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Fertilization has little effect on light-interception efficiency of *Picea abies* shoots

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Summary We investigated effects of nutrient availability on shoot structure and light-interception efficiency based on data from control (C) and irrigated + fertilized (IL) trees of Norway spruce (*Picea abies* (L.) Karst.). The sampling of 1-year-old shoots was designed to cover the variation in canopy exposure within the live crown zone, where current-year shoots were still found. Canopy openness was used as a measure of light availability at the shoot's position. Openness values for the sample shoots ranged from 0.02 to 0.77 on the IL plot, and from 0.10 to 0.96 on the C plot.

Among needle dimensions, needle width increased most with canopy openness. At fixed canopy openness, needle width was larger, and the ratio of needle thickness to width was smaller in IL trees than in C trees. Specific needle area (SNA) and the ratio of shoot silhouette area to total needle area (STAR) decreased with canopy openness, so that the combined effect was a threefold decrease in the ratio of shoot silhouette area to unit dry mass (SMR = STAR × SNA) along the studied range of openness values. This means that the light-interception efficiency of shoots per unit needle dry mass was three times higher for the most shaded shoots than for sun shoots. A test of the effect of fertilization on the relationships of SNA, STAR and SMR indicated statistically significant differences in both slope and intercept for SNA and STAR, and in the intercept for SMR. However, the differences partly cancelled each other so that, at medium values of canopy openness, differences between treatments in predicted SNA, STAR and SMR were small. At 0.5 canopy openness, predicted STAR of IL shoots was 6.1% larger than STAR of C shoots, but SMR of IL shoots was 10% smaller than that of C shoots. The results suggest that light-interception efficiency per unit needle area or mass of the shoots is not greatly affected by fertilization.

Keywords: LAI, nitrogen, Norway spruce, structural acclimation.

Introduction

The increase in stand productivity in response to fertilization can be attributed to an increase in photosynthetic performance and faster accumulation of leaf area index (LAI) (e.g., McMurtrie and Wolf 1983, Linder and Rook 1984). These factors can be analyzed separately, although they are in dynamic interaction, because the production of new foliage is part of the total canopy photosynthetic production. Leaf area can increase only as long as carbon uptake in photosynthesis is sufficient to meet the maintenance and construction costs of new leaves and associated woody structures and the export of carbon to developing buds (Givnish 1988, Schoettle and Fahey 1994). Net photosynthetic rate of a leaf in a given light environment is determined by its efficiency in capturing available photosynthetically active radiation (PAR, light-interception efficiency) and converting it to photosynthates (conversion efficiency) (Stenberg et al. 2001). Structural adjustment that changes leaf area display is the only available mechanism to allocate the incoming photons in some desired fashion onto leaf surfaces, and plasticity limits the extent to which different characteristics may be adjusted. It is known that morphological characteristics of needles and shoots change in response to shading (Del Rio and Berg 1979, Hager and Sterba 1985, Leverenz and Hinckley 1990, Schoettle and Smith 1991, Niinemets and Kull 1995*a*, 1995*b*, Sprugel et al. 1996), but the role of nutrients in these responses is not well understood. To assess the effect of nutrient availability on structural shade acclimation, we need to quantify and compare light-interception efficiencies along the naturally occurring light gradient within stands of different fertility.

Interception of PAR per unit needle area of a shoot situated in a given light environment is directly proportional to its shoot silhouette to total needle area ratio (STAR) (Stenberg et al. 2001). Because mean STAR ($\overline{\text{STAR}}$; Oker-Blom and Smolander 1988) is closely related to the light extinction coefficient, $\overline{\mathrm{STAR}}$ modifies the vertical gradient of PAR, thus providing a useful tool for analyzing the dynamic interaction between canopy structure and radiation regime. As a complement to STAR, we used the ratio of shoot silhouette area to needle dry mass (SMR) to quantify light-interception efficiency per unit dry mass invested in foliage. We determined the relationships of STAR and SMR with canopy openness in Norway spruce (*Picea abies* (L.) Karst.), and studied the effects of fertilization on these relationships.

Materials and methods

Measurements were made in the Norway spruce experimental stand situated at the Flakaliden research area (64°07′ N, 19°27′ E, 310 m a.s.l.) in Sweden. The stand was planted with 4-year-old seedlings in 1963, and the nutrient optimization experiment was established in 1987. The treatments are applied to plots of 50 × 50 m. Two treatments were used in this study: (1) a control (C) plot, and (2) an irrigated + fertilized (IL) plot, in which a complete nutrient solution has been injected into the irrigation water daily during the growing season constantly since 1987 (see Linder (1995) for further details on the experimental design). The development of the two canopies, since the start of the fertilization regime, has resulted in remarkable differences in tree size and LAI (see Table 1; S. Linder, Swedish University of Agricultural Sciences, personal communication), providing a setup for quantifying changes in needle and shoot structure with shading and for comparing those responses between fertilized and unfertilized trees.

In situ measurements

The data consisted of structural measurements taken in mid-July of 1995, 1996, 1997 and 1998. Results from 1997 have been reported previously by Stenberg et al. (1999). One-year-old shoots were selected from different canopy positions within the two experimental plots, representing two regimes of nitrogen availability. Sampling was designed to cover the range in canopy openness values within the crown zone, where current-year shoots could still be found. In practice, each year, two to four healthy trees from each of the two plots were selected and six to 16 shoots were sampled from different heights along the length of the living crown. This strategy ensured that the sampling (exposure) range was as wide as possible even without a priori knowledge about the distribution of openness values within the canopies and at the specific locations of the shoots. Nevertheless, maximum values of canopy openness for the sample shoots were somewhat lower on the IL plot, because the tops of the crowns were inaccessible with the ladder that was available. Minimum openness values were consistently lower on the IL plot than on the C plot.

Table 1. Diameter at breast height (DBH), mean height (Height), basal area (BA), stand volume (*V*), growth (CAI), and leaf area index (LAI) of trees in the irrigated + fertilized (IL) and control (C) plots used in this study. The estimates are from years 1995 and 1998.

Plot	Year	DBH (cm)	Height (cm)	BA (m^2 ha^{-1})	*V* (m^3 ha^{-1})	CAI (m^3 ha^{-1} $year^{-1}$)	LAI
IL	1995	10.8	701	23.4	97.6	12.9	5.9
	1998	12.8	845	32.6	143	17.4	8.4
C	1995	6.4	459	7.7	25.4	3.2	2.3
	1998	7.2	520	9.1	34.9	4.8	2.9

Canopy openness, defined as the unweighted fraction of unobscured sky (Sprugel et al. 1996), was used as a measure of light availability at the shoot's position. A measurement with the LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE) was taken at the location of each shoot applying no field of view restrictor. Above-canopy reference measurements were taken every 15 s by a second instrument placed in open conditions. To prevent direct sunlight from reaching the sensors, all measurements were taken in the evening when the sun was less than 16° above the horizon. Canopy openness was computed based on the gap fraction values in different sections of the sky provided by the LAI-2000. Canopy openness is mathematically defined as:

$$\text{openness} = \frac{1}{2\pi}\int_{\Omega} g_{\mathrm{f}}(\omega)\,\mathrm{d}\omega, \quad (1)$$

where $g_{\mathrm{f}}(\omega)$ denotes the gap fraction in the solid angle (dω) around the direction (ω) of the upper hemisphere (Ω).

Shoot and needle silhouette area measurements

Shoot silhouette areas (SSA) in different directions were measured photographically (see Table 2 for instrumentation). In our set-up design, the shoot was attached with a pin (at the mid-point of the twig) to a graduated dial that was fixed to a metal stand. Thus, the shoot's position with respect to the view direction of the camera could be adjusted by (1) changing the angle between shoot axis (twig) and the optical axis of the camera, and (2) reattaching the shoot to the pin so that different sides of the shoot were facing the camera. The camera was fixed at a distance of 160–300 cm from the shoot depending on the size of the shoot and the properties of the lens used, such that the maximum field of view obtained was 4°. The silhouette image was taken against the light table in an otherwise dark room. Excess light was minimized by covering the light table with 50% neutral dark film and the unused area of the light table was covered by curtains. The distance between the shoot and the light table was 15 cm.

In our coordinate system, the optical axis of the camera (or view direction) was horizontal, and the shoot inclination angle (ϕ) refers to the angle of the shoot axis (twig) to the vertical. Thus, for $\phi = 0°$, the twig was perpendicular to the direction of view, and for $\phi = 90°$ the twig was parallel to it (a view along the axis corresponding to the minimum shoot silhouette area). The rotation angle (γ) was defined such that $\gamma = 0°$ when the shoot's upper side was facing the viewer (camera). Thus, rotating the shoot 90° (along the shoot axis) from that gave the "side view" ($\gamma = 90°$). For Norway spruce shoots, the silhouette area commonly attains its maximum value at about $\phi = 0°$

Table 2. Equipment used in the photo analyses. Images were analyzed with a video band image analysis program (1995–1996) (Helsinki University of Technology, Espoo, Finland) and with Colan Colorimetric Image Analysis Software (1997–1998) (ColorSoft, Keminmaa, Finland).

Year	Field of view (°)	Film/camera	Lens	Pixel size (mm)	Pixels (cm^{-2})
1995	4	Film Tmax 100	Nikon 180 mm, Micro Nikkor 55 mm (needles)	0.4–0.6	280–625
1996	3	Film Tmax 100	Nikon 180 mm, Micro Nikkor 55 mm (needles)	0.08–0.13	5,900–15,600
1997	4	Kodak DCS-420	Nikon 180 mm	0.08–0.13	5,900–15,600
1998	2	Kodak DCS-460	Sigma 400, Micro Nikkor 60 mm (needles)	0.04	62,500

and $\gamma = 0°$, i.e., when the shoot axis and shoot's upper side are perpendicular to the view direction. Therefore, SSA (0,0) is commonly (although not quite accurately) referred to as the maximum silhouette area.

In 1995, 1997 and 1998, the measurement procedure was as follows. A set of measurements was taken where the inclination angle (ϕ) was changed in steps of 30° (ϕ = 0°, 30°, 60°, 90°, 120°, 150°). The rotation angle (γ) was 0° in the first set of measurements, and the procedure was repeated four times changing γ in steps of 45° (γ = 0°, 45°, 90°, 135°, 180°) or six times changing γ in steps of 30° (only in 1997). When changing γ, the previous view direction was marked before the shoot was detached. The shoot was then reattached to the stand at the desired rotation angle. In 1996, measurements were taken only at four rotation angles at a shoot inclination of ϕ = 0°.

After completing the shoot silhouette area and structural measurements (see below), the projected area (silhouette area) of all needles on the shoot was measured photographically. For this purpose, needles were laid out (not overlapping) on an acrylic plate as they fell. The acrylic plate, which was used to prevent the halo effect from burning the needle edges, was placed 35 mm above the horizontal light table. The silhouette area measuring system was calibrated with watch spindles or with precision wires with diameters from 0.8 to 2.0 mm that matched mean needle diameter.

The spherically averaged shoot silhouette area ($\overline{\mathrm{SSA}}$) was calculated by the method of Smolander and Stenberg (2001). In computing the spherically averaged shoot silhouette to total needle area ratio ($\overline{\mathrm{STAR}}$), the correction for the twig area was made as described by Stenberg et al. (1999). In addition to $\overline{\mathrm{STAR}}$, maximum shoot silhouette to total needle area ratio ($\mathrm{STAR}_{\max}$) was calculated by using SSA(0,0) instead of $\overline{\mathrm{SSA}}$. We used $\mathrm{STAR}_{\max}$ as a complement to $\overline{\mathrm{STAR}}$ mainly because measurements in 1996 did not allow computation of $\overline{\mathrm{SSA}}$. The spherically averaged ratio of shoot silhouette area to needle dry mass ($\overline{\mathrm{SMR}}$) was calculated by multiplying $\overline{\mathrm{STAR}}$ by the specific needle area (SNA).

Structural measurements

All needles of the shoot were detached and counted, and the length and diameter of the twig were measured. We estimated mean needle length by measuring the lengths of 10–30 sample needles with a ruler. In addition, three to six needles were picked from different sides of the central part of the shoot for determination of needle thickness and width. Needle dry mass (48 h at 60–70 °C) of the remaining needles of the shoot was determined and, in 1996 and 1997, foliar nitrogen concentration was determined with a LECO CHN-900 analyzer (LECO, St. Joseph, MI).

Anatomical leaf thickness (t_n) and width (w_n) were measured from needle cross sections (Figure 1) (see Stenberg et al. (1999) for details of the method). In 1995–1997, the cross sections were photographed on slide film, and needle thickness and width were measured by projecting the slides on the screen. In 1998, the dimensions were measured with a digital camera and the Colan Image Analysis Program (ColorSoft, Keminmaa, Finland).

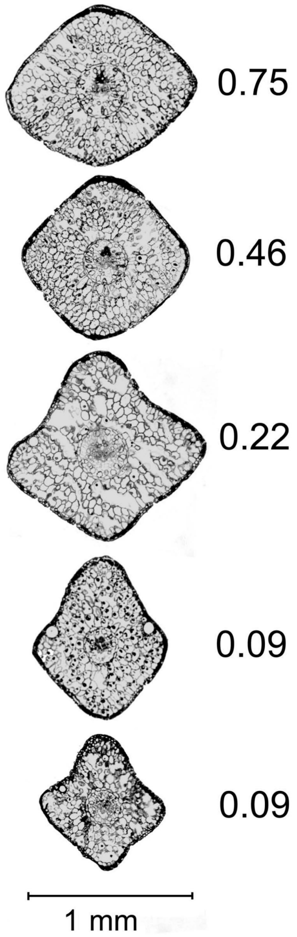

Figure 1. Cross sections of needles at different canopy openness values between 0.09 and 0.75. Data are from the IL plot in 1997.

Geometric needle area estimates

Total needle area (A_t) was estimated from mean needle length (l_n), t_n and w_n as:

$$A_t = 2l_n\sqrt{t_n^2 + w_n^2}. \quad (2)$$

Equation 1 applies to a rhomboidal prism, which was chosen to best approximate the shape of our Norway spruce needles (see Figure 1). Total needle area of a shoot (TNA) was estimated as A_t multiplied by the number of needles on the shoot.

A geometric estimate of projected needle area (A_p) was computed based on the rhomboid model (Niinemets and Kull 1995*a*) as:

$$A_p = l_n\frac{(\max(t_n,\ w_n))^2}{\sqrt{t_n^2 + w_n^2}}, \quad (3)$$

where A_p is the projected area of a needle lying on its side so that the angle to the horizontal is less for the larger diagonal. In our material, needle thickness was not consistently larger than needle width. Consequently, as indicated in the formula, we always used the larger dimension in the numerator in calculating A_p. The geometric estimate (A_p) agreed fairly well with the photographically measured projected needle area (Figure 2). On average, A_p calculated by the rhomboid model exceeded the photographically measured projected area by 2%.

Statistical analysis

Relationships of $\overline{\text{STAR}}$, $\text{STAR}_{\max}$, SNA and $\overline{\text{SMR}}$ with canopy openness (data from all years pooled) were described by a simple regression (reduced model): $y = \beta_0 + \beta_1X_1$, where X_1 denotes the logarithm (ln) of canopy openness, ln(openness), which linearized the response function. The difference between treatments in the relationships was studied by using an indicator ("dummy") variable to account for the effect of fertilization. Multiple linear regression models of the type (full model): $y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_1X_2$ were thus fitted to the whole data, where X_1 is ln(openness) and X_2 is the dummy variable, which was assigned the value 1 for IL shoots and 0 for C shoots (Neter et al. 1983, SYSTAT statistical software package, SYSTAT, Evanston, IL). The full model structure allows both the intercept and the slope of the regression to vary between the groups (indicated by 0 and 1). Testing for differences in intercept ($\beta_2 \neq 0$) and slope ($\beta_3 \neq 0$) was done by calculating partial *F* statistics for the coefficients of the full model.

Results

In trees on both the C and IL plots, there was a slightly increasing trend in needle nitrogen concentration (N_m) from the bottom to the top of the canopy (Figure 3), and N_m was lower in 1996 than in 1997. The ratio of needle thickness to width (t_n/w_n) ranged from 0.75 to 2.1 in IL trees, and from 0.79 to 1.9 in C trees. The ratio decreased with increasing canopy openness (Figure 4a) mainly because of an increase in needle width. For 88% of the needles t_n/w_n was between 0.75 and 1.25. The ratio of total to projected needle area (A_t/A_p) varied between 2.5 and 4.0 (Figure 4b). The value 4 is obtained when the needle cross section is a square ($t_n = w_n$ in Equations 2 and 3). The structural measurements of needle and shoot characteristics are summarized in Table 3.

Shoot size, quantified by twig length (l_t) and total needle area (TNA), was positively correlated with canopy openness (Table 4). There were decreases in STAR, SNA and SMR with increasing canopy openness in both control and fertilized trees (Figures 5–7). The combined effect of the changes in SNA

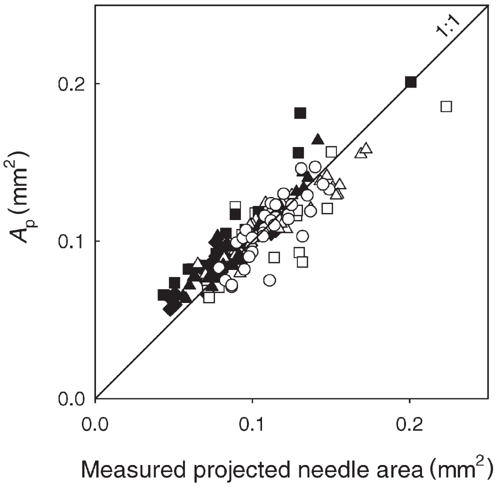

Figure 2. Projected needle area calculated with the rhomboid model (A_p) plotted against photographically measured projected needle area. Data are from 1995 (◇, ◆), 1996 (□, ■), 1997 (△ , ▲) and 1998 (○, ●). Closed symbols refer to the IL plot and open symbols to the C plot.

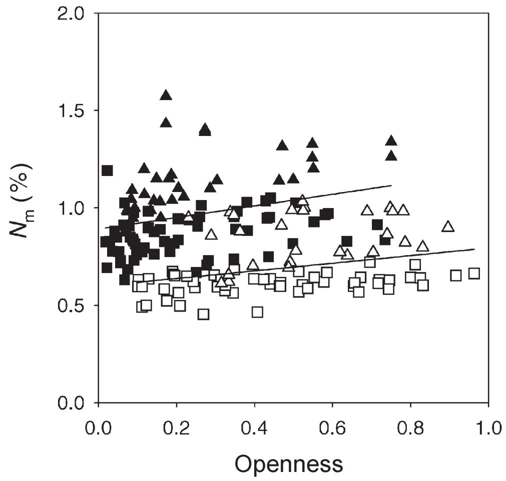

Figure 3. Foliar nitrogen concentration (N_m) as a function of canopy openness. Data are from 1996 (□, ■) and 1997 (△ , ▲). Closed symbols refer to the IL plot and open symbols to the C plot. The *P*-values of the regressions are 0.006 (IL) and 0.012 (C).

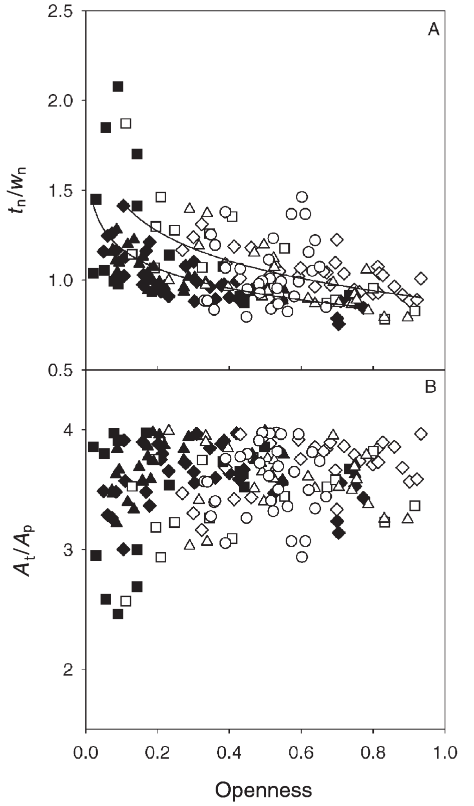

Figure 4. Ratio of needle thickness to needle width (t_n/w_n) (A) and total needle area to projected needle area (A_t/A_p) (B) as a function of canopy openness. Symbols as in Figure 2.

(Figure 5) and $\overline{\text{STAR}}$ (Figure 6) was a more than threefold change in $\overline{\text{SMR}}$ along the range of openness values in the study (Figure 7). The effects of fertilization on the relationships of $\overline{\text{STAR}}$, STAR_{max}, SNA and $\overline{\text{SMR}}$ with canopy openness are summarized in Table 5. The difference in intercept (values of the dependent variables at full canopy openness) was statistically significant for SNA ($P < 0.001$), $\overline{\text{STAR}}$ ($P < 0.01$) and $\overline{\text{SMR}}$ ($P < 0.01$). At full canopy openness, IL shoots had 21% smaller predicted SNA and 14% larger predicted $\overline{\text{STAR}}$ than C shoots. However, the slopes of the relationships were larger for SNA ($P < 0.05$) and smaller for $\overline{\text{STAR}}$ ($P < 0.05$) in the IL shoots than in the C shoots, implying that the predicted differences in SNA and $\overline{\text{STAR}}$ between C and IL shoots decreased at lower values of canopy openness. At an openness value of 0.5, predicted SNA of IL shoots was 12% smaller and predicted $\overline{\text{STAR}}$ was 6.1% larger than those of C shoots. No statistically significant differences ($P > 0.05$) between treatments were found in the relationships between STAR_{max} and canopy openness. For the relationships between $\overline{\text{SMR}}$ and canopy openness, the intercept (predicted value of $\overline{\text{SMR}}$ in unshaded conditions) was 26% smaller for IL shoots ($P < 0.01$) than for C shoots. However, because the rate of change in $\overline{\text{SMR}}$ with increased shading was smaller in C shoots than in IL shoots (although not statistically significant), at 0.5 canopy openness the predicted $\overline{\text{SMR}}$ was only 10% smaller for IL shoots than for C shoots.

Discussion

Fertilization increased foliage nitrogen concentration (N_m), but N_m varied only slightly with canopy openness (Figure 2). In both IL and C trees, needle width (w_n) increased more with canopy openness than needle thickness (t_n). At similar openness values, there was no clear effect of fertilization on t_n, but w_n was larger in IL trees than in C trees. As a result, IL trees had smaller t_n/w_n at a fixed canopy openness (see Figure 4a).

Table 3. Sampling protocol and the ranges of needle length (l_n), needle thickness (t_n), needle width (w_n), thickness to width ratio (t_n/w_n), total needle area to projected area ratio (A_t/A_p), specific needle area (SNA), foliar nitrogen concentration (N_m), twig length (l_t), total needle area (TNA), needle number density (N_n/l_t), needle area packing (TNA/l_t), spherically averaged shoot silhouette to total area ratio (STAR), maximum STAR (STAR_{max}) and shoot silhouette to foliage dry mass ratio (SMR).

	IL 1995	C 1995	IL 1996	C 1996	IL 1997	C 1997	C 1998
No. shoots/no. trees	35/3	30/3	62/4	55/4	32/2	28/2	48/8
Shoot order	1st	1st	1st	1st	Varying	Varying	1st
Openness	0.05–0.77	0.27–0.93	0.02–0.74	0.10–0.96	0.07–0.75	0.23–0.90	0.26–0.69
l_n (mm)	9.1–16.3	7.6–13.4	7.0–17.6	5.6–20.8	9.6–15.9	6.7–12.5	8.9–13.6
t_n (mm)	0.86–1.4	0.85–1.2	0.82–1.5	1.0–1.4	0.86–1.3	1.1–1.5	0.81–1.5
w_n (mm)	0.69–1.7	0.72–1.2	0.57–1.5	0.65–1.6	0.81–1.4	0.83–1.9	0.81–1.5
t_n/w_n	0.75–1.4	0.88–1.3	0.87–2.1	0.78–1.9	0.88–1.28	0.79–1.4	0.79–1.5
A_t/A_p	3.0–4.0	3.2–4.0	2.5–4.0	2.7–4.0	3.2–4.0	3.0–4.0	2.9–4.0
SNA ($\text{cm}^2\ \text{g}^{-1}$)	74–199	89–147	74–195	56–153	85–190	75–127	67–129
N_m (%)			0.63–1.2	0.45–0.72	0.96–1.6	0.65–1.1	
l_t (cm)	3.3–22	2.9–8.9	3.0–22	1.5–23	3.0–20	1.6–9.2	2.2–9.0
TNA (cm^2)	18.5–150	10.2–64.0	8.7–205	6.8–157	13.1–137	7.4–82.6	22.8–86.2
N_n/l_t (cm^{-1})	10–20	17–26	9–21	11–33	12–22	13–23	15–27
TNA/l_t ($\text{cm}^2\ \text{cm}^{-1}$)	3.6–7.8	4.5–11.4	2.9–9.2	3.1–12.7	4.0–11.6	3.4–9.7	4.5–11.4
STAR	0.121–0.209	0.105–0.169			0.122–0.188	0.103–0.166	0.103–0.173
STAR_{max}	0.153–0.310	0.133–0.224	0.127–0.364	0.122–0.240	0.143–0.246	0.115–0.234	0.116–0.251
SMR	10.5–41.7	10.0–21.9			12.1–29.6	8.5–21.8	9.8–16.4

Table 4. A Spearman correlation matrix for canopy openness, and needle and shoot characteristics. Symbols as in Table 3. Asterisks indicate statistical significance (* = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$) of the correlations.

	Treatment	Openness	l_n	t_n	w_n	t_n/w_n	SNA	l_t	TNA	N_n/l_t	$\overline{\text{STAR}}$
l_n	IL	0.32 **									
	C	0.28 **									
t_n	IL	0.51 ***	–0.16								
	C	–0.04	0.03								
w_n	IL	0.83 ***	0.13	0.82 ***							
	C	0.24 *	0.15	0.65 ***							
t_n/w_n	IL	–0.85 ***	–0.35 **	–0.31 **	–0.76 ***						
	C	–0.34 ***	–0.09	–0.06	–0.75 ***						
SNA	IL	–0.88 ***	–0.19	–0.57 ***	–0.77 ***	0.70 ***					
	C	–0.52 ***	–0.36 ***	–0.27 **	–0.52 ***	0.54 ***					
l_t	IL	0.69 ***	0.21	0.48 ***	0.72 ***	–0.67 ***	–0.70 ***				
	C	0.42 ***	0.35 ***	–0.00	0.35 ***	–0.53 ***	–0.60 ***				
TNA	IL	0.81 ***	0.46 ***	0.51 ***	0.82 ***	–0.78 ***	–0.72 ***	0.88 ***			
	C	0.45 ***	0.61 ***	0.20 *	0.51 ***	–0.51 ***	–0.61 ***	0.87 ***			
N_n/l_t	IL	–0.02	0.22 *	–0.30 **	–0.19	0.00	0.21	–0.39 ***	–0.13		
	C	0.16	0.12	–0.29 **	–0.21 *	0.14	0.18	–0.16	–0.05		
$\overline{\text{STAR}}$	IL	–0.58 ***	–0.32 **	–0.25 *	–0.58 ***	0.70 ***	0.28 *	–0.44 ***	–0.66 ***	–0.30 *	
	C	–0.50 ***	–0.25 *	–0.07	–0.39 ***	0.44 ***	0.19	–0.45 ***	–0.62 ***	–0.49 ***	
$\overline{\text{SMR}}$	IL	–0.96 ***	–0.26 *	–0.56 ***	–0.85 ***	0.80 ***	0.93 ***	–0.75 ***	–0.84 ***	0.07	0.58 ***
	C	–0.63 ***	–0.43 ***	–0.22 *	–0.60 ***	0.62 ***	0.77 ***	–0.70 ***	–0.82 ***	–0.14	0.70 ***

On both plots, t_n/w_n decreased with increasing openness, from values of > 1 to values of < 1, but the value of canopy openness at which the shift occurred was smaller in fertilized trees than in control trees. Ranges in the ratio of total to projected needle area (A_t/A_p) were also similar on both plots (2.5 to 4.0 in IL trees and 2.7 to 4.0 in C trees). Because A_t/A_p attains its maximum value (= 4) when $t_n = w_n$ (Equations 2 and 3), there was no monotonically increasing trend in A_t/A_p with light availability (Figure 4b). This is in contrast to results obtained in central European Norway spruce provenances (Niinemets and Kull 1995*a*, Sellin 2000).

Specific needle area is a function of needle dimensions and density. Needle flatness can be characterized by the ratio of the larger of t_n and w_n to the smaller of these dimensions (Sellin 2000). The smaller and flatter the needle, the larger the ratios of needle surface area to volume (V_n) ($A_t/V_n = 4\sqrt{(D_1^2 + D_2^2/D_1D_2)}$ and SNA (assuming constant density). The increase in SNA with shading in our material (Figure 5) was more closely associated with decreasing needle size than with increasing needle flatness, which did not show any clear trend over the common range of openness values. Needle width alone explained ~50% of the variation in SNA in IL

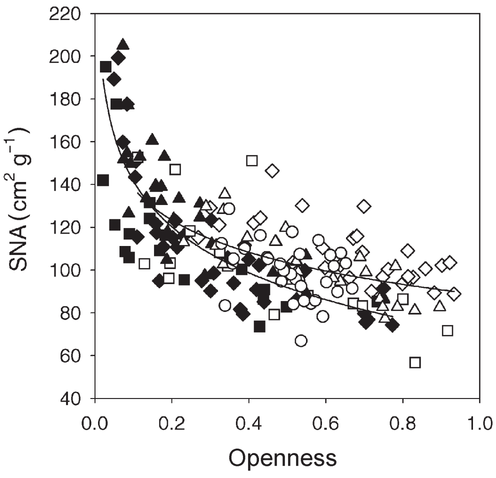

Figure 5. Specific needle area (SNA) as a function of canopy openness. See Table 5 for parameters of the fitted curves.

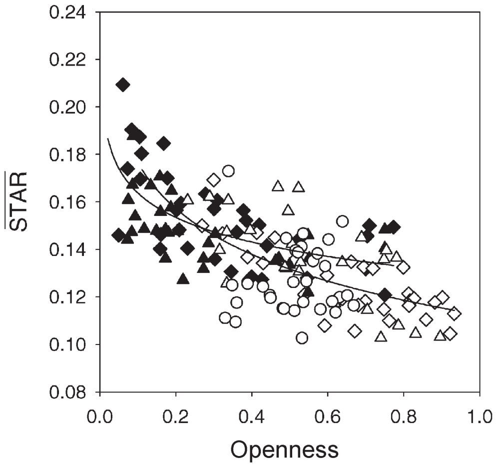

Figure 6. Mean shoot silhouette to total needle area ratio ($\overline{\text{STAR}}$) as a function of canopy openness. See Table 5 for parameters of the fitted curves.

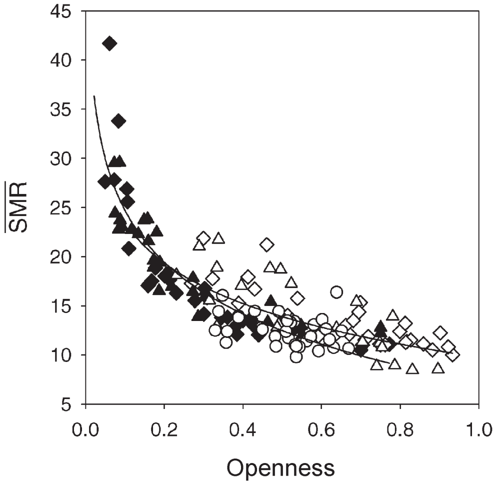

Figure 7. Mean shoot silhouette area per unit needle dry mass ($\overline{\mathrm{SMR}}$) as a function of canopy openness. See Table 5 for parameters of the fitted curves.

trees, and ~75% in C trees (data from 1995–1997). Needle density (needle dry mass/geometrically calculated V_n) changed little within the common range of observed openness values on the C and IL plots, but IL needles were somewhat denser than C needles. Thus, the higher SNA for C shoots than for IL shoots within this range was related to both smaller needles and lower needle density.

Statistically significant differences between treatments were found in the intercepts of the relationships of $\overline{\mathrm{STAR}}$ and $\overline{\mathrm{SMR}}$ with canopy openness (Figures 6 and 7). In open conditions, IL trees produced shoots that had somewhat higher STAR (less mutual shading within shoot) than C trees, but they had lower SMR (SMR = STAR × SNA) because of their smaller SNA. However, the differences in intercepts were offset by opposite differences in the rate of change with shading (slopes of the relationships) (Table 5). As a result, the differences between treatments in predicted $\overline{\mathrm{STAR}}$ and $\overline{\mathrm{SMR}}$ had different signs at high openness and low openness values, respectively, and were relatively minor at medium openness (e.g., 0.5, a value well within the common range of observed openness values on the C and IL plots). For $\mathrm{STAR}_{\mathrm{max}}$, which showed a strong positive correlation with $\overline{\mathrm{STAR}}$ ($r^2 = 0.88$), no significant effect of fertilization on either slope or intercept was found. This test covered a larger data set (including data from 1996, see Table 3), and the range of canopy openness values was wider.

Although total canopy PAR interception is a saturating function of LAI, mean canopy openness (available light) and mean light interception per unit leaf area or mass decrease with increasing LAI. The ability of trees to adjust shoot structure to increase light-interception efficiency of shade foliage is an important determinant of the amount of LAI that can be maintained. We looked at the light-interception efficiency of individual shoots along an openness gradient in two canopies differing in LAI. We found a twofold increase in STAR and a threefold increase in SMR with shading. The C and IL shoots were similar in terms of light-interception efficiency per unit area or mass within the overlapping range of canopy openness values. However, there were no current-year shoots below 10% canopy openness on the C plot, whereas on the IL plot current-year shoots were still found at 2% openness. This suggests that the higher capacity of fertilized trees to produce and maintain foliage at lower irradiances does not result from in-

Table 5. Reduced models ($y = \beta_0 + \beta_1 \ln(\mathrm{openness})$), where a single line was fitted to the whole data (IL + C) (upper section of table) together with individual regression models for SNA, $\overline{\mathrm{STAR}}$, $\mathrm{STAR}_{\mathrm{max}}$ and $\overline{\mathrm{SMR}}$ for fertilized (IL) and control (C) plots (lower section of table). Root mean square errors (RMSE) are given for the reduced model and the full model ($y = \beta_0 + \beta_1 \ln(\mathrm{openness}) + \beta_2 X_2 + \beta_3 \ln(\mathrm{openness}) X_2$), where X_2 is an indicator variable. Asterisks indicate statistical significance (* = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$) of the between-treatment differences in the intercept (β_0) and slope (β_1). Predicted values of the dependent variables are calculated at a canopy openness of 0.5.

		β_0	β_1	r^2	N	RMSE	y (0.5)
SNA	Reduced	83.3	–25.0	0.56	188	16.9	
	Full					16.3	
$\overline{\mathrm{STAR}}$	Reduced	0.118	–0.021	0.47	153	0.015	
	Full					0.014	
$\mathrm{STAR}_{\mathrm{max}}$	Reduced	0.144	–0.036	0.49	188	0.028	
	Full					0.028	
$\overline{\mathrm{SMR}}$	Reduced	9.01	–6.68	0.76	153	2.53	
	Full					2.47	
SNA	IL	70.3 ***	–31.0 *	0.66	83		91.8
	C	88.5	–21.7	0.28	105		104
$\overline{\mathrm{STAR}}$	IL	0.129 **	–0.015 *	0.38	64		0.140
	C	0.113	–0.028	0.28	89		0.132
$\mathrm{STAR}_{\mathrm{max}}$	IL	0.154	–0.032	0.41	83		0.176
	C	0.140	–0.039	0.30	105		0.167
$\overline{\mathrm{SMR}}$	IL	7.22 **	–7.60	0.81	64		12.5
	C	9.78	–5.95	0.42	89		13.9

creased light-interception efficiency at the shoot level. Rather, it may reflect higher conversion efficiency of shade foliage or changes in allocation between shoots and roots and, thereby, lower construction costs per unit new leaf area in terms of supporting woody tissues (Givnish 1988). Aboveground biomass and growth were higher on the fertilized plot than on the control plot. The associated increase in photosynthetic production is likely to be a combined effect resulting from higher LAI, increasing the total canopy PAR interception, and higher conversion efficiency per unit of intercepted PAR. In contrast, the difference in potential PAR capture per unit leaf mass of shoots developed at similar light environments was small.

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