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ON DISTRIBUTION OF GROWTH IN CROWN SYSTEM OF SOME YOUNG SCOTS PINE STANDS

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SELOSTE:

KASVUN JAKAUTUMISESTA NUORTEN MÄNTYKASVUSTOJEN LATVUSTOISSA

Branching and terminal growth of lateral shoots and needle growth of Scots pine *(Pinus sylvestris* L.) are investigated as a function of the position and age of the whorls and the prevailing light conditions. Number of buds per whorl was linearly and positively related to the whorl's position and the prevailing light conditions. An increasing whorl number, counting from the apex, was associated with a decrease in bud number. The terminal growth of the lateral shoots increased exponentially as a function of the whorl's position. In turn an increasing whorl number implied a curvilinear decrease in shoot growth, respectively, and only negligible growth occured when the whorl's age exceeded 10 years. The shoot growth was linearly related to the prevailing light conditions but differences between dominating and dominated threes were apparent. The distribution of needle growth in the crown system was similar to that of shoot growth.

INTRODUCTION

FARMER (1976) distinguishes three factors contributing to the wood producing capacity of deciduous trees: (1) net assimilation rate per unit leaf area; (2) canopy architecture; and (3) investment of photosynthates in different growth components, *i.e.* shoot growth, root growth and growth of crown system. The growth components are related to the assimilation rate and canopy architecture through source — sink relations which control plant growth and development. FARMER (1976) gives special emphasis to the individual tree variation in crown efficiency in contributing to the variation in the yield of hardwoods.

The canopy architecture is also of importance in the wood production of conifers (cf. for example MATTHEWS 1963). According to JAHNKE and LAWRENCE (1965), a vertically extended crown system has a higher light interception capacity than a horizontally arranged crown system. Also the horizontal arrangement of the needles, their optical properties etc. have an effect on the light absorption properties of coniferous canopies (cf. SAEKI 1963).

According to WAREING (1966), the size and shape of the canopy system of an individual tree is determined by (1) the number of growing points in the shoot system; (2) by the rate of leaf growth and (3) by the size, shape and arrangement of the leaves. FARMER (1976) assumes that these factors are fundamentally related to the degree to which photosynthates are reinvested in new shoot and leaf growth.

On the other hand, the amount of photosynthates reinvested in the growth of the shoot system is dependent on the total amount of photosynthates available for growth (cf. BATE and CANVIN 1971, EAGLES 1974). Branching of the shoot system and leaf production are assumed to be related to the amount of photosynthates available, as determined by environmental factors in different parts of the crown system (cf. LEDIG 1976). We assume, as argued by HORN (1971), that the reduction in light plays the main role in controlling the branching and leaf production in the crown system (cf. also MADGWICK 1968, BRUNIG 1976).

The aim of this paper is to describe the growth characteristics of the crown systems of young Scots pine *(Pinus sylvestris* L.) stands. The main emphasis is set on the growth and branching of lateral shoots and needle growth as a function of a whorl's position and age. The explanatory power of these factors is compared with the total estimated CO_2 accumulation in different layers of the crown system in order to investigate their functional significance.

MATERIAL AND METHODS

Stands

Three young Scots pine stands were selected for the study. The stands are located in Central Finland in the vicinity of the Forest Field Station of the University of Helsinki (60° 24′ N, 20° 20′ E, 150 m a.s.l.). They represent the *Myrtillus* and *Vaccinium* site types with underlying sandy soil. All the stands were artificially regenerated about 20—30 years. The stands had been thinned and invading deciduous tree species eliminated as in normally managed seedling stands. The characteristics of the stands are described in Table 1. Light measurements and sampling were carried out in the stand during July and August, 1977 and 1978.

Light measurements

Measurement principles

The aim of the light measurements was to approximate the amount of photosynthetic production available for needle and shoot growth in different parts of the crown system. Light intensity varies within the canopy system and it generates spatial and temporal variation in the photosynthetic rate. Let p(x, t) denote the photosynthetic rate (at the point x and the moment t).

If the variation in the photosynthetic rate is generated by variation in light, then

$$p(x, t) = p\,(l\,(x, t)), \quad (1)$$

where l (x, t) is the light intensity at the point x and the moment t. Within the chosen period $[t_o, t_1]$ the accumulation of photosynthetic production per unit leaf area is obtained as an integral of the photosynthetic rate

$$P\,(t_1) - P\,(t_o) = \int_{t_o}^{t_1} p\,(l\,(x, t)\,)\,dt, \quad (2)$$

where $P\,(t_1)$ and $P\,(t_o)$ are the amount of accumulated photosynthetic products by the moments t_o and t_1. Since the response of photosynthetic rate to the light intensity is curvilinear, the light intensity measurements cannot be directly utilized in the integration. A transformation must be carried out as argued by MCCREE (1965). The transformation was carried out by introducing the curvilinear response of the photosynthetic rate to light intensity into the measuring procedure as described by HARI *et al.* (1976). The applied measuring system is described in detail by KELLOMÄKI *et al.* (1979).

Measuring procedure

For the light measurements the crown system of each stand was divided into eight layers. One sensor unit of the measuring system was installed in each layer including the layer above the crown system. The sensor units were mounted on a pole erected at a chosen point in the sample area. The light conditions in each layer were monitored for five days in each stand. The measuring system was read twice a day, at 08.00 a.m. and 05.00 p.m.

Estimating amount of carbon product available for growth in the crown system

The concept of the photosynthetic light ratio PLR, is introduced in order to estimate the amount of carbon products produced for growth in each layer of the canopy system. It is defined as the ratio between the amount of CO_2 fixed in a particular layer x_i ($i = 0, 1, 2, 3, 4, 5, 6, 7, 8$) and the reference environment. It can be approximated as follows (Kellomäki 1977)

$$(3)\quad PLR(x_i) = \frac{\int_{t_o}^{t_1} p\,(l\,(x_i,\,t)\,)\,dt}{\int_{t_o}^{t_1} p\,(l\,(x_o,\,t))\,dt},$$

where x_o is the layer above the canopy where there is no shading. Thus, the ratio, PLR, indicates the amount of photosynthetic products available for growth in a particular layer during the period $[t_o, t_l]$ compared with the situation above the canopy. This index should be related to the growth characteristics of the crown system as assumed above (cf. Emmingham and Waring 1977).

Phytometric measurements

Twenty trees closest to the light measuring tower were sampled. In the first step the height and diameter at breast height (1.3 m above the soil level) of each tree were measured. Secondly, five to fifteen sample trees were selected from each sample area as presented in Table 1. The sample trees were selected so as to represent the height distribution of the stands. In addition, the tallest and the shortest stand member were included in the material. Trees with two leaders or other abnormalities were ommitted in the sampling.

In the third step, the sample trees were measured in detail in the laboratory. The following characteristics of the crown system of each sample tree were determined: length of the leader of the lateral shoot of the medium length in each whorl, the weight of needles in each whorl divided into four age categories (current, one-year-old, two-year-old and three-year-old) and the height of the whorl above the cutting level. The dry weight of the needles was obtained after drying for 24 hours at 105° C.

Table 1. Main characteristics of the study areas.

Stand	Site type	Stand[1]) age, yr	Stand density stems/ha	Mean diameter cm	Mean height m	Number of sample trees	Additional information
9	VT	20	6 300	6.7	6.8	12	Sown, on fine sand
12	MT	23	4 500	10.9	9.9	5	Planted
13	MT	23	7 000	6.8	7.5	5	»

[1]) Age at 1. 3 m above soil level

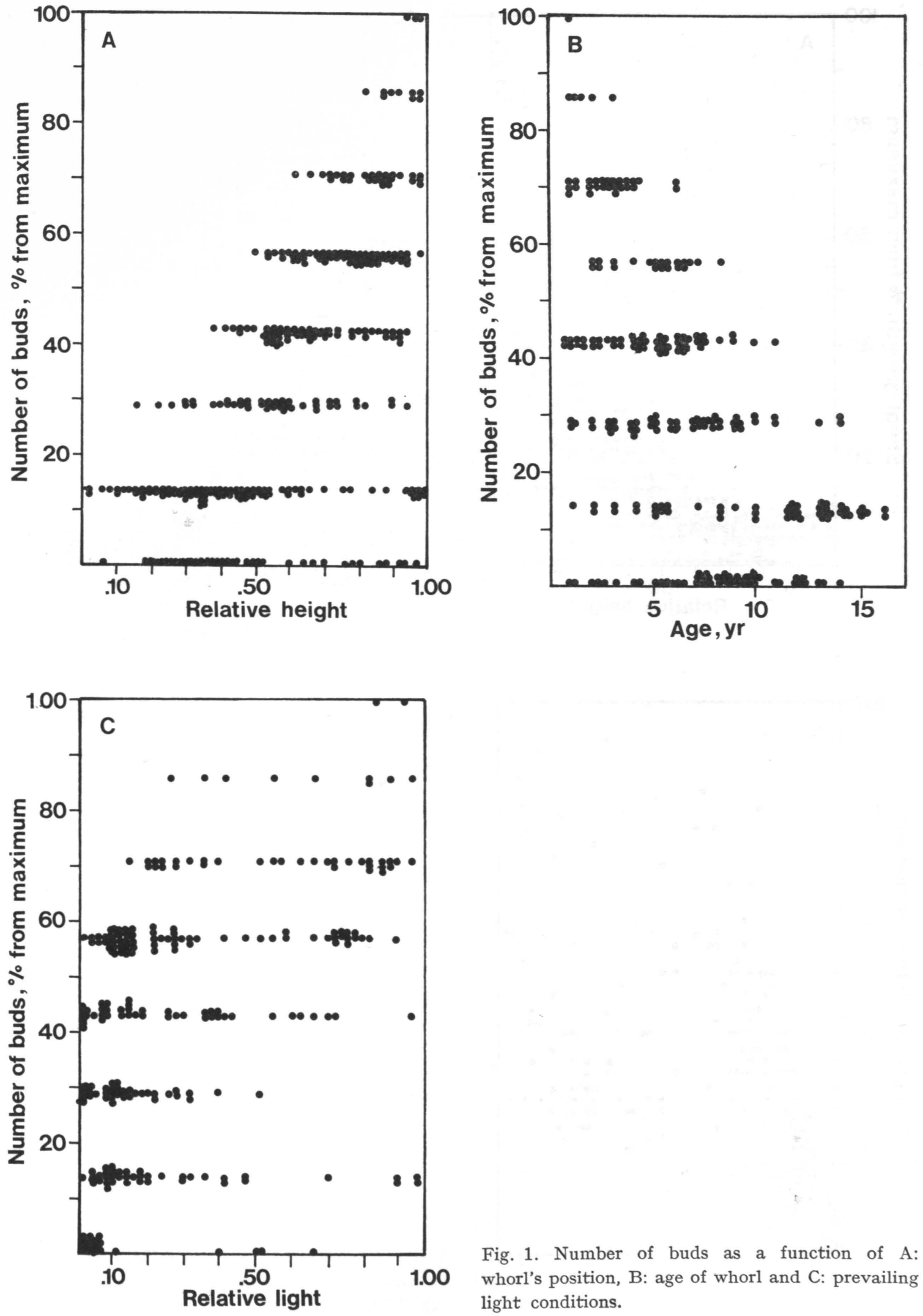
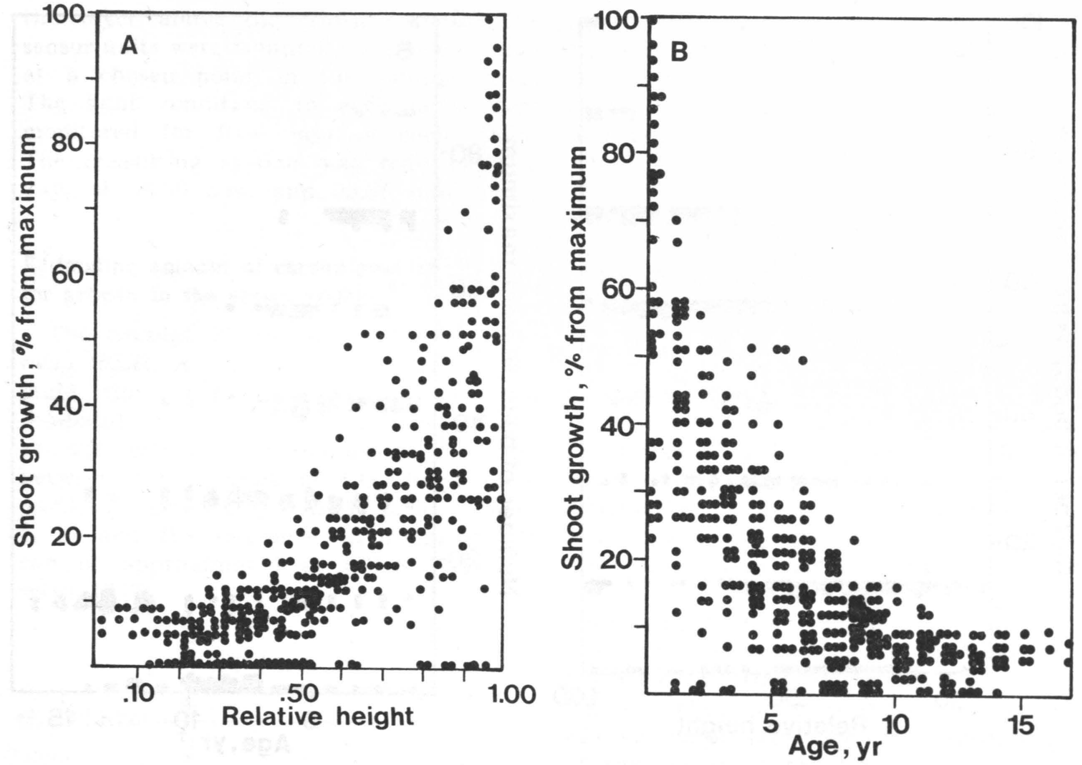


Fig. 1. Number of buds as a function of A: whorl's position, B: age of whorl and C: prevailing light conditions.



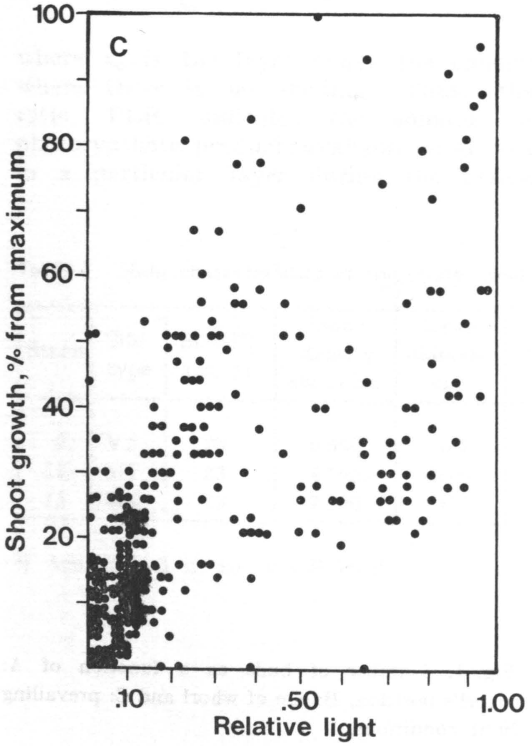


Fig. 2. Growth of lateral shoots as a function of A: whorl's position, B: age of whorl and C: prevailing light conditions.

Branching of lateral shoots

Branching of lateral shoots is presented in Fig. 1a as a function of relative height, *i.e.* the height of the whorl in relation to the total height of the sample tree. The number of buds in the current shoots reaches a maximum at the relative height of 1.0 – 0.9 of the stem *i.e.* at the first and second whorls from the apex (cf. Fig. 1b). The bud number per shoot also seems to be linearly correlated with the photosynthetic light ratio, and bud number decreases according to declining values of photosynthetic light ratio (Fif. 1c). The branching is negligible in the lowest whorls and it ceases at a photosynthetic light ratio value between .20 and .25.

Terminal growth of lateral shoots

Terminal growth of lateral shoots is presented in Fig. 2a as a function of relative height. The growth is the greatest at the height 0.8 – 1.0, *i.e.* in the current whorl and the whorls just above the closed canopy. The growth as a function of whorl age follows the same pattern (Fig. 2b). The growth increases, however, exponentially within the values 0.6 – 1.0. Growth lower down in the crown is negligible. On the other hand, an increasing whorl age implies a curvilinear decrease in shoot growth, respectively. The growth was negligible in shoots older than 10 years.

Considerable variation was found as

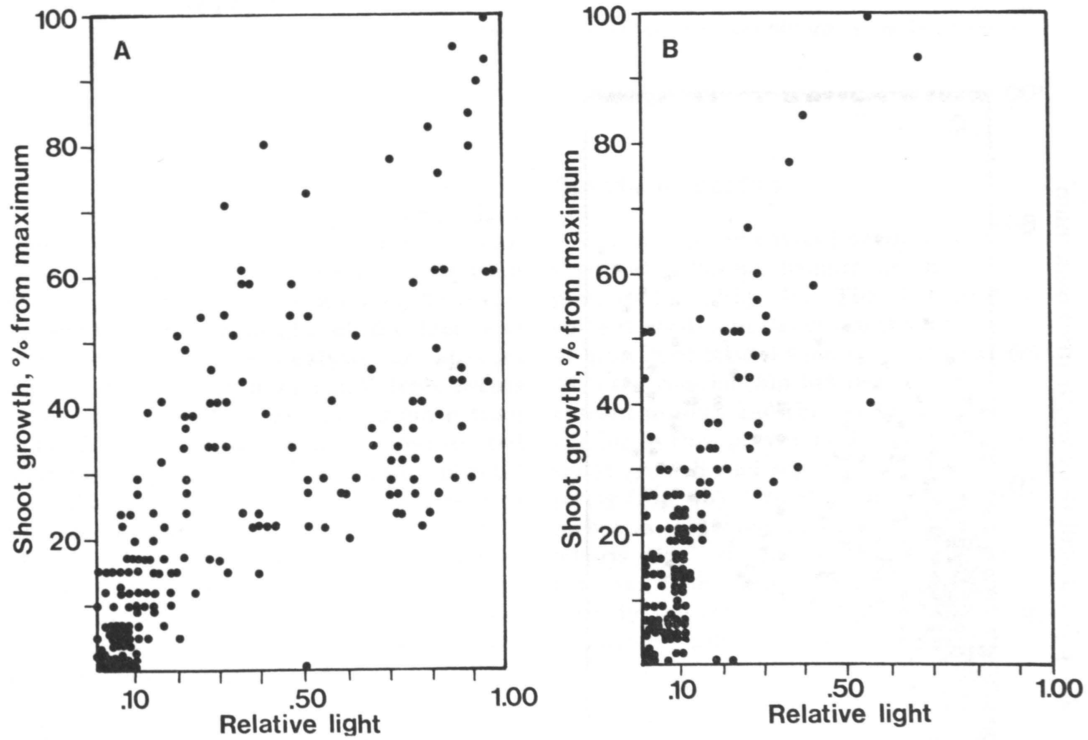
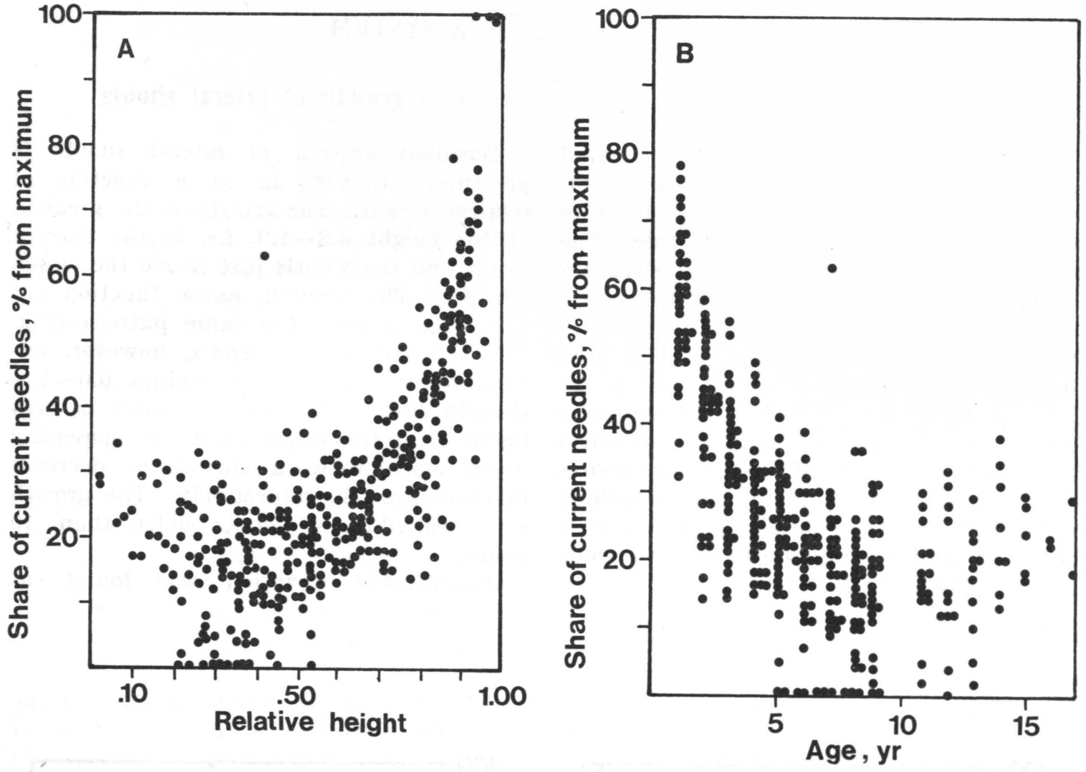


Fig. 3. Growth of lateral shoots as a function of prevailing light conditions A:in large trees and B: in small trees.



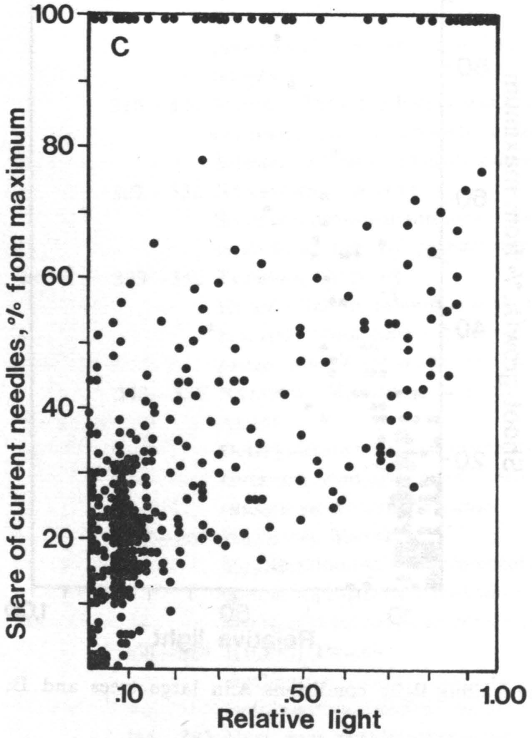


Fig. 4. Amount of current needles as a function of A: whorl's position, B: age of whorl and C: prevailing light condition.

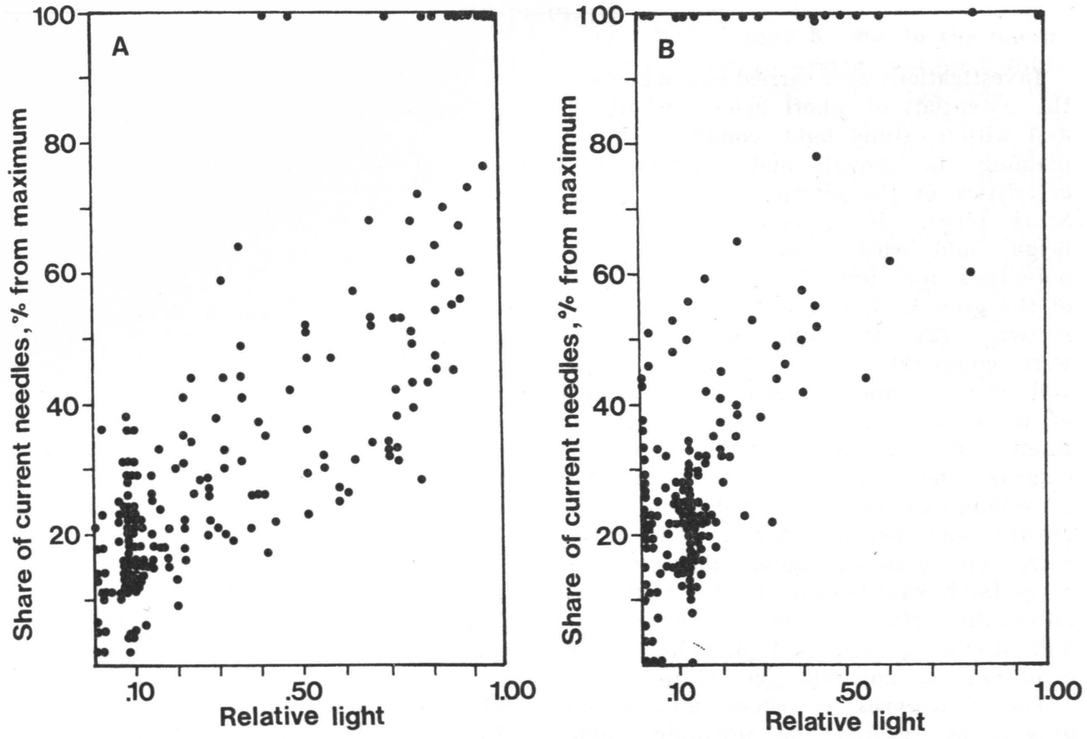


Fig. 5. Amount of current needles as a function of prevailing light conditions A: in large trees and B: in small trees.

regards the relationship between lateral shoot growth and the prevailing light conditions (Fig. 2c). In the case of small trees, especially, the linear correlation between these characteristics was, however, detected when the height of the tree was introduced into the analysis as appears from Fig. 3. Growth in small trees seems to be more sensitive to light climate than in large trees. This difference is interpretated as indicating the amount of photosynthates available for growth and the adaptation of the stand members to the prevailing situation. There are significant differences between the potential of the whorl's position and age and light climate for describing the distribution of shoot growth in the crown system.

Growth of needles

The amount of current needles per current shoot at different heights in the crown is presented in Fig. 4a. The distribution of current needles in the crown is similar to that of growth of lateral shoots, as was expected. Also the relationship between the amount of current needles and the age of the whorl was similar to that prevailing between the lateral shoot growth and age of the whorl, respectively (Fig. 4b). The share of current needles increases, however, in the oldest and lowest whorls due to the increased fall of old needles. The share of current needles was linearly related to the prevailing light conditions but considerable variation occured as a result of the height of the sample tree (Fig. 4c and 5). The differences were similar to that in lateral shoot growth.

DISCUSSION

Investigations were carried out to evaluate the potentials of whorl height, whorl age and within–stand light conditions in explaining the growth and biomass characteristics of the crown system of young Scots pines. It appeared that relative height and whorl number have similar potentials for describing the distribution of the growth characteristics of the crown system. The prevailing light conditions were comparable to the relative height and whorl number as regards the number of buds per whorl. Differences between small and large trees were apparent as regards the relationship between the prevailing light conditions and lateral shoot growth and needle growth. The linear regression between these characteristics suggests, however, that the functional relationship between lateral shoot growth and needle growth and prevailing light conditions is apparent (cf. HORN 1971).

The differences in shoot and needle growth as regards the prevailing light conditions are assumed to indicate the current supply of photosynthates available for growth and adaptation to the environmental conditions. As a result of adaptation the growth capacity of the stand member is maximized through functional and anatomical changes in photosynthetic vigour. For example, the ratio between the surface area and biomass of individual needles decreases according to decreasing light intensity. There are also structural and functional differences between light and shade leaves in response to the prevailing light conditions (cf. BJÖRKMAN 1971). Their ecological significance is poorly understood but they apparently increase the utilization of the amount of light available for growth (cf. DAUBENMIRE 1974, p. 217, KORPILAHTI and HARI 1978) as indicated by the present material. Additional studies are, however, needed to verify this assumption.

The role of one-year-old needles was the greatest in the upper part of the crown system, *i.e.* photosynthetically efficient needles are located in the most favourable light conditions (cf. for example KÜNSTLE and MITSCHERLICH 1975). On the other hand, the three- and four-year-old needles represented the major share of the needle biomass in the lower part of the crown system. Their photosynthetis rate is lower than that of the young needles, and their photosynthetic capacity remains low owing to the low photosynthetic rate and small needle biomass. HORN (1971) suggests that the decrease in length growth of lateral shoots in the bottom of the crown system is caused by the small supply of photosynthates, as indicated also by the results of this study. GRIER and RUNNING (1977) have, however, suggested that the actual leaf area of trees is a compromise between maximum photosynthesis and minimum transpiration. Therefore, the self-pruning of stems may also be affected by water supply and not only by the maximizing capacity through the leaf area.

The characteristic growth pattern of the crown system for each tree species is demonstrated under an unlimited supply of light, water and nutrients (cf. FARMER 1976). Competition for the growth factors modifies the canopy architecture. In limited light conditions the development of the crown system seems to be regulated by maximization of the photosynthetic production (GRIER and RUNNING 1977), *i.e.* the canopy architecture does not limit efficient light interception (cf. JAHNKE and LAWRRNCE 1965). In Scots pine the growth characteristics of the crown system seem to be related to the light conditions and the growth strategy seems to favour unobscured illumination of needles. Therefore the branching of the crown system decreases in reducing light intensity and most of the needle biomass and needle growth in dominated trees are located in the upper part of the crown system (cf. also MADGWICK 1968). Maximal needle biomass and needle growth occur within the area where crown closure takes place, *i.e.* within the area of maximum photosynthetic capacity. The percentage increase in needle biomass was highest in the upper part of the crown system as expected.

Self-pruning of the stem occured at a height of 0.15–0.20 *i.e.* at the 15th and 16th whorl from the apex. In terms of the prevailing light conditions it took place when the photosynthetic supply was about 20 percent of that above the canopy. In the lowest and oldest whorls the share of current needles increased, compared with the middle part of the crown. The high proportion of current needles in the lowest whorls may delay self-pruning due to their high photosynthetic efficiency. More comprehensive studies are, however, needed to verify this assumption.

The variation in each growth characteristic was quite poorly explained by crown characteristics and the light climate within the crown. The poor explaining power of these factors may be due to the microvariation in crown system not predictable by the chosen factors. For example, the homogenity of the crown system is not apparently as high as assumed in light measurements. Consequently, the variation in light climate important in growth processes has been ommitted in measuring procedure. Also the location of whorl and the age of whorl are too rough factors to indicate this kind of variation. Therefore a need of more sophisticated crown models is apparent for the studies of community production.

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