

# The effect of tree height on crown level stomatal conductance

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## ABSTRACT

Variation in stomatal conductance is typically explained in relation to environmental conditions. However, tree height may also contribute to the variability in mean stomatal conductance. Mean canopy stomatal conductance of individual tree crowns ( $G_{Si}$ ) was estimated using sap flux measurements in *Fagus sylvatica* L., and the hypothesis that  $G_{Si}$  decreases with tree height was tested. Over 13 d of the growing season during which soil moisture was not limiting,  $G_{Si}$  decreased linearly with the natural logarithm of vapour pressure deficit ( $D$ ), and increased exponentially to saturation with photosynthetic photon flux density ( $Q_o$ ). Under conditions of  $D = 1$  kPa and saturating  $Q_o$ ,  $G_{Si}$  decreased by approximately 60% with 30 m increase in tree height. Over the same range in height, sapwood-to-leaf area ratio ( $A_S:A_L$ ) doubled. A simple hydraulic model explained the variation in  $G_{Si}$  based on an inverse relationship with height, and a linear relationship with  $A_S:A_L$ . Thus, in *F. sylvatica*, adjustments in  $A_S:A_L$  partially compensate for the negative effect of increased flow-path length on leaf conductance. Furthermore, because stomata with low conductance are less sensitive to  $D$ , gas exchange of tall trees is reduced less by high  $D$ . Despite these compensations, decreasing hydraulic conductance with tree height in *F. sylvatica* reduces carbon uptake through a corresponding decrease in stomatal conductance.

**Key-words:** *Fagus sylvatica*; mean stomatal conductance; stomatal sensitivity; tree height

## INTRODUCTION

Responses of stomatal conductance ( $g_s$ ) to environmental variations have been described as a series of multiplicative functions formulated by Jarvis (1976):

$$g_s = f(Q_o)f(D)f(T_a)f(\Psi_L) \quad (1)$$

where  $Q_o$  is photosynthetic photon flux density,  $D$  is vapour pressure deficit,  $T_a$  is air temperature, and  $\Psi_L$  is leaf water potential. This approach was used with different sets of environmental variables and different functional forms.

More recently, a similar approach was successfully applied to quantify the effect of environmental variables on sap-flux scaled mean canopy stomatal conductance ( $G_S$ ) estimated according to Jarvis & McNaughton (1986; Dye & Olbrich 1993; Granier & Loustau 1994; Granier & Bréda 1996; Granier *et al.* 1996a; Martin *et al.* 1997). When soil moisture is not limiting, analysis of Eqn (1) can be simplified by partitioning data into classes of light or radiation, and described in relation to  $D$  within each class (Granier *et al.* 1996b):

$$G_s = G_{Sref} - m \cdot \ln D \quad (2)$$

where  $G_{Sref}$  is the intercept (i.e. the value of  $G_S$  at  $D = 1$  kPa in a log-linear relationship), and  $m$  is the slope of the regression fit, representing stomatal sensitivity to  $D$  (i.e.  $dG_S/d \ln D$ ).

Stomatal conductance decreases with tree height to control the minimum leaf water potential (Friend 1993; Sperry, Alder & Eastlack 1993; Sturm *et al.* 1996; Hubbard, Bond & Ryan 1999). Leaf water potential ( $\Psi_L$ ) decreases with height because of gravity ( $0.01$  MPa  $m^{-1}$ ; Scholander *et al.* 1965; Hellkvist, Richards & Jarvis 1974), and because the hydraulic conductance from soil to leaf decreases with increasing path length at a given transpiration rate (Ryan & Yoder 1997). To avoid potentially damaging effects of declining  $\Psi_L$  (e.g. cavitation), stomatal conductance should decline with height. Lower stomatal conductance in tall trees may limit carbon uptake (Yoder *et al.* 1994; Hubbard, Bond & Ryan 1999). Thus, a hydraulic limitation has been proposed as one of the mechanisms potentially limiting tree height (Ryan & Yoder 1997).

Scaled sap flux may provide a convenient way to evaluate the effect of tree height on stomatal conductance. Mean canopy stomatal conductance,  $G_S$ , has been increasingly estimated using sap flux measurements in representative trees in the stand. This approach is valid when (1) water stored in the plant contributes little to transpiration compared to water uptake from the soil, (2) there is no vertical pattern of  $D$  within the canopy, and (3) leaf boundary layer conductance is much higher than stomatal conductance (Aphalo & Jarvis 1991; Köstner *et al.* 1992). Sap flux is often measured in small patches of xylem, often one sensor in each sampled tree, and averaged and scaled to the stand (Hinckley *et al.* 1994; Cermák *et al.* 1995; Hatton, Moore & Reece 1995; Alsheimer *et al.* 1998; Cienciala *et al.* 1998;

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Oren *et al.* 1998a). From the scaled stand-level flux, conductance is estimated for the entire canopy (Miller *et al.* 1998) or, dividing by leaf area index, as mean canopy stomatal conductance (Oren *et al.* 1998b).

In a few studies, trees were either grouped by canopy position before analysing canopy conductance (Köstner *et al.* 1992), or analysed individually (Loustau *et al.* 1996; Martin *et al.* 1997; Andrade *et al.* 1998). When analysing single sensors as representative of individual trees, an implicit assumption is that the variability in xylem flux within a tree is small relative to the variability among trees. Although the variability in flux within a tree and among trees sharing a similar position in the canopy may be large (Dunn & Connor 1993; Hatton, Moore & Reece 1995; Oren *et al.* 1998a; Alsheimer *et al.* 1998), expected patterns in flux with respect to canopy position have been shown among trees equipped with single sensors (Köstner *et al.* 1992; Martin *et al.* 1997; Oren *et al.*, 1999). However, in a given stand, the influence of individual tree height on stomatal conductance is often confounded with the effect of light level because the latter is dependent on the tree's position in the canopy (Martin *et al.* 1997). For this reason, tall trees may have higher sap flux-scaled mean stomatal conductance than short, overtopped individuals when compared at a given level of above-canopy irradiance.

In a stand composed of European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl), under moist soil conditions, we accounted for variation in individual crown mean stomatal conductance ( $G_{Si}$ ) of the beech trees caused by  $Q_o$  and  $D$ . We then tested the hypothesis that tree height, ranging from 11 to 39 m, explains the remaining variability in  $G_{Si}$ .

## MATERIALS AND METHODS

### Study site

The stand is located in the Steigerwald, Bavaria, south-eastern Germany (49°52' N, 10°27' E) at an elevation of 200–490 m above sea level. The mean temperature in 1996 was 6.0 °C, somewhat lower than the mean annual temper-

ature of about 7.5 °C (German Weather Service). Annual precipitation in 1996 was 667 mm, 460 mm of which fell within the growing season (May–October). Soils at the site are partially podzolized cambisols derived from sandstones. The sandy loam texture supplies sufficient nutrients, and is well-drained (G. Lischeid, personal communication).

The mean age of the trees in the stand was 122 years (Forstrevierbuch IV, Ebrach). Tree density of the canopy component (not including immature trees with diameter < 0.07 m) was 373 trees ha<sup>-1</sup>, approximately 75% *F. sylvatica* with an average diameter of 0.26 m (SD 0.15) at 1.35 m above ground, and approximately 25% *Q. petraea* with an average diameter of 0.35 m (SD 0.07). A few *Carpinus betula* (L.), with an average diameter 0.08 m, occupied the sub-canopy, along with young *F. sylvatica*. Stem basal area at 1.35 m above ground was 29.3 m<sup>2</sup> ha<sup>-1</sup>, and total leaf area index was 6.2 m<sup>2</sup> m<sup>-2</sup>.

For the purpose of this study, we used a subset of data representing 13 d in June selected from a larger data set collected in 1996 from 1 May to 23 October. This subset was selected to coincide with a time at which the soil was moist (see Results), and after leaves were fully expanded.

### Sap flux measurements

Nine *F. sylvatica*, representing the range in size of mature trees in the stand, were selected for sap flux measurements (Table 1). Granier-type sensors (cf. Granier 1987, 1996) were used to measure sap flux density ( $J_s$ , g H<sub>2</sub>O m<sup>-2</sup> sapwood s<sup>-1</sup>). Each sensor consists of a pair of 20 mm long, 2 mm diameter probes inserted above each other in the hydroactive xylem (i.e. sapwood) approximately 15 cm apart. The upper probe was supplied with constant heat of 200 mW, and the temperature difference between this and the lower unheated reference probe was measured and converted to sap flux density according to Granier (1987, 1996). One to four sensors were inserted in each tree 1.5 m above ground at various depths (Table 1), such that none of the sensors protruded into the heartwood. Sensors inserted at different depths in the sapwood of a single tree were spaced as far as possible horizontally to minimize thermal inter-

**Table 1.** Characteristics of trees (*F. sylvatica*), and number and positions of sensors. Sapwood depth was obtained by coring; sapwood area was obtained using computed tomography

Tree diameter (m)	Tree height (m)	Crown length (m)	Sapwood depth (mm)	Sapwood area (cm <sup>2</sup> )	Sensor
0.12	11.0	8.1	118	94	1
0.13	15.3	13.6	45	95	1,3
0.16	15.5	10.3	56	166	1,4
0.25	21.7	13.5	75–82	437	1
0.29	24.3	15.2	90–110	611	1
0.26	24.4	13.8	75–85	500	1
0.29	25.9	17.6	82	489	1,2,3
0.39	27.8	16.4	152	960	1,2,4,5
0.59	38.6	23.9	144	2494	1,3,5

Sensor 1: 0–20 mm; 2: 20–40 mm; 3: 40–60 mm; 4: 50–70 mm; 5: 80–100 mm.

ference between probes. Heated probes thermally interfere with each other less than heated probes interfere with unheated probes; during periods of no flux, heated probes raise the local temperature similarly, and during periods of flux, the longitudinal heat dissipation dominates the radial dissipation (Granier *et al.* 1994). Phillips, Oren & Zimmermann (1996) have found that a heated probe has no thermal influence on an unheated, reference probe positioned a minimum of 50 mm away. In this study, the minimum distance between heated and unheated sensors was 108 mm, and the distance between two heated sensors was 42 mm. Temperature differences of all sensors were logged every 30 s, and stored as 10 min averages with a digital data logger (DL2, Delta T device, Cambridge, UK).

Whole-tree water uptake was estimated from: (1) continuous estimates of  $J_S$  from the outermost 20 mm of sapwood, (2) the relative decrease in  $J_S$  at consecutive sapwood depth intervals, and (3) the area representing each depth interval.

### Sapwood area and wood properties

Scaling  $J_S$  measured in a small patch of xylem to the transpiration of whole trees and stands requires an estimate of the conductive sapwood area corresponding to the different depths at which  $J_S$  is measured. To account for circumferentially varying sapwood depth, a computer tomograph was taken at breast height prior to installation of sap flux sensors. Computed tomography (Dobos *et al.* 1990; Tauchnitz *et al.* 1991; Habermehl & Ridder 1992, 1993) has been successfully used to quantify sapwood area (Wiebe & Habermehl 1994; Alsheimer 1997). With this technique, the attenuation of X-rays is measured to obtain a dimensionless absorption coefficient ( $\alpha$ ). Specific coefficients of absorption are related to wood density, and therefore to water content. To determine the range of  $\alpha$  within the sapwood, sapwood depth was estimated visually from wood cores extracted with a 5 mm diameter increment borer, and then dyed with bromocresol green (Sandermann, Hausen & Simatupang 1967). Sapwood depth from each increment core was compared to the tomographic image at the same radial position to identify the corresponding range in  $\alpha$ . After determining sapwood depth visually, the radial stem cores were used to quantify the uniformity of water content within the sapwood, and to assess whether the sapwood–heartwood boundary is delineated by a clear decrease in water content. Each core was divided into 10 mm sections of sapwood, and 20 mm sections of heartwood, and volumes and fresh and dry weights (70°C, 24 h), were then determined. Density of wood was calculated as mass divided by volume. Relative water content ( $R_w$ , %) was computed from dry ( $m_d$ ) and fresh mass ( $m_f$ ):

$$R_w = ((m_f - m_d) / m_d) \times 100\% \quad (3)$$

In all trees, sapwood determined both visually and based on  $R_w$  corresponded to  $\alpha$  ranging from 70 to 90. Thus, sapwood area was estimated after delineating on the tomographic image the area corresponding to this range in  $\alpha$ .

### Leaf area

To calculate mean canopy stomatal conductance in each tree ( $G_{Si}$ ), an estimate of sapwood area ( $A_S$ , m<sup>2</sup>) per unit of leaf area ( $A_L$ , m<sup>2</sup>) for each tree is required. An allometric relationship between leaf area and diameter at 1.35 m above ground ( $d$ ) was obtained through a destructive harvest of seven trees ( $r^2 > 0.96$ ; Schmitt 1997):

$$\log A_L = 1.6180 \times \log d - 0.2266 \quad (4)$$

The harvest was performed in a stand of similar density and age on a site of a similar soil in the same year. While these relationships do not account for seasonal dynamics in leaf area, both studies were performed using data collected in June, after full leaf expansion, and therefore  $G_{Si}$  calculation is not subject to errors caused by leaf area dynamics. Leaf area for each tree in this study was estimated using its diameter ( $d$ ) and Eqn (4).

### Environmental measurements

To calculate vapour pressure deficit ( $D$ , kPa; Goff & Gratch 1946), relative humidity and temperature were measured in an opening 300 m from the study plot (Type 2011, Skye Instruments Ltd, Cambridge, UK). Net radiation ( $R_n$ , W m<sup>-2</sup>) during the entire six-month study was calculated from radiation measured with two pyranometers vertically positioned in opposite directions (type 8111, Ph. Schenk, Wien, Austria); photosynthetic photon flux density ( $Q_o$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured with a quantum sensor (LiCor 190, Lincoln, Nebraska, USA) during the last three months of the study, after the period analysed here was over. We regressed  $Q_o$  against  $R_n$  for the three months in which data were available for both variables ( $r^2 = 0.98$ ), and estimated  $Q_o$  from the measured  $R_n$ , and the relationship between the two variables. Precipitation (tipping bucket type OMC 212, Eijelkamp, Germany) was measured at the same opening. All environmental parameters were logged every 30 s, and 10 min means were stored in a data logger (DL2, Delta T device, Cambridge, UK).

In the study plot, volumetric soil moisture ( $\theta$ , m<sup>3</sup> m<sup>-3</sup>) at three depths, beginning at 0.20, 0.35 and 0.90 m below the surface, was measured using 0.30 m long time domain reflectometer rods ( $n = 3$  at each depth; IMKO GmbH, Ettlingen, Germany). The rods were installed vertically in the soil through the bottom of auger holes 10 cm in diameter, similar to the diameter of the reflectometer heads, backfilling the holes with the extracted soil. Soil water potential ( $\Psi_s$ , MPa) at four depths, beginning at 0.20 m ( $n = 13$ ), 0.35 m ( $n = 10$ ), 0.90 m ( $n = 13$ ) and 2.00 m ( $n = 4$ ), was measured using tensiometers with a 0.10 m long ceramic cup installed similarly (IMKO GmbH Ettlingen, Germany). Both soil variables were measured every hour.

### Calculation of mean stomatal conductance

Calculating stomatal conductance with  $D$  as the driving variable (Jarvis & McNaughton 1986) is commonly done

for well-coupled species such as conifers. This approach is justified for other species with small leaves, especially when wind speed is sufficiently high, which reduces the boundary layer resistance and brings leaf temperature close to air temperatures (Pataki *et al.* 1998). Previously, a *F. sylvatica* stand of similar age, density and leaf area index showed a strong coupling between the canopy and the atmosphere, according to Jarvis & McNaughton (1986), with a decoupling coefficient  $\Omega$  of 0.2 (Herbst 1995). This indicates that transpiration in that stand was strongly controlled by the stomata. Thus, for our stand, we assumed that  $D$  approximates leaf-to-air vapour pressure difference at all levels of the canopy.

In well-coupled forests, mean stomatal conductance can be calculated based on a simplified equation (Köstner *et al.* 1992) derived from Whitehead & Jarvis (1981). Using whole-tree transpiration per unit leaf area ( $E_L$  in  $\text{g H}_2\text{O m}^{-2} \text{ leaf s}^{-1}$ ) and  $D$ , mean stomatal conductance for individual trees,  $G_{Si}$ , can be calculated as:

$$G_{Si} = (G_v T_a \rho E_L) / D \quad (5)$$

where  $G_v$  is the universal gas constant adjusted for water vapour ( $0.462 \text{ m}^3 \text{ kPa K}^{-1} \text{ kg}^{-1}$ ),  $T_a$  is the air temperature (K),  $\rho$  is the density of water ( $998 \text{ kg m}^{-3}$ ), and  $D$  is in kPa.  $G_{Si}$  calculated in Eqn (5) is in units of  $\text{mol H}_2\text{O m}^{-2} \text{ leaf s}^{-1}$ .

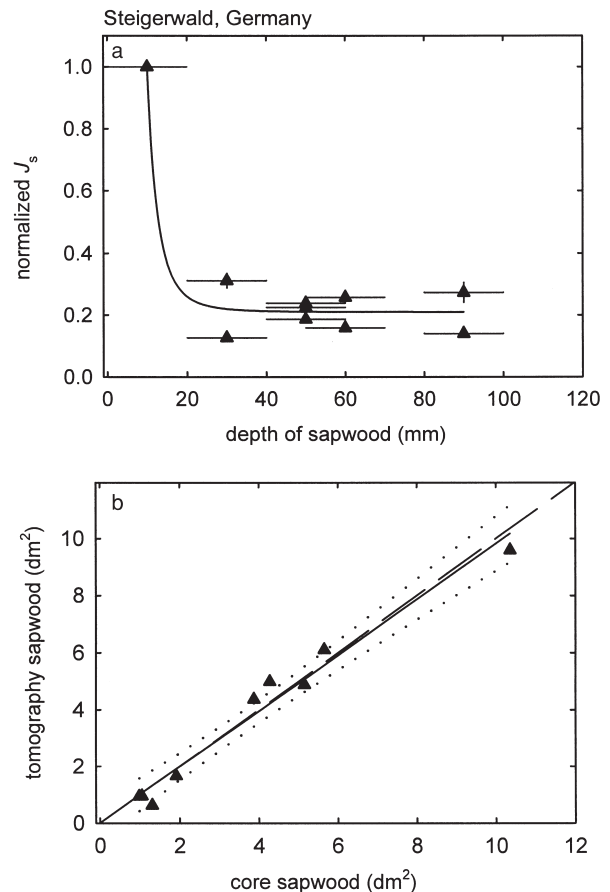
Whole-tree water uptake can be expressed as  $E_L$  (Eqn 5) by dividing by the leaf area of each tree ( $\text{m}^2$ ) estimated from Eqn (4). This approach is based on the assumption that the contribution of water stored in trees above the sensors to transpiration is negligible, or is explicitly accounted for. If the contribution of stored water is not negligible, then it can be accounted for by determining time lags between water uptake and an appropriate driving variable (Köstner *et al.* 1992; Granier & Loustau 1994). Employing a time lag may correct for shifts in the time series of uptake relative to transpiration, but does not correct for the diffusion of the transpiration signal measured as water uptake at the base of the stem (Phillips *et al.* 1997). Previous studies have shown that relatively large errors in  $E_L$  estimated from sap flux measurements occur only early and late in the day due to measurement errors, and the effects of stored water (Loustau *et al.* 1998; Phillips & Oren 1998; Ewers & Oren, 2000). Thus, in this study,  $G_{Si}$  was calculated after (1) performing cross-correlation analysis between  $D$  and  $E_L$ , and using the time lag (the lag with the highest correlation coefficient, Phillips *et al.* 1997) in order to infer a time-corrected  $E_L$ , and (2) filtering out data for  $D < 0.1 \text{ kPa}$ , corresponding to early and late daytime hours (Phillips & Oren 1998).

Statistical tests and time-lag analyses were performed using SAS version 6.12 (SAS Institute, Cary, North Carolina, USA). As necessary, curve fits were performed using non-linear regression in Sigmaplot version 4.0 (SPSS Inc., San Rafael, California, USA), calculated by using the Levenberg–Marquardt algorithm with maximal 100 iterations.

## RESULTS

### Radial pattern in $J_S$ and scaling of $J_S$ to transpiration

A sharp radial decline in  $J_S$  was observed from the outer 20 mm of sapwood to subsequent depth intervals for  $J_S$  normalized by the flux in the outermost xylem band (Fig. 1a;  $r^2 > 0.95$ ,  $P < 0.06$ ). The radial decrease in  $J_S$  varied among trees, but did not vary systematically with tree height (Table 1; paired Student's *t* test between large and small trees using depths as replicas,  $P = 0.85$ ,  $n = 4$ ). About 50% of water used by the average tree was transported in the outermost 20 mm of the xylem. A similar radial pattern in  $J_S$  has been found in a number of species representing ring, diffuse and non-porous tree species (Edwards & Booker 1984; Cermák *et al.* 1992; Granier *et al.* 1994; Phillips, Oren & Zimmermann 1996).



**Figure 1.** (a) Sap flux density ( $J_S$ ) normalized by the values in the outermost 20 mm of the xylem at five measurement depths. Horizontal lines indicate the depth interval of each sensor. Vertical lines indicate 1 SE of the slope of the relationship between outer and inner sap flux for each tree (see Table 1 for sensor position in each tree). (b) Relationship between sapwood area derived from computed tomography and sapwood area derived from stem cores. Dashed line represents the 1:1 line and dotted lines show 95% confidence interval.

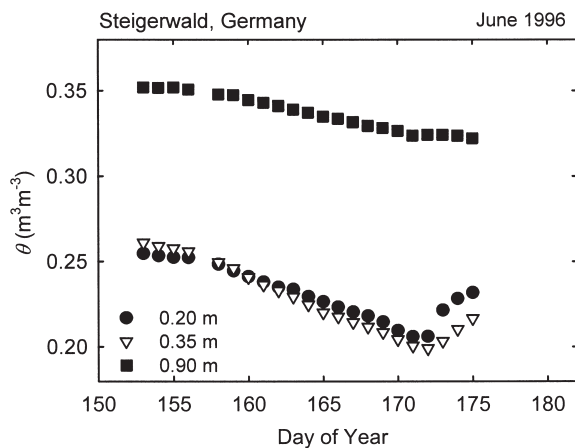
Relative water content was unrelated to depth in the sapwood ( $P = 0.165$ ), mirrored by low spatial variation observed in the tomographic images. However, there was a significant decrease in  $R_w$  (one-tailed  $t$  test,  $P = 0.029$ ) from sapwood (59.4%, SE 1.3) to heartwood (47.5%, SE 1.6), a decrease which was unrelated to specific wood density ( $P > 0.05$ ). Thus, sapwood area estimated from radial cores (i.e. from a linear measure) was highly correlated to the area estimated from tomography (i.e. from aerial measure) (Fig. 1b). This apparent homogeneity in the xylem permitted us to scale  $J_s$  to the flow in each xylem band by using the total corresponding sapwood area without the need to correct for spatial variability within each xylem band.

The mean transpiration of each tree on a leaf area basis,  $E_L$ , was estimated by summing water flow in all xylem bands, and dividing by leaf area estimated with Eqn (4). Time lags between  $E_L$  and  $D$  obtained with cross-correlation analysis for *F. sylvatica* ranged between 40 and 150 min, with no relation to tree basal area or height ( $P > 0.56$ ).

### Responses of $G_{Si}$ to environmental variables

Although the primary purpose of this study is to quantify the effect of tree height on mean stomatal conductance, it was necessary to first account for the variation in  $G_{Si}$  caused by  $\theta$ ,  $Q_o$  and  $D$ .

Water availability varies temporally and spatially. During the short period of the study,  $\theta$  in the upper soil layers (0.20 and 0.35 m depth) ranged from a maximum of  $0.27 \text{ m}^3 \text{ m}^{-3}$  to a minimum of  $0.19 \text{ m}^3 \text{ m}^{-3}$ , but remained high and was less variable with increasing depth (Fig. 2).  $G_{Si}$  was unrelated to either  $\theta$  or  $\Psi_s$  for any of the trees ( $P > 0.2$ ). Thus, temporal variation in soil moisture did not play a role during the study period. We note that, if taller trees were supported by a deeper root system, the spatial variability in soil moisture with depth (Fig. 2) would have provided them



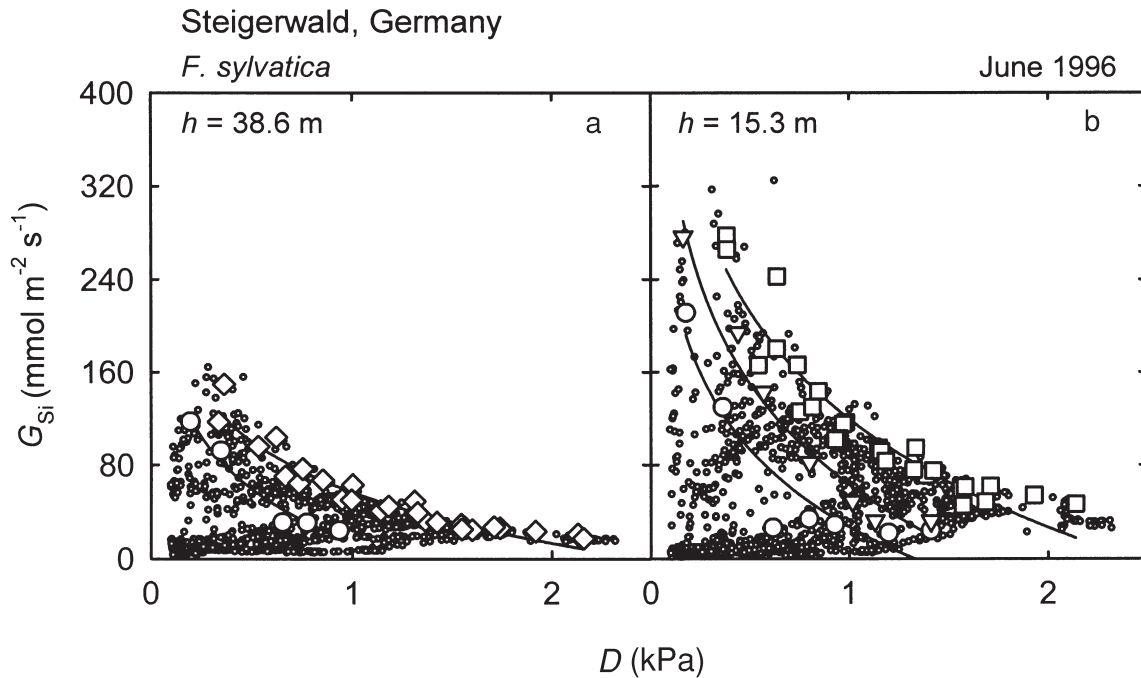
**Figure 2.** The course of soil water content  $\theta$  at three depths during the study period.

an advantage over short trees, resulting in increasing  $G_{Si}$  with tree height, which is opposite to the hypothesized relationship.

Analysis of the relationship between  $G_{Si}$  (Eqn 5) and  $D$  was performed after partitioning the data to six  $Q_o$  classes: five classes of  $150 \mu\text{mol m}^{-2} \text{ s}^{-1}$  up to  $750 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and one class representing the higher irradiance. With nine trees analysed, this resulted in 54 subsets of data. Each subset was subjected to a boundary line analysis, designed to select data representing maximum conductance for each tree in each  $Q_o$  class along the range of  $D$  (Dye & Olbrich 1993; Rico *et al.* 1996; Martin *et al.* 1997). The upper boundary line was derived by: (1) partitioning  $G_{Si}$  data of each light class into 0.2 kPa vapour pressure deficit intervals, (2) calculating the mean and standard deviation of  $G_{Si}$  in each interval, (3) removing outliers ( $P < 0.05$ ; Dixon's test according to Sokal & Rohlf 1995), (4) selecting the data falling above the mean plus one standard deviation, and (5) averaging the selected data for each  $D$  interval with  $n \geq 5$  remaining  $G_{Si}$  values. Excluding intervals with  $n < 5$  was done to prevent  $D$  intervals with too little information from affecting the relationship. For each tree and  $Q_o$  class, the mean  $G_{Si}$  values of all  $D$  intervals obtained in step (5) were then related to the natural logarithm of  $D$  (Eqn 2).

Figure 3 shows an example of  $G_{Si}$  calculated for one tall and one short tree of *F. sylvatica*. The tall tree reached a lower maximum  $G_{Si}$  (approximately  $60 \text{ mmol m}^{-2} \text{ leaf s}^{-1}$ ) than the short tree (approximately  $320 \text{ mmol m}^{-2} \text{ leaf s}^{-1}$ ). Using Eqn (2), we analysed the data selected through the boundary line analysis for each light class. Although the boundary line analysis was used to select data for six  $Q_o$  classes, used in six least-square regression fits between  $G_{Si}$  and  $\ln D$  for each tree, only a few relationships in each tree were distinct. In the tall tree example (Fig. 3), only two distinct relationships emerged: one for the lowest light class, and one for all the other classes. In the short tree example, the two lowest light classes are different from each other, and from all the other classes. In all, for the 54 separate regression analyses of  $G_{Si}$  versus  $\ln D$ , the  $P$  value for 52 was  $< 0.02$  (and  $P = 0.26$  and  $0.12$  for the remaining two regressions). The regression coefficient of determination ( $r^2$ ) ranged from 0.61 to 0.98. The poorest relationships were for regressions at intermediate light ( $150\text{--}450 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). Excluding the two poor relationships, average  $P$  and  $r^2$  for all trees in each light level were  $< 0.02$  and  $> 0.87$ , respectively.

In Fig. 3, it is shown that among light classes, the reduction in  $G_{Si}$  with increasing  $D$  is greater when  $G_{Si}$  at low  $D$  is higher. In fact, the sensitivity of stomata to  $D$  (e.g. the slope  $m$  in Eqn (2) or  $d G_{Si}/d \ln D$ ) was shown to be proportional to  $G_{Si}$  at low  $D$  (e.g. at 1 kPa, the intercept  $G_{Si\text{ref}}$  in Eqn 2, Oren *et al.*, 1999). This proportionality is convenient because the relative effect of height on  $G_{Si}$  will be the same regardless of the  $D$  at which the trees are compared. Thus, further analysis can focus on the effect of height on the intercept ( $G_{Si\text{ref}}$ ) of the relationship between  $G_{Si}$  and  $\ln D$  (Eqn 2).



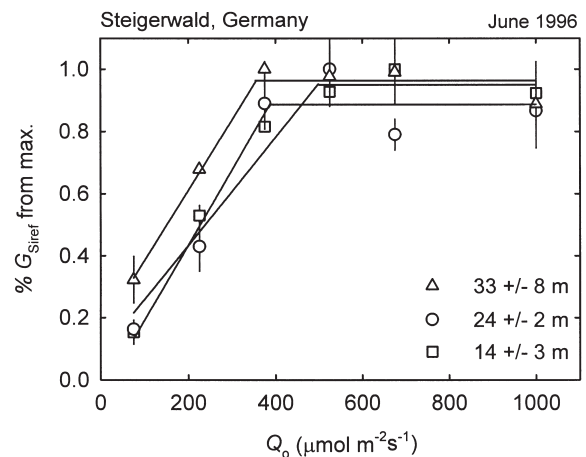
**Figure 3.** Mean stomatal conductance of individual trees ( $G_{Si}$ ) for (a) a tall tree and (b) a short tree in relation to vapour pressure deficit ( $D$ ). The lines represent the results of boundary line analysis selecting the maximum  $G_{Si}$  at different light levels (circles,  $Q_o < 150 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; diamonds in (a),  $Q_o > 150 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; triangles and squares in (b),  $Q_o = 150\text{--}450 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $> 450 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively; dots represent all data).

Analysis of the relationship between  $G_{Si}$  and  $\ln D$  resulted in 54 values of  $G_{Siref}$ , representing six light classes for each tree. In order to evaluate whether  $G_{Siref}$  is related to height, the confounding effect of light on  $G_{Siref}$  had to be removed. The effect of  $Q_o$  on  $G_{Siref}$  was evaluated after partitioning trees among three height classes, and expressing  $G_{Siref}$  in proportion to the highest value of each height class. Figure 4 shows that the patterns recognized in the examples in Fig. 3 were general.  $G_{Siref}$  reached saturation in all trees above  $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Thus, using only  $G_{Siref}$  obtained from the highest light class ensured that all trees are saturated with respect to light (Fig. 4).

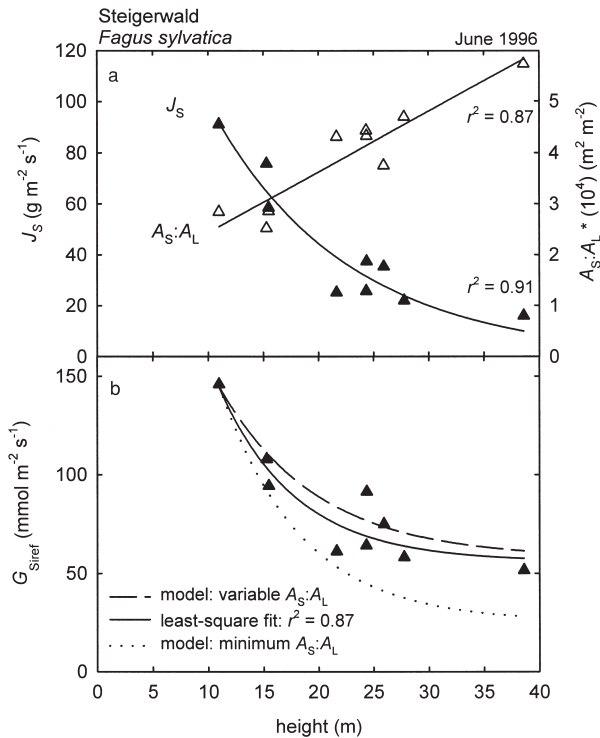
#### The effect of tree height on $G_{Siref}$

$J_S$  and  $A_S:A_L$  changed with height in opposite directions. Under saturating light and  $D = 1 \text{ kPa}$ ,  $J_S$  decreased exponentially with height ( $P < 0.0001$ ; Fig. 5a).  $A_S:A_L$  was calculated for each tree, using tree leaf area estimated from Eqn (4) and measured  $d$ , and sapwood area measured with tomography at the same height. Within the range of tree size in this study, estimated leaf area increased linearly with diameter, but measured sapwood area increased exponentially with diameter ( $r^2 = 0.98$ ,  $P < 0.0001$ ) despite a corresponding large increase in heartwood area. Both leaf and sapwood area increased exponentially with height, but the increase in sapwood area was proportionally greater, resulting in a value for  $A_S:A_L$  which increased twofold over 30 m in height (Fig. 5a,  $P = 0.0003$ ).

Similarly to  $J_S$ ,  $G_{Siref}$  decreased with height under non-limiting light conditions.  $G_{Siref}$  decreased in a log-linear fashion with height ( $P < 0.0001$ ; Fig. 5b), using, based on best distribution of residuals, a decay function with three parameters:



**Figure 4.**  $G_{Siref}$  is  $G_{Si}$  at a reference  $D (= 1 \text{ kPa})$ , averaged for arbitrarily chosen height classes, and is shown normalized to the highest value in each class in relation to mean values of six classes of photosynthetic photon flux density ( $Q_o$ ). Values next to the symbol legend are the mean of each height class ( $\pm 1 \text{ SE}$ ). Vertical lines represent 1 SE.



**Figure 5.** (a) Weighted mean sap flux density ( $J_S$ ) and sapwood-to-leaf area ratio ( $A_S:A_L$ ) in relation to tree height. (b) Mean stomatal conductance of individual trees ( $G_{Siref}$ ) at a reference vapour pressure deficit ( $D = 1$  kPa) in relation to tree height. The solid line represents a statistical fit using a non-linear model (Eqn 6). The dotted line represents the results from the hydraulic model obtained using Eqn (7-3), varying only the flow path length while using the sapwood-to-leaf area ratio ( $A_S:A_L$ ) of the shortest tree. The dashed line represents the results from the same model, but allowing  $A_S:A_L$  to increase with tree height.

$$G_{Siref} = G_{Smin} + ae^{-bh} \quad (6)$$

where the fitted parameters are:  $G_{Smin}$ , the minimum  $G_{Siref}$ ;  $a$ , the maximum  $G_{Siref}$ ;  $b$ , the sensitivity of  $G_{Siref}$  to tree height, and  $h$ , total tree height. Parameter values from this analysis were:  $G_{Smin} = 56$  mmol m<sup>-2</sup> s<sup>-1</sup>,  $a = 435$  mmol m<sup>-2</sup> s<sup>-1</sup>, and  $b = 0.10$  m<sup>-1</sup>.

The observed pattern in  $G_{Siref}$  with tree height could have emerged if a systematic bias corrupted the relationship between weighted average  $J_S$  and tree height (Fig. 5a). Errors in estimation of weighted average  $J_S$  may originate from errors in estimation of sapwood area, as well as neglecting systematic variation in  $J_S$  with depth (Phillips, Oren & Zimmermann 1996). However, because (1) two very different methods to estimate sapwood area of the trees were used, both of which provided similar estimates (Fig. 1b), and (2) no systematic difference in radial patterns of  $J_S$  between trees of different heights existed, it is highly unlikely that such potential errors could explain a systematic reduction in weighted  $J_S$  of approximately 85% with increase of approximately 30 m in tree height (Fig. 5a).

A simple hydraulic model was used to predict the reduc-

tion in  $G_{Siref}$  with height under light-saturating conditions. When  $D$  is fixed, here at 1 kPa, conductance is proportional to transpiration per unit leaf area ( $E_L$ ).  $E_L$  in turn is a function of hydraulic conductance from soil-to-leaf ( $k_{S-L}$ ) and the water potential difference between soil and leaf driving the flow ( $\Delta\Psi$ ):

$$G_{Siref} \propto E_L = k_{S-L}/A_L (\Delta\Psi_{S-L} - \Delta\Psi_g) \quad (7-1)$$

where  $\Delta\Psi_g$  is the portion of the  $\Delta\Psi_{S-L}$  water potential difference between root and leaf required to counteract gravity ( $\Delta\Psi_g = h \times 0.01$ , for  $\Psi$  in MPa and  $h$  in m). It is reasonable to assume that the hydraulic conductance of the shoot ( $k_{Shoot}$ ) will be proportional to the sapwood area ( $A_S$ ) because the more sapwood area, the more conducting tissue operating in parallel. The  $k_{Shoot}$  will also be inversely proportional to the length (or height,  $h$ ) of the shoot for the same length- and area-specific sapwood conductivity (defined as flow rate per pressure gradient per sapwood area). Limited information available from a study on pine shows that variations in sapwood conductivity are weakly related to age between 40 and 140 years, the range of ages for the beech in this study (Pothier, Margolis & Waring 1989b; Pothier *et al.* 1989a), and direct measurements of hydraulic conductance are consistent with an inverse relationship to height (Mencuccini & Grace 1996). Combining these proportionalities gives:

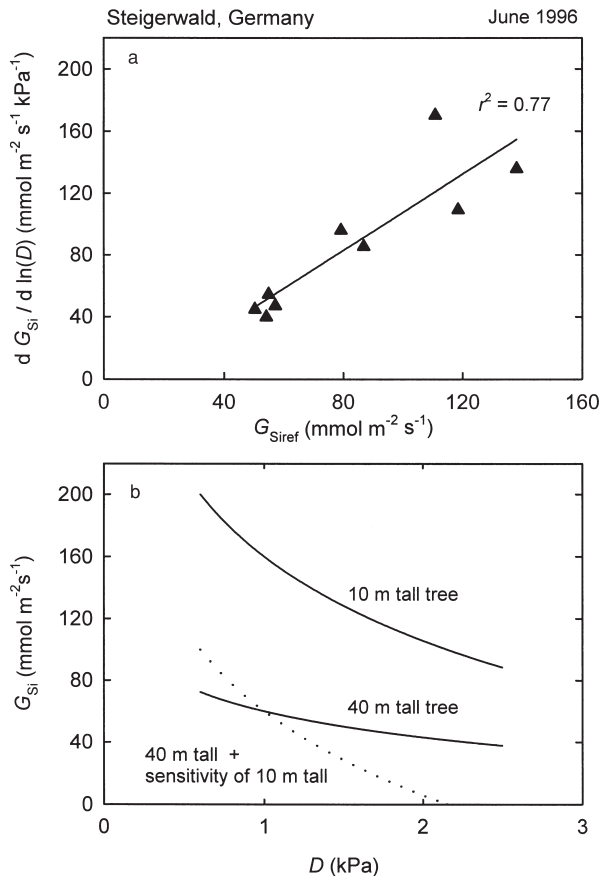
$$k_{Shoot} \propto A_S/h \quad (7-2)$$

If the ratio of  $k_{Shoot}$  and the hydraulic conductance of the root system is independent of height, the total root–shoot  $k_{S-L}$  in Eqn (7-1) will also follow the proportionality in Eqn (7-2). Substituting this proportionality for  $k_{S-L}$  in Eqn (7-1) gives the following relationship between  $G_{Siref}$  and  $h$ :

$$G_{Siref} \propto E_L = (1/h_M)(A_S:A_L)(\Delta\Psi_{S-L} - 0.01h_M) \quad (7-3)$$

where  $h_M$  is height at mid-crown in m (considered representative of the mean flow path length of each tree). If we assume that  $\Delta\Psi_{S-L}$  is constant with respect to height, as is often nearly the case for trees of the same species growing in a similar habitat (Scholander *et al.* 1965; Whitehead & Jarvis 1981; Hubbard, Bond & Ryan 1999), Eqn (7-3) leads to a prediction for how  $G_{Siref}$  should vary with  $h_M$ .

Using the hydraulic model, the reduction in  $G_{Siref}$  was estimated for each tree, based on mid-crown height and  $A_S:A_L$  varying as a function of mid-crown height ( $A_S:A_L = 1.528 \times 10^{-4} + 1.581 \times 10^{-5} h_M$ ,  $r^2 = 0.90$ ,  $P < 0.0001$ ; similar to Fig. 5a, but using  $h_M$  instead of total height). The values for all trees obtained from Eqn (7-3) were divided by the value of the shortest tree and then multiplied by  $G_{Siref}$  of that tree. The results are presented as a dashed line, which is anchored at  $G_{Siref}$  of the shortest tree and plotted against (Fig. 5b). The hydraulic model predicted a pattern of  $G_{Siref}$  decreasing with height entirely within the 95% confidence interval of the least squares fit to the data (full line, Fig. 5b). The fit suggests that the assumptions in our simple model were either valid or deviations from them were of little importance for the stomatal response to height.



**Figure 6.** Under non-limiting light conditions: (a) the sensitivity of mean stomatal conductance of individual trees ( $G_{Si}$ ) to vapour pressure deficit ( $D$ ) in relation to  $G_{Si}$  at a reference  $D$  ( $= 1$  kPa;  $G_{Siref}$ ); (b) schematic representations of the effect of stomatal sensitivity to  $D$  on  $G_{Si}$  for a short tree with high  $G_{Siref}$  and a tall tree with low  $G_{Siref}$ . Also shown is the hypothetical effect on  $G_{Si}$  of the tall tree if its stomatal sensitivity were similar to that of the short tree (dotted line).

In order to assess the compensatory effect of increasing  $A_S:A_L$  with height on  $G_{Siref}$ , the hydraulic model was used with an assumed constant  $A_S:A_L$  equal to that of the shortest tree. The model prediction was outside the confidence limits of the statistical fit at  $h > 17$  m, tending to underestimate actual  $G_{Siref}$  more with increasing height (dotted line Fig. 5b).

To assess an additional process which may accompany the reduction in  $G_{Si}$  with height, the relationship between individual tree parameter  $m$  ( $= d G_{Si} / d \ln D$ , or stomatal sensitivity to  $D$ ) and the parameter  $G_{Siref}$  in Eqn (2), under conditions in which light was non-limiting in all levels of the canopy ( $Q_0 > 750 \mu\text{mol m}^{-2} \text{s}^{-1}$ , Fig. 4), was quantified. The relationship between  $d G_{Si} / d \ln D$  and  $G_{Siref}$  (Fig. 6a) was highly significant ( $P = 0.0016$ ). This means that the stomata of tall trees were less sensitive to increasing  $D$  than stomata of smaller trees.

## DISCUSSION

Under conditions that maximize plant water loss, stomatal regulation limits  $\Psi_L$  and the associated dehydrative damage, such as the loss of hydraulic conductance via cavitation (Sperry *et al.* 1998). This mechanism is one of the hypothesized explanations to the limit imposed on maximum tree height (Friend 1993; Ryan & Yoder 1997). Thus far, a few studies provided indirect evidence for this mechanism (Yoder *et al.* 1994; Alsheimer 1997; Ryan & Yoder 1997; Hubbard, Bond & Ryan 1999). In these studies, greater tree height and age were confounded and neither factor was mechanistically linked to reduction in conductance. In contrast, Mencuccini & Grace (1996) investigated the effect of increasing flow path length on hydraulic conductance of *Pinus sylvestris* trees of different ages ranging in height from 1.6 to 24.2 m. Total tree above-ground conductance, calculated by summing the conductance of all branches and stem internodes, decreased with increase in tree height, in a manner expected from an inverse relationship with height (Whitehead & Hinckley 1991). The same pattern was repeated after normalizing total tree above-ground conductance by leaf area, and was also shown for branch 'leaf-specific' hydraulic conductance. However, in Mencuccini & Grace (1996), data on stomatal conductance were not available for a direct assessment of the effect of height.

In this study, we show that the reduction in mean stomatal conductance can be described well based on a hydraulic model that accounts for the increase in height, and in  $A_S:A_L$  with height (Eqn 7.3, dashed line in Fig. 5b). With increasing tree height, the area of leaves supported by a unit of sapwood decreased (Fig. 5a). This increases leaf-specific hydraulic conductance, and partially compensates for the increase in total soil-to-leaf flow path resistance with height, thus abating the effect of the longer flow path on stomatal conductance. The model estimates that, had trees been unable to adjust  $A_S:A_L$ , by increasing leaf area less than sapwood area with tree height, the reduction in  $G_{Siref}$  would have reached 80% over a 30 m increment in height (dotted line, Fig. 5b). With the increase in  $A_S:A_L$ , the modelled reduction in  $G_{Siref}$  with height was 60% (dashed line), similar to the observed reduction of 65% (solid line). Despite the adjustment in  $A_S:A_L$ , the drastic decrease in  $J_S$  with increasing flow path length reflects a large reduction in stomatal conductance necessary to maintain a reasonable  $\Psi_L$ .

In another study, Oren *et al.* (unpublished data) did not find a relationship between sap flux-scaled conductance and tree height in *Taxodium distichum* L. However, in that study,  $A_S:A_L$  was not available for individual trees, and it is conceivable that the shade-intolerant *T. distichum* may have adjusted its  $A_S:A_L$  to a greater extent than the highly shade-tolerant *F. sylvatica*. Alternatively, other hydraulic adjustments (e.g.  $k$ ,  $\Delta\Psi_{S-L}$ ) may be responsible for the absence of a reduction in stomatal conductance with height in some species and stands. Regardless of the mechanism, scaling sap flux to stand transpiration or canopy conduc-

tance requires a design that takes into account tree height in forests composed of species in which stomatal conductance decreases with height. A design emphasizing sampling of upper-canopy trees in forests that are well coupled to the atmosphere will lead to errors which are interestingly not always in the direction one might expect, namely that tall trees exposed to high light conditions have the highest mean stomatal conductance in the stand.

With such relatively low conductance and low foliage area per unit of respiring biomass, how do large trees maintain sufficiently high carbon uptake? Sandford & Jarvis (1986) suggested that the sensitivity of stomatal conductance to  $D$  should be positively related to the conductance in low  $D$ . This pattern, first demonstrated for non-woody species (Black & Squire 1979; Morison & Gifford 1983; Comstock & Ehleringer 1993), was recently shown to be general and consistent with the role of stomata in regulating  $E_L$  and plant water potential (Oren *et al.*, 1999). In the context of the findings in this study, this mechanism would reduce the impact of tree height on gas exchange by lowering the sensitivity of stomata in tall trees to diurnal changes in  $D$ .

We assessed the importance of this mechanism for sustaining gas exchange in tall trees by directly relating the stomatal sensitivity to  $D$  to  $G_{Siref}$ . The relationship between  $dG_{Si}/d \ln D$  and  $G_{Siref}$  (Fig. 6a) shows that trees with low  $G_{Siref}$  have proportionally lower stomatal sensitivity to increasing  $D$ . Because tall trees have lower  $G_{Siref}$  than short trees, lowered stomatal sensitivity in tall trees ensures a more stable carbon uptake rate over the wide diurnal range in  $D$ , and may serve as one mechanism supporting carbon exchange. This is shown as idealized response curves for a tall and short tree in Fig. 6(b). Were stomata of tall trees as sensitive to  $D$  as of short trees, gas exchange would be severely curtailed (dotted line in Fig. 6b).

In summary, reducing water stress in *F. sylvatica* in order to maintain a reasonable stomatal opening is achieved through increasing  $A_S:A_L$  with tree height (Fig. 5) by increasing sapwood area more than leaf area. The effect of increasing height on the reduction in gas exchange is more significant at high light (compare Fig. 3a,b), but is abated by compensatory reduction in the sensitivity of stomata to  $D$  (Fig. 6). It is interesting to note that, although shorter trees in the stand can reach higher  $G_{Si}$  than tall trees at high light, their greater sensitivity to  $D$ , coupled with the close correlation between diurnal  $D$  and  $Q_o$ , reduces considerably the advantage that shortness confers on leaf level gas exchange in a mixed-age stand. The advantage would be much greater if short and tall trees were compared at conditions in which light for both groups was unobstructed by overtopping canopy.

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