIRÉN 1949).

The site type classification developed by CAJANDER (1949) was applied in selecting the sample areas. There is therefore a certain degree of within-stand variation, for example, in soil properties due to stoniness and other abnormalities in the soil profile. The variation between the sample plots is, however, negligible, since all the sample plots represent different density classes of the same stand growing in a uniform forest area of the *Myrtillys* site type. It is therefore assumed that the variation in the light conditions plays a major role in modifying the crown structure and the stem growth of the undergrowth spruces.

The light conditions of the sample trees were determined by taking hemispheral photographs. The details of the procedure are well-documented in ecological literature (cf. EVANS and COOMBE 1959, ANDERSON 1964, 1971, DUCREY 1975 a, b, NILSON 1977, NILSON *et. al.* 1977, ONDOK 1977, NILSON and ROSS 1979). The computerized interpretation system applied in this study is described by HOLM (1979 a, b, c, 1980) and KELLOMÄKI *et. al.* (1979). Automized interpretation procedures applied in exploitation of hemispheral photographs have also been developed elsewhere (cf. BONHOMME and CHATIES 1969, MAGDWICK and BRUMFIELD 1969, DUCREY 1975 a, b).

Hemispheral photographs give values of the light intensity and its components for a particular point. Each sample tree is thus assumed to represent a point in space, since the light conditions above each sample tree were determined through one photograph. The within-crown variation in the light conditions is ommitted in the measuring procedure and the light conditions above the crown were assumed to be uniform all over the crown system. The bias in the results caused by this simplication is assumed to be negligible, since most of the measurements were made in the upper part of the crown within a limited area near the point represented by the photograph. A substantial number of photographs are, however, needed to obtain reliable estimates of the light conditions for a whole tree stand, as demonstrated by NILSON (1977), NILSON *et al.* (1977) and NILSON and ROSS (1979).

Hemispheral photographs tend to underestimate the light intensity in heavy shading. For example, DUCREY (1975 b) has demonstrated that the light estimates obtained from photographs in beech stand are reliable in moderate shading but in 90 percent shading the estimated light intensity is 30 percent less than the real value. Therefore biased light estimates may have been obtained for most of the shaded sample plots. The reliability of the present light measurements were, however, not studied in more detail. The order of the sample plots as regards degree of shading is, however, valid and only slightly affected by the measuring accuracy.

The characteristics of the crown structure and the stem growth were rather well correlated only to the diffuse radiation and the consequent photosynthetic production. This is interpreted as indicating that direct radiation has only a negligible role in the growth and development of spruce undergrowth, even though the major share of light energy available near the forest floor is in the form of direct radiation. The direct radiation near the forest floor is, however, characterized by massive but short-term pulses. The spruce undergrowth adapted to the type of diffuse radiation which prevails near the forest floor cannot utilize these impulses. On the other hand, the amount of direct radiation as calculated from hemispheral photographs is mainly determined by the frequency and duration of obtacles in the path of the sun's track and not by the crown closure as in the case of the diffuse radiation. Consequently, application of the duration of sunshine as an estimate of direct radiation should yield similar results as those obtained have in relation to diffuse radiation.

The variation in the intensity of the diffuse radiation is not substantial during the course of the day. The spruce undergrowth is thus influenced by almost constant radiation representing low intensity values. Consequently, the photosynthetic processes are not saturated resulting in a strong and linear response to the light intensity as suggested by the present results. For example, the best agreement, found in the computations, between the photosynthetic estimate and stem growth was obtained when parameter Ep was given a value 0,9 MJ $m^{-2}h^{-1}$ which was characteristic for a plant species adapted to the nonshaded conditions and having a more linear response to light intensity than shade-adapted plant species.

BOYSEN-JENSEN (1932), for example, suggested that the photosynthetic response of the subvolume of a plant or a stand to light intensity may be highly linear due to the properties of the light intensity and stand structure (cf. also LARCHER 1977, pp. 44–45, THORNLEY 1977). Photosynthetic production in a plant stand and even in a whole plant is, however, poorly documented.

The association between shading and the crown structure and stem growth was apparent in this study. The results for the crown structure and stem growth are in accordance with these of earlier studies. For example, PÖNTYNEN (1929) found that the crowns of suppressed spruces were short and broad due to decreased height growth of the stem and the dying-off of lower branches. He also found that the length increment of branches was substantial even under heavy shading. PÖNTYNEN (1929) suggested that also factors other than shading may cause morphogenesis of the crown of suppressed Norway spruces.

SIRÉN (1949) found that the branch length increment of suppressed spruces was greater than that of the stem as found in this study in heavy shading. SIRÉN (1949) also emphasized that in the relationship between branch and stem growth was reversed non-suppressed conditions. SIRÉN (1949) suggested that in addition to shading the competition for nutrients and water may also cause morphogenesis of the crown of spruce undergrowth (cf. also KALELA 1934, 1936). For example, BEADLE (1966, 1968) has demonstrated that the crown form of particular plant species in the tropics is dependent on the water and nutrient supply. Comparable results are not available from the boreal zone, but verification of this hypothesis maybe obtained in future studies.

CAJANDER (1914) suggested that the plate-shaped crown of suppressed spruces improves the capture of scarce light resources (cf. also JAHNKE and LAWRENCE 1965, HORN 1971). In any case, the adaptation of the crown of spruces growing in the shade seems to yield a crown system with a limited depth but a substantial surface area. This process seems to be further intensified by the horizontal inclination of the needles and their small thickness compared with the respective width. Consequently, unit biomass attains maximum exploitation of the scarce light resources. KUROIWA (1970) demonstrated theoretically that such a crown and branch form is formed under diffuse radiation such as that prevailing in the lower crown or near the forest floor. A similar hypothesis is also presented by BRUNING (1976).

The effect of radiation on the ratio between the length increment of the second and the first order lateral was less than on that between the first order lateral and the stem. In other words, the length increment of a branch is greater than the width increment, even under heavy shading. Both types of growth are comparable as regards light capture, since they occur at the same level. Consequently, neither the length increment nor the width increment are favoured decreasing the internal shading within the crown. A more comprehensive material is, however, needed to verify this hypothesis.

Shading also had an effect on the shape of the current-year shoots of the main branch axis. In heavy shading the shoots were broad. This was a consequence of the small needle inclination, and the concentration of the needles on the sides of the shoots thus producing horizontal arrangement emphasized by broad and thin needles (cf. also AUSSENAC 1973, TUCKER and EMMINGHAM 1977). In the open area, the needle inclination was vertically upwards, giving rise to narrow current-year shoots. In this case the needles were also located on the upper part of the shoot in contrast to the lateral location of needles under heavy shading. The applied measuring procedure was, however, unsatisfactory and requires further development in the future.

The radial growwth and height growth of the stemwere both linearly related to the prevailing light conditions and consequent photosynthetic production, as discussed above. Similarly, the height growth responded to the basal area of the dominating trees (cf. HAGNER 1962, HEISIG and THOMASIUS 1968, BERGAN 1971). There was also close correlation between the prevailing light conditions and the basal area of the dominating trees. The same relationship has earlier been recognized by KELLOMÄKI *et al.* (1977). (cf. also JACKSON and HARPER 1955, MITSCHARLICH et al. 1967). Thus the optimum stand density for natural regeneration of Norway spruce can, in principle, be determined through light studies. In other words, the hemispheral photographs and the respective stand density give satisfactory estimates of the degree of crown closure.

The spruce undergrowth appeared to be profoundly adapted to varying degrees of shading well illustrating its dominance in stand succession. The factors responsible for the adaptability of spruce and the consequent shade tolerance are only partially understood. In this study the factors associated with crown and needle morphology have been emphasized. However, there are several physiological processes capable of adapting to a varying shade pattern and hence improving the shade tolerance. For example, several changes, associated with the degree of shading, in chrolophyll-protein ratios, in the activity of chemical processes in chloroplasts, in respiration rates, photosynthetic rates and other metabolic processes have been reported (cf. KUROIWA 1960 a, b, HOLMGREN *et al.* 1965, LOACH 1967, KOZLOWSKI and KELLER 1966, TSEL'NIKER 1979 etc.). These may also be responsible for the shade tolerance of Norway spruce. The anatomical structure of needles growing in shade are also apt to improve the light capture under shading (cf. JACKSON 1967).

The growth strategy of Norway spruce seems to be such that a great variety of light conditions can be exploited through modification of the crown structure and associated physiological processes. In other words, the response of Norway spruce to the actual environment modifies the structure and the functions so that maximal esploitation of resources is possible (cf. BJÖRKMAN and HOLMGREN 1963, 1970, TOOMING 1970, GRIME 1977, BORMANN and LIKENS 1979, pp. 118–128). Therefore high phenotypic plasticity is one of the most important characteristics of the structure and functions of Norway spruce. This growth pattern enables survival in a great variety of sites but at the expense of a reduced growth rate even in the presence of an ample supply of resources.

REFERENCES

ANDERSON, M. C. 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. J. Ecol. Vol. 52 (41):27–41.

– " – 1970. Radiation, climate, crop architecture and photosynthesis. In: Prediction and measurement of photosynthetic productivity. (Ed. by I. Šetlik), pp. 71–78. Centre for Agriculturial Publishing & Documentation. Wageningen.

– " – 1971. Radiation and crop structure. In: Plant photosynthetic production. Manual and methods (Ed. by Šesták, Z., Čatskij, J. and Jarvis, P. G.), pp. 412–466. W. Junk. Hague.

AUSSENAC, G. 1973. Effect of different microclimates on the morphology and structure of needles. Ann. Sci. For. 30:375–392.

BEADLE, N. C. W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47:992–1007.

– " – 1968. Some aspects of the ecology and physiology of Australian xeromorphic plants. Aust. J. Sci. 30:348–354.

BERGAN, J. 1971. Skermförmyelse av gran sammanlinget med planting i grane i Nordland. Summary: Natural Norway spruce regeneration under shelterwood compared with plantations at grane in Nordland. Medd. Norske Skogforsøksv. Nr. 104:195–211.

BONHOMME, R. and CHARTIER, P. 1969. The interpretation and automatic measurement of hemispheral photographs to obtain sunlit foliage area and gap frequency. Israel J. Agric. Res. Vol. 22 (2):53–61.

BORMANN, F. H. and LIKENS, G. E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag. New York, Heidelberg, Berlin. 253 p.

BOYSEN-JENSEN, P. 1932. Die Stoffproduktion der Pflanzen. G. Fischer. Jena.

BRUNING, E. F. 1976. Tree forms in relation to environmental conditions: an ecological viewpoint. In: Tree physiology and yield improment (eds. M. G. R. Cannel and F. T. Last), pp. 139–156. Academic Press. London, New York, San Francisco.

CAJANDER, A. K. 1914. Onko metsää kasvatettava sekametsänä. Metsätaloudellinen aikakausikirja. Suppeampi painos. Vol. 1 (2):54–65.

– " – 1949. Forest types and their significance. Acta For. Fenn. 56:1–71.

DUCREY, M. 1975 a. Utilization des photographies hémisphériques pour le, calcul, de la perméabilité des couverts forestiers au rayonnement solaire. I. Analyse theorique de l'interception. Ann. Sci. Forest. Vol. 32 (2):73–92.

– " – 1975 b. Utilisation des photographies hémisphériques pour le calcul de la permeabilité des couvets forestiers au rayonnement solaire. II. Étude expérimentale. Ann. Sci. Forest., Vol. 32(4):205–221.

EVANS, G. C. and COOMBE, D. E. 1959. Hemispheral and woodland canopy photography and the light climate. J. Ecol. Vol. 47:103–113.

GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Natur. 11:1169–1194.

HAGNER, S. 1962. Ett exempel på beståndtäthetens betydelse för den naturliga föryngringens uppkomst och utveckling på god granmark i Skåne. Statens Skogsforskningsinstitut. Upps. 85.

HEISIG, J. and THOMASIUS, H. 1968. Studie über den Einfluss der Lichtenverhältnisse im Verstand sowie der Höhenlage auf die Verjüngungsfreudigkeit der Fichte. Arch. Forstw. 17:1173–1184.

HOLM, J. 1979 a. Metsäkuvien analyysi. Osa 1. Ohjelmadokumentti. Moniste. 24 p.

– " – 1979 b. Metsäkuvien analyysi. Osa 2. Ohjelmadokumentti. Moniste. 15 p.

– " – 1979 c. Metsäkuvien analyysiohjelma "vaakasäteily". Ohjelmadokumentti. Moniste. 17 p.

– " – 1980. Assimilaattien tuotannon arviointi kasvupaikalta otetun valokuvan perusteella. Moniste. 20 p.

HOLMGREN, P., JARVIS, P. G. and JARVIS, M. S. 1965. Resistance to carbon dioxide and water vapour transfer in leaves of different plant species. Physiol. Plant. 18:557–573.

HORN, H. S. 1971 The adaptive geometry of trees. Monographs in population biology 3. Princeton, N. J. Univ. Press. 144 pp.

JACKSON, L. W. R. 1967. Effect of shade on leaf structure of deciduous tree species. Ecology 48:498–499.

– " – and HARPER, R. S. 1955. Relation of light intensity to basal area of shortleaf pine stands in Georgia. Ecology 36:158–159.

JAHNKE, L. S. and LAWRENCE, D. B. 1965. Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. Ecology 46:319–326.

KALELA (CAJANDER), E. K. 1934. Kuusen taimistojen vapauttamisen jälkeisestä pituuskasvusta. Referat: Über den Höhenzuwachs der Fichtenpflanzenbestände nach der Befreiung. Commun. Inst. For. Fenn. 19 (5):1–59.

– " – 1936. Tutkimuksia Itä-Suomen kuusi–harmaaleppä–sekametsiköiden kehityksestä. Referat: Untersuchungen über die Entwicklung der Fichten–Weisserlen–Mischbestände in Ostfinnland. Acta For. Fenn. 44 (2):1–198.

KELLOMÄKI, S., HARI, P., HOLM, J. and SALMINEN, R. 1979. Application of hemispheral photographs for estimating photosynthetic production in a plant stand. In: Understanding and predicting tree growth. (ed. S. Linder). Swedish Coniferous Project. Tech. Report 25:41–43.

KELLOMÄKI, S., VÄISÄNEN, E., KAUPPI, P. & HARI, P. 1977. Production of structural matter by a plant community in successional environment. Seloste: Kasviyhdyskunnan kuiva-ainetuotos valaistukseltaan muuttuvassa ympäristössä. Silva Fenn. 11(4):276–283.

KOZLOWSKI, T. T. and KELLE, T. 1966. Food relations of woody plants. Bot. Rew. 32:293–382.

KUROIWA, S. 1960 a. Ecological and physiological studies on the vegetation of Mt. Shimagare. IV. Some physiological functions concerning matter production in young *Abies* trees. Bot. Mag. Tokyo. 73:133–141.

– " – 1960 b. Ecological and physiological studies on the vegetation of Mt. Shimagare. V. Intraspecific competition and productivity difference among tree classes in the *Abies* stand. Bot. Mag. Tokyo. 73: 165–174.

– " – 1970. Total photosynthesis of a foliage in relation to inclination of leaves. In: Prediction and measurement of photosynthetic productivity (Ed. by I. Šetlik), pp. 79–89. Centre for Agricultural Publishing & Documentation. Wageningen.

LARCHER, W. 1975. Physiological plant ecology. Springer-Verlag. Berlin, Heidelberg, New York. 252 pp.

LOACH, K. 1973. Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. 66:607–621.

MADGWICK, H. A. I. and BRUMFIELD, G. L. 1969. The use of hemispheral photographs to assess light climate in the forest. J. Ecol. 57:537–542.

MIKOLA, P. 1966. Alikasvosten merkitys metsien uudistamisessa. Summary: Significance of the undergrowth in reforestation. Metsätaloudellinen aikakausilehti 83 (1): 4–7.

MITSCHERLICH, G., KÜNSTLE, E. and LANG, W. 1967. Ein Beitrag zur Frage der Beleuchtunsstärke im Bestande. Allg. Forst-u. Jagdztg. 138:213–223.

NEWBOULD, P. J. 1967. Methods for estimating the primary production of forests. IBP Handbook 2. Blackwell Scient. Publ. Oxford, Edinburgh.

NILSON, T. 1977. Teoriya propuckaniya radiatsii neodnoronym pokrovom. Summary: A theory of radiation penetration into non-homogeneous plant canopies. In: Propuckaiya solnetsnoi radiatsii rastielnym pokrovom. pp. 5–70. Acad. Sci. Estonian SSR, Inst. Astrophys. and Phys. Atmosph. Tartu. 145 pp.

–"– and ROSS, V. 1979. Characterization of the transparency of a forest canopy by Fish-eye photographs. Estonian IBP Report 12:117–136.

–"– ROSS, V. and ROSS, J. 1977. Nekotorye voprosy arhitektoniki rastenii i rastitelnogo pokrova. Summary: Some problems on the architecture of plants and plant canopies. In: Propuckaiya solnetsnoi radiatsii rastielnym pokrovom. pp. 71–144. Acad. Sci Estonian SSR, Inst. Astrophys. and Phys. Atmosph. Tartu. 145 p.

ONDOK, J. P. 1977. Regime of global and photosynthetically active radiation in helophyte stands. Studie CSAV 10. – Academia. Praha. 112 p.

PÖNTYNEN, E. 1929. Tutkimuksia kuusen esiintymisestä alikasvoksina Raja-Karjalan valtion mailla. Referat: Untersuchungen über das Vorkommen der Fichte (*Picea excelsa*) als Unterwuchs in den finnischen Staatswäldern von Grenz-Karelien. Acta For. Fenn. 35 (1):1–235.

SIRÉN, G. 1949. Alikasvoskuusten biologiaa. Summary: On the biology of undergrown spruce. Acta For. Fenn. 58 (3):1–90.

THORNLEY, J. H. M. 1977. Modelling as a tool in plant physiological research. In: Environmental effects on crop physiology (eds. Landsberg, J. J. and Cutting, C. U.), pp. 339–350. Academic Press. London, New York, San Francisco. 388 pp.

TOOMING, H. 1970. Mathematical description of net photosynthesis and adaptation processes in the photosynthetic apparatus of plant communites. In: Prediction and measurement of photosynthetic productivity. Proc. IBP/PP technical meeting. Trebon. 1969. (ed. Šetlik), pp. 103–113. Centre for Agricultural Publishing & Cocumentation. Wageningen.

TSEL'NIKER, Y. L. 1979. Resistance to CO_2 uptake at light saturation in forest tree seedlings of different adaptation to shade. Photosynthetica 13 (2):124–129.

TUCKER, G. F. and EMMINGHAM, W. H. 1977. Morphological changes in leaves of residual western hamlock after clear and shelterwood cutting. For. Sci. 23 (2):195–203.

SELOSTE:

VARJOSTUKSEN VAIKUTUS ALIKASVOSKUUSIEN LATVUKSEN RAKENTEESEEN JA RANGAN KASVUUN

Työssä on tutkittu alikasvoskuusien (*Picea abies* (L.) Karst.) latvuksen rakenteen ja rangan kasvun suhdetta päällyspuuston alla vallitseviin valaistusolosuhteisiin sekä tämän perusteella laskettuun fotosynteesiin. Varjostus vähensi sekä oksien että rangan kasvua, jälkimmäistä kuitenkin selvästi voimakkaammin. Tämän vuoksi varjostus johtaa pitkähkönä aikavälinä muodoltaan litistyneeseen, sateenvarjomaiseen latvusrakenteeseen, joka on tunnetusti ominainen heikoissa valaistusolosuhteissa kasvaneille kuusille. Tällaisissa olosuhteissa neulaset asettuivat lähes vaakatasoon ja ne olivat ohuempia ja leveämpiä kuin hyvissä valaistusolosuhteissa kasvaneet neulaset. Sädekasvun ja pituuskasvun suuruus olivat lähes suoraviivaisesti riippuvia vallitsevista valaistusolosuhteista. Koska päällyspuuston pohjapinta-alan ja päällyspuuston alla vallitsevien säteilyolosuhteiden välillä vallitsi kiinteä riippuvuus, voidaan alikasvoskuusien kasvu suhteuttaa myös päällyspuuston pohjapinta-alaan.