

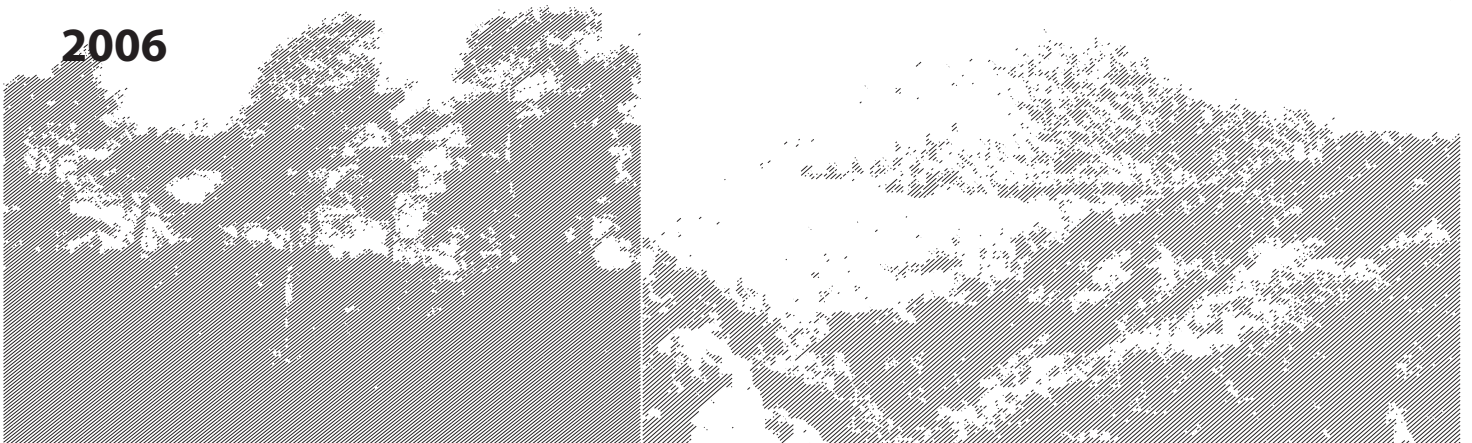


**Measuring and modelling transpiration
of pine and oak forest stands
in a Mediterranean mountain area (Vallcebre, NE Spain)**

TESI DOCTORAL

Rafael Poyatos López

2006



6. Plasticity in structural and functional hydraulic characters in Scots pine: Analysis of variability across Eurasia.

Poyatos, R.¹, Martínez-Vilalta, J.^{2,3}, Čermák, J.⁴, Ceulemans, R.⁵, Granier, A.⁶, Irvine, J.⁷, Köstner, B.⁸, Lagergren, F.⁹, Meiresonne, L.¹⁰, Nadezhdina, N.⁴, Zimmermann, R.¹¹, Llorens, P.¹, Mencuccini, M.²

In preparation for submission to *Oecologia*.

The botany of extreme climates has its special fascination. There is a thrill to be got from plants that surmount great natural difficulties, especially when they do so with excess and bravura

Gerald Brenan, South from Granada

- ¹ Institute of Earth Sciences 'Jaume Almera' (CSIC), ICTJA-CSIC, Lluís Solé i Sabarís, s/n , E-08028, Barcelona, Spain
- ² School of GeoSciences, University of Edinburgh, Crew Building, King's Buildings, Edinburgh EH9 3JN, UK
- ³ CREAM/Unitat d'Ecologia, Facultat de Ciències, Universitat Autònoma de Barcelona, Bellaterra 01893 (Barcelona), Spain
- ⁴ Institute of Forest Ecology, Mendel University of Agriculture and Forestry, Zemědělská 3, 613000 Brno, Czech Republic
- ⁵ Department of Biology, University of Antwerpen , Universiteitsplein 1, B-2610, Wilrijk, Belgium
- ⁶ Ecologie et Ecophysiologie Forestières, Centre de Nancy, F-54280 Champenoux, France
- ⁷ Department of Forest Science, Richardson Hall, College of Forestry, Oregon State University, Corvallis, OR 97331-5752, USA
- ⁸ Department of Meteorology, Institute for Hydrology and Meteorology, Technische Universität Dresden, D-01062 Dresden, Germany
- ⁹ Physical Geography and Ecosystems Analysis, Geobiosphere Science Centre, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden
- ¹⁰ Research Institute for Nature and Forest, Gaverstraat 4, B-9500 Geraardsbergen, Belgium
- ¹¹ Max Planck Institute for Biogeochemistry, PO Box 100164, 07743 Jena, Germany

Abstract

A meta-analysis of *Pinus sylvestris* L. sap flow and its response to environmental variables was conducted using datasets from across its whole geographical range. For each site, a Jarvis-type, multiplicative model was used to fit the relationship between sap flow and PAR, vapour pressure deficit (D) and soil moisture deficit (SMD); and a logarithmic function was used to characterize the response of stomatal conductance (G_s) to D . The fitted parameters of those models were regressed against climatic parameters to study the acclimation of Scots pine to dry/warm conditions. The absolute value of sap flow and its sensitivity to D and SMD increased with the average summer evaporative demand. However, relative sensitivity of G_s to D ($m/G_{s,ref}$) did not increase with evaporative demand across populations, and transpiration per unit leaf area (E_L) at a given D increased accordingly in drier/warmer climates. This physiological acclimation was linked to the previously reported climate- and size-related structural acclimation of leaf to sapwood area ratios ($A_L:A_S$). It is unclear why Scots pines have higher transpiration rates at drier/warmer sites, at the expense of lower water-use efficiency. In any case, our results suggest that these structural adjustments may not be enough to prevent higher xylem tensions at the driest sites. G_s at a reference D ($G_{s,ref}$) and its absolute sensitivity to D (m), generally decreased with age/height of the trees as previously reported for other pine species.

Resum

Aquest treball presenta una metanàlisi de mesures de flux de saba en *Pinus sylvestris* L. i de la seva resposta a les variables ambientals realitzada utilitzant bases de dades de tot el seu àmbit geogràfic. Per a cada localització, un model multiplicatiu de tipus *Jarvis* s'utilitzà per ajustar la relació entre flux de saba i PAR, dèficit de pressió de vapor (D) i dèficit hídric del sòl (SMD); i una funció logarítmica s'utilitzà per a caracteritzar la resposta de la conductància estomàtica (G_s) a D . Regressions entre els paràmetres ajustats d'aquests models i els paràmetres climàtics permeten l'estudi de l'aclimatació del pi roig a condicions seques/càlides. El valor absolut de flux de saba i la seva sensibilitat a D i SMD augmentaren amb la demanda evaporativa mitjana a l'estiu. Encara que la sensibilitat relativa de G_s a D ($m/G_{s,ref}$) no augmentà a l'incrementar la demanda evaporativa de les poblacions, i la transpiració per unitat d'àrea foliar (E_L) per a un determinat D augmentà en climes més secs/càlids. Aquesta aclimatació fisiològica es relacionà amb l'aclimatació climàtico-estructural de les relacions entre àrees de fulles i d'albeca ($A_L:A_S$) descrita prèviament. És poc clar perquè el pi roig té unes taxes de transpiració majors en localitzacions més seques/càlides a expenses d'una baixa eficiència en l'ús de l'aigua. En qualsevol cas, els resultats suggereixen que els ajusts estructurals poden no ser suficients per prevenir tensions més elevades al xilema en els llocs més secs. G_s a un D de referència ($G_{s,ref}$) i la seva sensibilitat a D (m), disminueix generalment amb l'edat/altura dels arbres tal i com s'havia descrit prèviament en altres pins.

Introduction

Tree species with extensive geographical distributions or living in contrasting habitats must develop a set of strategies that allow them to cope with a variety of climatic conditions, of which, atmospheric and soil moisture deficits are among the most relevant in determining plant growth and survival. Long-term drought acclimation of physiological responses and structural traits operate at different levels in the soil-plant-atmosphere continuum to maintain the hydraulic functioning of the tree (Mencuccini 2003). In the case of widely-distributed and abundant tree species at the global scale, these intraspecific climate-driven adjustments must be considered to understand the spatial variations in water and carbon exchange of forest ecosystems and the further implications of drought acclimation under climate change (DeLucia et al. 2000).

Short-term physiological regulation of tree transpiration by reducing stomatal conductance prevents excessive losses of water and too steep water potential drops in the soil-plant-atmosphere continuum (Meinzer 2002), which could lead to critical losses of xylem conductivity due to cavitation (Tyree and Sperry 1989). Thus, with the remaining hydraulic conditions being equal, trees growing in drier sites would benefit from an enhanced stomatal control of transpiration. Long-term structural changes operating in other compartments of the transpiration pathway also contribute to maintain a favourable hydric status under water-limiting conditions. A simple steady-state hydraulic model (Whitehead et al. 1984) predicts three mechanisms (in addition to stomatal regulation) to prevent the development of potentially damaging tensions in the xylem: (1) increased biomass allocation to conducting tissue, (2) higher sapwood conductivity or (3) an enhanced resistance to embolism (Maherali and DeLucia 2000). Recently, a more complex model has been proposed (Magnani 2000; Magnani et al. 2002) which also considers below-ground processes relevant for the hydraulic functioning of the tree. All these adjustments bear costs in terms of carbon gain and growth through reduced photosynthetic tissue, increased respiration (Ryan and Waring 1992) or construction costs (Hacke et al. 2001).

A reduction in the amount of leaf area relative to the conducting sapwood area with increasing evaporative demand has been shown to occur in several conifers, particularly pines (DeLucia et al. 2000), such as *Pinus ponderosa* Laws. (Callaway et al. 1994) or *Pinus sylvestris* L. (Mencuccini and Bonosi 2001). Less attention has been paid to plasticity of stomatal conductance and its response to water deficits, although some studies do report intraspecific variations in stomatal behaviour. Recent findings on ponderosa pine show that desert trees show higher maximum canopy stomatal conductance than montane trees (Maherali and DeLucia 2001), confirming previous results at the leaf level (DeLucia

and Schlesinger 1991). For Scots pine and ponderosa pine, there is some evidence for a strictly phenotypic, not ecotypic, origin for these climate-driven variation in hydraulic traits (Mencuccini and Grace, 1995; Maherali et al., 2002).

The phenomenological response of canopy-averaged stomatal conductance (G_s) to vapour pressure deficit (D), can be described by the equation (Oren et al. 1999),

$$G_s = G_{s,ref} - m \cdot \ln D \quad (1)$$

in which G_s sensitivity to D (slope m in Eq. 1) is tends to be linearly related to the magnitude of the reference conductance at $D=1$ kPa ($G_{s,ref}$) (Oren et al. 1999). Hence, if populations growing in warmer/drier climates showed an enhanced stomatal closure with increasing D , this response would be proportional to the value of $G_{s,ref}$. In this case, one would predict an increase in *absolute* sensitivity to D accompanied by a larger $G_{s,ref}$ in warmer/drier conditions (Fig. 1, black triangles compared to black dots). It is important to distinguish between absolute and relative stomatal sensitivity. The former is defined here as the absolute decline in G_s per relative increase in D (that is, the value of the parameter m ; see first derivative of G_s with respect to D in Eq. 1), whereas the relative stomatal sensitivity is defined in this study as the relative decline in G_s per relative increase in D (that is: $m/G_{s,ref}$). If there were a disproportional increase, with respect to $G_{s,ref}$, in the rate of stomatal closure with D , then an enhanced *relative* sensitivity would occur (Fig. 1, white circles). Alternatively, some authors (Mäkelä et al. 1996) predict a decrease in stomatal conductance with increasing evaporative demand (Fig. 1, white diamonds), which equates to proposing low values of G_s at low D and low sensitivity to D . In fact, this response has been shown in some acclimation experiments with plants grown under different levels of D (Leuschner 2002). Finally, one could predict a disproportional increase in $G_{s,ref}$ (with regards to m) at high D , which would correspond to a decline in relative stomatal sensitivity at high D (Fig. 1, inverted triangles). Note that these different scenarios have fundamental implications on transpiration rates per unit of leaf area (E_l) (Fig.1a) and on calculated leaf water potentials. Compared to the baseline scenario, Experimental evidence based on analysis of carbon isotope discrimination supports that indeed, stomatal control increases with aridity for different conifers (Warren et al. 2001) and more specifically, within the Pinaceae family (Martínez-Vilalta et al. 2004). In addition, pines show little plasticity in their vulnerability to embolism (Maherali and DeLucia 2000; Piñol and Sala 2000; Stout and Sala 2003), suggesting a dominant role of the abovementioned hydraulic adjustments and stomatal regulation as principal mechanisms of drought acclimation.

Scots pine (*Pinus sylvestris* L.) is one of the most widely distributed tree species on Earth, spanning across a vast climatic gradient from Eastern Siberia to Southern Spain. Hence, it has been the object of several studies on geographical variation of different functional

traits, including structural acclimation to drought (Berninger and Nikinmaa 1997; Mencuccini and Bonosi 2001; Mencuccini and Grace 1995; Palmroth et al. 1999). Scots pine maintains the integrity of the hydraulic continuum under atmospheric and edaphic drought by closing stomata (Irvine et al. 1998), but its low resistance to embolism (Cochard et al. 1992c; Jackson et al. 1995) makes it vulnerable to extremely dry periods in southernmost populations (Martínez-Vilalta and Piñol, 2002).

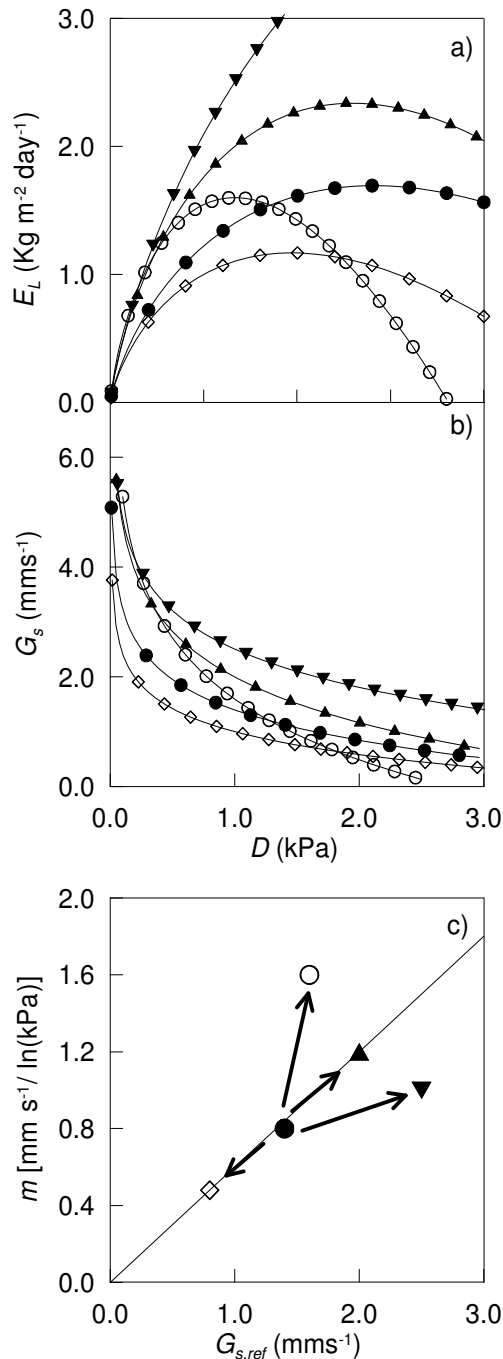


Figure 1. Theoretical relationship between transpiration per unit leaf area (E_L) and D according to stomatal responses described in (b) and (c). The notional baseline scenario is represented by the black dots. Phenotypic plasticity in stomatal responses to water deficits at warmer/drier sites is represented by two alternative cases, whereby $G_{s,ref}$ and m either decrease (diamonds) or increase (triangle) proportionally in warmer/drier sites. The proportionality between $G_{s,ref}$ and m is ca. 0.6 (Oren et al. 1999). Alternatively, $G_{s,ref}$ can increase (inverted triangles) or decrease (white dots) disproportionately with respect to m . Reductions in E_L at a given D are only obtained by either reducing $G_{s,ref}$ or by increasing the relative stomatal sensitivity (i.e., $m/G_{s,ref}$).

In this study we conducted a meta-analysis of Scots pine sap flow data from several sites across a climatic gradient in Eurasia, to compare the response of sap flow rates and canopy stomatal conductance to the main environmental variables. Regarding

physiological acclimation to drought, we hypothesized that populations growing in warmer/drier sites should have (1) higher transpiration rates per unit leaf area at a reference D and (2) an enhanced *absolute* stomatal sensitivity to atmospheric drought, proportional to the value of conductance at low D (Oren et al. 1999). Finally, we hypothesized that (3) physiological and structural acclimation combine to maintain homeostasis in plant water transport across different climates.

Materials and methods

Study sites: climatic and stand parameters

The eight studied sites were highly representative of the broad range of climatic conditions across Scots pine's geographical distribution (Table 1), from Siberian boreal forests to montane populations in NE Iberian Peninsula. Mediterranean, continental, coastal and subarctic climates were represented in this meta-analysis.

Mean annual temperature (MAT), mean annual precipitation (MAP), elevation and geographical coordinates were available for all sites from the literature. Potential evapotranspiration (PET), calculated with a modified Thornthwaite method, was taken from a global dataset with a resolution of 0.5 degrees (UNEP 1992), in order to make it comparable across the sites. VPD_{summer} was calculated averaging the monthly VPD of June, July and August, which were also taken from a global dataset (New et al. 1999). Note that for vapour pressure deficit the symbol D will be used for the daytime averages and VPD for the climatic parameter referring to the long-term evaporative demand.

Table 1. Summary of climatic characteristics of the studied sites.

Site	Location	Latitude	Longitude	Elevation (m)	MAT (°C)	MAP (mm y ⁻¹)	VPD_{summer} (kPa)	P/PET
Zotino	C Siberia	60 43' N	89 08' E	100	-3.7	493	1.36	2.3
Norunda	C Sweden	60 05' N	17 29' E	41	5.5	527	0.99	1.7
Guisachan	N Scotland	57 16' N	04 49' W	300	6.5	1215	0.66	5.3
Devilla	C Scotland	56 02' N	03 43' W	75	8.5	820	0.80	3.3
Brasschaat	N Belgium	51 18' N	04 31' E	16	9.8	767	1.16	1.9
Nedamov	Czech Rep.	50 28' N	14 35' E	300	8.5	456	1.45	0.9
Hartheim	SW Germany	47 56' N	07 37' E	201	9.8	647	1.17	1.3
Vallcebre	NE Spain	42 12' N	1 49' E	1260	8.6	924	1.35	1.3

MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation. Taken from the respective publications.

VPD_{summer} : Summer Vapour Pressure Deficit. Taken from the climatic database in New et al. (1999). P/PET : Precipitation to Potential Evapotranspiration Ratio. Taken from the climatic database in UNEP (1992).

The stands at the different sites, most of which were monospecific, varied in their origin, structure and age (Table 2). Leaf to sapwood area ratios ($A_L:A_S$) were always related to sapwood measured at breast height. Leaf area (projected, summertime values) was either measured on harvested trees or calculated from reported values of stand sapwood basal area and maximum leaf area index (LAI) of each site.

Dataset preparation

The main meteorological factors which determine transpiration from forest canopies (i.e. radiation, vapour pressure deficit and soil moisture) were first converted into comparable quantities. Global shortwave radiation (R_g) was converted into photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) wherever necessary. PAR was estimated as 45% of R_g (González and Calbó 2002), and the coefficient used to convert energy to photon flux units was 4.6 $\mu\text{E}/\text{J}$. If two different measurements of radiation were taken simultaneously (i.e. PAR and net radiation, R_n) linear regressions were performed to fill in the gaps in PAR or R_g data. We used 24-hour averages of PAR, thus taking into account differences in daylength across the sites.

Table 2. Main biometric characteristics of the studied stands.

Site	Age (years)	Basal Area ^a ($\text{m}^2 \text{ha}^{-1}$)	Density ^a (Trees/ha)	LAI _{max} ($\text{m}^2 \text{m}^{-2}$)	DBH (cm)	Height (m)	$A_L:A_S$ ($\text{m}^2 \text{cm}^{-2}$)	Management
Zotino	138	622	1110	1.3	18.0	15.2	0.226	natural
Norunda	50	28.9 (64%)	872 (59%)	5.0	20.0	17.4	0.141	natural
Norunda	100	39.1 (63%)	735 (42%)	4.5	32.2	26.8	0.099	natural
Guisachan ^c	28	20	316	0.9	10.8	7.2	0.188	natural
Guisachan ^c	49	20	316	0.9	37.6	11.7	0.180	natural
Guisachan ^c	195	20	316	1.6	83.1	17.6	0.153	natural
Devilla	40	28.0	836	2.3	20.1	15.0	0.108	plantation
Brasschaat ^b	70	31.4/27.0	560/376 (80%)	3/3	26.8/30.0	20.6/21.3	0.160	plantation
Nedamov	100	17.2	266	2.0	42.1	13.8	-	plantation
Hartheim ^b	36	36.7/24.1	3753/1754	3/1.9	10.8/12.9	11.5/12.3	0.090	plantation
Vallcebre	40	44.7	2165	2.4	15.2	11	0.065	natural

^a In multispecific stands, the total is given, with the corresponding percentage of Scots pine in brackets, where available

^b Pre/Post thinning values

^c Trees belonging to the different age classes are growing in the same stand. Basal area and density are given for the whole stand.

Vapour pressure deficit was present in all datasets, except for the dataset from Nedamov for the year 1980, where only radiation, temperature and PET data were available. In this specific case, we used meteorological data from the same site during the previous year, when relative humidity measurements were available, to perform a multiple regression analysis including air temperature (T_a), R_g and PET. This regression, which explained 84% of the variance in D , was used to estimate such variable for the Nedamov dataset in 1980. Soil moisture deficit (SMD) in the upper soil was calculated as (Granier and Loustau 1994):

$$\text{SMD} = \frac{\theta_{\max} - \theta}{\theta_{\max} - \theta_{\min}} \quad (2)$$

where θ is volumetric soil moisture ($\text{cm}^3 \text{ cm}^{-3}$), and θ_{\min} and θ_{\max} represent minimum and maximum values measured at each site during the period of study. Soil moisture was measured in the first 20 to 30 cm below the surface for all sites, except Brasschaat, where it was measured in the top 50 cm.

Table 3. Dataset coding, age of the stand, years of measurement, sap flow method used in each site and relevant references.

Site	Age	Code ^a	Years	Sap flow method	References
Zotino	130	ZO	1995-1997	HD	(Zimmermann et al. 2000)
Norunda	50	NO#1 ^a	1998-2000	THB	(Lagergren and Lindroth 2002; Lagergren and Lindroth 2004)
Norunda	100	NO#2	2001-2002	THB	(Lindroth et al., unpublished results)
Guisachan	28	GU#1	2003	HD	(Martínez-Vilalta et al., submitted)
Guisachan	49	GU#2 ^a	2003	HD	(Martínez-Vilalta et al., submitted)
Guisachan	195	GU#3	2003	HD	(Martínez-Vilalta et al., submitted)
Devilla	40	DV ^a	1995	HPV	(Irvine et al. 1998)
Brasschaat	70	BR	1997, 2000	HFD	(Meiresonne et al. 2003)
Nedamov	100	NE	1980	THB	(Čermák et al., unpublished results)
Hartheim	36	HA ^a	1993-1994	HD, THB	(Granier et al. 1996; Köstner et al. 1996)
Vallcebre	40	VA ^a	2003-2004	HD	(Poyatos et al. 2005)

^aDatasets included in the climatic analysis
HFD, heat field deformation; HPV, heat pulse velocity; HD, heat dissipation; THB, tissue heat balance

Sap flow measurements

Sap flow was measured at breast height in all locations using thermal methods (Table 3). Heat dissipation (Granier 1985; Granier 1987) and tissue heat balance (Čermák et al. 1973; Čermák et al. 2004) were the most employed methods, whereas the heat pulse velocity (Marshall 1958; Swanson and Whitfield 1974) and heat field deformation (Nadezhdina et al. 1998) techniques were applied in only one site. Tissue heat balance (THB) and heat dissipation (HD) methods have already been cross-compared for Scots pine (Köstner et al. 1996; Lundblad et al. 2001) and some disagreement in the quantitative estimates of sap flow density was found. We concluded therefore, that these methods obtain similar qualitative responses to environmental variables, but that there may be a degree of uncertainty in the absolute sap flow density values and in the subsequent scaling-up to whole-stem sap flow which should be taken into account when interpreting the results. This will be considered further in the Discussion.

Tree sap flow per unit leaf area (Q_L) was obtained from sap flow measurements and tree leaf area, except for Devilla, where sapwood areas, but not leaf areas were available. However, a stand-level leaf to sapwood area ratio ($A_L:A_S$) was locally available for this site and Q_L was obtained by dividing individual-tree, sapwood-related sap flow by the stand-level $A_L:A_S$ ratio. Transpiration on a leaf area basis (E_L) for each site was obtained averaging the individual values of Q_L , except for Nedamov, where it was derived from stand transpiration (E_c) divided by LAI. When the measurement period extended to early spring, autumn or winter, data were corrected for seasonal changes in leaf area, as supplied by the authors of the studies or estimated from data published elsewhere (Beadle et al. 1982; Gond et al. 1999; Wang et al. 2005).

Analysis of sap flow responses to environmental variables across the sites

We used a Jarvis-type, multiplicative model, originally developed for stomatal conductance (Jarvis 1976), but also applicable to sap flow (Oren and Pataki 2001), in which daily totals of sap flow per unit leaf area (E_L , kg m⁻² day⁻¹) were related to daytime averages of the main meteorological variables:

$$E_L = \frac{\text{PAR}}{\text{PAR}_{\max}} (a + b \cdot \ln D) (1 - k \cdot \exp(\text{SMD})) \quad (3)$$

In the following sections the parameters a , b and k (Eq. 3) fitted for each dataset are related to the main climatic (Table 1) and structural (Table 2) parameters of each site. Each of these parameters bears a physiological meaning: a is related to the absolute value of sap flow; whereas b and k measure the sensitivity to changes in D and SMD, respectively. As we are primarily interested in the climate-driven changes in stomatal behaviour, in order to avoid the confounding effects of age-related decline in sap flow (Delzon and

Loustau 2005), we first separately analysed the five sites with stand ages between 35 and 50 years old (climatic analysis). We considered all datasets only when we were analyzing specifically the effects of tree age/height or we were relating functional properties across sites. Note that for the Devilla dataset (Scotland) we only considered the control treatment to avoid the possible interference of the experimental drought in the analysis of general climatic patterns.

Analysis of canopy stomatal conductances (G_s)

As Scots pine stands are well coupled to the atmosphere (Whitehead and Jarvis 1981), canopy stomatal conductance (G_s , mm s^{-1}) was calculated from daily values of sap flow and meteorological variables using the inversion of the Penman-Monteith equation for well-coupled canopies (Phillips and Oren 1998):

$$G_s = \frac{\gamma \lambda E_L}{\rho_a c_p D} 10^3 \quad (4)$$

where γ is the psychrometric constant (kPa K^{-1}), λ is the latent heat of vaporisation of water (J kg^{-1}) ρ_a is air density (kg m^{-3}), c_p is specific heat of air ($\text{J K}^{-1} \text{kg}^{-1}$), D is daytime average vapour pressure deficit (kPa) and the 10^3 factor is used to convert conductance units from m s^{-1} into mm s^{-1} .

The relationship between G_s and D was analysed using boundary-line analysis performed with quantile regression (Cade and Noon 2003; Koenker and Basset 1978), using the statistical package R (R v. 2.0.1, R Development Core, Vienna, Austria). Regression results for the upper quantiles yield optimal relationships between a pair of variables when other factors not included in the model may also be affecting the response of the dependent variable. We assumed that the linear regression results for the 95th quantile were representative of the boundary-line relationship between G_s and $\ln D$ (Eqn. 1), and identified the obtained intercept and slope with the model parameters $G_{s,ref}$ and m , respectively (Eqn.1).

Other statistical analyses

Model fitting was carried out using the Levenberg-Marquardt algorithm in SPSS v.13.0 (SPSS Inc., Chicago, USA), after discarding data with average daytime $D < 0.05$ kPa . The results of the analysis of sap flow and canopy stomatal conductance were compared with climatic and structural parameters by means of correlation analysis, using linear or power fits. We considered that correlations were marginally significant when $0.05 < P < 0.1$. To test the sensitivity of these correlations to the variability posed by the use of different sap flow

methods, we carried out a sensitivity analysis based on a Monte Carlo approach. For each detected significant relationship ($P < 0.05$) we repeated the correlation analysis 1,000 times after multiplying the (sap flow-related) value for each site by a coefficient, which was different for each sap flow method. We then analyzed the percentage of realizations in which the original relationship was retained. The coefficient, specific for each sap flow method, was sampled independently for each realization from an homogeneous distribution between 0.75 and 1.25, simulating differences of $\pm 25\%$ in the estimates of sap flow across methods. Dataset coding for each site, years of measurement and relevant references for each study are summarised in Table 3.

Table 4. Model parameters (\pm SE), valid N and R-squared for the sap flow multiplicative model. For explanations of site codes and datasets see Table 3.

Dataset	N	R ²	Parameter values		
			<i>a</i>	<i>b</i>	<i>k</i>
NO#1	377	0.54	1.47** \pm 0.12	0.16* \pm 0.07	0.13** \pm 0.03
NO#2	155	0.42	0.65** \pm 0.08	0.39** \pm 0.08	0.12* \pm 0.05
GU#1	80	0.75	1.01** \pm 0.09	0.16** \pm 0.04	0.06 ^{ns} \pm 0.04
GU#2	90	0.78	0.65** \pm 0.07	0.14** \pm 0.03	0.10* \pm 0.04
GU#3	82	0.71	0.74** \pm 0.06	0.14** \pm 0.03	0.13** \pm 0.03
DV	177	0.49	1.46** \pm 0.10	0.09 ^{ns} \pm 0.05	0.16** \pm 0.02
BR	298	-	-	-	-
HA	178	0.54	2.12** \pm 0.12	0.32** \pm 0.10	0.33** \pm 0.01
NE	117	0.71	0.67** \pm 0.08	0.16** \pm 0.04	0.23** \pm 0.04
VA	382	0.67	2.38** \pm 0.09	0.46** \pm 0.06	0.24** \pm 0.01

** $P < 0.01$, * $0.01 < P < 0.05$, † $0.05 < P < 0.1$, ^{ns} $P > 0.05$

Results

Sap flow multiplicative model and the boundary-line analysis of G_s

The sap flow multiplicative model explained 49-78 % of the variance in E_L across the different datasets. Parameter *a* was found to be highly significant in all the datasets and sensitivity to *D* and SMD (parameters *b* and *k*) were non-significant only in Devilla and for one age class in Guisachan, respectively (Table 4). When fitted to the Brasschaat data, the model yielded negative values for parameters *b* and *k*, meaning that sap flow would decrease with *D* and increase with SMD (data not shown). Similar results were obtained when using alternative nonlinear regression algorithms. The reason for this problem lies in the similarity in the relationships between sap flow and both PAR and *D* for the range

of D values of the Brasschaat dataset, together with the high correlation between these two variables. This has likely lead to collinearity problems and the inability to fit this particular model. Since negative values of b and k are not consistent with our present understanding of sap flow responses to meteorological variables and are likely artefactual, this dataset was excluded from some of the analyses.

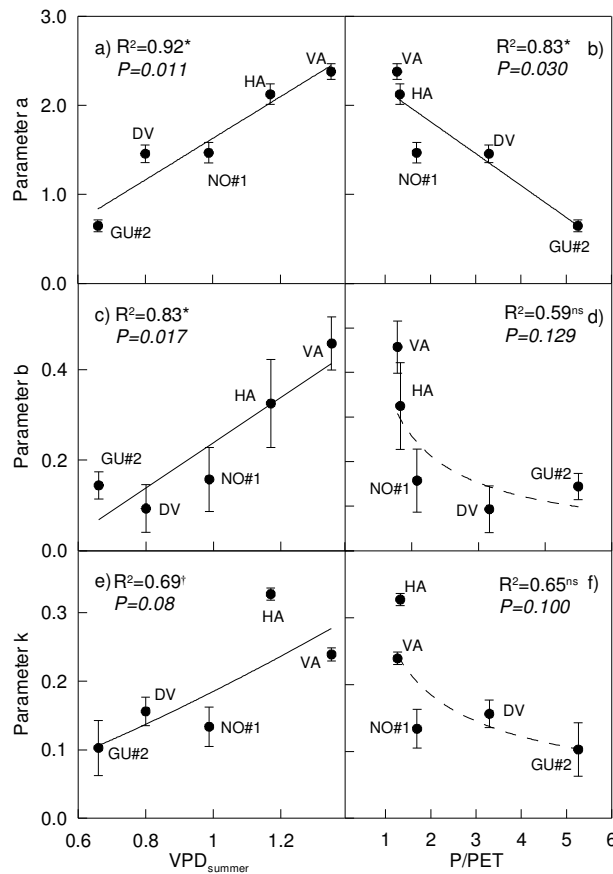


Figure 2. Relationships between the three parameters (\pm SE) of the sap flow multiplicative model (Eq. 3) and the long-term summer vapour pressure deficit (VPD_{summer}) and annual precipitation to potential evapotranspiration ratios (P/PET) for the different study sites. See Table 3 for meaning of site abbreviations. Statistically significant relationships are marked with full lines. ** $P < 0.01$, * $0.01 < P < 0.05$, [†] $0.05 < P < 0.1$, ^{ns} $P > 0.1$.

Considering only the datasets included in the climatic gradient analysis ($35 < \text{stand age} < 50$), none of the parameters, either from the sap flow model or the G_s analysis, was related to either MAT or MAP, except for sensitivity to soil moisture which was marginally and positively correlated with MAT ($R^2 = 0.71$, $P = 0.074$). Absolute values of sap flow and sensitivity to D were negatively related with latitude (parameter a : $R^2 = 0.67$, $P = 0.086$; parameter b : $R^2 = 0.88$, $P = 0.017$). Finally, parameters a and k showed a positive correlation with stand density (parameter a : $R^2 = 0.83$, $P = 0.034$; parameter k : $R^2 = 0.97$, $P = 0.003$).

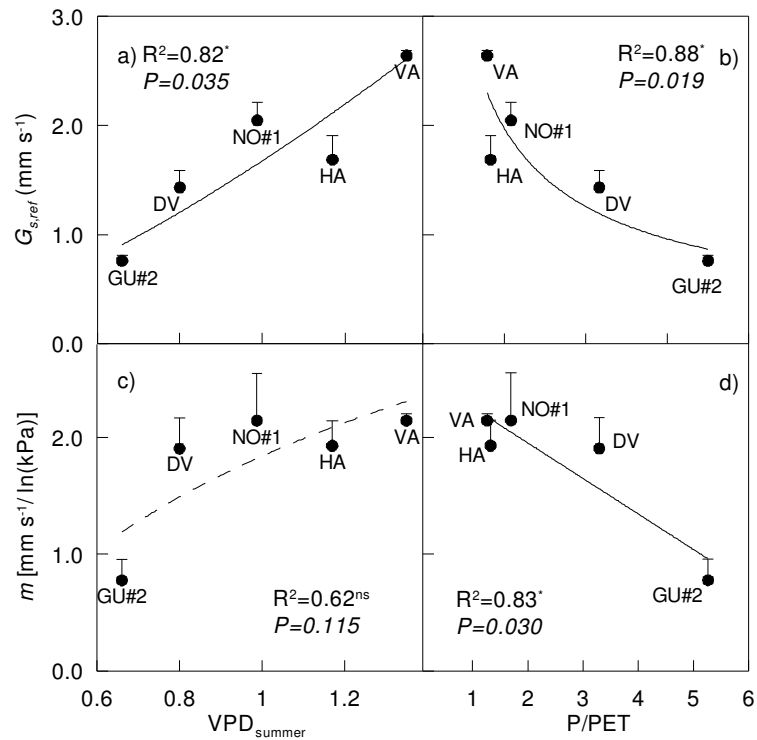


Figure 3. Relationship of canopy stomatal conductance at 1 kPa ($G_{s,ref}$, Eq. 1) and absolute sensitivity of G_s with respect to $\ln D$ (m ; Eq. 1) with long-term summer vapour pressure deficit ($\text{VPD}_{\text{summer}}$) and annual precipitation to potential evapotranspiration ratios (P/PET) for the different study sites. Error bars are positive standard errors. See Table 3 for meaning of site abbreviations and Fig. 2 for meaning of statistical significance symbols.

Physiological acclimation

The parameters resulting from the analysis of sap flow and canopy stomatal conductance were correlated with the main climatic parameters of each site describing local conditions of water balance and evaporative demand ($\text{VPD}_{\text{summer}}$, P/PET , PET). In the sap flow multiplicative model, parameter a , related to the absolute magnitude of sap flow, was positively correlated with $\text{VPD}_{\text{summer}}$ and negatively correlated with P/PET (Figs. 2a,b). Sensitivity to D and soil moisture deficit, as described in our model, showed similar trends against $\text{VPD}_{\text{summer}}$ and P/PET : both parameters increased with higher $\text{VPD}_{\text{summer}}$ and decreased with higher P/PET ratios (Figs. 2c-f). The relationships with P/PET were only significant for parameter a , though. Positive correlations between parameters a and b , and PET were also observed (parameter a : $R^2=0.77$, $P=0.051$; parameter b : $R^2=0.96$, $P=0.003$). Multiplying parameter a by $A_L:A_S$ (representing a value of reference sap flow per unit sapwood) did not result in any significant relationship with $\text{VPD}_{\text{summer}}$ or P/PET . The observed relationships with P/PET did not change when PET was obtained with alternative methods (Turc, Penman-Monteith reference evapotranspiration) (data not shown).

Reference canopy stomatal conductance ($G_{s,ref}$) was positively correlated with VPD_{summer} and negatively correlated with P/PET (Figs. 3a,b). Canopy stomatal conductance also showed an increased sensitivity to D at lower P/PET values (Fig. 3d) and an apparent trend with VPD , which was not statistically significant (Fig. 3c). In fact, except for Guisachan, the rest of the locations showed very similar values of parameter m (ca. $2 \text{ mm s}^{-1} \ln \text{ kPa}^{-1}$). Overall, the general trends in stomatal parameters with respect to climate were consistent with the results of the sap flow model.

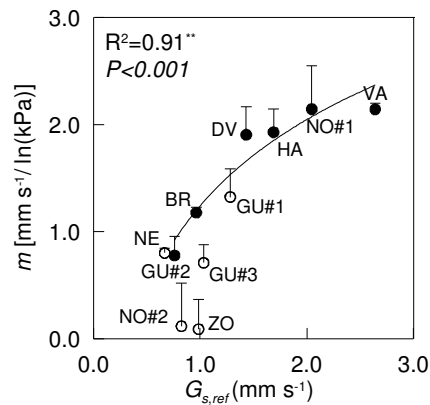


Figure 4. Relationship between canopy stomatal conductance at 1 kPa ($G_{s,ref}$; Eq. 1) and absolute sensitivity of G_s with respect to $\ln D$ (m ; Eq. 1). Error bars are positive standard errors. See Table 3 for meaning of site abbreviations and Fig. 2 for meaning of statistical significance symbols.

The parameters $G_{s,ref}$ and m were positively related in a logarithmic fashion, showing a tendency for sensitivity to D to plateau at high $G_{s,ref}$ (Fig. 4). No significant trend was found between the ratio of these two parameters ($m/G_{s,ref}$) and VPD_{summer} ($R^2=0.30$, $P=0.342$) or P/PET ($R^2=0.06$, $P=0.680$) for the mature stands. We also observed a positive linear relationship between $G_{s,ref}$ and the maximum PAR of the site, when all sites were considered ($R^2=0.55$, $P=0.009$), but not when only the sites in the climatic analysis were included ($R^2=0.32$, $P=0.320$).

Structural and physiological acclimation

Leaf to sapwood area ratios increased with decreasing evaporative demand (VPD_{summer}) and increasing P/PET but the observed relationships were not overly strong, with only a marginal statistical significance in the case of VPD_{summer} (Fig. 5). However, the inclusion of the stands reviewed in Mencuccini and Bonosi (2001) which lied within the age range of our climatic analysis, resulted in a much stronger linear trend ($R^2=0.60$, $P=0.003$).

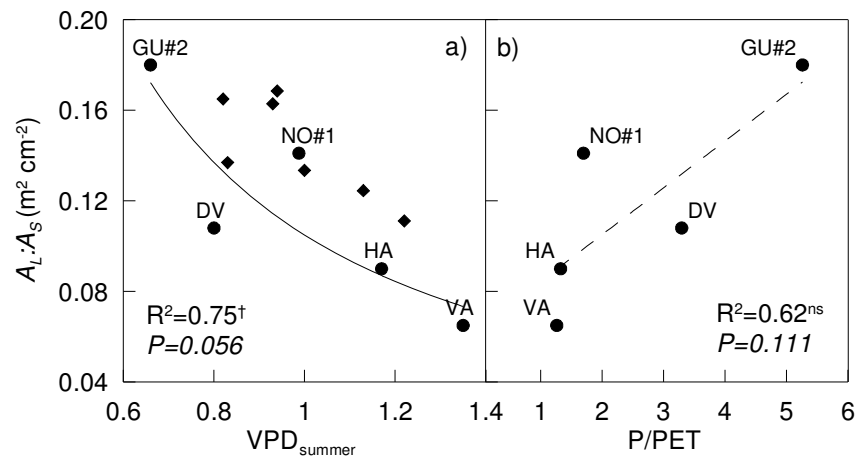


Figure 5. Relationships between leaf-to-sapwood area ratios ($A_L:A_S$) and (a) long-term summer vapour pressure deficit (VPD_{summer}) and (b) annual precipitation to potential evapotranspiration ratios (P/PET) across sites included in the climatic analysis. In figure 5a, data from stands reviewed in Mencuccini and Bonosi (2001) within the age range of our climatic analysis are also shown (black diamonds). See Table 3 for meaning of site abbreviations and Fig. 2 for meaning of statistical significance symbols.

We examined the relationships between the parameters describing the stomatal behaviour of Scots pine (a , b , k , $G_{s,ref}$ and m) and $A_L:A_S$, pooling all the datasets regardless of their stand age. All the parameters of the multiplicative model showed significant decreasing trends with increasing $A_L:A_S$, except parameter a , for which the correlation was very close to being significant at the 0.05 level (Fig. 6). However, multiplying $A_L:A_S$ by mean tree height resulted in a stronger correlation, while for the other two parameters the relationships were then better described by a second order polynomial fit (Fig. 6, see Discussion section for further information regarding rationale for such an analysis). Similarly, $G_{s,ref}$ and m also decreased with $A_L:A_S$, although in both cases the relationships were only marginally significant (Fig. 7). These two relationships disappeared when only the sites included in the climatic analysis were considered ($G_{s,ref}$, $R^2=0.61$, $P=0.119$; and m , $R^2=0.58$, $P=0.132$).

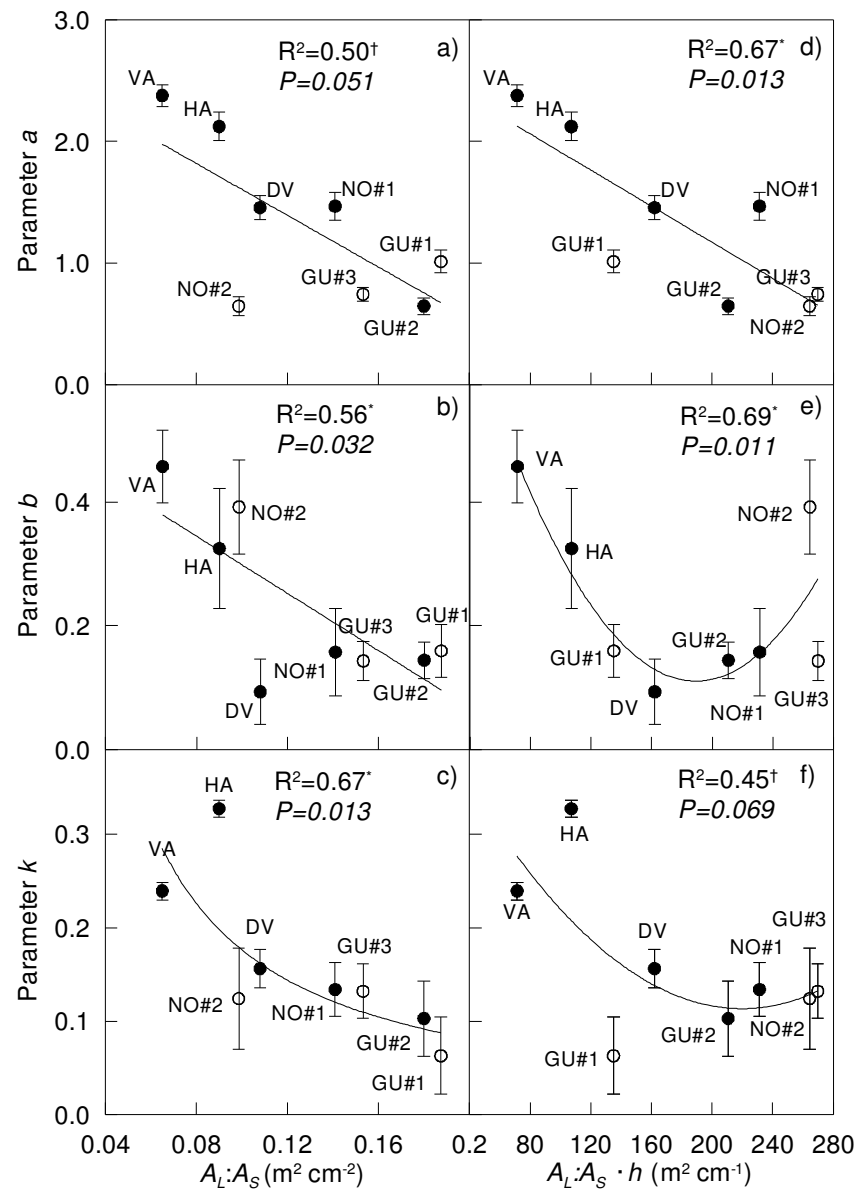


Figure 6. Relationships between the three parameters of the sap flow multiplicative model (Eq. 3) and leaf-to-sapwood area ratios ($A_L:A_S$) across sites (a,b,c). The same parameters are also regressed against the product of $A_L:A_S$ and mean tree height ($A_L:A_S \cdot h$). Error bars are standard errors. See Table 3 for meaning of site abbreviations and Fig. 2 for meaning of statistical significance symbols.

A noteworthy point is the departure of the parameter m for the 100 year-old stand in Norunda (NO#2) from the observed general relationship (Fig. 7). In this site, trees are appreciably taller than in any other site (Table 2), and this result suggests a decrease in stomatal sensitivity to D with increasing mean height of the trees, which was supported by our results (Fig. 8c). However, the relationship was tighter with age, and both $G_{s,ref}$ and m decreased with age of the stand (Fig. 8b,d). The ratio between these two parameters $m/G_{s,ref}$ was found to decrease with age, but the trend was only marginally significant ($R^2=0.32$, $P=0.07$).

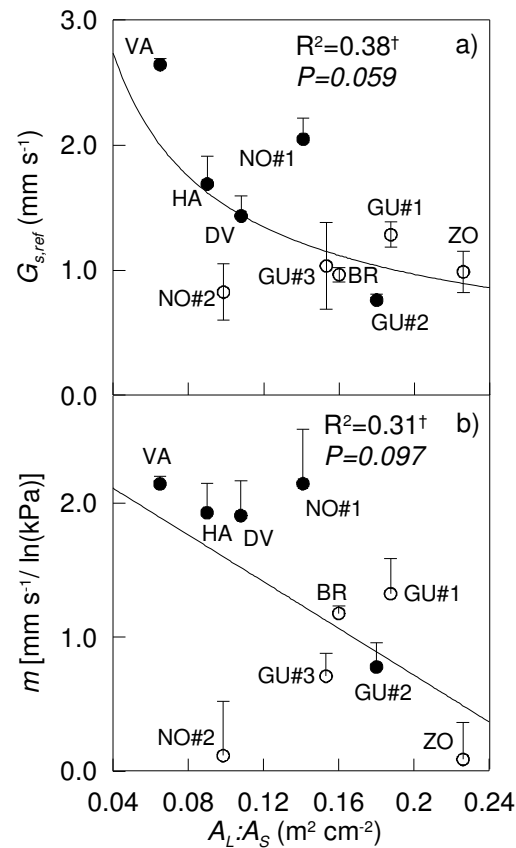


Figure 7. Relationship between (a) stomatal conductance at 1 kPa ($G_{s,ref}$, Eq. 1) and (b) absolute sensitivity of G_s with respect to $\ln D$ (m ; Eq. 1) and leaf-to-sapwood area ratios ($A_L:A_S$) across sites. Error bars are positive standard errors. See Table 3 for meaning of site abbreviations and Fig. 2 for meaning of statistical significance symbols.

Finally, the results of the sensitivity analysis showed that only in two out of nine cases the original significant relationship was retained in less than 50% of the realizations. This was the case of the relationship between the parameter a and P/PET (retained in 45% of the realizations) and between m and P/PET (retained only in 40% of the realizations). In this two cases, the relationship remained at least marginally significant in >60% of the realizations. Overall (considering the nine tested relationships) in 79% of the realizations the result was consistent with the original conclusion (significance at the 0.05 level). We thus conclude that our main results are robust with regards to potential quantitative differences between sap flow methods.

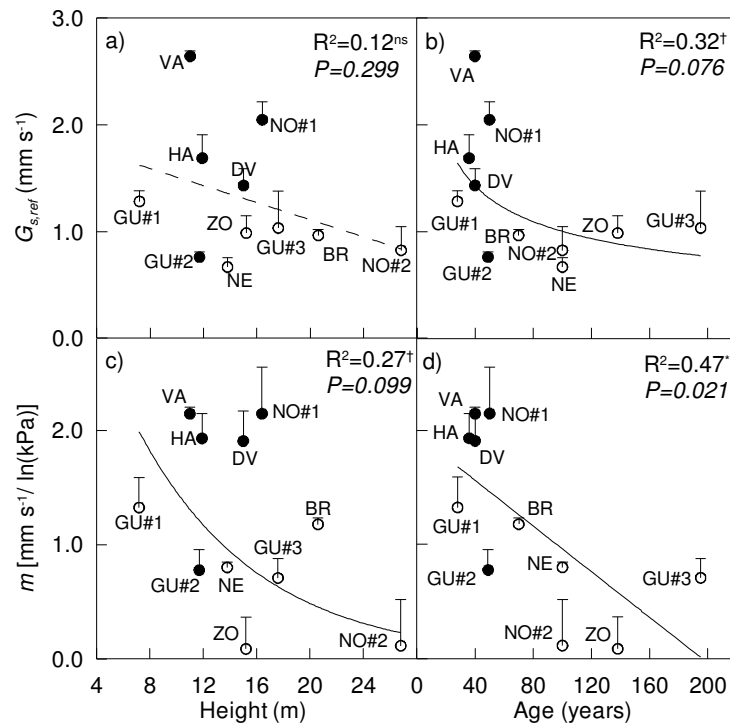


Figure 8. Variation of conductance at 1 kPa ($G_{s,ref}$, Eq. 1) and absolute sensitivity of G_s with respect to $\ln D$ (m ; Eq. 1) with respect to the age and height of the stand. Error bars are positive standard errors. See Table 3 for meaning of site abbreviations and Fig. 2 for meaning of statistical significance symbols.

Discussion

Methodological issues

The range of environmental conditions in this meta-analysis is greater than in previous studies concerning structural adaptation to drought in *P. sylvestris* (Palmroth et al., 1999; Mencuccini and Bonosi, 2001), although the strictly climatic analysis is applied to sites within the climatic limits of the mentioned studies. To our knowledge, this is the first study comparing the physiological responses of sap flow across the range of a tree species, although a review of stand transpiration across Europe for *Fagus sylvatica* has recently been published (Schipka et al. 2005).

Except for the Brasschaat site, the performance of the multiplicative sap flow model in describing sap flow responses to environmental variables was reasonably good, given the fact that a common model was used for all sites (Table 4). Because of the methodological differences in sap flow measurement across sites, the possibility exists that some or all of our trends are artefactual. We think this is unlikely. First, because of the form of our model, one would expect that parameter a would be most affected, and yet significant correlations were also found for parameters b and k , and always in the directions expected from our physiological understanding of these processes. Second, the extreme

sites with regard to summer VPD and P/PET (Vallcebre and Guisachan), whose values strongly affect the regressions, were both obtained using the HD method. Hence, it is more likely that variability in methods employed resulted in random noise around the regression line. Besides, the results of the sensitivity analysis confirm that the observed relationships are robust with regards to potential differences between methods, including the uncertainties derived from the radial and azimuthal variability of sap flow.

Climate-driven physiological acclimation

Our results showed that E_L at reference conditions increases with long-term evaporative demand (Fig. 2a) and that the increase in E_L with vapour pressure deficit is steeper in warmer/drier sites (Fig. 2c). As a result, evapotranspiration per unit leaf area at a given D was always greater in warmer/drier sites. Indeed, stomatal conductance at reference conditions was shown to increase significantly in warmer/drier sites whereas sensitivity to D did not increase proportionally (Figs. 3,4). Therefore, we have found evidence that sensitivity of G_s to D increases in warmer/drier climates in absolute terms but decreases in relative terms. In ponderosa pine maximum G_s estimated using sap flow techniques was *ca.* 4 times larger in desert than montane populations (Maherali and DeLucia 2001), but the sensitivity to D was not studied in that case. Although stomatal control has been reported to increase with aridity within the Pinaceae family (Martínez-Vilalta et al. 2004), information on climate-driven intraspecific variations in stomatal sensitivity to D is scarce. Recently, an experimental study at the leaf level, has shown that (absolute) stomatal sensitivity to D , defined in the same way as in our study (Eqn. 1), increases with maximum summer VPD of the geographic origin of the species for several seedlings of temperate and rainforest trees (Cunningham 2004). However, in the same study, seedlings grown under experimentally manipulated low VPD showed an increase in parameter m , contrary to the acclimation patterns shown in our results. We could not relate our results of increased $G_{s,ref}$ with evaporative demand to a parallel increase in stomatal density, as previous observations on this parameter in Scots pine needles across a similar climatic gradient as the one studied here, showed a rather uniform value for all sites (Luoma 1997). However, maximum stomatal aperture also depends on other physical and biological properties of guard cells and stomata (Lushnikov et al. 1995), which were not reported in the previous study.

Climate-driven structural acclimation

Although many factors beside climate also play a role in $A_L:A_S$ variability across sites (Long and Smith 1988), Scots pine has been shown to reduce the ratio between transpiring and conducting area when evaporative demand increases (Mencuccini and Bonosi 2001; Mencuccini and Grace 1995), a pattern that has also been observed for other pine species (DeLucia et al. 2000). Indeed, using a smaller sample size than Mencuccini & Bonosi (2001), this trend was also observed in our stands but merging both data sets, a much tighter relationship emerged (Fig. 5). In addition, there was a close link between this structural acclimation and the physiological behaviour of Scots pine across the studied climatic gradient (Fig. 6,7). These findings are consistent with the observed patterns in stomatal behaviour if we analyse the results within the framework of the hydraulic model proposed by Whitehead et al. (1984):

$$A_L : A_S = \frac{cK_s}{G_s D} \frac{\Delta\psi}{h} \quad (5)$$

where K_s is sapwood conductivity, $\Delta\psi$ is the leaf-to-soil difference in water potential including the gravity effect, h is the height of the tree, and c groups a series of variables with a weak dependence on temperature. Although E_L at reference conditions was only marginally related to $A_L:A_S$, the strength of the correlation improved considerably when, as suggested by Eq. 5, $A_L:A_S$ was multiplied by mean stand height (Fig. 6). Because of the relevance of size-related structural changes, $A_L:A_S \cdot h$ is a better descriptor of the hydraulics of a developing stand than $A_L:A_S$ on its own. Overall, our results show that in warmer/drier climates, the product $G_s D$ was larger than in cooler/more humid conditions for any value of D . Therefore climate-driven adjustments in $A_L:A_S$ are necessary for an homeostatic regulation of $\Delta\psi$ within the operative limits for Scots pine.

Notwithstanding this, homeostasis in water transport may not entirely hold across the complete geographic distribution of Scots pine, as the abovementioned hydraulic adjustments may still not be enough to entirely regulate water potentials, leading to lower values of ψ in more arid environments. Although minimum ψ in *P. sylvestris* has been set at ca. -1.4 MPa in a recent review (Magnani et al. 2002), water potentials below -2 MPa have been measured in the Vallcebre site (Poyatos et al. unpublished results), confirming previous observations in other populations from NE Spain (Martínez-Vilalta and Piñol 2002). Consequently, one would expect some degree of acclimation to occur across populations with respect to vulnerability to embolism. Water potentials causing 50% loss of conductivity at these Mediterranean sites (Martínez-Vilalta and Piñol 2002) are much lower than the values reviewed in Magnani (2000). Finally, increasing sapwood K_s

with evaporative demand, as found for *P. ponderosa* (Maherali and DeLucia 2000), would also increase the conducting efficiency and allow higher transpiration rates in drier climates. In that particular case, an elevated K_s was not associated to an increase in vulnerability to embolism (Maherali and DeLucia 2000). Indeed, high vapour pressure deficits have been related to larger tracheid lumen diameter in *Pinus radiata* Don seedlings (Whitehead et al. 1983) and higher temperatures have also been positively correlated with larger lumen diameter in Scots pine (Antonova and Stasova 1993).

Other climatic factors and size/age related constraints

Comparing the responses of sap flow and stomatal conductance to soil moisture deficits across climates is much more difficult than observing patterns in the responses to atmospheric drought, due to our comparatively limited knowledge of the soil characteristics relevant to processes in the soil-plant-atmosphere hydraulic continuum (soil depths, vertical and horizontal extent of root systems, hydrodynamic properties of the soil) and the inherent heterogeneity of the soil matrix. Therefore, it is possible that the observed relationships with climate are due to differences in root systems across sites. Nevertheless, if we examine the values obtained for the parameter k in the climatic analysis (Fig. 2), the highest value corresponds to Hartheim forest, where shallow soils and restricted access to groundwater makes it prone to intense soil water deficits (Sturm et al. 1998), and the lowest are found for the clayey and organic-rich soils in Guisachan.

Apart from climate-driven hydraulic constraints, the increase of path length in tall trees poses an additional limitation on long-distance water transport. For most conifer species, $A_L:A_S$ is inversely related to tree height (McDowell et al. 2002), but these reductions in $A_L:A_S$ with height do not fully compensate for the size-related hydraulic constrictions and hence canopy conductance still declines with tree height (McDowell et al. 2002; Schäfer et al. 2000). Despite not finding a direct relationship between $G_{s,ref}$ and h (Fig. 7), we demonstrated the interaction between climate- and size-related hydraulic variation in $A_L:A_S$ (Fig. 6). Relationships between physiological parameters and age were generally better than those found for size (Fig. 8). We reported a decline in $G_{s,ref}$ (Fig. 8b) and $m/G_{s,ref}$ with tree age, consistent with the results for other pine species (Ewers et al. 2005; Irvine et al. 2004). It must be noted that, unlike Scots pine, some conifers with higher $A_L:A_S$ do not show plasticity in this trait with respect to evaporative demand (DeLucia et al. 2000) or even increase their $A_L:A_S$ with height (McDowell et al. 2002) or age (Köstner et al. 2002).

Acclimation or adaptation?

It seems obvious that the studied populations belong to different ecotypes of the same species (Molotkov and Patlaj 1991), but whether the observed gradient in stomatal responses to air humidity is due to ecotypic differentiation must be investigated. It has recently been shown that the contrasting hydraulic traits observed in montane and desert stands of *Pinus ponderosa* are not a result of ecotypic divergence (Maherali et al. 2002). Structural acclimation to high evaporative demands in Scots pine was first shown in two stands with identical genetic origin (Mencuccini and Grace 1995). These findings are consistent with the general view that pioneer species such as Scots pine show high phenotypic plasticity (Sultan 2000).

Effects of the observed patterns on carbon and nutrient dynamics

One of the consequences of maintaining high stomatal conductances in dry climates is the decline in water use efficiency due to the non-linear relationship between G_s and carbon assimilation (Cowan 1982). Our results contradict theoretical models of optimal gas exchange, which predict a decrease in stomatal conductance with increasing evaporative demand (Farquhar et al. 2002; Mäkelä et al. 1996), and agree with the results of gradient and common garden experiments showing that Scots pine intrinsic water use efficiency is not higher under warmer/drier conditions (Palmroth et al. 1999). Maintaining a high stomatal aperture could be beneficial for trees growing in warmer/drier sites, because photosynthetic rates under full light conditions would not be limited by CO_2 diffusion into the stomata.

Other processes are likely to influence the patterns observed in this study, for example the increased needle retention in cooler climates (Oleksyn et al. 2003). A full understanding of the mechanisms underlying the observed patterns may require the consideration of the complex interactions that determine the resource economy of trees, taking into account explicitly that plants are likely to be regulated in order to maximize carbon gain, and that photosynthesis may be limited by hydraulic factors, but also by other resources, such as nitrogen and light (Buckley and Roberts 2006).

Implications at the global scale

The observed variability in stomatal behaviour across climates in Scots pine undoubtedly influences the spatial variation of canopy fluxes of water vapour and carbon dioxide, and

has further implications in the parameterisation of ecosystem models, because this intraspecific variation is not usually considered (but see Berninger (1997)).

The results of this study are consistent with the observed vulnerability of southernmost populations to extreme drought events (Martínez-Vilalta and Piñol 2002). As previously shown, structural adjustments of Scots pine at these latitudes are not able to compensate for the higher transpiration rates, and thus lower water potentials are likely to be reached at warmer/drier sites, with the corresponding increase in the risk of cavitation. The predicted increase in the intensity and frequency of acute droughts can seriously threaten Scots pine stands in the Mediterranean basin. Extensive drought-induced mortality has been identified elsewhere as the cause of extreme vegetation changes at the landscape level (Allen and Breshears 1998; Mueller et al. 2005).

Conclusions

In conclusion, we have found that relative sensitivity of stomatal conductance to D does not increase with evaporative demand across Scots pine populations, and transpiration rates at a given D increase accordingly in drier/warmer climates. These patterns were associated with a decline in $A_L:A_S$ values in drier/warmer sites, as previously reported. We could not entirely explain why trees in warmer/drier climates reduced leaf area and kept high stomatal conductances, and not the opposite. Clearly, this topic deserves further attention, probably using a fully coupled photosynthesis-water transport model. More comprehensive surveys of climate-driven variation in hydraulic traits are also needed to complete the picture of physiological and structural hydraulic acclimation in Scots pine, and thus predict how climate change will affect this species across Eurasia.

References

- Allen, C.A. and D.D. Breshears 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Science USA*. 95:14839-14842.
- Antonova, G.F. and V.V. Stasova 1993. Effects of environmental factors on wood formation in Scots pine stems. *Trees*. 7:214-219.
- Beadle, C.L., H. Talbot and P.G. Jarvis 1982. Canopy structure and leaf area index in a mature Scots pine forest. *Forestry*. 55:105-127.
- Berninger, F. 1997. Effects of drought and phenology on GPP in *Pinus sylvestris*: a simulation study along a geographical gradient. *Funct Ecol*. 11:33-42.
- Berninger, F. and E. Nikinmaa 1997. Implications of varying pipe model relationships on Scots Pine growth in different climates. *Funct Ecol*. 11:146-156.

- Buckley, T.N. and D.W. Roberts 2006. DESPOT, a process-based tree growth model that allocates carbon to maximize carbon gain. *Tree Physiol.* 26:129-144.
- Cade, B.S. and B.R. Noon 2003. A gentle introduction to quantile regression for ecologists. *Front Ecol Environ.* 1:412-420.
- Callaway, R.M., E.H. DeLucia and W.H. Schlesinger 1994. Biomass allocation of montane and desert ponderosa pine: an analog for response to climate change. *Ecology.* 75:1474-1481.
- Čermák, J., M. Deml and M. Penka 1973. A new method of sapflow rate determination in trees. *Biol Plant (Praha).* 15:171-178.
- Čermák, J., J. Kučera and N.Nadezhdina 2004. Sap flow measurements, integration within trees and scaling up from sample trees to entire forest stands. *Trees.* 18:529-546.
- Cochard, H., P. Cruziat and M.T. Tyree 1992. Vulnerability of several conifers to air embolism. *Tree Physiol.* 11:73-83.
- Cowan, I.R. 1982. Water use and optimisation of carbon assimilation. *In Physiological plant ecology* Eds. O.L. Lange, C.B. Nobel, C.B. Osmond and H. Zeigler, Berlin, pp. 589-630.
- Cunningham, S.C. 2004. Stomatal sensitivity to vapour pressure deficit of temperate and tropical evergreen rainforest trees of Australia. *Trees.* 18:399-407.
- DeLucia, E.H., H. Maherali and E.V. Carey 2000. Climate-driven changes in biomass allocation in pines. *Global Change Biol.* 6:587-593.
- DeLucia, E.H. and W.H. Schlesinger 1991. Resource-use efficiency and drought tolerance in adjacent great basin and sierran plants. *Ecology.* 72:51-58.
- Delzon, S. and D. Loustau 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. *Agric For Meteorol.* 129:105-119.
- Ewers, B.E., S.T. Gower, B. Bond-Lamberty and C.K. Wang 2005. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell Environ.* 28:660-678.
- Farquhar, G.D., T.N. Buckley and J.M. Miller 2002. Optimal stomatal control in relation to leaf area and nitrogen content. *Silva Fenn.* 36:625-637.
- Gond, V., D.G.G. de Pury, F. Veroustraete and R. Ceulemans 1999. Seasonal variations in leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon balance in a multilayer, multispecies temperate forest. *Tree Physiol.* 19:673-679.
- González, J.A. and J. Calbó 2002. Modelled and measured ratio of PAR to global radiation under cloudless skies. *Agric For Meteorol.* 110:319-325.
- Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann Sci For.* 42:193-200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3:309-320.
- Granier, A., P. Biron, B. Köstner, L.W. Gay and G. Najjar 1996. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots Pine. *Theor Appl Clim.* 53:115-122.
- Granier, A. and D. Loustau 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric For Meteorol.* 71:61-81.

Hacke, U.G., J.S. Sperry, W.P. Pockman, S.D. Davis and K.A. McCulloh 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*. 126:457-461.

Irvine, J., B.E. Law, M.R. Kurpius, P.M. Anthoni, D. Moore and P.A. Schwarz 2004. Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine. *Tree Physiol*. 24:753-763.

Irvine, J., M.P. Perks, F. Magnani and J. Grace 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol*. 18:393-402.

Jackson, G.E., J. Irvine and J. Grace 1995. Xylem cavitation in two mature Scots pine forests growing in a wet and a dry area of Britain. *Plant Cell Environ*. 18:1411-1418.

Jarvis, P.G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philos Trans R Soc Lond B Biol Sci*. 273:593-610.

Koenker, R. and G. Basset 1978. Regression quantiles. *Econometrica*. 46:33-50.

Köstner, B., P. Biron, R. Siegwolf and A. Granier 1996. Estimates of water vapour flux and canopy conductance of Scots Pine at the tree level utilizing different xylem sap flow methods. *Theor Appl Clim*. 53:105-113.

Köstner, B., E. Falge and J. Tenhunen 2002. Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. *Tree Physiol*. 22:567-574.

Lagergren, F. and A. Lindroth 2002. Transpiration response to soil moisture in pine and spruce trees in Sweden. *Agric For Meteorol*. 112:67-85.

Lagergren, F. and A. Lindroth 2004. Variation in sapflow and stem growth in relation to tree size, competition and thinning in a mixed forest of pine and spruce in Sweden. *For Ecol Manag*. 188:51-63.

Leuschner, C. 2002. Air humidity as an ecological factor for woodland herbs: leaf water status, nutrient uptake, leaf anatomy and productivity of eight species grown at low or high vpd levels. *Flora*. 197:262-274.

Long, J.N. and F.W. Smith 1988. Leaf area-sapwood area relations of Lodgepole Pine as influenced by stand density and site index. *Can J For Res*. 18:247-250.

Lundblad, M., F. Lagergen and A. Lindroth 2001. Evaluation of heat balance and heat dissipation methods for sapflow measurements in pine and spruce. *Ann Sci For*. 58:625-638.

Luoma, S. 1997. Geographical pattern in photosynthetic light response of *Pinus sylvestris* in Europe. *Funct Ecology*. 11:273-281.

Lushnikov, A.A., T. Vesala, M. Kulmala and P. Hari 1995. A semiphenological model for stomatal gas transport. *J Theor Biol*. 171:291-301.

Magnani, F. 2000. Carbon allocation and tree growth under hydraulic constraints in Scots pine (*Pinus sylvestris* L.). University of Edinburgh, Edinburgh, UK, p. 236.

Magnani, F., J. Grace and M. Borghetti 2002. Adjustment of tree structure in response to the environment under hydraulic constraints. *Funct Ecol*. 16:385-393.

Maherali, H. and E.H. DeLucia 2000. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiol*. 20:859-867.

- Maherali, H. and E.H. DeLucia 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia*. 129:481-491.
- Maherali, H., B.L. Williams, K.N. Paige and E.H. DeLucia 2002. Hydraulic differentiation of Ponderosa pine populations along a climate gradient is not associated with ecotypic divergence. *Funct Ecol*. 16:510-521.
- Mäkelä, A., F. Berninger and P. Hari 1996. Optimal control of gas exchange during drought: a theoretical analysis. *Annals of Botany*. 77:461-467.
- Marshall, D.C. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiology*. 33:385-396.
- Martínez-Vilalta, J. and J. Piñol 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For Ecol Manag*. 161:247-256.
- Martínez-Vilalta, J., A. Sala and J. Piñol 2004. The hydraulic architecture of Pinaceae - a review. *Plant Ecol*. 171:3-13.
- McDowell, N., H. Barnard, B. Bond, T. Hinckley, R. Hubbard, H. Ishii, B. Köstner, F. Magnani, J. Marshall, F. Meinzer, N. Phillips, M. Ryan and D. Whitehead 2002. The relationship between tree height and leaf area: sapwood area ratio. *Oecologia*. 132:12-20.
- Meinzer, F.C. 2002. Co-ordination of vapour and liquid phase water transport properties in plants. *Plant Cell Environ*. 25:265-274.
- Meiresonne, L., D.A. Sampson, A.S. Kowalski, I.A. Janssens, N. Nadezhdina, J. Čermák, J. Van Slycken and R. Ceulemans 2003. Water flux estimates from a Belgian Scots pine stand: a comparison of different approaches. *J Hydrol*. 270:230-252.
- Mencuccini, M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant Cell Environ*. 26:163-182.
- Mencuccini, M. and L. Bonosi 2001. Leaf/sapwood area ratios in Scots pine show acclimation across Europe. *Can J For Res*. 31:442-456.
- Mencuccini, M. and J. Grace 1995. Climate influences the leaf/sapwood area ratio in Scots pine. *Tree Physiol*. 15:1-10.
- Molotkov, P.I. and I.N. Patlaj 1991. Systematic position within the genus *Pinus* and intraespecific taxonomy. *In Genetics of Scots pine* Eds. M. Giertych and C. Mátyás. Elsevier, Amsterdam, pp. 31-40.
- Mueller, R.C., C.M. Scudder, M.E. Porter, R.T.I. Trotter, C.A. Gehring and T.G. Whitham 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *J Ecol*. 93:1085-1093.
- Nadezhdina, N., J. Čermák and V. Nadezhdin 1998. Heat field deformation method for sap flow measurements. *In 4th International Workshop on measuring sap flow in intact plants* Eds. J. Čermák and N. Nadezhdina. IUFRO Publications, Zidlochovice, Czech Republic, pp. 72-92.
- New, M.G., M. Hulme and P.D. Jones 1999. Representing 20th century space-time climate variability. I: Development of a 1961-1990 mean monthly terrestrial climatology. *J Climate*. 12:829-856.
- Oleksyn, J., P.B. Reich, R. Zytowski, P. Karolewski and M.G. Tjoelker 2003. Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations. *Oecologia*. 136:220-235.
- Oren, R. and D.E. Pataki 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. *Oecologia*. 127:549-559.

Oren, R., J.S. Sperry, G.G. Katul, D.E. Pataki, B.E. Ewers, N. Phillips and K.V.R. Schafer 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ.* 22:1515-1526.

Palmroth, S., F. Berninger, E. Nikinmaa, J. Lloyd, P. Pulkkinen and P. Hari 1999. Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecologia.* 121:302-309.

Phillips, N. and R. Oren 1998. A comparison of daily representations of canopy conductance based on two conditional time averaging-methods and the dependence of daily conductance on environmental factors. *Ann Sci For.* 55:217-235.

Piñol, J. and A. Sala 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. *Funct Ecol.* 14:538-545.

Poyatos, R., P. Llorens and F. Gallart 2005. Transpiration of montane *Pinus sylvestris* L. and *Quercus pubescens* Willd. forest stands measured with sap flow sensors in NE Spain. *Hydrol Earth Syst Sci.* 9:493-505.

Ryan, M.G. and R.H. Waring 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology.* 73:2100-2108.

Schäfer, K.V.R., R. Oren and J.D. Tenhunen 2000. The effect of tree height on crown level stomatal conductance. *Plant Cell Environ.* 23:365-375.

Schipka, F., C. Leuschner and J. Heimann 2005. Regional variation in canopy transpiration of Central European beech forests. *Oecologia.* 143:260.

Stout, D.L. and A. Sala 2003. Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. *Tree Physiol.* 23:43-50.

Sturm, N., B. Köstner, W. Hartung and J.D. Tenhunen 1998. Environmental and endogenous controls on leaf- and stand-level water conductance in a Scots pine plantation. *Ann Sci For.* 55:237-253.

Sultan, S.E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5:537-542.

Swanson, R.H. and D.W.A. Whitfield 1974. A numerical analysis of heat pulse velocity: theory and practice. *J Exp Bot.* 32:221-239.

Tyree, M.T. and J.S. Sperry 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology.* 40:19-38.

UNEP 1992. *World Atlas of Desertification.* Edward Arnold, London,UK. 69 p.

Wang, Q., J. Tenhunen, N.Q. Dinh, M. Reichstein, T. Vesala and P. Keronen 2005. Similarities in ground- and satellite-based NDVI time series and their relationship to physiological activity of a Scots pine forest in Finland. *Remote Sens Environ.* 93:225-237.

Warren, C.R., J.F. McGrath and M.A. Adams 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia.* 127:476-486.

Whitehead, D., W.R.N. Edwards and P.G. Jarvis 1984. Conducting sapwood area, foliage area and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can J For Res.* 14:940-947.

Whitehead, D. and P.G. Jarvis 1981. Coniferous forests and plantations. *In Water Deficits and Plant Growth* Ed. T.T. Kozłowski. Academic Press, New York, pp. 49-152.

Whitehead, D., D.W. Sherriff and D.H. Greer 1983. The relationship between stomatal conductance, transpiration rate and tracheid structure in *Pinus radiata* clones grown at different vapour saturation deficits. *Plant Cell Environ.* 6:703-710.

Zimmermann, R., E.D. Schulze, C. Wirth, E.E. Schulze, K.C. McDonald, N.N. Vygodskaya and W. Ziegler 2000. Canopy transpiration in a chronosequence of Central Siberian pine forests. *Global Change Biol.* 6:25-37.

