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EFFECT OF NITROGEN FERTILIZATION ON PHOTOSYNTHESIS AND GROWTH IN YOUNG SCOTS PINES – PRELIMINARY RESULTS

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Seloste

ALUSTAVIA TULOKSIA TYPPILANNOITUKSEN VAIKUTUKSESTA NUORTEN MÄNTYJEN FOTOSYNTEESIIN JA KASVUUN

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Application of nitrogen at levels of 200, 400 and 600 kg ha^{-1} resulted in increases of 35, 18 and 12 per cent in the photosynthetic rate in young Scots pines (*Pinus sylvestris* L.) The number of buds, degree of branching, and needle size were positively related to the amount of nitrogen applied. A 10–40 per cent increase in the average needle area was found. A positive correlation was found between total photosynthesis and stem growth.

1. INTRODUCTION

Intensive studies on forest fertilization have been carried out in Finland. The response of stem growth to fertilizers is well documented (cf. Metsänlannoitustutkimuksen ... 1979). Stem growth is, however, determined by several physiological processes in crown system primarily affected by fertilization measures. Helms (1964) reported an increase in the photosynthetic rate and an increased needle area of Douglas fir (*Pseudotsuga menziesii)* as a result of nitrogen fertilization. Keya et al. (1968), Brix and Ebell (1969), Brix (1971, 1972) and Ågren et al. (1977) observed post-fertilization changes in the photosynthesis and crown structure of conifers. Nevertheless, the effect of fertilizers on physiological processes and the crown dynamics of trees is rather poorly understood.

The aim of the present study is to investigate the effect of nitrogen fertilization on the photosynthetic capacity of Scots pine (*Pinus sylvestris* L.). The influence of three levels of nitrogen on the relationship between photosynthetic response to illumination and temperature is studied first. Secondly, the needle mass and dimensions are related to the nitrogen applications. Finally, the effect of fertilization on diameter growth is studied.

The participation of the authors in the study was the following:

Seppo Kellomäki and Carl Johan Westman:	initiation of the study, general lay-out, establishment of the study area and preparation of the manuscript.
Pasi Puttonen:	implementation of the photosynthetic measuring system and supervision of measurements.
Heikki Tamminen:	photosynthetic and phytometric measurements, preliminary manuscript in Finnish.

All the members of the study group contributed to the final compilation of the manuscript.

2. MATERIAL AND METHODS

2.1. Tree stand and sample plots

The experiment was conducted in an 18-year-old Scots pine stand growing on podsolic silty moraine in central Finland (61°55′ N, 24°34′ E, 150 m. a. s. l.). The area was burnt over in 1960 and regenerated by spot sowing in 1961. Deciduous trees were removed mechanically in 1977–78. Four sample plots (15×20 m) laid out in the area, were fertilized on June 6th, 1978, with commercial calcium amonium nitrate (27,5 % N) at the following levels: 0, 200, 400 and 600 N kg ha^{-1}. Treatments of the sample plots were randomised. The stem number at the time of fertilizing was 1650 stems ha^{-1} and the mean height of the stand 4,6 m.

One year after fertilization three sample trees were taken from each plot. At the first phase of the sampling the diameter distribution ($D_{1,3}$) of the tree stand was determined. Separate sampling was then conducted randomly within each third of the diameter distribution. South-facing branches representing the lowest living whorl, the uppermost whorl and the middle crown section of the selected trees were sampled. Branches with dead twigs or other abnormalities were rejected and the nearest branch fulfilling given requirements were used. A total of 12 sample trees and 36 sample branches was measured.

2.2. Measurements

For photosynthetic measurements, sample branches were cut and immersed in water. To ensure an uninterrupted flow of water, a further five to ten centimetres were removed from the submerged end of the branch. The photosynthetic response to light and temperature in one-year-old needles was measured. Current-year needles were removed immediately before inserting the branch in the measuring cuvette.

The photosynthetic rate was monitored for one day in an open system consisting of trap-type cuvettes and an IRGA (Uras 2T) gas analyser (Hari et al. 1979). The light intensity (W m^{-2}) was measured by a pyranometer (model Kipp & Zonen). In addition, the light conditions inside the cuvettes were measured by a system which integrated the light available for photosynthesis during the measurement period (ELP-measurements in arbitrary units) (Hari et al. 1976). Air temperature was measured using thermocouples placed just outside the cuvettes. The measurements were carried out in June, 1979.

After the photosynthetic measurements were completed, the fresh weight of the branch section enclosed in the cuvette was determined to an accuracy of 1 g. The width, length and thickness of needles representing 10 per cent of the corresponding needle mass were determined to an accuracy of 0,01 mm. In calculating needle area, the cross-section of the needles was assumed to be an ellipse. The unit area of the needles per unit needle mass was converted into total area using the total needle mass of the measured branch sample. In addition, the number of needles per length unit, bud number and length of current-year shoots were recorded. The dry weight of the needles in the sample branches was determined after drying at 105°C for 24 h.

The radial growth of the sampled trees was obtained by measuring the annual rings of increment cores to an accuracy of 0,01 mm. The measurements represent the breast height, i.e. 1,3 m above soil surface. The measurements were made in August 1979.

2.3. Computation of photosynthetic response

The photosynthetic response to light and temperature conditions was described by means of regression coefficients for the linear relationship between the photosynthetic rate and the light available for photosynthesis (ELP measurements) in a series of temperature classes as well as for the whole temperature range. The numeric values of the regression coefficients obtained from models forced through origo were related to the amount of nitrogen added.

The relationship between the photosynthetic rate and total radiation were described with the following function:

$$(1) \quad \frac{dP}{dt} = p_{max} \tanh \left(\frac{I - I_C}{I - I_p}\right),$$

where dP/dt is the photosynthetic rate (CO_2 mg dm^{-2} h^{-1}), p_{max} the maximum rate of photosynthesis (CO_2 mg dm^{-2} h^{-1}), I the light intensity (W m^{-2}), I_C the light intensity representing the compensation point (W m^{-2}), I_p the light intensity at which the photosynthetic rate is 75 per cent of the maximum (W m^{-2}) and h a parameter having the value 0,761. The values of p_{max}, and I_p were related to the amount of nitrogen applied.

3. RESULTS

3.1. Gas exchange and nitrogen fertilization

Nitrogen fertilization affected the photosynthetic response to light (ELP-measurements) within each temperature class (Fig. 1). In the class 5–10°C the regression coefficient increased more than 50 per cent for applications of 200 and 600 kg ha^{-1}. In the temperature classes being 10–15°C and 15–20°C, the regression coefficient increased by 20–50 per cent. The change was least in the highest temperature class being in the 10 to 35 per cent range. For the whole temperature range (5–25°C) 200 kg ha^{-1} nitrogen had the greatest influence on the photosynthetic response, i. e., the increase was about 35 per cent for a dosage of 200 kg ha^{-1} of nitrogen and 20 and 10 per cent for dosages of 400 and 600 kg ha^{-1} of nitrogen, respectively. Thus the smallest amount of nitrogen applied seems to have the most favourable effect on the relationship between photosynthesis and light (ELP measurements). The photosynthetic response of fertilized trees to temperature followed the well-documented pattern of Scots pine with an optimum at 15–20°C (Table 1).

The fertilization affected most clearly the properties of the photosynthetic response at the level of 200 kg ha^{-1} of nitrogen, i. e., the value of the parameter p_{max} – the maximum level of net photosynthetic rate in Equation (1) increased more than 40 per cent (Fig. 2). On the other hand, the light intensity for a photosynthetic rate of 75 per cent of the maximum, i. e. the parameter I_p, increased 20, 75 and 50 per cent for the nitrogen dos-

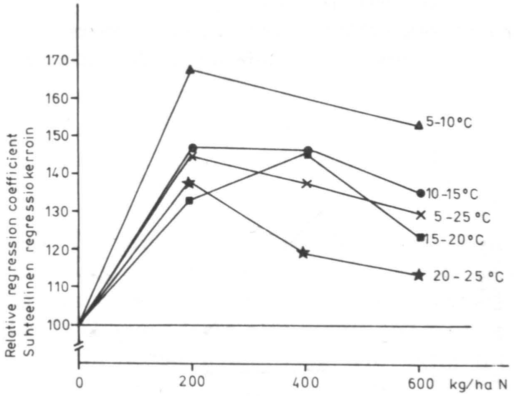

Fig. 1. Regression coeffients (a) between light available for photosynthesis (ELP measurements) and photosynthetic rate (y = ax) per temperature classes in relative terms plotted against the nitrogen application. Unfertilized trees = 100.

Kuva 1. Valon voimakkuuden (ELP-mittaukset) ja neulasten fotosynteesinopeuden välinen regressiokerroin (y = ax) suhteellisena eri lannoituskäsittelyillä lämpötilaluokittain. Lannoittamaton = 100

Table 1. Regression coefficients (x 10^{-2}) for the linear relationship (y = ax) between photosynthetic rate and light available for for photosynthesis (ELP measurements) per temperature classes and nitrogen applications.

Taulukko 1. Kasveille käyttökelpoisen valon voimakkuuden ja neulasten fotosynteesinopeuden väliset regressiokertoimet (x 10^{-2}) lämpötilaluokittain eri lannoituskäsittelyillä (y = ax).

Temperature *Lämpötila*	Fertiliztion, kg ha $^{-1}$ – *Lannoitus, kg ha^{-1}*			
	0	200	500	600
	Regression coefficient (a) – *Regressiokerroin (a)*			
°C	a	a	a	a
5–10	0,1878	0,3163	–	0,2892
10–15	0,2185	0,2920	0,3195	0,2957
15–20	0,2413	0,3538	0,3509	0,2980
20–25	0,2163	0,2926	0,2541	0,2433

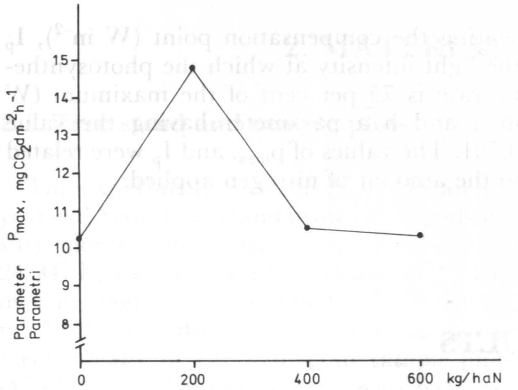

Fig. 2. Maximum photosynthesis relative to light intensity in Equation (1) plotted against the nitrogen application.

Kuva 2. Neulasten maksimifotosynteesinopeus eri lannoituskäsittelyillä laskettuna yhtälön (1) avulla.

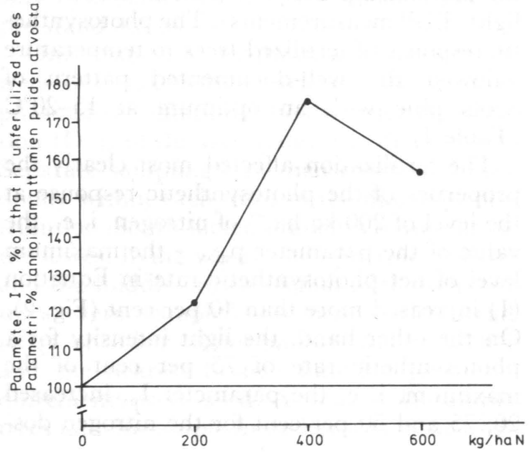

Fig. 3. Relative light intensity resulting in a photosynthetic rate being 75 per cent of maximum (I_p in Eq. 1). Unfertilized trees = 100.

Kuva 3. Suhteellisen valon intensiteetti, jolla fotosynteesinopeus on ¾ osaa maksimistaan laskettuna yhtälön (1) avulla. Lannoittamaton = 100.

ages 200, 400 and 600 kg ha $^{-1}$, respectively (Fig 3). Due to distributional properties of the measurements the parameter I_c, i. e. compensation of photosynthesis in Equation (1), takes negative values and will thus be omitted here. However, it was apparent that in fertilized trees the compensation of photosynthesis was lower than in the unfertilized trees, indicating that net photosynthesis is positive in the fertilized trees at lower light intensities than in unfertilized trees.

3.2. Nitrogen fertilization and growth

3.2.1. Needle dimensions

Nitrogen fertilization also affected the needle area/mass ratio, i. e., the specific needle area, indicating a more succulent structure after nitrogen application (Table 2). The increase in specific needle area varied for the tree crown sections between 5 and 15 per cent. The greatest individual increase, 25 per cent, was recorded in the lowest crown section as a result of 400 kg ha^{-1} of nitrogen. These changes were also associated with increase in needle length (Fig. 4). In the first year the application of 600 kg ha $^{-1}$ of nitrogen gave the greatest increase, but in the second year 200 kg ha^{-1} of nitrogen. Despite these irregularities in the individual needle dimensions, the average needle surface area for a single needle increased about 10–20 per cent, depending on the dosage of nitrogen (Fig. 5). In the second year the growth of the needle area was substantially higher than in the first year.

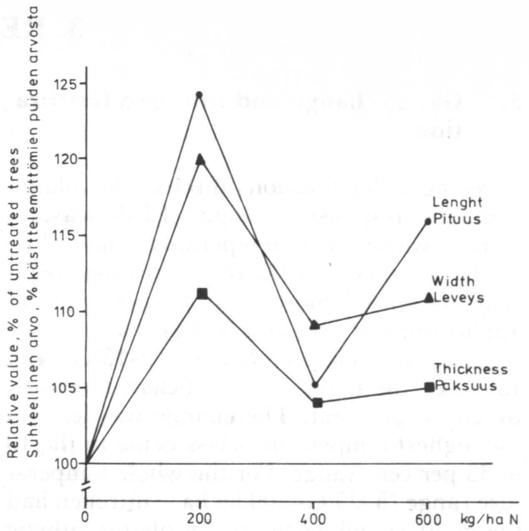

Fig. 4. Relative needle length, width and thickness in the year of fertilizing plotted against the nitrogen application. Unfertilized trees = 100.

Kuva 4. Vuoden 1978 neulasten pituus, leveys ja paksuus suhteellisina arvoina eri lannoutuskäsittelyillä. Lannoittamaton = 100.

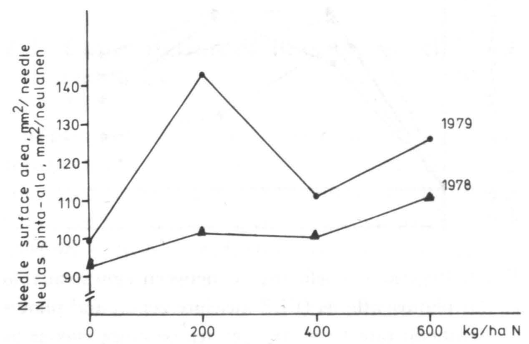

Fig. 5. Average needle area of an individual needle (mm^2) in the year of fertilizing and a year after fertilizing plottet against the nitrogen application.

Kuva 5. Neulasten keskimääräinen pinta-ala (mm^2), vuosina 1978 ja 1979 syntyneissä kasvaimissa eri lannoituskäsittelyillä.

Table 2. Specific needle area (cm^{2}g^{-1}) of the needles formed in the year of fertilization in various sections of the crown per nitrogen application. Unfertilized trees = 100.

Taulukko 2. Vuoden 1978 neulasten pinta-alan ja painon suhde (cm^{2}g^{-1}) eri lannoituskäsittelyillä absoluuttisena ja suhteellisina arvoina. Lannoittamaton = 100.

Branch location *Oksien sijainti puussa*	Fertilization, kg ha^{-1} – *Lannoitus kg ha^{-1}* 0 Absolute *Absol.*	0 Relative *Suht.*	200 Absolute *Absol.*	200 Relative *Suht.*	400 Absolute *Absol.*	400 Relative *Suht.*	600 Absolute *Absol.*	600 Relative *Suht.*
Lower crown *Alaoksat*	62,9	100	68,7	109	78,7	125	65,8	105
Middle crown *Keskioksat*	58,9	100	56,7	96	63,9	108	64,3	109
Upper crown *Yläoksat*	50,4	100	53,1	105	53,6	106	56,4	112
x̄	57,4	100	59,5	104	65,4	114	62,2	108

Table 3. Number of buds on the sampled branches in the year before and two years after the fertilization. Data given in absolute and relative figures, unfertilized trees = 100.

Taulukko 3. Näyteoksien silmujen lukumäärä absoluuttisina ja suhteellisina arvoina eri lannoituskäsittelyillä ennen lannoitusta (1977) sekä kahtena lannoitusta seuranneena vuotena. Lannoittamaton = 100.

Fertilization, kg ha^{-1} *Lannoitus kg ha^{-1}*	Before fertilization *Ennen lannoitusta* (1977) Number/branch *kpl/oksa*	Before fertilization Relative *Suht.*	1978 Bud number – *Silmujen lukumäärä* Number/branch *kpl/oksa*	1978 Relative *Suht.*	1979 Number/branch *kpl/oksa*	1979 Relative *Suht.*
0	2,6	100	3,6	100	3,1	100
200	2,4	95	3,3	104	4,0	129
400	2,3	91	4,1	115	3,4	111
600	2,9	113	3,9	109	3,4	111

3.2.2. Branching of laterals

A faint tendency towards an increasing number of buds was possible (Table 3). There were, however, considerable differences in the number of buds between the different sample plots already before the nitrogen application. Due to this heterogeneity no clear response to nitrogen fertilization in bud formation was detectable.

3.2.3. Stem growth

Nitrogen application increased the radial growth (Fig. 6). On the other hand, elimina-

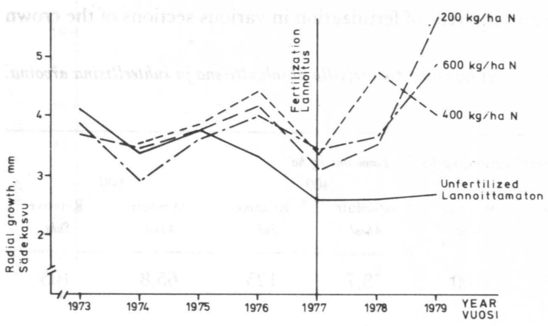

Fig. 6. Radial growth of sample trees 1,3 m above ground level per the nitrogen application in the years 1973–1979.

Kuva 6. Koepuiden sädekasvu rinnankorkeudella eri lannoituskäsittelyillä vuodesta 1973 vuoteen 1979.

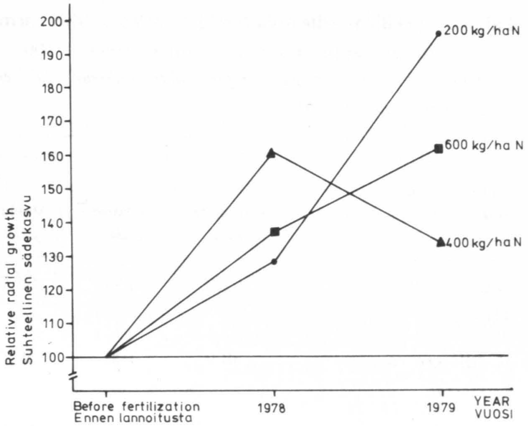

Fig. 7. Relative radial growth of sample tree 1,3 m above ground level per the nitrogen application in the years 1978 and 1979. Radial growth of unfertilized trees and the average growth of fertilized trees during five years before fertilizing = 100.

Kuva 7. Koepuiden suhteellinen sädekasvu eri lannoituskäsittelyillä vuosina 1978 ja 1970. Lannoittamaton ja viiden vuoden keskiarvo ennen lannoitusta = 100.

tion of the deciduous trees prior to fertilization may also have affected growth (see control). In 1978, 400 kg of nitrogen per hectare gave the greatest response (Fig. 7). In the following year, the maximum effect was given by a nitrogen application of 200 kg ha^{-1}, as would be expected from the photosynthetic response measurements. Nitrogen applications of 400 and 600 kg ha^{-1} also clearly increased radial growth. However, the application of 400 kg ha^{-1} gave the weakest effect in 1979.

4. DISCUSSION

In this study it was apparent that the nitrogen fertilization considerably impinged on the photosynthetic response to radiation. The same has been found in several earlier studies as appears from Table 4. The study by Brix and Ebell (1969) showed a smaller response of Douglas fir to nitrogen fertilization than that of Scots pine in our study. In the study by Helms (1964), the response of Douglas fir was smaller than that of Scots pine to the particular nitrogen application in our study. Brix (1971) got, however, a greater response of Douglas fir to a particular nitrogen application. According to Miller and Miller (1976), the nitrogen application of 168 kg ha^{-1} gave the greatest photosynthetic response in *Pinus nigra,* when the nitrogen application was 84, 168, 336, and 504 kg ha^{-1}. These results are in accordance with our study emphasising that the maximum photosynthetic response is obtained, when the nitrogen application is 100 to 200 kg ha^{-1} (cf. also Ågren et al. 1977).

The values of the photosynthetic rate obtained in different investigations are plotted against the respective nitrogen dosage in Fig. 8. The nitrogen application of 200 kg ha^{-1} gave the greatest photosynthetic response, the response decreasing considerably when nitrogen applications exceeding this amount are used. The comparison is, however, based on different conifers grown on sites of varying quality and different types of fertilizer. The reliability of the comparison is also decreased by the fact that the measurements in the different studies are based on shoots from different parts of crown.

Reasons for the decreased influence on

Table 4. Photosynthetic rate of unfertilized and fertilized conifers in various studies.

Taulukko 4. Lannoittamattomien ja lannoitettujen havupuiden suhteelliset fotosynteesinopeudet eri tutkimusten mukaan.

Source and tree species *Lähde ja puulaji*	Treatment *Käsittely*	Relative photosynthesis *Suhteellinen fotosynteesinopeus* Unfertilized *Lannoittamaton*	Fertilized *Lannoitettu*
This study *Tämä tutkimus* *Pinus sylvestris*	200[1] kg ha^{-1} nitrogen *typpi*	100	135
	400[1] " " " "	100	117
	600[1] " " " "	100	112
Brix ja Ebell (1969) *Pseudotsuga mentziesii*	336[1] kg ha^{-1} nitrogen *typpi*	100	111
Keya ym. (1968) *Pinus pinaster*	104[1] kg ha^{-1} nitrogen *typpi* 323[3] " " phosphorus *fosfori*	100	240
Helms (1964) *Pseudotsuga menziesii*	560[4] kg ha^{-1} nitrogen *typpi*	100	108
Brix (1971) *Pseudotsuga menziesii*	448[1] kg ha^{-1} nitrogen *typpi*	100	125

1) ammoniumnitrate based fertilizers
1) *ammoniumtyppipohjaiset lannoitteet*
3) superphosphate based fertilizer
3) *superfosfaattipohjainen lannoitus*
2) urea based fertilizers
2) *ureapohjainen lannoite*
4) fertilizer unknown
4) *tuntematon lannoite*

photosynthetic rate following nitrogen applications of 400 and 600 kg ha^{-1} were not studied. The needle mass in fertilized shoots increases, and mutual shading may thus limit the photosynthetic rate as suggested by the magnified response to fertilization due to thinning of the stand just before the fertilizer application (cf. Brix 1971, Haapanen et al. 1979). On the other hand, thinning also improves the water supply for the trees which also may increase the photosynthetic rate. For example, Brix (1972) and Ågren et al. (1977) have found that irrigation may magnify the photosynthetic response due to nitrogen application.

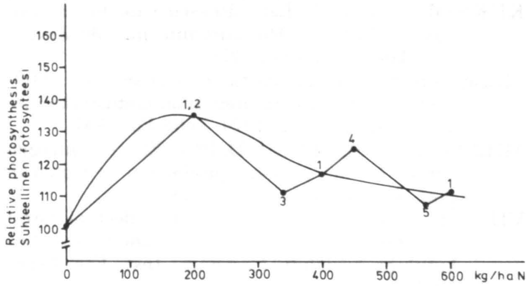

Fig. 8. Relative photosynthesis plotted against the nitrogen application in various studies as indicated by numbers.

Kuva 8. Suhteelliset fotosynteesinopeudet eri tutkimusten mukaan eri lannoitemäärillä. Kunkin tutkimuksen lannoittamattomat puut = 100.

The effect of nitrogen application on the needle dimensions, especially length and width, was evident. Brix and Ebell (1969) have demonstrated that a nitrogen application of 336 kg ha^{-1} results in an increase of 23 per cent in needle length and of 10 per cent in needle width. According to Brix (1972), a nitrogen application of 448 kg ha^{-1} yielded, however, only a 4 per cent increase in length and width of Douglas fir needles. In the present study, the effect was considerably greater than those reported above (cf. also Viro 1965, 1972, Miller and Miller 1976).

Nitrogen application appeared to increase branching of the laterals. However, relative figures of 5–15 per cent in this study were consistantly smaller than those by Brix and Ebell (1969). In a study of Douglas fir they found that fertilizing with nitrogen doubled the number of buds. Consequently, the increased branching of laterals affects the crown biomass and thus also the photosynthetizing needle mass. On the other hand, a stronger mutual shading is a related effect with a probable negative influence on net photosynthesis as discussed above.

Nitrogen fertilization seems primarly to increase the photosynthetic capacity of conifers through the increase in needle mass, as emphasized earlier (cf. Helms 1964, Brix 1971, Fagerström and Lohm 1977). However, changes in the photosynthetic rate due to the nitrogen application may also occur. The increased rate of net photosynthesis measured in this study may, however, be also a consequence of the altered balance between total photosynthetic rate and respiration rate due to the nitrogen application.

The stem growth of Scots pine has been found to increase linearly when the nitrogen dosage increases from 60 to 200 kg ha^{-1}. Increasing amounts of nitrogen leave a clearly diminishing effect on stem growth, which, however, is positive up to 600 kg ha^{-1} nitrogen. This agrees with the findings in this study, according to which the maximum increase in the photosynthetic rate was obtained with 200 kg ha^{-1} nitrogen.

Haapanen et al. (1979) found that 145 kg ha^{-1} nitrogen gave a small response in radial growth the first year after fertilization. The growth effect accelerated later and culminated three to four years after the fertilizer application. In this study, the growth during the first two years only was measured, but the results seem to be in accordance with those by Viro (1965), Brantseg et al. (1970) and Kukkola (1978). In the second year after nitrogen fertilization, the radial growth in the trees fertilized with 200 kg ha^{-1} nitrogen was almost twice that of the unfertilized trees. This is in accordance with the recommendations that a nitrogen application of greater than 200 kg ha^{-1} is too large (Metsänlannoitustutkimuksen . . . 1979).

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SELOSTE

ALUSTAVIA TULOKSIA TYPPILANNOITUKSEN VAIKUTUKSESTA NUORTEN MÄNTYJEN FOTOSYNTEESIIN JA KASVUUN

Työssä on tutkittu ammoniumnitraattina annetun typpilannoituksen vaikutusta männyn fotosynteesiin ja kasvuun. Lannoittamattomiin puihin verrattuna antoi 200, 400 ja 600 kg typpilisäys hehtaaria kohti 35, 18 ja 12 prosentin lisäyksen fotosynteesinopeudessa. Myös silmujen lukumäärä, oksien haarominen, neulasten lukumäärä sekä neulasten mitat, erityisesti leveys ja pituus, lisääntyivät lannoituksen vaikutuksesta. Puiden fotosynteesikapasiteetin ja rungon sädekasvun välillä vallitsi selvä positiivinen vuorosuhde.