

SPECIFIC NEEDLE AREA OF SCOTS PINE AND ITS DEPENDENCE ON LIGHT CONDITIONS INSIDE THE CANOPY

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SELOSTE:

MÄNNYN NEULASTEN OMINAISPIINTA-ALA JA SEN RIIPPUVUUS KASVUYMPÄRISTÖN VALAISTUS-SUHTEISTA

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The specific needle area of young Scots pines (*Pinus sylvestris* L.) showed a substantial within-tree and between-tree variation which was associated with the position of the tree and the position of the whorl as indicated by the prevailing crown and branch illumination. In suppressed trees the values of the specific needle area were three to four times greater than those in dominating trees. A similar morphogenesis was discernible in comparison of the lower and the upper part of the crown. The mean specific needle area value for the whole stand was 184 cm² g⁻¹.

INTRODUCTION

Plants adapt to the actual environment through several physiological and morphological changes in function and structure. At the physiological level, changes in light compensation, for example, have frequently been found as a response to variations in the light regime (cf. for example LIETH and ASHTON 1961, BJÖRKMAN and HOLMGREN 1963, BJÖRKMAN 1970). Other changes in the characteristics of the photosynthetic response to the growing environment have also been documented (cf. for example JARVIS 1964).

At the morphological level the attention is drawn especially to the changes in specific leaf area, i.e., leaf area per leaf biomass. For example, GHOLZ (1978) found that the decrease in the specific leaf area of *Rhododendron macrophyllum* is associated with

increasing illumination of the growing site. The same phenomenon has been documented by DEL RIO and BERG (1979) for Douglas fir (*Pseudotsuga menziesii*). Such morphogenesis in the characteristics of the foliage may prove to be of importance in the successional power of different plant species and to be one of the determinates of the succession of plant stands. Therefore, they may also be important for silvicultural decisions, for example, regarding thinning and fertilization.

The aim of the present work was to study the specific needle area of Scots pine (*Pinus sylvestris* L.). The specific needle area was studied in relation to the light regime of the growing habitat. The within-tree and between-tree variation in light regime was taken into account.

MATERIAL AND METHODS

Description of the study area

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

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

The stand was sown in 1961 on prescribed burnt ground. It had undergone the thinning and elimination of invading deciduous trees such as *Betula* species. However, scatter undergrowth of deciduous trees and Norway spruce (*Picea abies*) were still present in the study area. Their role in stand dynamics is negligible due to suppression by the dominating pines.

The main characteristics of the pine-dominated tree stratum are given in Table 1. The stand density of 3200 stems per hectare exceeded somewhat the recommended density for commercial forests. The mean height of the stand was 3,8 m. The pattern of the stand was not fully regular due to the stoniness of the soil, but an east-west orientation of sowing rows was discernible.

Sampling of the study area

A sample area 10 × 10 m in size was chosen as the first step of the phytometric measure-

ments. The diameter distribution of the trees at a height of 1,3 m above ground level was determined in the first phase of the sampling. The distribution was determined to the accuracy of one centimeter. In the sampling the minimum number of sample trees was one for each diameter class. Trees with two leaders or other abnormalities were omitted in the sampling.

Light measurements

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

Phytometric measurements

The sample trees were cut 5 cm above ground level and sent to the laboratory for further analysis. Several characteristics were determined from each sample tree, but only the following were utilized in the present analysis: tree height, diameter at 1,3 m above ground level, position of each whorl and number of branches in each whorl.

The analysis of the sample branch was as follows. In the first phase, the needle biomass divided into four age classes was determined to an accuracy of one gram.

Table 1. Some main characteristics of the study area.

Characteristic	Value
Density	3200 stem/ha
Mean height	3,81 ± 0,99 m
Mean diameter at 1,3 m above ground level	6,28 ± 2,68 cm
Mean diameter of the crown of pines	156,31 ± 54,76 cm

At the same time, five needles from the middle part of the current-year shoot of the branch main axis were taken as the sample for needle area measurements, *i.e.*, from the area representing the light measurement.

The length, width and thickness of each needle were measured. The last two measurements represent the maximum values of each needle area measurements, *i.e.*, from the area representing the light measurement. It was determined that the needle cross-section is a half ellipse. The needle dry weight was determined to an accuracy of 10^{-3} g after 24 h drying at 105°C .

Computations

The amount of total radiation and its division into direct and diffuse radiation in $\text{MJ m}^{-2} \text{day}^{-1}$ was computed from the hemispherical photographs as follows

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

where $I(t, x_i)$ denotes the total solar radiation at point x_i and moment t , $I_s(t, x_i)$ the direct radiation and $I_d(t, x_i)$ the diffuse radiation. The value of i varies within the range $i = 0, 1, \dots, n$, where $i = 0$ denotes the point above the canopy. A detailed description of how to approximate the values of Equation (1) has been given by KELLOMÄKI *et al.* (1980) (see also ANDERSON 1964, 1971).

The light measurements were used in determining the whorl position, p_w , and the tree position, p_{tr} . The former concept is determined from Equation (2).

$$(2) p_{wij} = \frac{\int_{t_1}^{t_2} I(x_{ij}, t) dt}{\int_{t_1}^{t_2} I(x_{0j}, t) dt},$$

where I is light intensity in MJ m^{-2} , t a moment of time, x_{ij} the place of the i :th whorl of the j :th tree ($i = 0, 1, \dots, n$, where $i =$

0 represents the place above the canopy) and t_1 and t_2 the beginning and the end of the integration period. In this study it was one day, June 15.

The concept of tree position is defined as follows

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

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

The light measurements were also used in determining the photosynthetic production, P_{tot} , of each sample branch and sample tree as follows

$$(4) P_{tot}(t_1, t_2) = \delta_{ij} \int_{t_1}^{t_2} p(I(x_{ij}, t)) dt,$$

for a branch and

$$(5) P_{tot}(t_1, t_2) = \sum_{i=1}^n \delta_{ij} \int_{t_1}^{t_2} p(I(x_{ij}, t)) dt,$$

for a tree

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

The specific needle area in terms of $\text{cm}^2 \cdot \text{g}^{-1}$ was determined for each whorl as the mean of five sample needles. This value was further employed in determining the needle area of the current-year needles of the whole whorl and the whole tree. The same value was also applied for other needle age classes. The total number of branches in a whorl was employed in converting the measurements of the sample branch to represent the whorl or the whole tree.

RESULTS

Variation in specific needle area

The within-tree variation of specific needle area in each sample tree is presented in Fig. 1. In most of the trees there was a tendency towards increasing specific needle area in the lower part of the crown. The tendency was

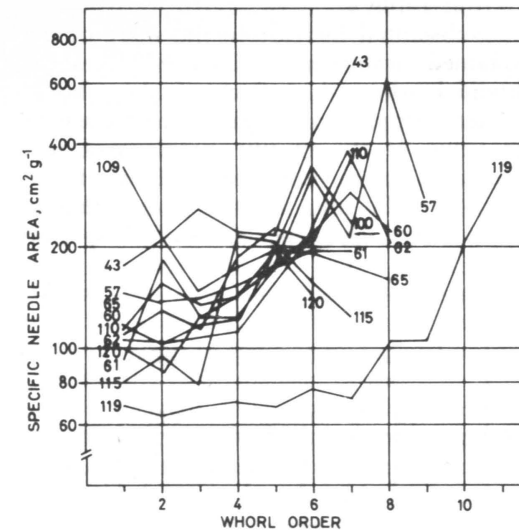


Fig. 1. Whorl-to-whorl variation in specific needle area of the sample trees. Numbers in the Figure are those of the sample trees.

apparent both in small and suppressed trees and in large and dominating trees. It also appeared that in suppressed trees the magnitude of specific needle area was considerably greater than in the dominating trees, *i.e.*, 2–4 fold that in dominating trees. The within-tree variation, however, was considerable, which complicated the interpretation.

Dependence of specific needle area on the within-stand light regime and photosynthetic supply.

The within-tree and between-tree variation in specific needle area correlated fairly well with the depth of the canopy, as appears from Fig. 2. The increase in the specific needle area in the lower crown was emphasized, suggesting that both the whorl position and the tree position affect the specific needle area of a particular branch, *i.e.*

$$(6) NA_{ij} = NA(p_{tr}, p_w),$$

where NA_{ij} is the specific needle area of a branch in the i :th whorl of the j :th tree. Further, these factors are assumed to have a multiplier affect

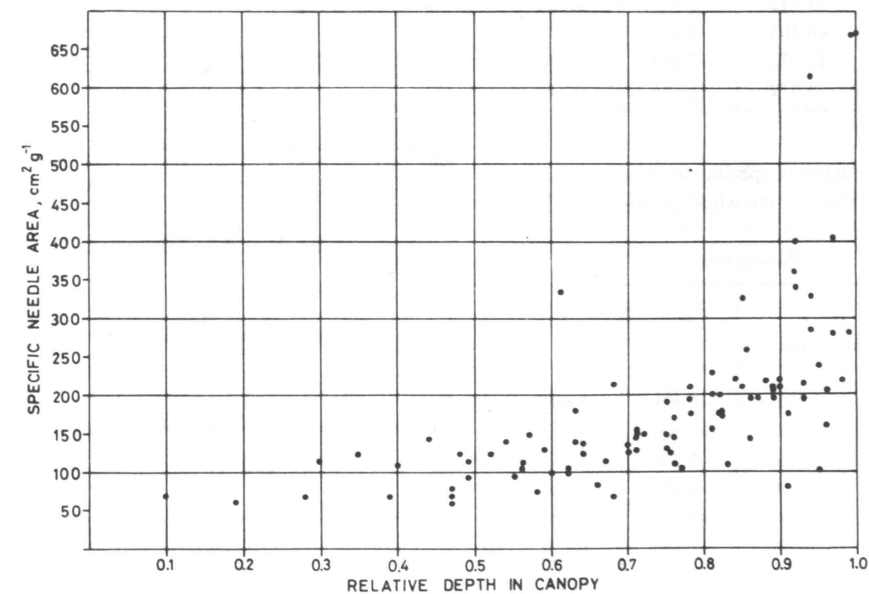


Fig. 2. Specific needle area plotted against the position of the branch in the canopy.

$$(7) NA_{ij} = a \cdot (p_{tr} \cdot p_w)^b,$$

where a is a parameter representing the magnitude of the specific needle area in terms of $\text{cm}^2 \cdot \text{g}^{-1}$ and b the effect of the light regime on the specific needle area. The results of the calculations are given in Table 2.

As expected, the specific needle area increased when the light regime in the branch growing environment deteriorated. There was, however, no whorl-specific regularity in parameter b . This suggests that in each whorl the dependence of specific needle area on the light regime is similar. The same seems to hold for parameter a . Only the correlation coefficients greater than 0,520 were statistically significant ($p < 0,100$) due to the limited number of observations.

Table 2. Dependence of specific needle area on the whorl position.

Whorl order	Parameters		r
	a $\text{cm}^2 \text{g}^{-1}$	b	
1	22.220	-1.735	0.260
2	45.195	-1.290	0.622
3	42.478	-1.320	0.688
4	60.153	-1.038	0.571
5	83.512	-0.833	0.423
6	40.165	-1.782	0.637
7	46.572	-1.664	0.517
8	73.972	-1.175	0.216

Table 3. Dependence of specific needle area per photosynthetic unit (phu) on the whorl position.

Whorl order	Parameters		r
	a' $\text{cm}^2 \text{g}^{-1} \text{phu}^{-1}$	b'	
1	0.224	-7.408	0.692
2	0.498	-4.309	0.811
3	0.086	-5.258	0.768
4	0.0048	-8.005	0.901
5	0.0057	-7.663	0.849
6	0.0066	-7.765	0.722
7	0.0014	-9.434	0.889
8	0.0151	-7.101	0.595

The variation in the specific needle area was only partly explained by the tree position and branch position. This suggests that also other factors than the light regime may affect the variation in specific needle area. Several alternatives were studied and it appeared that the magnitude of the photosynthetic supply also affected the variation in specific needle area. The results of these calculations are given in Table 3.

A substantial increase in the share of the explained variance in specific needle area was obtained when the effect of the photosynthetic supply from a particular branch to the value of the specific needle area was eliminated by dividing the values of the specific needle area by the photosynthetic supply values. The dependence of the specific

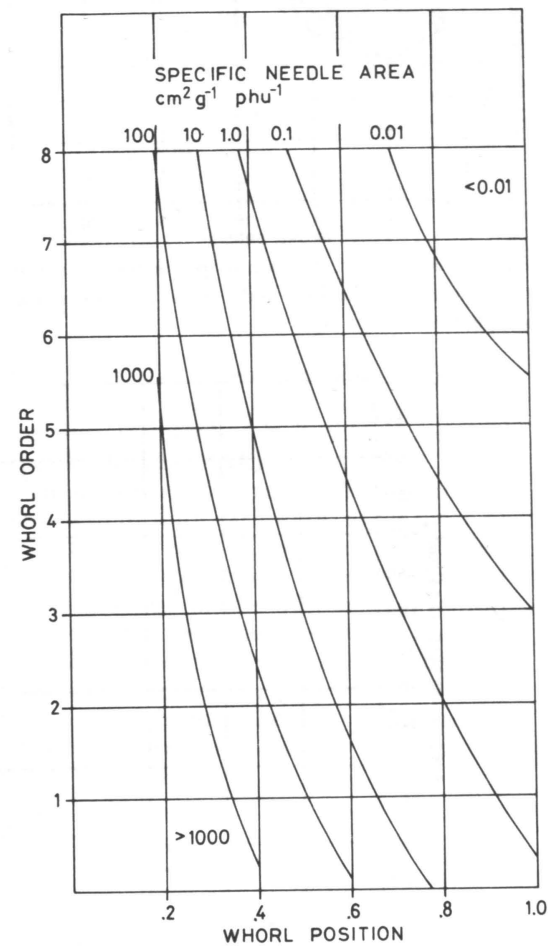


Fig. 3. Specific needle area per photosynthetic unit plotted against whorl position and whorl order.

needle area on the light regime was statistically significant ($p < 0,100$) in each whorl.

It appears that the specific needle area per photosynthetic unit decreases substantially in the lower crown and it is only one hundredth of that in the upper crown. The decrease is not systematic, but the tendency is evident. On the other hand, the dependence of specific needle area on the light regime as indicated by parameter b has no regularity as regards the whorl order. The results suggest that the light regime modifies the specific needle area within the limits set by the magnitude of photosynthetic supply for needle growth.

The effect of the whorl position on specific needle area is demonstrated in Fig. 3, where the specific needle area per photosynthetic unit is plotted against whorl position and whorl order. In interpreting the results one must keep in mind that the computations cover also variation in the tree and whorl position outside the basic material.

As expected, under poor light conditions, the specific needle area per photosynthetic unit exceeded considerably that in good light conditions due to the sensitivity of the specific

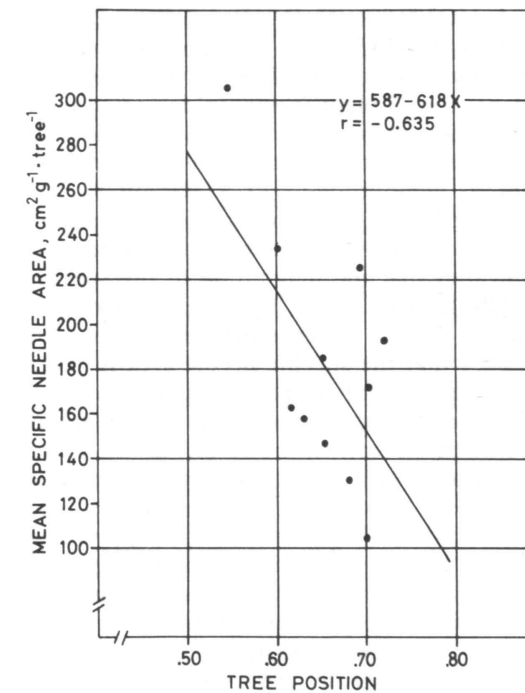


Fig. 4. Mean specific needle area per tree plotted against tree position.

needle area to the prevailing light conditions (cf. Tables 2 and 3). Therefore, the specific needle area in absolute terms is also greater in the lower crown than in the upper crown, although the photosynthate supply in the lower crown is limited (cf. Fig. 2). Thus, the effect of light regime seems to be overwhelming compared with the photosynthetic supply even though the latter factor clearly limits the actual magnitude of the specific needle area.

Implications for growth studies

The implications of the change in specific needle area for growth are evident when the mean needle area of the tree is computed as presented in Fig. 4. It appears that in suppressed trees the mean specific needle area is threefold that in dominating trees. It may

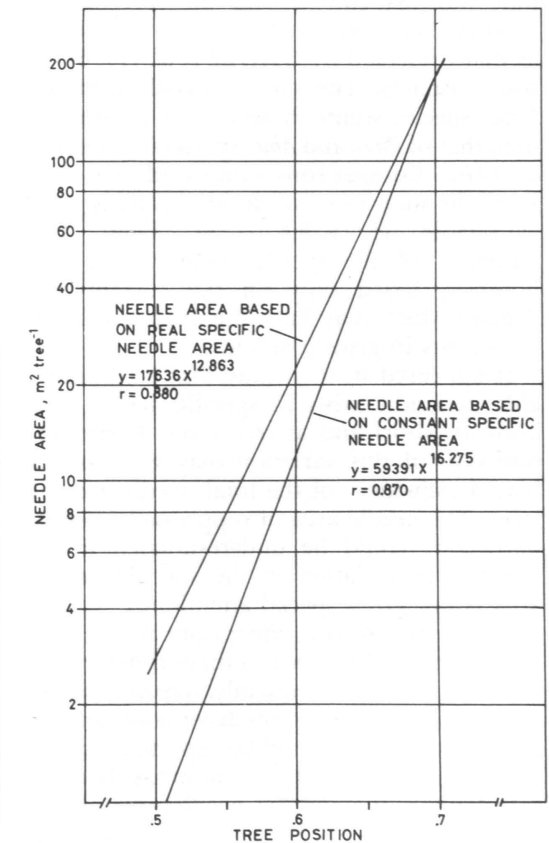


Fig. 5. Estimates of total needle area based on real values of specific needle area and constant value of specific needle area plotted against tree position.

have an important role in growth studies. In Fig. 5 the total needle area values of the sample trees based on the real values of the specific needle area and the constant value of the specific needle area are presented as a function of tree position. The constant value of the specific needle area was that of the biggest sample tree, *i.e.* 112 cm² .g⁻¹. Thus, the calculations represent the maximal differences which may occur depending on the premises. The difference between the estimates of the

total needle area was greatest in the lower crown where the real values of the specific needle area yielded nearly twofold the needle area of that based on the constant value. An improved tree position resulted in decreasing differences between the estimates. Hence, the stratification of the canopy of a tree stand into horizontally different layers results in a considerable increase in the total needle area of the stand compared with the situation in which there is no stratification.

DISCUSSION

The specific needle area of Scots pine (*Pinus sylvestris* L.) was studied in a material representing a stand aged 20 years. The unweighed mean specific needle area of Scots pine was 184 cm² .g⁻¹ for the current-year needles. The value is of the same magnitude as that presented by GHOLZ *et al.* (1976) for some conifers. The specific needle area for *Pinus* species seems, however, to be smaller than that of *Picea* and *Abies* species (GHOLZ *et al.* 1976). Comparisons with deciduous trees show the superiority of deciduous trees, as is expectable (cf. KIRA *et al.* 1969). The estimates of the specific needle area are, however, based only on the current-year needles which may limit the applicability of the results in growth studies.

It appeared in this study that a considerable variation exists in specific needle area both at whorl and at tree level. Therefore, omission of this variation may give rise to biased estimates of the total needle area of trees. The needle area of suppressed trees, in particular, could be underestimated if the tree-to-tree variation in the specific needle area is not given special attention.

In suppressed trees, the specific needle area values were as high as 3–5 times those in dominating trees. Consequently, the total needle areas in suppressed trees have considerably higher values than could be expected only on the basis of the total needle biomass. In these calculations, the specific needle area of the different needle age classes is assumed to be the same as that of the current-year needles. The validity of this assumption cannot be verified from the present material. For further

details of the problems of estimating the total needle areas of coniferous trees see the study by GHOLZ *et al.* (1976).

The variation in the specific needle area was associated with the prevailing light conditions around a particular branch and the illumination of the crown to which the branch belonged. DEL RIO and BERG (1979) found the same in crowns of Douglas fir undergrowth. The increased specific leaf area in herbs was reported earlier by BJÖRKMAN and HOLMGREN (1964), and in *Quercus rubra* by JARVIS (1964) as regards decreasing light intensity (cf. also KIRA *et al.* 1969). The adaptation of plant species to decreased light intensities through increased specific leaf area seems to be common among plant species, as demonstrated by GRIME (1978).

The effect of the photosynthetic supply on the specific needle area was also evident. It appeared that the magnitude of the specific needle area is limited by the photosynthetic supply. In the lower crown especially, this implies that the specific needle area is lower than expected for the prevailing light regime. The role of the prevailing light climate in leaf morphogenesis seems, however, to be more important than that of the photosynthetic supply but the effect of light regime seems to be limited by the photosynthetic supply. The role of genetic factors in leaf morphogenesis is also important, but cannot be evaluated on the basis of the present material.

Only the role of the light regime affecting the specific needle area was studied. For example, GHOLZ (1978) has demonstrated that also temperature and nutrient and water

supply affect the specific needle area (cf. also WOODMAN 1971). This may be valid also for the present material, as the dependence of the specific needle area on the depth of the canopy suggests (cf. Fig. 2). It implies that light measurements describe only partially the characteristics of the growing environment affecting the needles properties. The light measurements themselves present problems. One is synchronizing the light measurements and the phytometric measurements due to the limited area represented by one hemispherical photograph (cf. DUCREY 1975). In this analysis, the same light measurements are also utilized in computing estimates for light regime and photosynthetic production. This complicates the interpretation of the results and special care should be taken as regards causal interpretation.

DEL RIO and BERG (1979) assume that the increased leaf area in shaded conditions

possesses a great strategic value in competition in a plant stand. Apparently, the increased resource capture through increased leaf specific area improves the survival of suppressed trees (cf. GRIME 1978). In light-demanding trees light-induced modifications in the structure and function of the photosynthetic apparatus seems to be common, as demonstrated by GRIME (1978). This is in accordance with the results of the present study, since Scots pine is considered to be a light-demanding tree species in Finnish conditions. This study implies that this is partly based on the growth strategy which yields crown structure allowing substantial penetration of light in the upper crown, but increased capture of light in lower crown. This kind of growth strategy seems to allow sufficient illumination of the whole crown in addition to efficient capture of light resources.

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SELOSTE:

MÄNNYN NEULASTEN OMINAISPINTA-ALA JA SEN RIIPPUVUUS KASVUYMPÄRISTÖN
VALAISTUSSUHTEISTA

Männyn (*Pinus sylvestris* L.) neulasten ominaispinta-ala eli neulasen pinta-alan ja painon suhde ($\text{cm}^2 \cdot \text{g}^{-1}$) vaihtelee puittain sekä puiden latvusten sisällä. Vaihtelu näyttää liittyvän puun latvuksen saaman valaistuksen määrää sekä valaistukseen, jossa neulasen edustama oksa kasvoi. Alistetussa asemassa olevien mäntyjen neulasten

ominaispinta-ala oli nelinkertainen verrattuna vallitsevien puiden neulasten ominaispinta-alaan. Samanlainen muutos havaitaan, kun verrataan puun latvuksen yläosia ja alaosia keskenään. Tutkitussa tapauksessa oli koko metsikölle laskettu neulasten ominaispinta-ala $184 \text{ cm}^2 \cdot \text{g}^{-1}$.