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Arne Sellin, Priit Kupper. Within-crown variation in leaf conductance of Norway spruce: effects of irradiance, vapour pressure deficit, leaf water status and plant hydraulic constraints. *Annals of Forest Science*, 2004, 61 (5), pp.419-429. 10.1051/forest:2004035 . hal-00883772

**HAL Id: hal-00883772**

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Submitted on 11 May 2020

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# Within-crown variation in leaf conductance of Norway spruce: effects of irradiance, vapour pressure deficit, leaf water status and plant hydraulic constraints

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(Received 2 January 2003; accepted 20 August 2003)

**Abstract** – Responses of leaf conductance ( $g_L$ ) to variation in photosynthetic photon flux density, leaf-to-air vapour pressure difference, shoot water potential and soil-to-leaf hydraulic conductance ( $G_T$ ) were studied in *Picea abies* (L.) Karst. foliage with respect to shoot age and position within the canopy. The upper canopy shoots demonstrated on average 1.6 times higher daily maximum  $g_L$  as compared to the lower canopy shoots growing in the shadow of upper branches. Functional acclimation of the shade foliage occurred in the form of both a steeper initial slope of the light-response curve and a lower light-saturation point of  $g_L$ . The mean  $G_T$  was 1.6–1.8 times bigger for the upper canopy compared to the lower canopy. We set up an hypothesis that stomatal conductance at the base of the live crown is constrained not only by low light availability but also by plant's inner hydraulic limitations.

**foliage age / leaf conductance / photosynthetic photon flux density / soil-to-leaf conductance / vapour pressure difference**

**Résumé** – **Variation de la conductance foliaire dans les couronnes de l'Épicéa : effets de l'éclairage, du déficit de vapeur d'eau dans l'air, de l'état hydrique des feuilles et des contraintes hydrauliques des arbres.** Les réponses de la conductance foliaire ( $g_L$ ) aux variations de la densité de flux photosynthétique de photons, du déficit de saturation de l'air, du potentiel hydrique des rameaux et de la conductance hydraulique ( $G_T$ ) dans le transfert Sol-feuille ont été étudiées chez *Picea abies* (L.) Karst. En relation avec l'âge des rameaux et leur position dans la canopée. Les rameaux de la partie supérieure de la canopée présentent des valeurs journalières maximum moyennes de  $g_L$  1,6 fois plus élevées que les valeurs correspondantes de  $g_L$  des rameaux des parties basses de la canopée se développant à l'ombre des branches les plus hautes. Une acclimatation fonctionnelle du feuillage à l'ombre se manifeste par une pente initiale plus élevée de la courbe de réponse à la lumière et un point de saturation de  $g_L$  plus bas. La moyenne de  $G_T$  était de 1,6 à 1,8 fois plus grande pour la partie basse de la canopée. Nous avançons l'hypothèse que la conductance stomatique à la base de la couronne vivante est conditionnée par les bas niveaux de lumière disponible mais aussi par les limitations hydrauliques internes de l'arbre.

**âge du feuillage / conductance foliaire / densité de flux photosynthétique de photons / conductance du transfert sol-feuille / déficit de saturation**

## 1. INTRODUCTION

Compared to herbaceous species, trees present a more complicated case for the study of physiological processes, even due to the large size of the woody plants and considerable environmental gradients within deep canopies. Besides, environmental conditions change permanently with stand development. Trees have to develop foliage with both physiological and morphological traits permanently acclimatizing to spatially and temporally changing conditions within the canopy. Both stomatal conductance and light-saturated photosynthetic capacity exhibit a declining trend with the decrease in light availability from the top to the bottom of the canopy [1, 6, 34], and it is generally

accepted that at the base of the canopy these processes are limited by low irradiance, i.e. by light competition. At the base of a live crown, there is insufficient light energy to maintain a positive carbon balance within branches, and the branches are not able to develop new buds and support leaves [38, 55].

There is evidence for many plant species that variation in stomatal conductance, crown conductance and transpiration is closely associated with variation in the total hydraulic conductance of the soil-to-leaf pathway,  $G_T$  [16, 21, 50, 51]. Thus, a homeostatic balance has to exist between transpiration rate, leaf area, sapwood area, and the hydraulic capacity of the stem to supply water to leaves [53, 57, 58]. The long-term implication of this

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balance would be that adjustment of these characteristics could serve to maintain similar water potential gradients in trees despite environmental differences between growth sites [23]. The functional relationship between water loss from the foliage and water transport capacity of the stem maintains leaf water status remarkably constant over a wide range of environmental conditions. For a given soil-to-leaf hydraulic conductance, the value of stomatal conductance required to maintain leaf water potential at its daily minimum set point will depend on the atmospheric evaporative demand. Therefore, stomatal responses to atmospheric humidity must also be considered in interpreting co-ordination of vapour and liquid phase water transport properties, because homeostasis of bulk leaf water status can only be achieved through regulation of the actual transpirational flux [19].

There is a growing body of evidence that trees' hydraulic conductance may limit stomatal conductance and net photosynthesis, and therefore the growth of older and higher trees [11, 16, 37]. McDowell et al. [18] suggested that the path length from bulk soil to leaf rather than tree height per se is the relevant term. As trees grow taller,  $G_T$  declines causing stomata to close earlier in the day to restrain water losses and prevent the development of damaging water potential gradients. This leads to lower intercellular  $\text{CO}_2$  concentration, decreased net photosynthetic rate and net primary production during forest maturation. Fischer et al. [8] reported a decrease in the whole-tree hydraulic conductance with increasing tree size in *Pinus flexilis* James growing in a high-elevation meadow, while  $G_T$  did not show clear trends with tree size in *Pinus ponderosa* Dougl. ex Laws. The experiments carried out on seedlings of *P. ponderosa* by manipulating the stem hydraulic conductivity confirmed that changes in  $G_T$  affect both stomatal conductance and plant carbon gain [12]. However, Niinemets [28] recently analyzed a huge amount of data on *Picea abies* (L.) Karst. and *Pinus sylvestris* L., covering 126 stands of various height and age, and concluded that stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size. In addition to size-related changes in foliar morphology, stomatal conductance, and carboxylation activity, he supposed the effect of increasing diffusive resistance between the intercellular air space and carboxylation sites in chloroplasts due to modifications in leaf structure with increasing tree height.

Overall, trees' hydraulic capacity has undoubted implications for their performance, influencing also other aspects of plant life (e.g. duration of leaf growth [26]) besides stomatal conductance, net photosynthesis, and primary production. Even geographic distribution of woody species is considered to be associated with xylem hydraulic properties, and with xylem vulnerability to cavitation in particular [3]. At the same time, the relationships between leaf functioning within an individual crown and traits of the plant hydraulic architecture are still poorly understood [10, 13]. In the recent past a great deal of data has been published on the hydraulic conductance of whole trees, obtained by using the evaporative flux method. However, Meinzer et al. [22] warned against possible errors due to the big variation in transpiration rate and leaf water potential within the crown.

Leaf conductance is one of the factors controlling water transfer through the soil-plant-atmosphere continuum and, thus, it is a key variable for understanding water and gas exchange

**Table I.** Meteorological data on the study periods in 1997 and 2000 from Jõgeva Meteorological Station of the Estonian Meteorological and Hydrological Institute, situated 21 km west of Vooremaa Ecology Station.

Characteristic	Month	Jõgeva	
		1997	2000
Mean air temperature (°C)	June	15.8	14.0
	July	17.6	16.1
	August	17.9	15.0
Mean vapour pressure deficit (kPa)	June	0.59	0.53
	July	0.55	0.38
	August	0.74	0.36
Precipitation (mm)	June	79.6	66.8
	July	59.4	126.3
	August	32.0	70.1
Number of rainy days (precipitation $\geq$ 1 mm)	June	11	9
	July	7	16
	August	3	11
Duration of sunshine (h)	June	284	302
	July	319	205
	August	374	213

processes in trees, both at plant and stand scales.  $g_L$  is regulated by biological and environmental variables, but the relative importance of various control mechanisms is poorly understood. The goals of the present study were to: (1) establish the within-crown variation in leaf conductance of Norway spruce depending on the level of irradiance and vapour pressure deficit; (2) assess the contribution of the leaf water status and liquid phase conductance to the control of leaf conductance in relation to the shoot position within a canopy. The results provided here can be used in further studies of trees' water relations and gas exchange. They may be useful for developing dynamic tree models, so far complex structural-functional models mostly disregard stomatal function [46].

## 2. MATERIALS AND METHODS

### 2.1. Study area and sample trees

The study was carried out at Vooremaa Ecology Station (58° 44' N, 26° 45' E), eastern Estonia, from June to August in 1997 (on 18 days) and 2000 (on 21 days). The annual precipitation in the Vooremaa area ranges from 600 to 630 mm, while 400 to 410 mm of this falls during the growing season, i.e. during the period when the mean diurnal air temperature is above +5 °C. The mean monthly air temperature ranges between -6.6 °C and +17.3 °C. The annual sum of the global short-wave radiation averages 3518 MJ·m<sup>-2</sup>, and the annual radiation budget, 2552 MJ·m<sup>-2</sup> [35]. Main meteorological data on the study periods in 1997 and 2000 is presented in Table I.

The studies were carried out on 20-year-old Norway spruce (*Picea abies* (L.) Karst.) trees growing in a well-conditioned forest plantation of the *Oxalis* site type [31]. Height of the sample trees ranged from

11.2 to 12.0 m, their diameter at breast height varied from 10.1 to 15.8 cm in 2000. The soil was a rich, well to moderately drained, brown forest soil (Calcaric Cambisol according to FAO classification) formed on red-brown calcareous moraine [33]. The  $\text{pH}_{\text{H}_2\text{O}}$  of the rooted zone was 5.2. A detailed description of the climate, soil and vegetation of the study area has previously been published by Frey [9].

## 2.2. Plant water relations

Plant water relations were studied in the basal and top thirds of the crowns of three neighbouring spruce trees accessible from a wooden tower erected between the sample trees. Bulk water potential ( $\Psi_x$ ; MPa) of shoots was measured by the balancing pressure technique using a Scholander-type pressure chamber [2]. On each day of observation, 6 current-year shoots (3 from the lower and 3 from the upper canopy) taken from the trees were sampled just before sunrise (i.e., 0300 to 0500 h), and then at two-hourly intervals from 0500 to 2100 h, East European standard time. Leaf conductance ( $g_L$ ;  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) to water vapour and transpiration rate ( $E$ ;  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) were measured with a LI-1600M steady-state diffusion porometer (LI-COR, Lincoln, USA) equipped with a cylindrical leaf chamber. In 1997 the porometric measurements were carried out on current-year, 1-year-old and 2-year-old shoots in both the basal and top thirds of the crowns. In 2000, the current-year to 3-year-old shoots were sampled in the upper canopy, while in the lower canopy the exact determination of shoot age was impossible. Because of the deep shadow in the lower canopy layers no new buds or shoots had developed during the previous years; the age of the existing shoots was estimated at  $\geq 3$  years. The porometric measurements were made at two-hourly intervals from 0500 to 2100 h, the number of replications was 3 per each shoot age class and canopy layer. Both  $E$  and  $g_L$  were expressed on the basis of projected area of needles. Leaf temperature was measured with fine copper-constantan thermocouples installed in the porometer.

The changes in leaf conductance, depending on the vapour pressure difference ( $VPD$ ) between the leaf interior and the bulk air, were analysed according to Oren et al. [29, 30]:

$$g_L = -m \cdot \ln VPD + b, \quad (1)$$

where  $m$  and  $b$  are parameters generated in a least-squares regression analysis. The parameter  $b$  is a reference conductance at  $VPD = 1$  kPa, the parameter  $-m$  quantifies the stomatal sensitivity to  $VPD$ .

$$-m = -dg_L/d \ln VPD, \quad (2)$$

while  $m$  is constant over the entire range of  $VPD$  and thus permits comparison of the data independently of specific  $VPD$  ranges.

On the basis of transpiration rates and water potential differences between the soil and leaves, soil-to-leaf hydraulic conductance ( $G_T$ ;  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ ) was determined and expressed per unit leaf area [47, 60], while the boundary layer conductance was assumed to approach infinity:

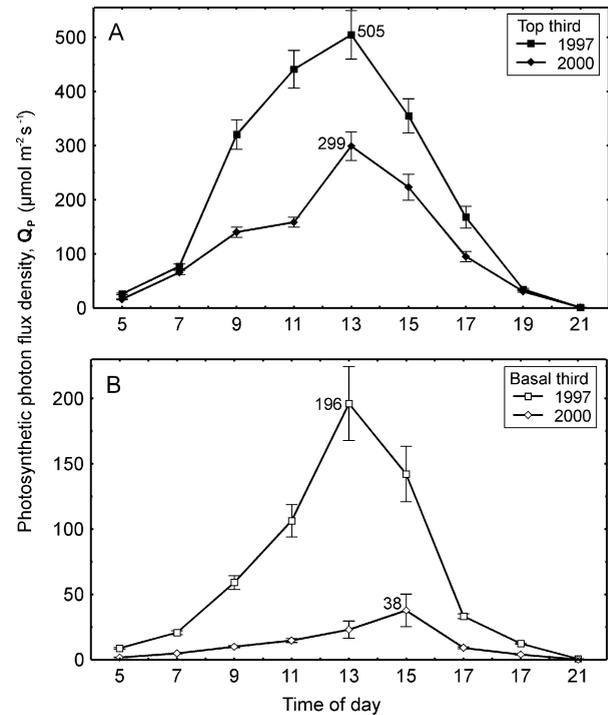
$$G_T = \frac{E}{\Psi_s - \Psi_x}, \quad (3)$$

where  $\Psi_s$  is water potential (MPa) of the wettest soil layer of those monitored with soil hygrometers.  $G_T$  was calculated as a slope of the regression of  $E$  from  $\Delta\Psi$ ; it is a measure of whole-plant water transport efficiency based on the liquid water flux per unit driving force.

To determine an optimum water potential for leaf conductance, the data of  $g_L$  were plotted against shoot water potential and smoothed using a polynomial of the third order. As the dependence of  $g_L$  on  $\Psi_x$  was assumed to have one maximum,  $\Psi_x^*$  at which the first derivative of the equation equals zero, was taken as the water potential optimum.

## 2.3. Environmental characteristics

Soil water potential ( $\Psi_s$ ) at a depth of 20, 40 and 60 cm was determined by using a dew-point microvoltmeter HR-33T-R equipped with



**Figure 1.** Generalized daily patterns of photosynthetic photon flux density within the crowns of trees. The numbers beside some symbols indicate the means of the daily maxima. The data points represent arithmetic means of the measurements at certain times of day, and the bars indicate  $\pm$  SE of the means.

soil hygrometers PCT-55 operating in the psychrometric mode [4]. Relative humidity of the air (%) was recorded using a Vaisala HUMICAP humidity sensor, and air temperature with copper-constantan thermocouples installed in the porometer. Vapour pressure difference ( $VPD$ ) was calculated from the saturation vapour pressure at the leaf temperature and the ambient vapour pressure. Photosynthetic photon flux density ( $Q_p$ ;  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) was measured with a LI-190S-1 quantum sensor attached to the porometer.  $Q_p$  was recorded simultaneously with stomatal conductance measurements at 15 to 24 points within the crowns depending on the number of sample shoots. Care was taken to hold the sensor head of the porometer horizontally and to match cuvette conditions to ambient temperature and humidity during the measurements. The differences in photosynthetic photon flux densities between the lower and upper canopy have been presented in Figure 1.

## 2.4. Projected area of needles

After porometer measurements, shoots were brought to the laboratory and the needles were carefully detached from the twigs with tweezers. All needles were fixed on a transparent adhesive tape and photographed with a standard, using opaque background illumination to produce black-and-white images of the needle projections. The standard was a drawing consisting of black needle-like shapes on a transparent film. After that the needles were removed from the tape, oven-dried at 80 °C for 48 h, and then weighted.

The slides of the needle projections were scanned with HP ScanJet 4c/T scanner (Hewlett-Packard Co., Palo Alto, USA) and digitized using Corel Photo-Paint, version 5.0 (Corel Corp., Ottawa, Canada).

The area of the digitized images was measured using a program PIN-DALA, version 1.0 (designed by I. Kalamees, Eesti Loodusfoto, Tartu, Estonia), while all measurements were corrected separately using the standard with known area. The error of the area measurements was 1.5% on average, maximally 2.6%.

## 2.5. Leaf conductance model

To explore the combined effects of irradiance, atmospheric evaporative demand, and the plant liquid phase conductance, on the dynamics of  $g_L$ , a phenomenological model was developed. We used a Jarvis-type approach, assuming that leaf conductance is affected by non-synergistic interactions between plant and environmental variables [14, 46]. Specific model parameters were derived for each shoot age class and canopy level. As for irradiance, we proceeded from the equation describing curvilinear increase in  $g_L$  in response to growing irradiance and allowing for the possibility that stomata are open in the dark [7, 14, 43]:

$$g_L = \frac{g_{\max} \cdot c_1 \cdot (Q_p + q)}{g_{\max} + c_1 \cdot (Q_p + q)}, \quad (4)$$

where  $Q_p$  is the incident photosynthetic photon flux density,  $g_{\max}$  is the maximum value of  $g_L$  at infinite  $Q_p$ , and  $c_1$  is  $dg_L/dQ_p$  at  $Q_p = 0$ .

$$q = \frac{c_2}{c_1}, \quad (5)$$

if it is assumed that the initial slope of the response curve is nearly linear.  $c_2$  is the value of  $g_L$  in the dark, and is given by the intercept on the ordinate.  $c_2$  is introduced to allow for the stomata being open at night, and is not intended to be a cuticular conductance.  $c_2$  was computed as an absolute term and  $c_1$  as a slope of the regression of leaf conductance from photon flux density at low irradiance ( $Q_p < 30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) in the morning and evening:

$$g_L = c_1 \cdot Q_p + c_2. \quad (6)$$

The light-saturation point of leaf conductance to water vapour was taken as the value of  $Q_p$  corresponding to the value of 95% of  $g_{\max}$  calculated from equation (4) by using the boundary line technique [49, 56].

Preliminary data analysis indicated that maximum leaf conductance depends asymptotically on plant hydraulic conductance, therefore  $g_{\max}$  was expressed as a logistic function of  $G_T$ :

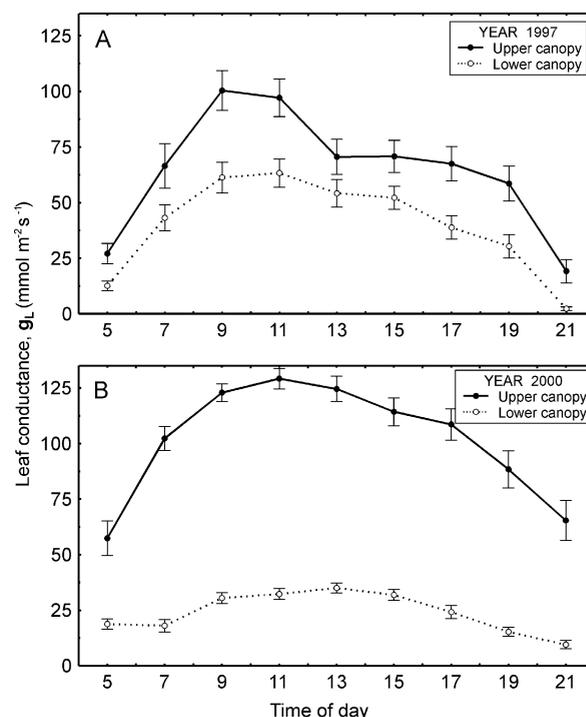
$$g_{\max} = \frac{g_{\text{asy}}}{1 + c_3 \cdot e^{c_4 \cdot G_T}}, \quad (7)$$

where  $g_{\text{asy}}$  is the asymptotic value of leaf conductance at saturating light intensities found for each data set using the boundary line technique.  $c_3$  and  $c_4$  are empirical constants, while  $c_4$  affects the rate of decline in  $g_L$  from the asymptotic value.

To account for the effect of atmospheric evaporative demand on leaf conductance, the additional term  $f(VPD)$  was included in the model:

$$g_L = \frac{g_{\max} \cdot c_1 \cdot (Q_p + q)}{g_{\max} + c_1 \cdot (Q_p + q)} \cdot \frac{1}{\sqrt{(1 + (c_5 \cdot VPD)^2)^{c_6}}}, \quad (8)$$

where  $c_5$  and  $c_6$  are empirical constants, while  $c_6$  affects the decline in the leaf conductance from its daily maximum values. The higher the value of  $c_6$ , the greater the decline in  $g_L$  at high  $VPD$ . When  $c_6 = 0$ , the second term of equation (8) equals one. The empirical parameters  $c_3$  to  $c_6$ , specific for each age class of the shade and sun foliage, were found using multivariate optimization based on the least squares estimation procedure.



**Figure 2.** Spatial and temporal variation in leaf conductance in the current-year and older (lower canopy in 2000) foliage. The number of replications ranged from 20 to 60 at different times of day in different data sets. The bars indicate  $\pm$  SE of the means.

Model performance was estimated by the coefficient of determination ( $R^2$ ) and index of agreement ( $d$ ) developed by Willmott [49, 59]:

$$d = 1 - \frac{\sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n [ |P_i'| + |O_i'| ]^2} \quad (9)$$

where  $P_i$  and  $O_i$  are the predicted and observed values, respectively.  $P_i' = P_i - \bar{O}$ , and  $O_i' = O_i - \bar{O}$ , where  $\bar{O}$  is the average observed value. The index of agreement is a measure of the degree to which model's predictions are error free, varying between 0 and 1. A value of 1.0 expresses perfect agreement between observed and predicted values, and 0.0 describes complete disagreement.

## 3. RESULTS

### 3.1. Responses of leaf conductance to irradiance

Responses of leaf conductance to  $Q_p$  depended on foliage position within a canopy (i.e., sun or shade foliage) and foliage age. Sun needles demonstrated substantially higher leaf conductances as compared to shade needles (Fig. 2). In sun shoots of younger age classes, the overall maxima of  $g_L$ , calculated as an arithmetic mean of the 10 largest records during the study period [54], were 1.3–1.4 times higher, and the means of daily maxima, 1.6 times higher than those in shaded shoots (Tab. II).

**Table II.** Main parameters characterizing the daily patterns of leaf conductance for shade and sun foliage of different ages (zero denotes the current-year foliage) depending on irradiance. <sup>a</sup> Arithmetic mean of the 10 largest records during the study period; <sup>b</sup> mean of the records at 0900 h; <sup>c</sup> mean of the records at 1100 h; <sup>d</sup> mean of the records at 1300 h.

Foliage age (yr)	Year	Mean leaf conductance if $Q_P = 0$ ( $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )			Mean initial slope of the light-response			Light-saturation point of leaf conductance ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )		Maximum leaf conductance $\pm$ SE ( $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )			
		Shade	Sun	$P$	Shade	Sun	$P$	Shade	Sun	Overall maximum <sup>a</sup>		Mean of daily maxima	
										Shade	Sun	Shade	Sun
0	1997	5.4	17.5	ns	1.65	0.48	< 0.05	82	131	151 $\pm$ 5.4	198 $\pm$ 5.6	63 <sup>c</sup> $\pm$ 6.3	100 <sup>b</sup> $\pm$ 8.9
	2000	–	68.6	–	–	0.39	–	–	57	–	193 $\pm$ 4.8	–	129 <sup>c</sup> $\pm$ 4.6
1	1997	12.1	20.6	ns	1.59	0.75	ns	26	138	137 $\pm$ 5.9	188 $\pm$ 10.3	56 <sup>c</sup> $\pm$ 5.4	90 <sup>b</sup> $\pm$ 8.1
	2000	–	70.3	–	–	0.51	–	–	53	–	170 $\pm$ 1.1	–	117 <sup>c</sup> $\pm$ 3.9
2	1997	18.5	34.0	ns	1.85	1.14	ns	27	146	149 $\pm$ 7.1	194 $\pm$ 7.4	58 <sup>c</sup> $\pm$ 5.4	91 <sup>c</sup> $\pm$ 7.7
	2000	–	102.5	–	–	0.32	–	–	26	–	219 $\pm$ 3.3	–	126 <sup>c</sup> $\pm$ 4.7
$\geq 3$	2000	17.1	67.6	< 0.001	0.84	0.63	ns	6	17	74 $\pm$ 1.9	153 $\pm$ 2.0	35 <sup>d</sup> $\pm$ 2.3	88 <sup>c</sup> $\pm$ 3.7

For older ( $\geq 3$  years) shoots, the differences in maximum leaf conductance between the lower and upper canopy were considerably larger. There were no significant differences between the current-year and up to 2-year-old shoots, while the older foliage demonstrated substantially lower maxima of  $g_L$ .

The shade needles demonstrated a steeper initial slope of the  $g_L$  response curve as compared to the sun needles, although the difference was statistically significant ( $P < 0.05$ ) only for the current-year shoots (Tab. II). Stomata of the sun foliage were more open at dawn and sunset as compared to shade foliage, this evidently being related to the maximum level of  $g_L$ . Stomatal openness increased with age from the current-year to 2-year-old shoots, while in older shoots ( $\geq 3$  years),  $g_L$  in the darkness was lower. The light-saturation of leaf conductance to water vapour in the lower canopy was achieved at photon flux densities substantially lower than those for the upper canopy. The initial slope of the light-response curve, the leaf conductance at zero irradiance, as well as the light-saturation point, varied among the study years, giving evidence of the stomatal acclimation to specific meteorological conditions. The summer of 2000, July and August in particular, were substantially cooler, cloudier and rainier than those of 1997 (Tab. I). There was no statistically significant relationship between  $g_L$  and  $Q_P$  in the midday period, except for the current-year sun foliage in 1997 (slope  $-0.0223$ ,  $P < 0.05$ ).

### 3.2. Effects of atmospheric evaporative demand, leaf water status and plant hydraulic conductance

The effects of atmospheric evaporative demand and plant hydraulic factors on  $g_L$  were analysed in the midday period (1100 to 1300 h), when the irradiance had mostly achieved saturating levels. Leaf conductance tended to respond more sensitively to changes in  $VPD$  in sun shoots (Tab. III), although the differences between the means for the lower and upper canopy were statistically insignificant. On the other hand, the differences in stomatal sensitivity to  $VPD$  between the two study years for the current-year and 1-year-old foliage were significant ( $P < 0.05$ ): the stomata were less sensitive to atmospheric evaporative demand in the cool and rainy summer of 2000. Stomatal sensitivity was positively related to the overall maximum

**Table III.** Mean stomatal sensitivity ( $\pm$  SE) to the vapour pressure difference ( $VPD$ ) between the leaf interior and the bulk air in the midday period. Zero denotes the current-year foliage. Statistical significance for mean values: <sup>a</sup>  $P < 0.05$ , <sup>b</sup>  $P < 0.01$ , <sup>c</sup>  $P < 0.001$ .

Foliage age (yr)	Year	Stomatal sensitivity to $VPD$ , $-m$	
		Shade	Sun
0	1997	54.8 <sup>c</sup> $\pm$ 10.7	68.6 <sup>c</sup> $\pm$ 13.4
	2000	–	37.0 <sup>c</sup> $\pm$ 10.1
1	1997	43.2 <sup>c</sup> $\pm$ 9.4	61.3 <sup>c</sup> $\pm$ 13.4
	2000	–	27.9 <sup>b</sup> $\pm$ 8.6
2	1997	52.6 <sup>c</sup> $\pm$ 8.1	60.8 <sup>c</sup> $\pm$ 8.9
	2000	–	47.8 <sup>c</sup> $\pm$ 9.5
$\geq 3$	2000	13.3 <sup>a</sup> $\pm$ 5.6	25.2 <sup>b</sup> $\pm$ 8.0

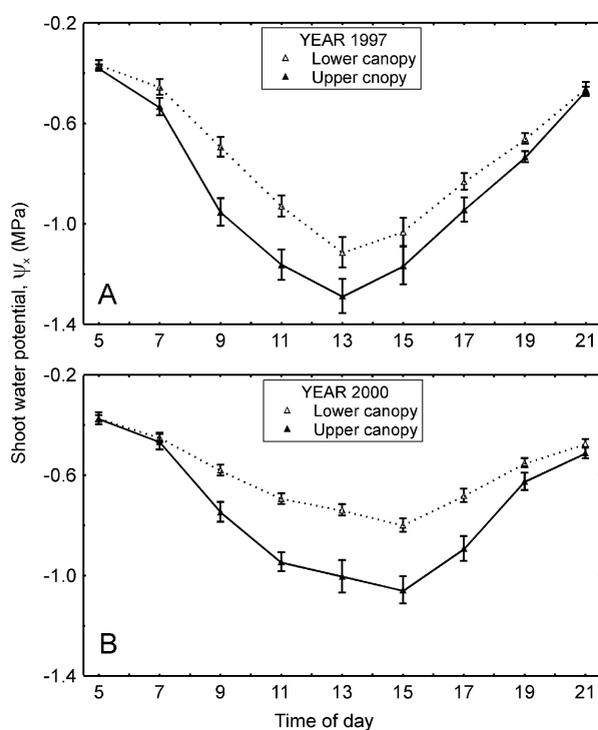
$g_L$  ( $R^2 = 0.403$ ,  $P < 0.05$  for all data sets taken together), while there was a strong relationship ( $R^2 = 0.944$ ,  $P < 0.001$ ) between  $-m$  and  $g_{\text{max}}$  when the 1997 data sets were analysed separately.

The daily patterns of shoot water potential in the lower and upper canopy have been presented in Figure 3. The optimum water potential for leaf conductance turned out to be  $-0.76$  and  $-0.86$  MPa for the shade and sun foliage, respectively. The effect of leaf water potential on  $g_L$  of the shade foliage around midday in 1997 was rather marginal ( $R^2 = 0.097$ – $0.102$ ) or insignificant, the effect on the sun foliage was stronger ( $R^2 = 0.276$ – $0.316$ ). In summer 2000, the relationship between  $\Psi_x$  and  $g_L$  was still weaker. Overall, the effect of  $\Psi_x$  on leaf conductance was more pronounced in sun foliage if to judge by higher values of the slopes for the  $g_L = f(\Psi_x)$  regressions (Tab. IV). For all data sets, leaf conductance tended to respond more sensitively to changes in  $VPD$  at lower shoot water potentials.

The mean hydraulic conductance of the soil-to-leaf transport pathway was 1.6–1.8 times higher ( $P < 0.001$  for all needle age classes) for the upper canopy as compared to that for the lower canopy, and in 2000 it was 1.3–1.4 times higher ( $P < 0.001$  for all age classes) than in 1997 (Fig. 4). Smaller apparent  $G_T$  in the lower branches resulted from greater reductions in water flow, while there were no significant differences in  $\Delta\Psi$  between the lower and upper canopy (Fig. 5) recorded at the

**Table IV.** Effect of shoot water potential ( $\Psi_x$ ) on leaf conductance ( $g_L$ ): the numbers indicate slopes of the  $g_L$  regressions from  $\Psi_x$  before and after the midday. Zero denotes the current-year foliage. Statistical significance for the slopes: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ; ns, not significant.

Foliage age (yr)	Year	Shade foliage			Sun foliage		
		0900 h	1100 h	1300 h	0900 h	1100 h	1300 h
0	1997	-137**	83*	ns	ns	138***	ns
	2000	-	-	-	ns	59*	50*
1	1997	-119**	ns	ns	ns	124***	ns
	2000	-	-	-	37*	ns	49**
2	1997	ns	74*	ns	ns	117***	ns
	2000	-	-	-	78**	93***	79***
$\geq 3$	2000	ns	72**	ns	ns	49*	32*

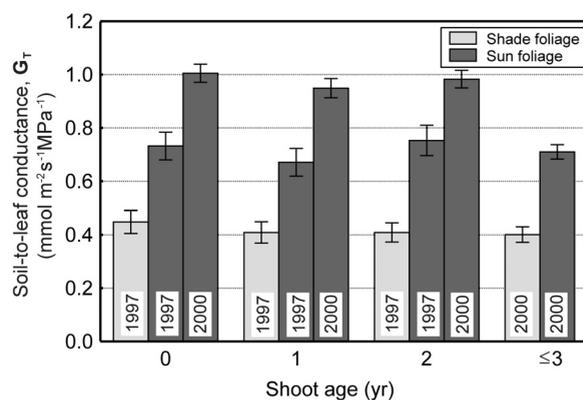


**Figure 3.** Generalized daily patterns of shoot water potential in the lower and upper canopy. The number of replications ranged from 42 to 126 at different times of day in different data sets. The bars indicate  $\pm$  SE of the means.

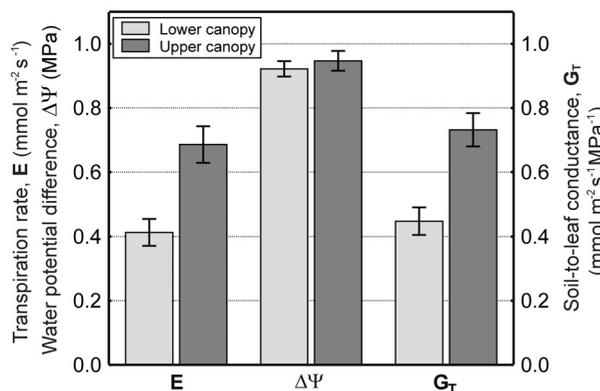
daily maximum level of  $g_L$ . In 1997, the liquid phase conductance explained 77–82% and 53–75% of the variation in  $g_L$  around midday in the shade and sun foliage, respectively. In 2000, the corresponding numbers were 62% and 28–42%.

### 3.3. Leaf conductance model

The model, developed for analysing the dynamics of leaf conductance in relation to the variation in  $Q_p$ ,  $VPD$  and  $G_T$ , fitted the empirical data sets obtained in 1997 to a similar degree (Tab. V). The model described 83.3–89.0% of the total variance of leaf conductance and there was a high correspondence



**Figure 4.** Mean soil-to-leaf conductance in the midday period calculated for shoots of different age (zero denotes the current-year shoots). The number of measurements ranged from 45 to 57 in different data sets. The bars indicate  $\pm$  SE of the means.

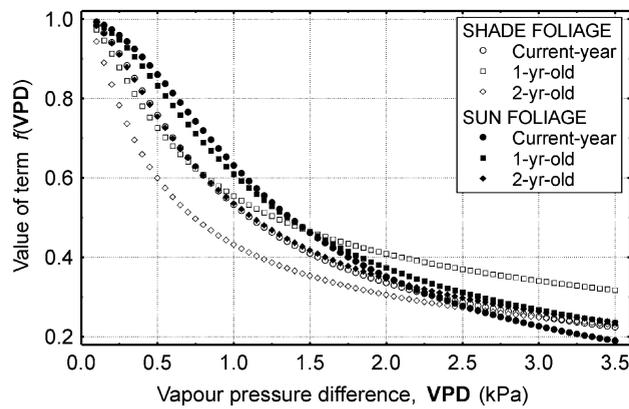


**Figure 5.** Mean transpiration rates, water potential differences between the soil and foliage, and soil-to-leaf conductances recorded at the daily maximum level of  $g_L$  for the current-year shoots in 1997. The number of measurements was 45 for the lower and 51 for the upper canopy. The bars indicate  $\pm$  SE of the means.

between the observed and predicted values. The analysis of the model's residuals revealed that the residual values depended on different combinations of atmospheric, soil and leaf factors,

**Table V.** Quantitative measures of the model performance using the 1997 data sets: coefficient of determination ( $R^2$ ) and index of agreement ( $d$ ). Zero denotes the current-year foliage.

Foliage age (yr)	Foliage type	Number of measurements	$R^2$	$d$
0	Shade	370	0.870	0.961
	Sun	368	0.890	0.969
1	Shade	369	0.861	0.959
	Sun	369	0.859	0.959
2	Shade	369	0.863	0.959
	Sun	367	0.833	0.951



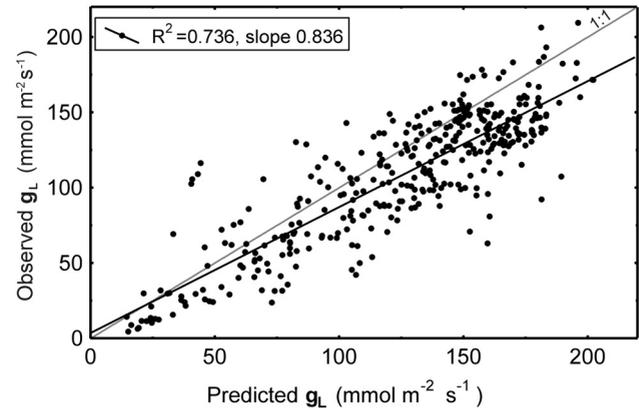
**Figure 6.** Values of term  $f(VPD)$  in equation 8 for different age classes of shade and sun foliage.

and there was no uniform relationship for different age classes of the sun and shade foliage. Applying stepwise linear regression procedure, different factors together explained 13.5–35.3% of the variance of the residuals. The most relevant environmental factors were relative humidity of the air ( $RH$ ) and soil water potential ( $\Psi_s$ ). At high relative air humidity ( $RH > 90\%$ ) the model tends to underestimate the leaf conductance, however, this may be caused by the relatively large errors of the porometric method applied at high atmospheric humidity. Soil water potential had a very weak but statistically significant ( $P < 0.001$ ) effect on the model's residuals, although there was no soil water deficit in summer 1997 and  $\Psi_s$  did not fall below  $-0.03$  MPa in the wettest soil layer of those monitored with soil hygrometers during the entire study period.

At low atmospheric evaporative demand,  $g_L$  in shade foliage responded more sensitively to the changes in  $VPD$ , while at high atmospheric demand it was on the contrary, the sun leaves tended to be more sensitive (Fig. 6). When we were developing the model, we tried out other forms of the term  $f(VPD)$  as well (see [49]), but they resulted in poorer predictions than those achieved with the term included in the model (Eq. (8)). To assess comparatively the sensitivity of leaf conductance in foliage of different age and position to the atmospheric demand and liquid phase conductance,  $VPD$  and  $G_T$  were changed by 10% from

**Table VI.** Modelled changes (%) in leaf conductance in response to the changes in soil-to-leaf conductance ( $G_T$ ) and vapour pressure difference ( $VPD$ ) by  $\pm 10\%$  from the average values in the midday period. Zero denotes the current-year foliage.

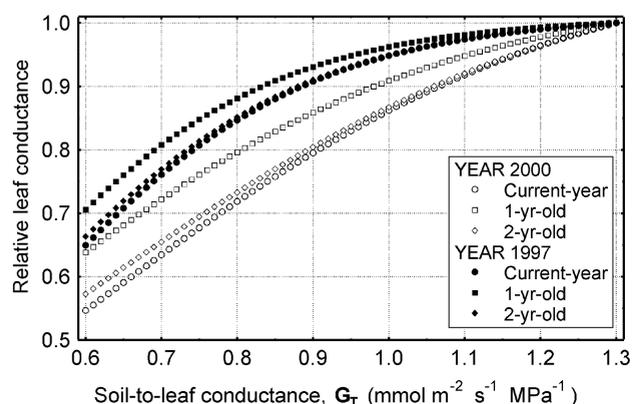
Foliage age (yr)	Foliage type	$G_T$		$VPD$	
		Decrease	Increase	Decrease	Increase
0	Shade	-11.7	10.6	5.8	-5.2
	Sun	-9.3	7.6	5.7	-5.4
1	Shade	-11.5	10.2	4.3	-3.8
	Sun	-9.1	7.5	5.4	-5.1
2	Shade	-11.3	10.1	5.2	-4.5
	Sun	-8.4	6.7	6.6	-5.8



**Figure 7.** Predicted versus observed values of leaf conductance ( $g_L$ ) in the current-year sun foliage in 2000.

the average values in the midday period, specific for each data set. The analysis indicated that changes in  $G_T$  induce bigger changes in leaf conductance than those induced by  $VPD$ , and the lower canopy foliage is more sensitive in this respect (Tab. VI). In the sun foliage  $VPD$  caused slightly bigger effects than in the shade shoots:  $g_L$  changed by 5–7 and 4–6%, respectively.

To perform a more rigorous test of the model, it was validated with data on sun foliage collected at the same site in the year 2000. The validation resulted in a fair agreement between the observed and predicted values of leaf conductance:  $R^2$  ranged from 0.624–0.736, and  $d$  from 0.881–0.895 for different needle age classes. However, the model developed using the 1997 data tended in all data sets to underestimate  $g_L$  for the year 2000 (Fig. 7). The comparative analysis of the data of both years confirmed that the underestimation could not result from stomatal responses to  $VPD$ . On the contrary, one could suspect the opposite effect, as the leaf conductance proved to be less sensitive to atmospheric evaporative demand in the cool and rainy summer of 2000. Most probably, the underestimation resulted from differential stomatal responsiveness to changes in conducting capacity of the soil-to-leaf transport pathway in



**Figure 8.** Modelled response of leaf conductance (normalized values) to soil-to-leaf conductance in sun foliage.

different years. In summer 2000, leaf conductance declined more steeply with decreasing  $G_T$  than in summer 1997 (Fig. 8).

## 4. DISCUSSION

### 4.1. Effects of irradiance and atmospheric evaporative demand

Responses of leaf conductance to irradiance varied widely within a canopy of Norway spruce, depending on both shoot position and age (Fig. 2 and Tab. II). The upper canopy shoots (i.e. sun foliage) demonstrated substantially higher daily maximum leaf conductances as compared to the lower canopy shoots (i.e. shade foliage). The primary reason for this difference is considered to be a limited light availability in the lower canopy (Fig. 1), although there was no statistically significant relationship between  $g_L$  and  $Q_P$  in the midday period, except for the current-year sun foliage ( $P < 0.05$ ) in 1997. Around midday the photosynthetic photon flux density has mostly achieved a saturating level with respect to  $g_L$ , and the effects of other factors (high  $VPD$ , low  $\Psi_x$ ) probably mask the influence of the irradiance. The higher leaf conductances observable at higher light availability are a universal regularity, common for both temperate [25] and tropical tree species with different shade tolerance [34]. If the current-year to 2-year-old shoots demonstrated rather similar maximum levels of leaf conductance, then the older foliage of Norway spruce had significantly lower maxima of  $g_L$ .

Because most leaves in a spruce canopy are shaded to various degrees, variation in stomatal behaviour depending on shoot position contributed to functional acclimation of *P. abies* to a shady environment. The shade acclimation in spruce trees, revealed in the present study, occurred in the form of higher stomatal sensitivity of the shade foliage to changes in irradiance (Tab. II). Both a steeper initial slope of light-response curve and a lower light-saturation point in shade leaves enable a longer daily period of stomatal opening, and thus permit efficient utilization of the existing microenvironment. As a rule  $g_L$  changed in response to irradiance faster in the evening, i.e. at decreasing irradiance [43], however, in the present study we did

not analyse the morning and evening data separately. Shade acclimation of trees is actually a complex process including both morphological and physiological adjustment of the foliage. Morphological adjustment of Norway spruce foliage to light availability was extensively studied in our previous paper [43]. Modifications in leaf morphology and acclimation of the photosynthetic apparatus allow leaves to photosynthesize efficiently despite the very biased distribution of light within the canopy [24, 52].

Stomatal responses to irradiance also varied between the years giving evidence of the acclimation to specific meteorological conditions. In 2000, under darker conditions (Fig. 1) due to denser canopy and cloudy weather (Tab. I) the foliage exhibited lower light-saturation point of  $g_L$ . However, the initial slope of the light-response curve was smaller because the stomata were more open at zero irradiance if compared to summer 1997 (Tab. II). Under the cool and rainy weather conditions prevailing in Estonia in the summer months of 2000, trees had not adjusted for economical water-use and exhibited weaker stomatal control of transpirational water loss. This conclusion is confirmed also by higher means of daily maximum  $g_L$  as well as the smaller stomatal sensitivity to atmospheric evaporative demand (Tab. III). Other data [8, 20] suggests weaker stomatal control of transpiration in both tropical and temperate tree species during the wet season than during the dry season. Comparing the data on the spruce shade and sun foliage collected in 1997, one might claim that sun needles, being exposed to higher irradiance, temperature and wind, as well as drier air in the daytime, are slightly more sensitive to changes in atmospheric evaporative demand than shade needles (Tabs. III and VI). Stomatal sensitivity to atmospheric evaporative demand was positively related to the overall maximum  $g_L$ , thus, the higher the leaf conductance, the more sensitively stomata respond to increasing  $VPD$ . This result is in accordance with the prediction made by Oren et al. [30] that stomatal sensitivity to water vapour pressure deficit is proportional to stomatal conductance at low  $VPD$ .

### 4.2. Effects of leaf water status versus hydraulic constraints

The mean hydraulic conductance of the soil-to-leaf transport pathway was 1.6–1.8 times higher ( $P < 0.001$ ) for the upper canopy than for the lower canopy (Fig. 4), thus, the water flow to the shade foliage has to overcome a bigger resistance than to the sun foliage. This result is supported also by the data indicating that  $g_L$  in the lower canopy depended more strongly ( $R^2 = 0.62$ – $0.82$ ) on the liquid phase conductance and the shade foliage responded more sensitively to changes in  $G_T$  around midday (Tab. VI). Anyway, one may conclude that the path length from bulk soil to leaf was not the term responsible for the variation in soil-to-leaf conductance within crowns of Norway spruce. The distinction in  $G_T$  between the lower and upper canopy resulted most likely from differences in xylem anatomical structure, leaf area to sapwood area ratio and/or number of branch junctions (i.e. nodes) on the path that water must take to get from the soil to a certain shoot. As for old trees, Rust and Roloff [36] suggested that in addition to increasing pathway length and lower xylem conductivity, structural changes in shoot and crown architecture need to be considered when analyzing

reasons for the size-related decrease in stomatal conductance and photosynthesis.

Our results on *P. abies* are in contrast with those published for *Pinus ponderosa*: there were no differences, either in leaf specific hydraulic conductance from soil to leaf or leaf gas exchange, between the upper and lower canopy [13]. We suppose that the disparity between the two studies could result from two matters: (1) spruces as shade tolerant species form long and densely foliated crowns as compared to shade intolerant pines; (2) the present study was carried out on closed-canopy trees exposed to large environmental gradients within the canopy (Fig. 1), while the sampled ponderosa pines were open-grown trees receiving full sunlight nearly throughout the day. Relatively even environmental conditions throughout the whole crowns of the pines probably did not promote the development of differences in hydraulic properties of branches between the upper and lower canopy. Besides, effects arising from methodological differences between the studies cannot be ruled out, e.g. Hubbard et al. [13] assumed equal sapwood permeability for all branches irrespective of their position.

In the cool and rainy summer of 2000 the water supply for leaves in Norway spruce turned out to be less critical and the co-ordination between the liquid and gaseous phase conductances less tight than in 1997. In 2000, average  $G_T$  for the upper canopy was 1.3–1.4 times higher ( $P < 0.001$ ) as compared to year 1997 (Fig. 4), when the second half of the study period was characterized by very warm and dry weather in Estonia [44]. The high atmospheric evaporative demand probably induced a massive cavitation of tracheids, yielding a strong dynamic water stress in trees, although there were sufficient water reserves in the soil. The mean  $G_T$  calculated from daily maximum values of transpiration recorded throughout the whole crown for the first half of the study period in 1997 ( $1.04 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ ; see [44]) coincides with the values for corresponding needle age classes of the sun foliage recorded in 2000 ( $0.95$  to  $1.00 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ ). In contrast to the soil-to-leaf conductance, the effect of leaf water potential on  $g_L$  was weak around midday, supporting once more the finding of Meinzer et al. [20] that stomatal adjustments to  $G_T$  co-ordinate transpiration with liquid phase transport efficiency rather than bulk leaf water status.

Our earlier studies [40, 41] on *P. abies* revealed that low resistance to water flow throughout most of the trunk, except the very top, creates more equal prerequisites for water supply to branches situated at different heights in the crown. However, there may be a remarkable systematic variation in xylem hydraulic capacity between the branches [15, 17, 32], and trees growing under low-light conditions produce sapwood with poor water conducting capacity [39, 45]. Recently, both the specific and leaf-specific hydraulic conductivity ( $LSC$ ) have been found to increase with branch insertion height [5, 17, 32], while in *Eucalyptus grandis*  $LSC$  declined as the branch grew larger [5]. Higher specific conductivity in the upper branches was a result of larger vessel diameter and higher vessel density. Therefore, the leaves growing on lower long branches, characterized by small radial increments and containing smaller tracheids/vessels, are hydraulically more constrained, although this effect is not reflected in leaf water potentials (Fig. 3). Differences in water supply between the leaves attached to upper and lower branches are offset by sensitive stomatal control of the transpi-

rational water loss. Lemoine et al. [17] indicated differential stomatal responses within a crown of *Fagus sylvatica* L., which depended on the hydraulic properties of branches to maintain  $\Psi_x$  above the values critical for cavitation, and thus avoid xylem embolism. However, the results of the experiments carried out in eleven woody species by Nardini and Salleo [27] suggested that some cavitation-induced embolism could not be avoided, and the loss of hydraulic conductance could act as a signal for the reduction of  $g_L$ . We hypothesize that stomatal conductance at the base of the live crown is constrained not only by low light availability but also by plant's inner hydraulic limitations. The data on *Pinus contorta* Dougl. ex Loud. published by Protz et al. [32] seems to support our hypothesis. Of course, further experimental studies on the co-ordination of liquid and gaseous phase conductances in large forest trees should be encouraged at different scales to verify the hypothesis.

Overall, the conducting capacity of the soil-to-leaf transport pathway determines the daily maximum level of  $g_L$ . Sensitivity analysis proved that the transport capacity of the water-conducting system in Norway spruce is a more relevant factor in respect to leaf conductance than the atmospheric evaporative demand (Tab. V). Our results point to the dominant role of a tree hydraulic capacity in determining patterns of stomatal behaviour in spruce trees. In addition to maintaining a long-term balance between vapour and liquid phase water conductances in plants, stomata are exquisitely sensitive to short-term, dynamic perturbations of liquid water transport [19].

### 4.3. Leaf conductance model

The model developed from the data obtained in 1997, accounting for the interactive effects of irradiance,  $VPD$ , and plant hydraulic conductance, described 83.3–89.0% of the total variance of leaf conductance and demonstrated a high correspondence between the observed and predicted values (Tab. IV). The validation of the model by applying it to the independent 2000 data sets resulted in a fair agreement between the observations and predictions, while the model tended to underestimate  $g_L$  as compared to the observed values (Fig. 7). The comparative analysis of the data of both years revealed that the biased predictions resulted most likely from different stomatal responsiveness to changes in the liquid phase conductance in different years, not taken into account in the model. Thus, stomatal sensitivity to hydraulic signals may differ from year to year, and it is probably affected by weather conditions characteristic of specific years. Of course, we cannot exclude also other reasons, e.g. there could be effects, produced by some other environmental variable or by xylem capacitance, significant for leaf conductance in Norway spruce in 2000, but not included in the model. In general, it is common to find that models fitted to the data of one particular year result in much poorer predictions if applied to the data of another year [48, 49].

To summarize, the results revealed that the responses of leaf conductance to irradiance and atmospheric evaporative demand varied widely within a canopy of Norway spruce, depending on shoot position, age and year. Norway spruce trees are able to adjust their water relations to the prevailing environment by co-ordinating hydraulic capacity with changes in stomatal conductance to prevent leaf water potential from reaching critical values. Our earlier studies [42] indicated that the mean minimum

values of  $\Psi_x$  usually do not drop below  $-1.5$  MPa under meteorological conditions prevailing in Estonia. The liquid phase transport capacity determines the maximum levels of  $g_L$ , but stomatal sensitivity to hydraulic signals varies among years and positions as well. Therefore, one must be careful in transferring data on plants' hydraulic properties not only from trees growing at one site to those at another site, but also from one year to another for trees at the same site.

**Acknowledgements:** This study was supported by grant No. 5296 from the Estonian Science Foundation. We are grateful to Mr. Ilmar Part for language correction.

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