

Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*

BRENT E. EWERS,^{1,2} RAM OREN,¹ NATHAN PHILLIPS,^{1,3} MONIKA STRÖMGREN⁴ and SUNE LINDER⁴

¹ Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

² Present address: Department of Forest Ecology and Management, University of Wisconsin, 1630 Linden Dr., Madison, WI 53706, USA

³ Department of Geography, Boston University, Boston, MA 02215, USA

⁴ Department for Production Ecology, Swedish University of Agricultural Sciences, P.O. Box 7042, SE-750 07 Uppsala, Sweden

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Summary We compared sap-flux-scaled, mean, canopy stomatal conductance (G_S) between *Picea abies* (L.) Karst. in Sweden and *Pinus taeda* (L.) in North Carolina, both growing on nutritionally poor soils. Stomatal conductance of *Picea abies* was approximately half that of *Pinus taeda* and the sensitivity of G_S in *Picea abies* to vapor pressure deficit (D) was lower than in *Pinus taeda*. Optimal fertilization increased leaf area index (L) two- and threefold in *Pinus taeda* and *Picea abies*, respectively, regardless of whether irrigation was increased. Although it increased L , fertilization did not increase G_S in *Picea abies* unless irrigation was also provided. In *Pinus taeda* growing on coarse, sandy soils, the doubling of L in response to fertilization reduced G_S sharply unless irrigation was also provided. The reduction in G_S with fertilization in the absence of irrigation resulted from the production of fine roots with low saturated hydraulic conductivity. When *Pinus taeda* received both fertilization and irrigation, the increase in L was accompanied by a large increase in G_S . In *Pinus taeda*, a reference G_S (defined as G_S at $D = 1$ kPa; G_{SR}) decreased in all treatments with decreasing volumetric soil water content (θ). In *Picea abies*, θ varied little within a treatment, but overall, G_{SR} declined with θ , reaching lowest values when drought was imposed by the interception of precipitation. Despite the large difference in G_S both between *Picea abies* and *Pinus taeda* and among treatments, stem growth was related to absorbed radiation, and stem growth response to treatment reflected mostly the changes in L .

Keywords: fertilization, irrigation, loblolly pine, Norway spruce, sap flux, shade tolerance.

Introduction

Across tree species, the combination of a long leaf life span, and high leaf-to-sapwood area ratio ($A_L:A_S$) and leaf area in-

dex (L) is associated with shade tolerance, and a relatively low maximum stomatal conductance, g_s , and assimilation rate (Larcher 1983, Meinzer and Grantz 1991, Whitehead 1998, Reich et al. 1999). Among conifers, *Picea spp.* generally have a greater leaf life span (Reich et al. 1999), $A_L:A_S$ (Waring et al. 1982), and L (Whitehead et al. 1984) than *Pinus spp.*, as exemplified by a comparison of *Picea abies* (L.) Karst. and *Pinus taeda* (L.). Reflecting these differences, maximum g_s in *Picea abies* is approximately half that of *Pinus taeda* under optimal conditions (e.g., compare Roberntz and Stockfors (1998) with Murthy et al. (1996)).

The intensification of mutual leaf shading with increasing L , and the decline in gas-exchange rates with increasing needle age (Oren et al. 1986, Zimmermann et al. 1988) reduce mean canopy stomatal conductance (G_S) relative to leaf-level maximum g_s . We therefore postulated that, because of differences between the species in leaf longevity and L , the difference in G_S between *Picea abies* and *Pinus taeda* should be greater than the difference in g_s . In this study, we investigate whether differences in G_S , calculated from scaled sap flux (Köstner et al. 1992, Martin et al. 1997, Pataki et al. 1998), are even greater between *Picea abies* and *Pinus taeda* than differences in leaf-level measurements of g_s .

Species with high G_S under optimal conditions commonly show high G_S sensitivity to environmental variation. Stomata regulate the minimum xylem water potential in a way that prevents excessive cavitation (Sperry et al. 1998). When G_S is high at low vapor pressure deficit (e.g., at $D = 1$ kPa; hereafter reference G_S , or G_{SR}), G_S is more sensitive to increasing D than when G_{SR} is low (Oren et al. 1999). For a wide range of species, the proportionality between G_{SR} and the sensitivity of G_S to D averages ~ 0.6 (Oren et al. 1999). Given that maximum g_s is approximately twice as high in *Pinus taeda* as in *Picea abies*, and given that *Pinus taeda* crowns have less mutual shading and support on average younger foliage, we postu-

lated that, under similar conditions, G_{SR} in *Pinus taeda* will be more than twice that in *Picea abies*, and that G_S will be more sensitive to D in *Pinus taeda* than in *Picea abies*.

In addition to differences among species, G_{SR} responds to natural and imposed variation in environmental conditions. To investigate such variation, we conducted parallel experiments with *Pinus taeda* in North Carolina (Albaugh et al. 1998) and *Picea abies* in northern Sweden (Bergh et al. 1999), in which irrigation (I), fertilization (F) and the combination of both (IL with liquid fertilizers in Sweden, or IF with solid fertilizers in North Carolina) were added and compared with control (C).

The aim of these experiments was to test the response of G_S to increasing L (Table 1), foliar N and changing difference between water demand and supply. To summarize results previously reported, we found that when soil water content was raised in the coarse, sandy soil in which the *Pinus taeda* grew, G_S among treatments ranked as $F < C = I < IF$ (Ewers et al. 2001). The lower G_S of F trees was due to the combination of roots produced under the prevailing water stress conditions of the sandy soil (Ewers et al. 1999, 2000) and the lower amount of fine roots in F trees (Ewers et al. 2000). Water stress was induced by a doubled L in F relative to C (Table 1), without an increase in root surface area (Ewers et al. 2000). In response to this change in root-to-leaf area ratio, the fine roots in F trees have low xylem vulnerability to cavitation, accompanied by low root hydraulic conductance (Ewers et al. 2000). The consequence of the change in fine root physiology was that F trees could extract water to a lower soil water content than trees in the other treatments, although their G_S was only half that of trees in the other treatments. When water stress is relieved naturally or artificially, F trees cannot change the morphology of existing roots or replace roots fast enough to acclimate to the change. Thus, their lower G_S reflected a carry-over effect from more stressful periods. Higher G_S in IF trees relative to I trees reflected the positive effect of higher foliar N, which was greater than the negative effect of lower mean leaf surface irradiance. For the shade-intolerant *Pinus taeda*, this was possible because the maximum L attained in IF was well below the species' maximum.

Table 1. Leaf area index (L), leaf-to-sapwood area ratio ($A_L:A_S$ m² cm⁻²) stand density (trees ha⁻¹) and annual transpiration (E_C , mm) for control (C), irrigated (I), fertilized (F), irrigated-fertilized (IF/IL), and drought trees (Dr), respectively.

	C	I	F	IF/IL	Dr
<i>Pinus taeda</i>					
L	1.8	2.0	3.3	3.6	
$A_L:A_S$	0.20	0.22	0.23	0.17	
Stand density	1260	1260	1260	1260	
E_C	331.3	325.0	385.0	580.7	
<i>Picea abies</i>					
L	1.9	1.9	6.1	6.4	1.8
$A_L:A_S$	0.33	0.2	0.31	0.27	0.38
Stand density	2100	2200	2400	2200	2100
E_C	94.5	113.4	206.4	407.6	75.2

Here we hypothesize that the parallel treatments in *Picea abies*, in which F caused a tripling of L , will cause less water stress than the same treatment in *Pinus taeda*, especially if G_S is as low as predicted above, because the sandy soil of the *Picea abies* stand can provide more water than the coarse sand of the *Pinus taeda* stand. Furthermore, we hypothesized that an artificially imposed drought (Dr) in the *Picea abies* stand will impact G_S minimally because G_S is already low in *Picea abies*. In addition, because unfertilized *Picea abies* stands can support much higher L than was attained with fertilization in this study (Oren et al. 1988), we hypothesize that, like *Pinus taeda*, stomata of *Picea abies* will respond positively to fertilization when irrigation is also provided, despite the large increase in L .

Materials and methods

Site descriptions

The *Picea abies* stand was located at the Flakaliden research site in northern Sweden (64°07' N, 19°27' E, elevation 320 m). Flakaliden has a mean annual temperature of 2.3 °C and the growing season lasts 120 days on average. The mean annual precipitation is 600 mm, one-third of which falls as snow. The soil is thin, podzolic, sandy, glacial till with mean depth of 120 cm, and the humus layer varies in depth from 2 to 6 cm with a mean depth of 4.3 cm (Bergh and Linder 1999). The trees were planted in 1963 after prescribed burning and soil scarification. A nutrient and water optimization experiment began in 1987 with five treatments: C, I, F, IL and Dr. The Dr treatment was established in 1989 by means of an under-canopy roof that reduced summer precipitation by 65% over an area of approximately 1000 m². Treatments were replicated four times in 50 × 50-m plots. In the F treatment, a complete mix of solid fertilizer was applied in early June each year. In the IL treatment, all essential macro- and micronutrients were supplied as liquid fertilizer every second night during the growing season, to maintain an optimal needle nutrient status. The needle nitrogen concentrations were 1.0, 1.5 and 1.8 % for C, F and IL, respectively (Linder 1995). Water was supplied to the irrigated plots to maintain a soil water potential (Ψ_s) above -100 kPa. For further details of the treatments see Linder (1995).

The *Pinus taeda* stand was located at the Southeast Tree Research and Education Site (SETRES) in the geological formation known as the Sandhills of North Carolina (34°55' N, 79°30' W). The climate permits gas exchange year round. Annual precipitation averages 1210 mm with occasional growing season water deficits. The soil is infertile, well drained, coarse, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series). The stand was planted in 1985 with mixed genetic lines from the North Carolina Piedmont. The four treatments were a 2 × 2 factorial combination of nutrition and water additions replicated four times in 50 × 50-m plots established in 1992. Nutrient treatments commenced in March 1992 and water additions in April 1993. Foliar nutrient status was monitored monthly and fertilizer was applied annually to meet tar-

get values. The needle nitrogen concentrations were 0.95%, for C and I, and 1.29% for F and IF (Albaugh et al. 1998). Water additions were made to keep available soil water content between field capacity and 40% of available soil water in the upper 0.50 m of the soil profile. For details of nutrition and water treatments see Abrahamson et al. (1998), Albaugh et al. (1998) and Murthy et al. (1996). Although the specific nutrient application rates varied between *Picea abies* and *Pinus taeda*, both stands were fertilized based on an approach for optimal nutrition (Linder 1995).

Sap flux measurements

At Flakaliden, ten 20-mm-long, Granier-type sap flux sensors (Granier 1987) were installed in the outer 20 mm of xylem below the live crown on the north side of the stem in one replicate of each treatment. The C, Dr and F trees were measured from May 31 to July 25, 1996, IL from May 5 to May 30, 1996 and I from June 8 to September 11, 1997, with several interruptions in data collection. Information on the radial pattern in flux developed on site with Granier-type sensors installed from 20 to 40 mm inside the sapwood area (Phillips et al. 1996, 2001), was combined with site specific information on active xylem area (Stockfors and Linder 1998, Phillips et al. 2001) to calculate the mean weighted sap flux of the stem (J_S ; Oren et al. 1998a). The outer sap flux was weighted by the sapwood area represented in that xylem band and the inner sap flux by the sapwood area internal to the outer band (Ewers et al. 1999, Ewers and Oren 2000). This assumes that inner sap flux represents the flux inside of 40 mm from the cambium.

At SETRES, eight 20-mm-long, Granier-type sensors were installed in the treatment plots of one block (Ewers et al. 1999, Ewers and Oren 2000). The same methodology as described for Flakaliden was used to calculate mean weighted J_S in stems of each treatment (Ewers et al. 1999, Ewers and Oren 2000).

Biomass measurements

At Flakaliden, diameter increment was measured weekly during the growing season by means of dendrometer bands. Projected leaf area index (L , $m^2 m^{-2}$) and whole-tree sapwood-to-leaf area ratio ($A_S:A_L$) were estimated from allometric relationships based on tree harvests in 1986, 1992 and 1996 (T. Albaugh, North Carolina State University, unpublished data). Leaf area index was assumed to increase linearly during the period of needle elongation, which started with bud break on about June 15 and ended on about July 31, and was assumed to be constant during the remainder of the growing season.

At SETRES, diameters of trees monitored for sap flux were measured on April 1996, March 1997, March 1998 and January 1999. Intra-seasonal growth patterns were determined from diameter measurements made every 2 weeks. Projected L was calculated using allometric relationships before bud break, corrected for seasonal pattern based on canopy area analyzer (LAI-2000, Li-Cor, Inc., Lincoln, NE) measurements (Albaugh et al. 1998, Ewers et al. 1999). Allometric and canopy area analyzer estimates of subplot L agreed to within 10%

(B. Ewers, unpublished data). Whole-tree $A_S:A_L$ was calculated from L and sapwood area determined with cores (Ewers et al. 1999, Ewers and Oren 2000).

Environmental measurements

At Flakaliden, meteorological data were monitored at a standard weather station situated within 250 m from the sap flux measurement trees. Vapor pressure deficit (D) was calculated from air temperature (T) and relative humidity based on Goff and Gratch (1946). A relative humidity and temperature probe (Vaisala HMP 35C, Campbell Scientific Ltd., Logan, UT) was positioned 1.7 m above ground. Photosynthetically active radiation (Q_o) was measured above canopy with a quantum sensor (Li-190s, Li-Cor, Inc.). All data were sampled every minute, and averaged and stored every 10 min. Soil water potential (Ψ_s ; kPa) was measured with ceramic tensiometers at three depths (15, 30 and 45 cm), and soil volumetric water content (θ ; $m^3 m^{-3}$) was measured by automated time domain reflectometry (Theta probe, Delta-T Devices, Cambridge, U.K.) at 15-cm soil depth in the I plot. One Ψ_s vertical measurement profile at 15, 30 and 45 cm was positioned in each plot, at a distance not exceeding 50 m from the trees monitored for sap flux. The tensiometers were measured twice a week from June to September. A relationship was established between Ψ_s and θ from concurrent measurements taken at I ($\theta = 81.3/(270.9 + \Psi_s)$; $r^2 = 0.71$) to calculate θ for all the treatments for comparison with SETRES. The resulting θ values were averaged across the three depths in each treatment because there was no consistent vertical pattern in Ψ_s and there were no data on vertical root profiles, although no roots were observed below 45 cm (M. Strömgen, Swedish University of Agricultural Sciences, unpublished data).

At SETRES, D was calculated as above from measurements made at 7 m above ground, approximately two-thirds of tree height, in the center of each subplot. Under the prevailing conditions, there was no vertical change in D at SETRES (Ewers and Oren 2000). Soil volumetric water content was measured with Theta probes along a vertical profile at 0.05, 0.1, 0.25, 0.5, 1.0 and 2.0 m depths in the center of the sap flux measurement cluster in each treatment. The 2.0-m probe was available from June to July 1998 and averaged only $0.002 m^3 m^{-3}$ higher than the 1.0-m probe with little variation. This deviation was used to estimate θ at 2 m for the rest of the data set. A mean root surface area weighted θ (θ_R) was calculated from root profiles to 1.9 m (Ewers et al. 2000). Xylem flux and all environmental sensors were sampled every 30 s and 30-min means were logged (DL2, Delta-T Devices).

In addition, an experiment of 8 days of continuous irrigation was performed to raise soil water content beyond that observed with natural precipitation (Ewers et al. 2000, 2001). The artificially elevated soil water content provides conditions more similar to those experienced by *Picea abies* in the less coarse sand of Flakaliden. The artificially elevated soil water content also provides data that are more similar to *Pinus taeda* in heavier soils (Hacke et al. 2000).

Calculation of transpiration

To calculate transpiration per unit leaf area (E_L), J_S was combined with $A_S:A_L$ as follows (Pataki et al. 1998, Oren et al. 1998a):

$$E_L = J_S \frac{A_S}{A_L} \quad (1)$$

Analyses of daily water use were performed on sums of E_L over 24-h periods beginning at 0500 h, which approximately corresponded to the time of zero flow, and therefore accounts for nighttime recharge (Phillips and Oren 1998). Diurnal mean D was calculated by averaging daytime D values only, the period in which D affects canopy transpiration, and therefore uptake (Phillips and Oren 1998). This value was normalized by daylight hours (determined as all half-hour intervals in which $Q_o > 0$) divided by 48 (D_Z ; Oren et al. 1996, Phillips et al. 1999) to permit analysis over a period with changing day length.

Canopy stomatal conductance

Mean canopy stomatal conductance to water vapor ($m\ s^{-1}$), was calculated from E_L and D using the simplification suggested by Monteith and Unsworth (1990):

$$G_S = \frac{K_G(T)E_L}{D} \quad (2)$$

where K_G is the conductance coefficient ($115.8 + 0.4236T$; kPa $m^3\ kg^{-1}$), which accounts for temperature effects on the psychrometric constant, latent heat of vaporization, specific heat of air at constant pressure and the density of air (Phillips and Oren 1998). This simplification requires the following conditions: (i) D is close to the leaf-to-air vapor pressure deficit, i.e., boundary layer conductance is high; (ii) there is no vertical gradient in D through the canopy; and (iii) there is negligible water stored above the J_S measurement position. Ewers and Oren (2000) showed that all three conditions are generally met at SETRES, as has been found for all treatments in Flakaliden (Phillips et al. 2001). To keep the measurement errors in G_S below 10%, G_S was calculated for $D \geq 0.6$ kPa only (Ewers and Oren 2000).

Annual transpiration

Annual transpiration (E_C) was calculated from relationships between D_Z and E_L and then multiplying E_L by the appropriate L . Annual E_C for *Picea abies* (Table 1) was calculated from D_Z for mid-April to October, which corresponds to the period when gas exchange occurs at Flakaliden (Bergh et al. 1998).

Statistical analysis

All statistical analyses were performed using GLM and MIXED procedures of the SAS statistical software package (Version 6.12, SAS Institute, Cary, NC). Nonlinear curve fits were performed with SIGMAPLOT software (Version 4.5, SPSS, San Rafael, CA) on individual trees with one of the fol-

lowing three functions: (1) $y = a + bx$; (2) $y = a(1 - e^{-bx})$; and (3) $y = a + b \ln x$. Subsequently, differences among the parameters were evaluated by ANOVA. Individual tree sap flux measurements and the resulting scaled variables were used as replicates. Therefore, standard errors for regression parameters are based on individual sap flux measurements scaled from the appropriate scalars from the subplot measurements. Boundary line analyses were performed with a program based on the methodology in Schäfer et al. (2000).

Data reduction

One approach to data reduction is to distill data to parameters that contain the information stored in the entire data set. Variation in diurnal G_S can often be explained mostly by D . By partitioning data into categories of soil water content, light and temperature, and performing a boundary line analysis on G_S versus D within each category, it can be reduced to the parameters describing the relationship between G_S and D (e.g., Chambers et al. 1985, Pezeshki and Hinckley 1988, Schäfer et al. 2000). The boundary line was derived by (1) partitioning the D into at least five different ranges; (2) calculating the mean and standard deviation of the G_S variable within each range of D ; (3) removing outliers ($P < 0.05$ Dixon's test, Sokal and Rohlf 1995); and (4) selecting data above the mean and standard deviation of G_S (Schäfer et al. 2000). These parameters can then be related to the categorizing variables. When a boundary analysis is made on the entire data set of each tree or a population, it produces the response under the best of the measured conditions (Martin et al. 1997). We used the function (3) $G_S = a - b \ln D$, in which a is G_{SR} , and b is $dG_S/d \ln D$, to describe the response of G_S to D . Applying them to the entire data set of each tree produced the highest G_{SR} of each tree and the accompanying G_S sensitivity to D . We verified that both species conformed to the general relationship of a proportionality between the two parameters (Oren et al. 1999), which facilitates another step in data reduction—where $dG_S/d \ln D$ can be expressed as a function of G_{SR} , all further evaluation of environmental effects on G_S can be restricted to analyses of G_{SR} .

Results

In *Picea abies*, the relationship between G_{SR} and $dG_S/d \ln D$ was similar in all treatments ($P > 0.5$; Figure 1A). Combining all trees from the five treatments resulted in a slope of 0.57 ($r^2 = 0.83$; $P < 0.001$), not significantly different from the general relationship ($P > 0.3$; Figure 1A). Because of the proportionality between G_{SR} and $dG_S/d \ln D$ in *Picea abies*, which was similar ($P > 0.8$) to that shown elsewhere for *Pinus taeda* in SETRES (0.57 in Ewers et al. 2000, Ewers et al. 2001), the hypothesized treatment effects on G_S were tested using G_{SR} . The ranking of mean G_{SR} in *Picea abies* was $Dr < F = C = I < IL$, based on a least significant difference test ($\alpha = 0.05$). In the *Pinus taeda* study, G_{SR} ranked $F < C = I < IF$ (the mean response from both studies is shown in Figure 1B). A two-way ANOVA with species and treatment as variables revealed a significant interaction ($P < 0.05$). In both *Pinus taeda* and *Picea abies*, G_{SR} in IF/IL trees was greater than in trees in all of

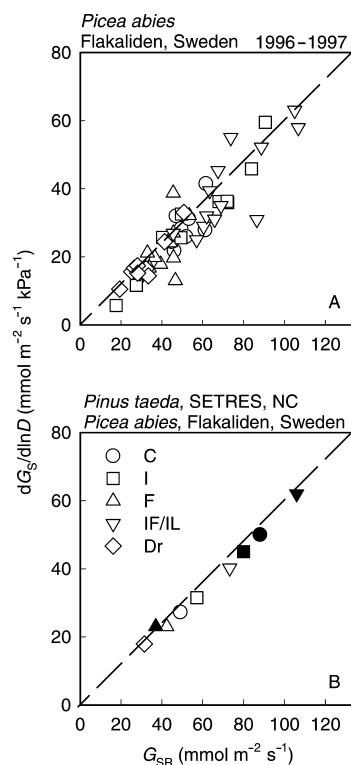


Figure 1. (A): Sensitivity of sap-flux-scaled, mean, canopy stomatal conductance to D ($dG_S/d\ln D$) versus stomatal conductance at vapor pressure deficit (D) = 1 kPa (G_{SR}) in control, irrigated, fertilized, irrigated/fertilized, and drought-exposed trees (C, I, F, IF/IL and Dr, respectively). (B): Mean $dG_S/d\ln D$ versus mean G_{SR} in *Picea abies* (open symbols) and *Pinus taeda* (closed symbols). Dashed lines represent the average relationship from Oren et al. (1999).

the other treatments ($P < 0.05$), and thus the difference between the species among the four similar treatments was that G_{SR} in F trees was less than in trees in the other treatments in *Pinus taeda*, but only tended to be lower in *Picea abies*. Under the best of conditions, G_{SR} in *Pinus taeda* was approximately twice that of *Picea abies* (Figure 1B) when the same treatments were compared.

Because the effect of D on G_S is captured in G_{SR} , the response of G_S to environmental variables in both species can be readily evaluated in terms of G_{SR} . In *Pinus taeda*, the data set was partitioned into days in which the minimum value of T was either \geq or $<$ 10 °C (Ewers et al. 2001). When T was \geq 10 °C, Q_o did not explain the variation in G_{SR} ($P > 0.3$), and only θ_R affected G_{SR} (Figure 2). The relationship between G_{SR} and θ_R for C, I and IF trees was described by Function 1 (Table 2; $P < 0.001$) but had a low coefficient of determination (Figure 2). The IF trees had a greater slope than the C and I trees (Table 2; $P < 0.05$). For F trees, the response was nonlinear ($P > 0.3$), and the exponential saturation Function 2 (Table 2) was used ($P < 0.001$). For clarity of presentation, the mean value of G_{SR} was plotted every 0.01 θ_R with the lines fitted through the data (Figure 2). To illustrate the range of data, an upper and lower boundary line analysis was performed,

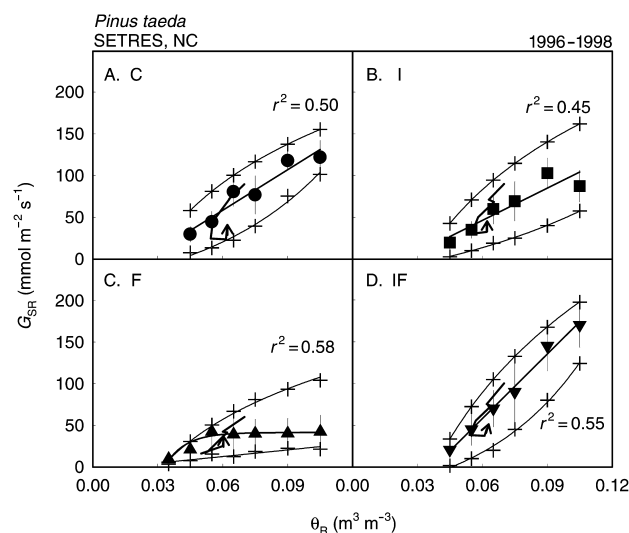


Figure 2. Sap-flux-scaled, mean, canopy stomatal conductance at vapor pressure deficit (D) = 1 kPa (G_{SR}) versus root weighted, volumetric soil water content (θ_R) in (A) control, (B) irrigated, (C) fertilized and (D) irrigated/fertilized *Pinus taeda*. Crosshairs represent the minimum and maximum boundary conditions, symbols represent the mean G_{SR} for every 0.01 θ_R and curves ending with arrows show hysteresis from consecutive days of a drying cycle.

again, for clarity, plotting only the mean of the boundary data in the 0.01 θ_R intervals. The breadth of G_{SR} response at each θ_R could be related to hysteresis in the relationship. This was evaluated by plotting the longest, continuously measured drying cycle (from August 15 to September 1, 1997) and the subsequent increase in θ_R as the curves ending with arrows in Figure 2. In each case, as drying occurred, G_{SR} declined with θ_R , but when the soil water content increased, a time lag became apparent in the response of G_{SR} .

In contrast to the large data set of *Pinus taeda* that allowed presentation of G_{SR} with θ_R for each treatment (Figure 3A), there was no overlap of θ_R among treatments in *Picea abies*. Thus, θ_R and treatment effects on G_{SR} were confounded. An upper boundary analysis on G_{SR} (G_{SRB}) with data for all treatments in *Picea abies* is shown in Figure 3B (for comparison, upper boundaries of *Pinus taeda* from Figure 2 are in Figure 3A). The boundary data represents conditions of low D (= 1 kPa) and most likely G_{SR} in the “upper portion” of the hysteresis curve for *Pinus taeda* (Figure 2). As can be seen, it was not possible to differentiate between a response of G_{SRB} to θ_R and treatment in *Picea abies* (Figure 3B). Note that although G_{SRB} in *Pinus taeda* reached high values in response to continuous irrigation (to the right of the dashed line in Figure 3A), the values under the highest native θ_R were approximately half the maximum value.

The effect of light on G_{SR} was investigated based on mean absorbed Q_o (Q_A) calculated with the Beer-Lambert law, a mean extinction coefficient of 0.5 (T. Albaugh for *Pinus taeda* and J. Bergh, Swedish University of Agricultural Sciences, for *Picea abies*, unpublished data) and the appropriate L . Mean Q_A of the canopy was calculated as Q_A/L . In *Pinus taeda*, only

Table 2. Regression parameters corresponding to the appropriate figure and function in the text for control (C), irrigated (I), fertilized (F), irrigated fertilized (IF/IL) and drought (Dr) trees, respectively.

Figure	Relationship	Parameters	C	I	F	IF/IL	Dr
<i>Pinus taeda</i>							
4	$G_S = f(Q_A/L)$	Function	2	2	2	2	
		a	10.7	8.8	4.0	7.2	
		b	0.01	0.01	0.01	0.01	
		r^2	0.53	0.52	0.49	0.40	
5	$E_L = f(D_Z)$	Function	2	2	2	2	
		a	0.52	0.49	0.26	0.48	
		b	3.0	2.5	2.4	2.8	
		r^2	0.79	0.76	0.75	0.82	
<i>Picea abies</i>							
4	$G_S = f(Q_A/L)$	Function	2	2	2	3	2
		a	3.9	2.6	4.3	3.4	6.8
		b	0.03	0.02	0.02	0.04	1.4
		r^2	0.44	0.30	0.50	0.65	0.48
5	$E_L = f(D_Z)$	Function	3	3	3	3	3
		a	0.40	0.27	0.39	0.32	0.55
		b	0.15	2.45	0.15	0.13	0.25
		r^2	0.94	0.91	0.82	0.87	0.90

Q_A/L explained the variation in G_{SR} when minimum T was $< 10^\circ\text{C}$, based on Function 2 (Table 2). For clarity, lines fitted to the data are plotted together with symbols for mean G_{SR} at every $50 \mu\text{mol m}^{-2}$ leaf area s^{-1} interval for each treatment and species (Figure 4A). In *Picea abies*, Function 2 (Table 2) was appropriate for all treatments except IL, which was best described by the log-linear Function 3 (Table 2, Figure 4B). There was no difference in the relationship between Q_A/L and G_{SR} for C, I and IF trees of *Pinus taeda* ($P > 0.1$), whereas F trees had a lower saturation value ($P < 0.05$; Table 2). In *Picea abies*, Dr trees had a lower saturation value than trees in the other treatments (Table 2; $P < 0.01$). A comparison between

species was not possible because data for *Pinus taeda* was limited to the temperature range that clearly affected G_{SR} .

Given the greatly differing G_{SR} between the species, and among treatments within each species, one might expect large differences in the rate of transpiration per unit leaf area at comparable vapor pressure deficits. This possibility was evaluated by relating daily E_L to D_Z with Function 2 (Figure 5A, Table 2). In *Pinus taeda*, E_L saturated at a lower value in F trees than in trees in the other treatments ($P < 0.01$). In *Picea abies*, Function 2 (Table 2) did not yield a significant relationship ($P > 0.2$) and the best fit for all treatments was provided by Function 3 (Table 2). The range of E_L at a given D_Z was similar, but there was a greater tendency for saturation at high D_Z in *Pinus*

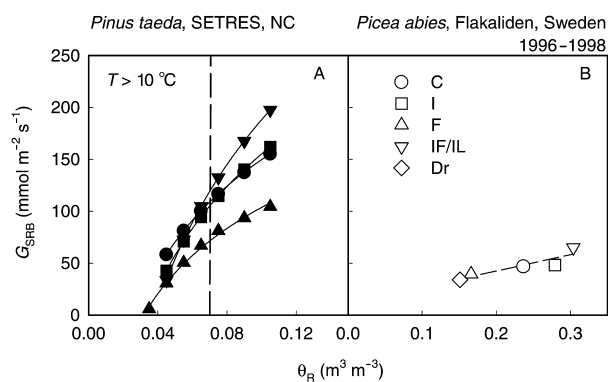


Figure 3. Sap-flux-scaled, mean, canopy stomatal conductance at vapor pressure deficit (D) = 1 kPa (G_{SRB}) versus maximum boundary conditions of root weighted volumetric soil water content (θ_R , from Figure 2) for control, irrigated, fertilized, irrigated/fertilized and drought trees (C, I, F, IF/IL and Dr, respectively) of (A) *Pinus taeda* and (B) *Picea abies*.

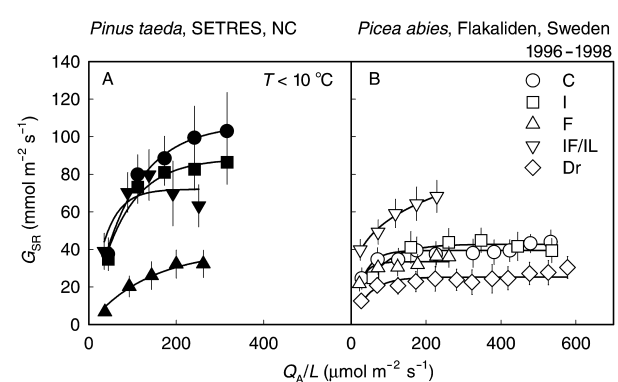


Figure 4. Sap-flux-scaled, mean, canopy stomatal conductance at vapor pressure deficit (D) = 1 kPa (G_{SR}) versus absorbed photosynthetic photon flux density per unit leaf area (Q_A/L) for control, irrigated, fertilized, irrigated/fertilized and drought-treated (C, I, F, IF/IL and Dr, respectively) trees of (A) *Pinus taeda* and (B) *Picea abies*. The parameters and coefficient of determination are provided in Table 2.

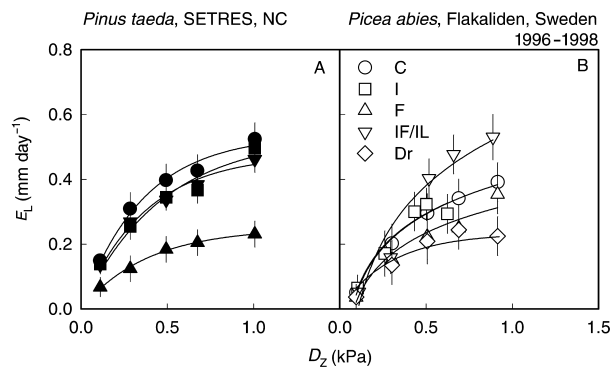


Figure 5. Transpiration per unit leaf area (E_L) versus mean daily vapor pressure deficit normalized by light hours (D_z) for control, irrigated, fertilized, irrigated/fertilized and drought-treated (C, I, F, IF/IL and Dr, respectively) trees of (A) *Pinus taeda* and (B) *Picea abies*.

taeda (Figures 5A and 5B). Annual transpiration (E_C) for both *Pinus taeda* and *Picea abies* is shown in Table 1.

Discussion

Although G_S was lower in *Picea abies* than in *Pinus taeda* under optimal soil water conditions (Figure 3) and at high irradiances (Figure 4), in contrast to our hypothesis, the ratio is similar to that reported from porometric measurements of maximum g_s . Our hypothesis that lower G_S would be accompanied by lower G_S sensitivity to D , was supported by the data, because both species in all treatments conformed to the same proportionality in their sensitivities to D and G_{SR} (Figure 1B). This is similar to the proportionality shown by many species (Oren et al. 1999), and is consistent with the role of stomata in regulating minimum xylem water potential (Sperry et al. 1998).

Values of G_{SR} for *Picea abies* were lower in F and Dr trees, but the difference, as hypothesized, was not as dramatic as in *Pinus taeda* (Figure 1B). In *Pinus taeda*, F trees produced fine roots with half the maximum hydraulic conductance found in trees in the other treatments (Ewers et al. 2000). However, unlike the comparisons among treatments for *Pinus taeda*, the comparisons for *Picea abies* are confounded by non-overlapping soil water contents among treatments (Figure 3B). Nevertheless, despite relatively similar soil water contents in the I and IL treatment plots (Figure 3B), and low maximum mean absorbed light (Q_A/L) in IL (Figure 4B), IL trees of *Picea abies* had higher G_{SRB} (maximum boundary of G_{SR}) than trees in the other treatments, a tendency also found in IF trees of *Pinus taeda* (Figure 3). Improved nutrition in the absence of a strong limitation of soil water content enhances photosynthesis (Linder and Troeng 1980). As a result, both species had a higher conductance in IF/IL despite the high leaf area index.

Soil water content plays a dominant role in regulating G_{SR} in *Pinus taeda* when $T \geq 10$ °C (Figure 2). This is because the coarse sandy soil, even at its highest native θ , is unable to supply water at an adequate rate (Hacke et al. 2000). When soil water content was maintained artificially high, G_S increased

sharply (Figure 2, θ_R values above $0.07 \text{ m}^3 \text{ m}^{-3}$). However, in F trees, G_S was limited, even at artificially high soil water contents, by maximum root hydraulic conductance (Ewers et al. 2000). Continuous decline in G_S , at a rate determined by soil texture, is indicative of deep rooting system such as in SETRES ($> 1.9 \text{ m}$), whereas a sudden sharp decline indicates a shallow root system ($< 0.3 \text{ m}$) in fine soils (Oren et al. 1998b).

The relationship between G_{SR} and θ_R in SETRES showed hysteresis (Figure 2) that may reflect (1) a hysteresis in the relationship between soil Ψ_s and θ following rehydration (Jury et al. 1991), (2) time lags in refilling cavitated xylem conduits (Tyree and Yang 1992) or (3) a non-hydraulic signal from the roots (Davies et al. 1990), and perhaps a combination of these processes. Hacke et al. (2000) found that, in *Pinus taeda* trees in C, E_L could only be modeled from hydraulic considerations during a monotonic decline in soil water, presumably because of time lags in recovery from cavitation. Uninterrupted estimates of G_{SR} were rare because of electrical failures at the site, so the time it takes for G_{SR} to recover completely (i.e., reach G_{SRB}) is unknown, but a partial recovery was noticeable 3 days after rehydration (Figure 3). For accurate modeling of the effect of soil water on G_S , the causes of hysteresis, and especially the time constants for recovery, must be quantified.

In *Pinus taeda*, Q_A/L appeared to affect G_{SR} only when minimum T was < 10 °C, i.e., not during the growing season. This is because the conditional sampling criteria for accepting data to estimate G_S ($D \geq 0.6 \text{ kPa}$) exclude most low light conditions during the growing season, but not during the cooler season when irradiances are generally lower, and soil water contents are higher (Ewers et al. 2001). In *Pinus taeda*, G_{SR} in the cooler season saturated with Q_A/L in all treatments, but reached lower values in F trees (Figure 4A). In *Picea abies*, G_{SR} saturated at much lower values of Q_A/L than *Pinus taeda*, except in IL trees, in which it showed no saturation (Figure 4B, Table 2). Thus, the increased water supply combined with high nutrition allows IL trees to use light more efficiently than F trees.

Soil water content played no important role in controlling G_S in *Picea abies*. Withholding water from Dr trees caused an insignificant reduction in L (Table 1) and G_S (Figure 1B), accompanied by an insignificant reduction in stem growth (6%). Similar results were noted in *Pinus sylvestris* L. in Sweden (Linder and Troeng 1980, Bengtson 1980). In contrast, *Pinus taeda* in sand may be under soil water content limitations continuously as seen by the response to θ_R above native values (Figure 3A). The G_{SRB} at high soil water content (Figure 3A) may better reflect G_S of *Pinus taeda*. If the G_{SRB} values from IL trees (Figure 3b) represent maximum G_S of *Picea abies*, then the difference between *Pinus taeda* and *Picea abies* is substantially greater than that shown between porometric measurements of maximum g_s (compare Roberntz and Stockfors 1998 to Murthy et al. 1996), and more in line with our hypothesis.

Higher G_{SR} in *Pinus taeda* leads to a greater decline in G_{SR} with increasing D than in *Picea abies* (Figure 1B). As a result of this and the soil water content limitations to *Pinus taeda* (Figure 3A), both species share a similar daily E_L in several

treatments, despite the much higher G_{SR} in *Pinus taeda* under native soil water conditions (Figure 5). Both species are similar unless soil water content is artificially elevated (Figure 3). This means that for F and IF/IL trees, daily stand transpiration at an equivalent D_Z will be higher in *Picea abies* because of its higher L (Table 1). Although daily transpiration was higher in IL trees of *Picea abies*, the seasonal transpiration was 0.70 that of IF trees of *Pinus taeda* (Table 1). The disparities between species were even greater in the other treatments (*Picea abies* was 0.29, 0.35 and 0.54 of *Pinus taeda* for C, I and F, respectively). The seasonal transpiration data represent more of a comparison of climate between SETRES and Flakaliden than between the species. The differences were large because the climate allows year-round photosynthetic activity in *Pinus taeda* (Ellsworth 1999) but only from mid-April to October in *Picea abies* (Bergh et al. 1998), and because during the active period, the mean D_Z at Flakaliden is half the mean D_Z of SETRES.

Although the daily E_L of *Pinus taeda* is similar to *Picea abies*, stem growth rate of *Pinus taeda* was 2–3 times higher than that of *Picea abies* in the respective treatments (Albaugh et al. 1998, Bergh et al. 1999), which is similar to the magnitude of E_C . A diagnostic analysis by Timmer (1985) was adapted to investigate the relative treatment response of G_{SR} , L , Q_A and stem growth (including branches). The value of Q_A was summed over the growing season, June through September in Flakaliden, and April through October in SETRES. The analysis quantifies the vector of a response relative to a reference position. In the analysis, either C or I trees were used as references for F (and Dr) or IF/IL tree responses, respectively. We set G_{SR} , L , Q_A and stem growth of C and I trees to 1.0, and positioned the responses of trees in other treatments relative to that of their respective reference. The resulting changes from C to F, I to IF/IL, or C to Dr are shown as vectors (Figure 6).

In *Pinus taeda*, improved nutrition increased L by ~ 1.8 in both treatments, accompanied by an increase in G_{SR} of 1.1 in IF trees, but a sharp decline in F trees to ~ 0.5 . In contrast, in

Picea abies, improved nutrition increased L by ~ 3.5 in both treatments, accompanied by an increase in G_{SR} of 1.3 in IL trees, and a small decrease to 0.9 in F trees. Thus, the shade-tolerant *Picea abies* responded to nutrient and water amendments by increasing L nearly twice as much as the shade-intolerant *Pinus taeda*, but both increased their G_S . Unlike *Picea abies*, *Pinus taeda*, faced with water limitations, responded to increased demand for water created by higher L by greatly reducing its G_S .

The increase in L in response to increased nutrition caused different impacts on G_{SR} depending on water supply (Figure 6A). Nevertheless, stem growth of both species increased in similar proportion with nutrition (~ 2.5 -fold in *Pinus taeda* and ~ 3.0 -fold in *Picea abies*), regardless of water supply, and in relation to the growing season increase in Q_A , which is highly correlated with L (Figure 6B). The decoupling between the responses of mean canopy conductance and stem growth was especially evident in F trees of *Pinus taeda*, where G_{SR} decreased to about half, whereas growth more than doubled, a growth response similar to IF trees where conductance actually increased. It is possible that G_S in F trees is still above the values that restrict carbon assimilation. In *Pinus taeda* seedlings with high foliar N, photosynthesis was 0.75 of maximum when g_s was 0.5 of maximum (Green and Mitchell 1992). Such a response, combined with a significant reduction in carbon allocation to coarse and fine roots in F trees (Ewers et al. 2000), may explain the ability of F trees to keep up stem wood production similar to IF trees, despite a similar leaf area index and much lower stomatal conductance.

With increased nutrition, shade-intolerant *Pinus taeda* responded less with increased leaf area than *Picea abies*, but all trees of both species produced stemwood in direct proportion to the radiation absorbed, which is dependent on leaf area, the length of growing season and irradiance (cf. Bergh et al. 1999). With more favorable environmental conditions, *Pinus taeda* produced more than twice as much stemwood in each treatment as *Picea abies*. However, on a relative basis, *Picea abies* responded to nutrition more than *Pinus taeda*, mostly because of a greater increase in L (Figure 6). Thus, differences in canopy stomatal conductance between these species growing in very different environments had little effect on the difference in stemwood production, in absolute or relative terms. On the other hand, the reduction in stomatal conductance in F trees of *Pinus taeda* may have been responsible for lowering total production to 0.83 relative to IF trees (Albaugh et al. 1998).

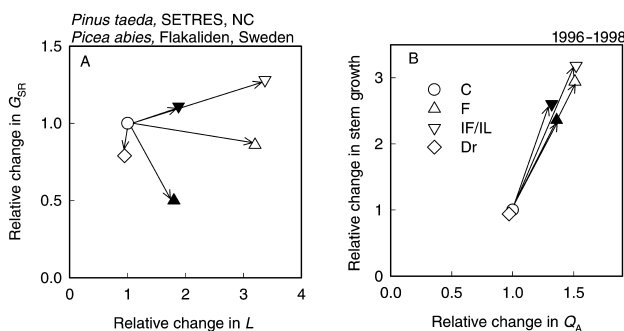


Figure 6. (A): Relative change in mean canopy sap-flux-scaled stomatal conductance at vapor pressure deficit (D) = 1 kPa (G_{SR}) in fertilized (F) relative to control (C), irrigated-fertilized (IL/IF) relative to irrigated (I), and drought (Dr) relative to C in relation to respective relative change in leaf area index (L). (B): Same relative changes between each two treatments as in (A) except that growing season absorbed radiation (Q_A) is related to stem growth. The parameters and coefficient of determination are provided in Table 2.

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