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Transpiration response to soil moisture in pine and spruce trees in Sweden

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Abstract

Variation in transpiration and conductance between individual trees of Scots pine and Norway spruce was investigated in a mixed 50-year-old stand in central Sweden. Daily transpiration rates were measured by the tissue heat balance method on five trees of each species during a dry, warm growing season. Daytime averages of sapflow, climatic variables and soil water content were used to fit an empirical model of tree conductance for each tree. Conductance per unit needle area was about twice as high in pine as in spruce, while equal-sized trees transpired similarly in both species. Conductance generally decreased more steeply with increasing vapour pressure deficit and increased faster with increasing light in pine than in spruce, although one individual spruce behaved more like the pines. Inclusion of a linear or exponential function for air temperature improved the model for pine, but of the spruces, only one tree showed a clear temperature dependency. The response to decreasing soil water content varied widely; the spruces tended to be more sensitive to drought than the pines. When the drought was at its worst, no sapflow could be detected in some of the trees. On average, the reduction in transpiration began when ca. 80% of the extractable water in the rooting zone had been depleted.
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1. Introduction

Tree transpiration is the major pathway for both water and energy leaving the forest ecosystem. Measurement of transpiration provides access to the canopy conductance of the forest, a key parameter in models of water- and carbon-exchange (Collins and Avissar, 1994), since the water and carbon fluxes are strongly linked by their common passage through the stomata (Morén et al., 2001).

The scale at which the forest is studied answers different questions in the context of exchanges of energy and matter (Jarvis, 1995). Studies at shoot or branch level (e.g. Harley and Baldocchi, 1995; Roberntz and Stockfors, 1998), for instance, are particularly useful in the study of physiological processes; scaling-up to stand level from single shoots is intrinsically complex but can give firm results (e.g. Baldocchi and Harley, 1995). Studies at tree level (e.g. Cermak et al., 1995; Granier et al., 1996) provide an average response of the mostly non-linear physiological processes, and are therefore, more useful for empirical modelling. Such studies are particularly useful for scaling-up fluxes for a certain stand or plot if a sufficient number of trees are measured (Cermak et al., 1995), and provide

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answers about the variation within it. The ecosystem or landscape level (e.g. Tenhunen et al., 1998; Grelle et al., 1999) provides answers about net exchange and the variation between stands or regions.

The sapflow technique (Swanson, 1994) is very useful for obtaining the total water use of a single tree. Sapflow is commonly scaled up to stand level and considered as representing transpiration. A problem with this approach is that, because of the capacitance of the trunk and branches, sapflow lags somewhat behind transpiration (Granier and Loustau, 1994; Köstner et al., 1996). The lag is not constant over the course of the day, between days or between trees (Lundblad and Lindroth, 2002; Phillips et al., 1997), even though in many approaches it is assumed to be constant; modelling the lag is consequently not a simple task. However, daily sapflow totals can often be assumed to equal the sum of transpiration, although under some conditions, e.g. after a dry period followed by some rainy days, this may not be true (Waring et al., 1979; Zweifel and Häsler, 2001). Another drawback of a daily time step is that the processes which affect transpiration are non-linear, hence, any model would be truly empirical and should be used with caution outside the range for which it was calibrated. The daily pattern of the variables can also vary between different days; this will affect conductance, even though the mean of the variables may be unchanged.

Soil moisture is considered to be a critical parameter in many models of evaporation or surface energy partitioning. Many models show large sensitivity to soil moisture, and general circulation models, which are used to predict future climate change, are no exception (e.g. Viterbo and Beljaars, 1995). Unfortunately, it is inherently difficult to establish firm relationships between transpiration (or canopy conductance) and soil water content, mainly because of the large spatial variation in soil properties and soil moisture, but also because of transpiration's strong dependence on other weather parameters. There are, however, several empirical studies of such relationships in which firm relationships have been established; e.g. for Scots pine by Rutter (1967), Sturm et al. (1996) and Irvine et al. (1998), for Norway spruce by Lu et al. (1995) and Lu et al. (1996), and for mixed stands of these species by Cienciala et al. (1998). As far as the present authors are aware, variation in individual response in a mixed stand has not previously been estimated and modelled.

Evaluation of individual variation can increase our understanding of the response of the entire stand.

The primary aim of this study was to quantify how tree conductance, and thus, the transpiration of individual trees in a mixed pine and spruce forest, depends on soil moisture. In order to do that it was also necessary to quantify the influence of weather conditions on the conductance of individual trees under non-limiting soil water conditions. Daily data from a growing season with large variation in soil water content were used to estimate and model conductance and its dependence on weather parameters and soil moisture.

2. Material and methods

2.1. The stand

Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) are dominant species in most of the Eurasian Taiga. Scots pine is a pioneer species that is well adapted to dry conditions. Norway spruce is a secondary species that is shade-tolerant and prefers wetter habitats that are not frequently disturbed. Mixed stands are, however, very common. The studied stand was located in the Norunda forest in central Sweden (60°5′N, 17°29′E, altitude 45 m). The stand was ca. 50 years old and was growing on a boulder-rich, sandy glacial till. The stand was naturally regenerated and was a mix of Scots pine (64% of the basal area (BA) at 1.3 m height), Norway spruce (33%) and deciduous trees (3%). A plot, 60 m × 120 m, was established in 1997 for studies of tree water relations, and the diameter of all trees on it was measured. The mean diameter was 20 cm, mean height was 17 m, BA was 29 m² ha⁻¹ and there were 872 trees per hectare.

2.2. Sapflow

Sapflow was measured by the tissue heat balance method (Cermak et al., 1973; Cermak et al., 1976; Cermak et al., 1982) with a P4.1 sapflow meter (Ecological Measuring Systems, Bruno, Czech Republic). This is a method that has previously been proven to give reliable transpiration estimates in the studied forest (Grelle et al., 1997; Cienciala et al., 1999) and the method was evaluated in Lundblad et al. (2001). The system used five electrodes inserted in parallel, and

supplied with a constant power of 1 W, to heat a segment of the stem. The temperature difference between the heated and unheated part of the stem was measured with a thermo battery consisting of eight sensors.

The measured temperature difference, ΔT (K), is correlated to sapflow for the heated segment as

$$Q_w = \frac{P}{c_w \, \Delta T} - \frac{k}{c_w} \quad (\text{kg s}^{-1}) \tag{1}$$

where P (W) is the heat input, c_w the specific heat of water (4186.8 J kg^{-1} K^{-1}) and k (W K^{-1}) is the coefficient of heat loss from the heated segment, obtained under zero-flow conditions. Tree level sapflow, Q, was calculated by dividing Q_w by the width of the heated segment (8 cm) and multiplying by the circumference under bark at the measuring point.

To record as much as possible of the variation in sapflow, both between trees and around the circumference of a tree, with the 12 sapflow channels available, the following set-up was used: the installations were made on five pines and five spruces in July 1998 (denoted P1–5 and S1–5). On each tree, two measuring points were installed, on the eastern and western side, respectively. On one pine and one spruce, both measuring points were continuously measured. Only one side of the other trees was connected on each measurement period. In 1999, measurements were shifted from the east to the west side on 16 June and shifted back on 5 August. The two relationships, before and after the shifts, to the sapflow in the continuously measured tree of the same species, was used to calculate a mean value based on measurements of both sides, as in Lundblad et al. (2001). There was a difference in sapflow between opposite sides, but the relationship was relatively stable (see Lundblad et al., 2001). In the present study, sapflow measurements from 16 April to 27 October 1999 were used. In 2000, the systems were installed in another sample of trees, sapflow from this year was used to validate the final model of the transpiration, this year sapflow was measured 19 May to 22 October. No severe visual injuries were detected when the electrodes were removed in autumn 1999.

For the 2 days during which the measured side was shifted, sapflow was calculated as the mean fraction of the flow a few days before and after the shift, in the trees that was not shifted. Similarly, the missing days for P1, P3, P5, S1 and S4 on 6–9 July were replaced. For S5, the heating control malfunctioned from 16 June to 6 July and from 6 to 11 August. Data from these periods were replaced by data generated from the relationship with the remainder of the pines before and after the heating failure.

2.3. Weather and soil moisture

Soil water content (θ) at 0–20 and 0–50 cm depth, was measured with the TDR-technique (Topp et al., 1980) at eight positions located in a transect through the stand. This transect was not in the same direction as the sapflow transect, so it was not possible to link 'local' soil moisture to the individual trees. A general formula for mineral soils was used to obtain θ from the measurements. At each position, one pair of 20 cm rods and one pair of 50 cm rods were placed vertically. The signal was read manually about every tenth day during the growing season, by means of a Tektronix 1502C cable tester (Tektronix Corp., Beaverton, OR, USA). Additionally, θ was measured with two ThetaProbes (ML1, Delta-T Devices Inc., Cambridge, UK), installed at 10–15 cm depth, which were read every minute with a Campbell CR10-datalogger and a Campbell AM32-multiplexer (Campbell Scientific Inc., NE, USA). Data were stored as 10 min means. The dynamic information from the ThetaProbes was used to obtain interpolated daily values of θ, based on the level of the mean of the TDR measurements. From θ, the relative extractable water (REW) (θ_{REW}) was calculated as

$$\theta_{REW} = \frac{\theta - \theta_m}{\theta_{FC} - \theta_m} \tag{2}$$

where θ_m is minimum θ (0.02 for 0–20 cm and 0.05 for 0–50 cm depth in the present study) and θ_{FC} is θ at field capacity (0.30 in the present study, both depths). The θ_m was taken as the minimum θ found in the present study, and was in accordance with the wilting point found by Lundin et al. (1999) in an adjacent stand. The θ_{FC} was taken as the θ in the spring shortly after the groundwater table had fallen to the lower limit of the measured soil volume.

Climatic data were taken from a tower ca. 500 m from the site and, for missing values, from a scaffold tower 50 m from the site (instrumentation is given in Table 1). The data from the tower 500 m away were preferred, because the instruments in the scaffold tower were below the height of the tallest trees.

Table 1
Meteorological instrumentation in the Norunda tower and the scaffold tower

Quantity	Instrument
Air temperature	Thermocouple (in situ, Ockelbo, Sweden)[a]
	Hygrometer MP probe (Rotronic Instruments Ltd., Horley, UK)[b]
Relative humidity	Hygrometer MP probe (Rotronic Instruments Ltd., Horley, UK)[a, b]
Global radiation	Pyranometer CM-21 (Kipp & Zonen, Delft, The Netherlands)[a]
	LI-190SZ quantum sensor (LI-COR Inc., Lincoln, NE, USA)[b]
Precipitation	IS200W rain gauge (in situ, Ockelbo, Sweden)[a]

Data were recorded every minute with Campbell CR10-datalogger (Campbell Scientific Inc., NE, USA) and stored as 10 min means.
[a] Norunda tower.
[b] Scaffold tower.

2.4. Leaf area of the sapflow trees

The leaf area index (LAI) of the stand ($L_{LAI2000}$) was estimated three times in 1999 with the LAI2000 plant canopy analyser (LI-COR Inc., Lincoln, NE). The measurements were corrected for foliage clumping by the factor 1.65 provided by the manufacturer, and averaged.

The functions obtained from a detailed biomass sampling (Morén et al., 2000) were used to find projected leaf area (L_{tree}) for all individual trees in the stand, with diameter as input. The L_{tree} was corrected to sum up to the level of $L_{LAI2000}$, because the sampled stand differed somewhat in age and the sampling was done in a different year:

$$L_{treecor} = L_{tree} \frac{L_{LAI2000} A}{\sum L_{tree}} \tag{3}$$

where A is the area of the plot (m²).

Tree height and live crown length were measured both on the sapflow trees and on a sample of 115 pines and 85 spruces. The needle mass according to Marklund (1988), was calculated from diameter at breast height, height and live crown length. For pine, the north co-ordinate, according to the Swedish co-ordinate system, was also included in the input parameters. A relationship between diameter and needle

mass was established for pine and spruce, respectively and was applied to all trees in the plot.

Functions between needle mass and $L_{treecor}$ could then be fitted for pine and spruce, respectively. The functions were used to obtain the projected leaf area of the sapflow trees from needle mass (in which tree height and live crown length were taken into account). The polynomial functions, on average, corresponded to specific leaf areas of 7.3 and 4.5 m² kg⁻¹ for pine and spruce, respectively which is close to the values in Morén et al. (2000).

The final leaf area of the sapflow trees was used to express sapflow per unit leaf area. The properties of the sapflow trees are summarised in Table 2.

2.5. Tree conductance

The mean daytime value of temperature (T_{day} (°C)), vapour pressure deficit (D_{day} (Pa)) and global radiation (R_{day} (W m⁻²)) were calculated for the period when global radiation (R) > 0. Daily sums of sapflow for each tree were calculated with no restriction in R, but were divided by the duration of $R > 0$ to obtain mean daytime transpiration per unit needle area (E_{day} (g m⁻² s⁻¹)). This was done because sapflow may be expected to lag behind transpiration, but transpiration will only occur when $R > 0$. For pine and spruce, respectively mean values of E_{day}, weighted by the leaf area were calculated, for which the conductance also was modelled. Tree conductance (g_{tday}) was then calculated according to Monteith and Unsworth (1990):

$$g_{tday} = \frac{\lambda E_{day} \gamma}{\rho c_p D_{day}} \tag{4}$$

where λ is the latent heat of vaporisation of water (2465 J g⁻¹), γ the psychrometer constant (65.5 Pa K⁻¹), ρ the density of the air (1225 g m⁻³), and c_p is the specific heat of air (1.01 J g⁻¹ K⁻¹). The use of this simplified equation for calculating conductance is valid if the trees are well coupled to the atmosphere, which can be assumed for conifers (Jarvis et al., 1976; Granier and Loustau, 1994; Phillips and Oren, 1998). The advantage of using a daily time step when modelling conductance is that the problem of the time-lag between sapflow and transpiration is overcome. The disadvantage is that Eq. (4) rightfully should be used on instantaneous values, but the error

Table 2
Dendrological properties of the pines (P1–5) and spruces (S1–5) in the present study and their distance to the centre of the nearest strip road (see Section 4)

	P1	P2	P3	P4	P5	S1	S2	S3	S4	S5
Diameter (cm)	24.5	21.8	22.3	19.0	15.8	24.6	21.6	20.4	19.6	16.4
Height (m)	17.0	16.8	16.7	15.4	16.9	19.0	16.6	17.2	16.5	16.0
Crown length (m)	9.0	8.0	7.9	8.7	6.3	15.3	14.1	12.4	13.7	13.1
Leaf area (m^2)	62.7	47.4	48.9	44.3	23.5	107.1	96.4	77.1	83.2	66.1
Needle mass (kg)	8.81	6.35	6.60	5.86	2.48	25.2	21.3	14.9	16.8	11.8
Distance to road (m)	8.4	2.0	7.5	2.1	6.8	2.6	1.5	3.8	10.7	2.8

is generally small, and thus acceptable, as described by Phillips and Oren (1998).

To estimate the effect of soil moisture on tree conductance, it is necessary to analyse the influence of weather conditions on conductance under non-limiting soil moisture conditions. Thus, the aim of the modelling described later was primarily to obtain a tool to 'normalise' conductances with respect to different weather parameters, i.e. not to obtain a general model of individual tree conductance. An empirical model of the calculated g_{tday} was fitted to vapour pressure deficit, radiation, temperature and soil moisture:

$$g_{tday} = g_{tmax} f(D_{day}) f(R_{day}) f(T_{day}) f(\theta) \qquad (5)$$

The modelling approach was stepwise, first g_{tmax} and $f(D_{day})$ was decided by using data when the other functions were close to 1. Then $f(R_{day})$ was fitted when $f(T_{day})$ and $f(\theta)$ were close to 1, thereafter $f(T_{day})$ when θ was not limiting, and finally $f(\theta)$.

The period 18 May to 15 June was used to fit the functions for D_{day} and R_{day}; this was a period with little variation in T_{day} (mean 15.2 °C; $\sigma = 2.2$) and sufficient soil moisture. The function for T_{day} was fitted after the period from 7 July to 27 September had been excluded (during this period, $\theta_{REW\,0-50\,cm}$ was <0.30). Days with Penman potential evaporation (E_p) (Penman, 1948) less than 1 mm were also excluded as a small absolute measured error is likely to have a large effect when two small numbers are divided.

When fitting the functions for θ, the period 1 June to 15 September was used, days with E_p less than 1 mm being excluded, as also days with D_{day} above 2000 Pa, because maximum D_{day} during the period when $f(D_{day})$ was fitted was 1355 Pa. In total, there were 11, 2 and 12 days, respectively, outside the range

for which the functions for D_{day}, R_{day} and T_{day} were fitted, from a total of 189 days for which the final model was applied.

3. Results

3.1. Weather

The winter and early spring of 1999 were wet. Precipitation from December to April was 270 mm, i.e. 64% more than for the normal period 1960–1990 (Uppsala Weather Station, 30 km south). The growing season began with high soil water content (θ) and with the ground water table at or close to the soil surface at many points. May, June and August had precipitation and temperature close to the normal, while July and September were warmer than normal, by 1.9 and 3.2 °C, respectively (Fig. 1a). In July, only about one-third of the normal precipitation fell, and the first half of September was also very dry. This depleted the soil water, and $\theta_{0-50\,cm}$ decreased to minimum values <6% on 4 August and 15 September (Fig. 1b). After some rainy days at the end of June, at the end of July and at the beginning of August, θ recovered temporarily. In the middle of July, and at the turn of the month to August, there were some days with very warm and dry conditions. The mean daytime vapour pressure deficit (D_{day}) then had a maximum value of ca. 2400 Pa (Fig. 1c).

3.2. Sapflow

The decreasing θ had a high impact on the sapflow rate. In spite of high demand, i.e. high vapour pressure deficit and global radiation (Fig. 1c) in middle of July,
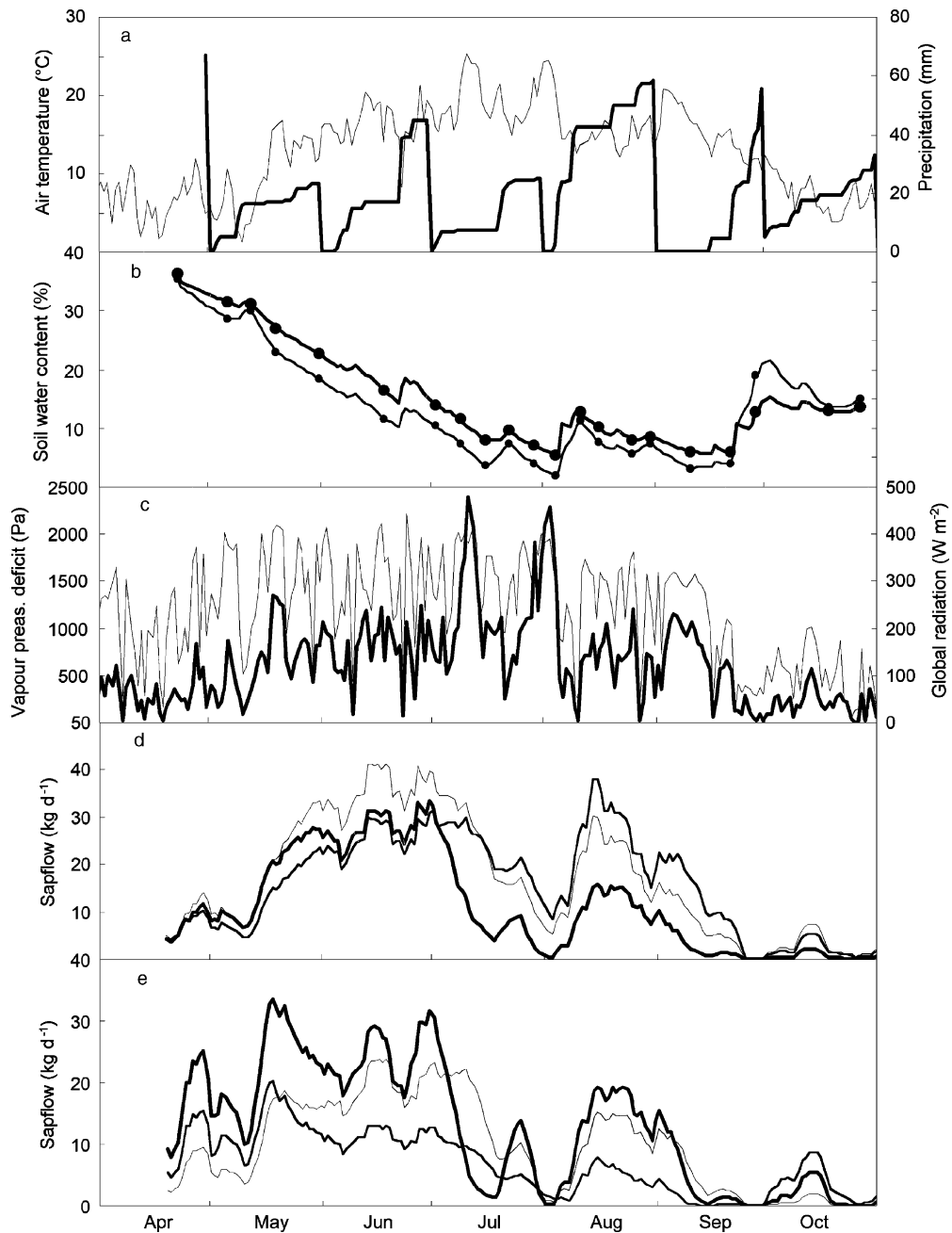
Fig. 1. Environmental conditions and sapflow for the 1999 season. (a) Mean daytime temperature, T_{day} (thin line) and accumulated monthly precipitation (bold line). In April, a manual rain gauge was emptied a few times and only a total for this month is presented. (b) Soil water content at 0–20 cm (normal line) and 0–50 cm (bold line) depth. The points are means from manual reading of eight positions with TDR rods and the lines are calculated from the dynamics of continuously measured ThetaProbes. (c) Mean daytime vapour pressure deficit, D_{day} (bold line) and mean daytime global radiation, R_{day} (thin line). (d) Seven-day running means of sapflow for the pines P1 (thin line), P2 (normal line) and P4 (bold line). (e) Seven-day running means of sapflow for the spruces S1 (thin line), S2 (normal line) and S3 (bold line). The presented trees were selected to represent the range in soil moisture response.

at the beginning of August and the end of September, sapflow decreased dramatically (Fig. 1d and e). At the beginning of July, the first trees began to respond to the decreasing θ, while others maintained transpiration a few weeks longer. This individual behaviour can be demonstrated by comparing the relationship in sapflow rates between trees at the beginning of June, when soil water content was high, with a period in September, when soil water content was low and decreasing (Fig. 2). The three selected pines did not differ by more than about 20% at most in June, whereas the difference in mid-September was 15 orders of magnitude between the tree with the highest maintained sapflow rate, and that which was least able to transpire (Fig. 2a). It may also be noted that the tree with the highest sapflow rate in June decreased most in September, while the tree with the lowest rate in June maintained its flow rate best. The picture was similar for the spruces, but here all trees decreased their sapflow rates to almost zero in mid-September.
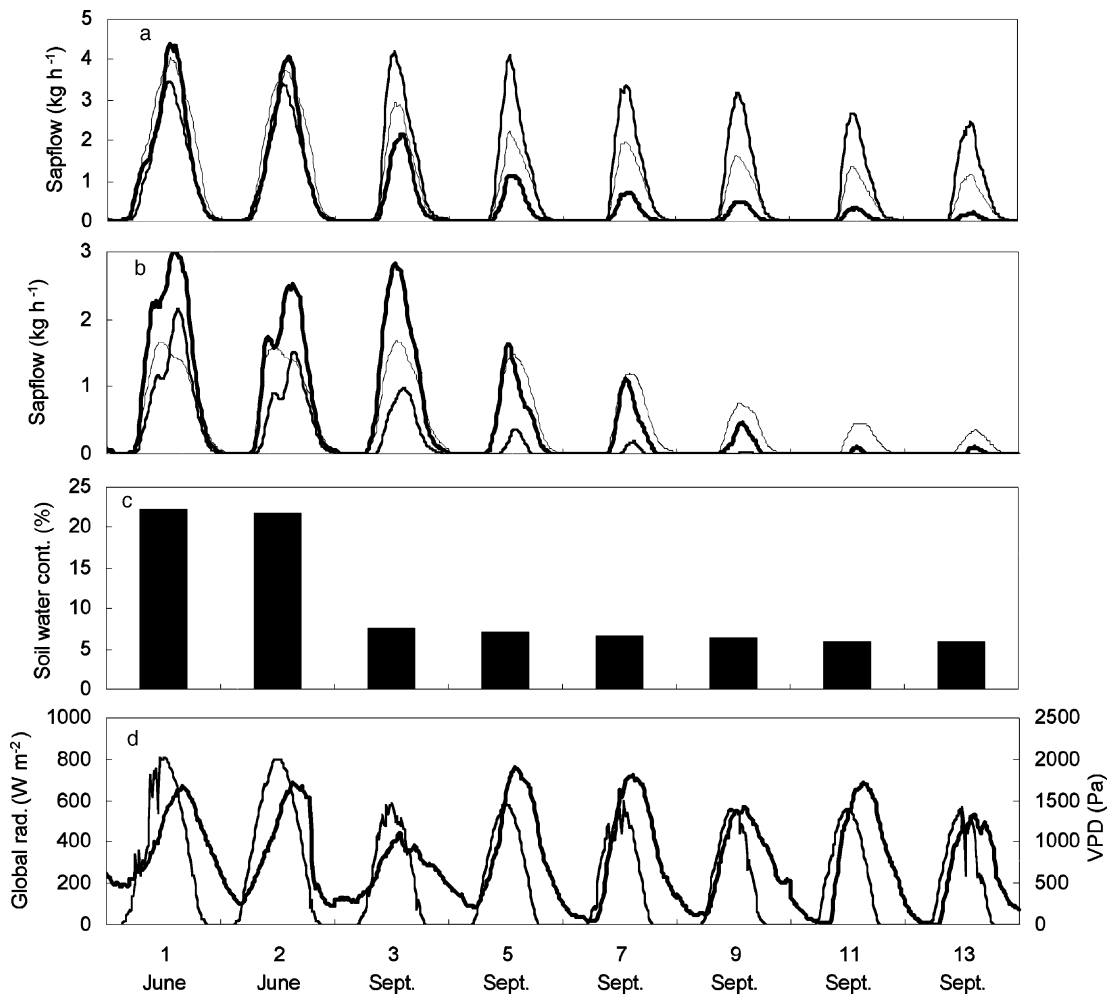

Fig. 2. Sapflow and environmental conditions for 2 days in June and 6 days in September 1999 (note that the x-axis is not continuous). (a) Sapflow for the pines P1 (thin line), P2 (normal line) and P4 (bold line). (b) Sapflow for the spruces S1 (thin line), S2 (normal line) and S3 (bold line). (c) Soil water content at 0–50 cm. (d) Global radiation (normal line) and vapour pressure deficit (bold line). The presented trees were selected to represent the range in soil moisture response.

3.3. Tree conductance

The period 18 May to 15 June was selected to fit the functions $f(D_{day})$ and $f(R_{day})$, because soil moisture was high at the same time as there was a large variation in vapour pressure deficit and global radiation. Tree conductance showed the characteristic behaviour for conifers, i.e. decreasing conductance with increasing D_{day}, with a large scatter for low D_{day} and increasing conductance with increasing R_{day} (Fig. 3). The pines showed a stronger response to high D_{day} than the spruces. The g_{tday} increased with increasing R_{day} in a logarithmic fashion. For the pines, there was a tendency towards decreasing g_{tday} at the highest radiation levels, which was caused by the steep response to D_{day}. The correlation between D_{day} and R_{day} was high, $r^2 = 0.65$.

As the first step, the dependence on D_{day} was considered by applying boundary-line analysis (Webb, 1972; Martin et al., 1997). Lines were fitted to the up-

per right part of Fig. 3a and b, where no limitation due to low radiation could be expected. Although the relationships seemed linear for the pines, exponential functions of the form:

$$g_{tday} = g_{tmax} \exp(-aD_{day}) \qquad (6)$$

were used, where g_{tmax} and a are fitted parameters whose values are given in Table 3; g_{tmax} is a hypothetical conductance at zero D_{day} and saturated radiation, which varied between 5.9 and 14.3 mm s^{-1} for the pines and between 1.3 and 2.6 for the spruces. The parameter a was ca. 0.002 for the pines and 0.001 for the spruces. Exponential functions were preferred, to make extrapolation possible, as this is the known common behaviour (e.g. Stewart, 1988).

As the next step, the dependence on global radiation was considered. The quotient between measured conductance (Eq. (4)) and $g_{tmax} \times f(D_{day})$ was regarded as a function of R_{day} (Fig. 4). The relationships were
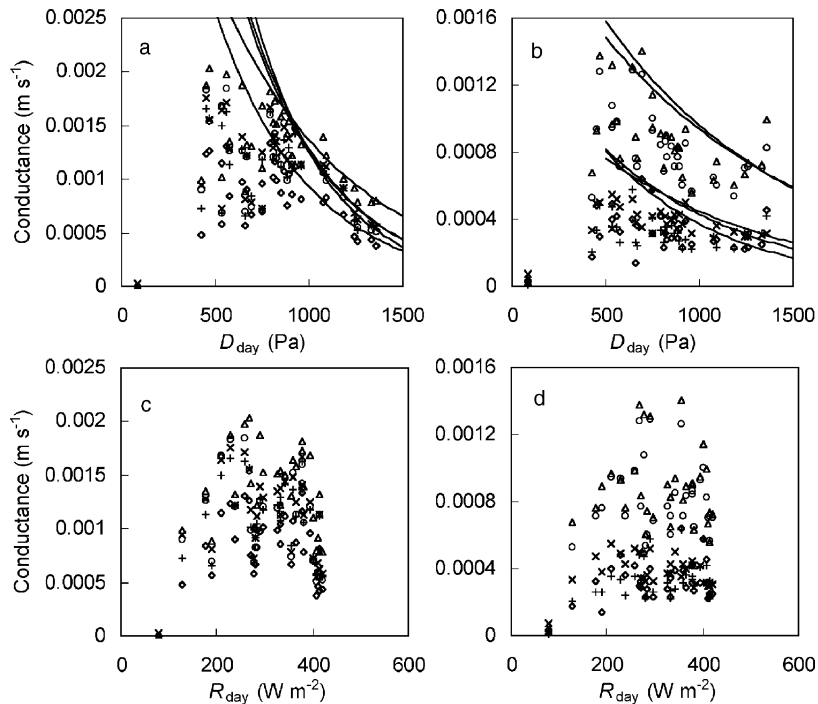

Fig. 3. Tree conductance, based on sapflow per unit projected needle area, dependence on daytime vapour pressure deficit (D_{day}) and daytime radiation (R_{day}) for the period 18 May to 15 June 1999. (a) Dependence on (D_{day}) for pines, P1 ($\times$), P2 (+), P3 ($\bigcirc$), P4 ($\triangle$) and P5 ($\diamondsuit$), the lines are fitted through boundary-line analysis (see text). (b) Dependence on D_{day} for spruces, S1 ($\times$), S2 (+), S3 ($\bigcirc$), S4 ($\triangle$) and S5 ($\diamondsuit$). (c) The pines' dependence on R_{day} (symbols as in (a)). (d) The spruces' dependence on R_{day} (symbols as in (b)).

Table 3
Parameters for the conductance, g_{tday}, functions of vapour pressure deficit, D_{day}, and radiation, R_{day} ($g_{tday} = g_{tmax} \exp(-aD_{day})(b \ln R_{day} - c)$), for the pines P1–5, the spruces S1–5 and for a weighted average for respective species

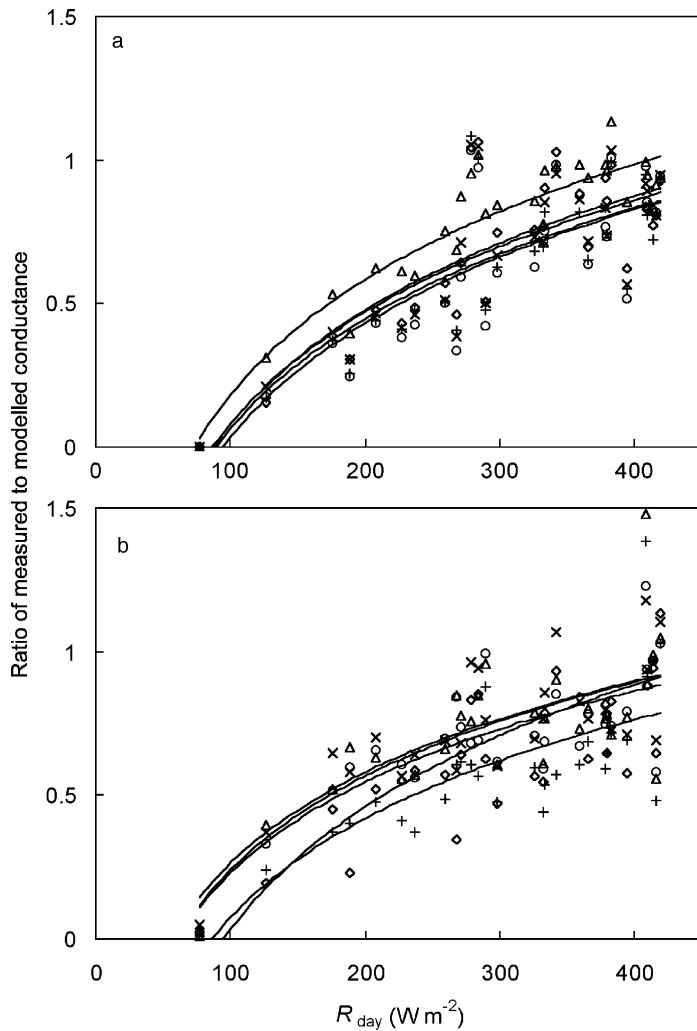|	P1	P2	P3	P4	P5	S1	S2	S3	S4	S5	Pine	Spruce
g_{tmax} (mm s^{-1})	11.05	10.43	14.31	5.91	7.12	1.55	1.31	2.35	2.60	1.76	10.44	1.48
$a \times 10^3$	2.15	2.12	2.44	1.46	2.04	1.29	1.08	0.92	0.99	1.55	2.12	0.92
b	0.563	0.555	0.573	0.582	0.576	0.458	0.497	0.457	0.471	0.615	0.578	0.470
c	2.51	2.49	2.60	2.50	2.57	1.84	2.21	1.87	1.93	2.79	2.59	1.91

Fig. 4. The ratio of measured conductance (g_{tday}) to conductance modelled using vapour pressure deficit ($g_{tmax}f(D_{day})$) plotted against global radiation; the lines are logarithmic regressions and data are from 18 May to 15 June 1999. (a) Pines P1 (×), P2 (+), P3 (○), P4 (△) and P5 (◇). (b) Spruces S1 (×), S2 (+), S3 (○), S4 (△) and S5 (◇).

best described by logarithmic functions:

$$f(R_{\text{day}}) = b \ln R_{\text{day}} - c \tag{7}$$

where b and c are parameters. When the functions delivered negative values (if $b \ln R_{\text{day}} < c$), the function was set to zero. This point, below which no transpiration occurred during the day according to the model, accorded to R_{day} values between 60 and 95 W m^{-2}. The values of the parameters, b and c, are listed in Table 3. For the mean pine, b and c were 0.58 and 2.6, respectively and for spruce 0.47 and 1.9, respectively. S5 deviated somewhat from the other spruces, by exhibiting values more like those of the pines.

Finally, the effect of air temperature on the conductances was dealt with in the following manner. For the pines, there was a strong relationship between the quotient between measured conductance (Eq. (4)) and conductance modelled with R_{day}, D_{day} and mean daytime air temperature (Fig. 5). For four of the trees, the relationship was best described by an exponential function:

$$f_1(T_{\text{day}}) = k \exp(l T_{\text{day}}) \tag{8}$$

For one tree, the relationship was linear:

$$f_2(T_{\text{day}}) = m T_{\text{day}} \tag{9}$$

The quotient showed a clear linear response to temperature for one of the spruces only, for the rest of the spruces, there was no relationship, i.e.

$$f_3(T_{\text{day}}) = 1 \tag{10}$$

The parameter values (k, l and m) and the function used for each tree are given in Table 4.

Accordingly, it was now possible to assess the effect of soil moisture on tree conductance. The quotient between measured conductance (Eq. (4)) and conductance modelled with radiance, vapour pressure deficit, and temperature, showed a strong dependence on the

relative amount of extractable water, θ_{REW} (Fig. 6). Linear functions up to a threshold value (x) were used to describe the relationships:

$$f(\theta) = \frac{\theta_{\text{REW}}}{x}, \quad x < \theta_{\text{REW}} \tag{11}$$

$$f(\theta) = 1, \quad x = \theta_{\text{REW}} \tag{12}$$

To obtain x, Eqs. (11) and (12) were combined to one equation (Eq. (13)) which was solved by the 'nlin procedure' in SAS statistical software (version 6.12, SAS Institute, Cary, NC):

$$f(\theta) = \left(\frac{\theta_{\text{REW}}}{x} \left(\frac{|x - \theta_{\text{REW}}|}{(x - \theta_{\text{REW}})} + 1 \right) \right.$$
$$\left. + \frac{|\theta_{\text{REW}} - x|}{(\theta_{\text{REW}} - x)} + 1 \right) \times 0.5 \tag{13}$$

The threshold value (x) was derived for both $\theta_{\text{REW}\,0-20\,\text{cm}}$ and $\theta_{\text{REW}\,0-50\,\text{cm}}$; the values of x are listed in Table 5. The variation in x was large, between 0.04 and 0.37 $\theta_{\text{REW}\,0-50\,\text{cm}}$ for the pines and between 0.18 and 0.39 for the spruces.

The slope and the r^2 values for the relationship between measured conductance and conductance modelled with all functions in Eq. (5), are given in Table 6. The conductance in the early spring and late autumn was difficult to explain by the model for some of the spruces, for which reason, the relationships restricted to the period 1 May to 30 September are also given. For the pines, there was little difference between the model fitted to $\theta_{\text{REW}\,0-20\,\text{cm}}$ or $\theta_{\text{REW}\,0-50\,\text{cm}}$; it explained 46–74% of the variation, and underestimated conductance by 0–14%. For the spruces, when the spring and autumn period were excluded, the model was improved by 1–6% if $\theta_{\text{REW}\,0-20\,\text{cm}}$ was used instead of $\theta_{\text{REW}\,0-50\,\text{cm}}$; r^2 was between 0.59 and 0.80, and the slope was between 0.94 and 1.0 when the restricted period and $\theta_{\text{REW}\,0-20\,\text{cm}}$ were used.

Table 4
The function used for temperature, T_{day}, dependence of the conductance and the derived parameters ($f_1(T_{\text{day}}) = k \exp(l T_{\text{day}})$, $f_2(T_{\text{day}}) = m T_{\text{day}}$, $f_3(T_{\text{day}}) = 1$), for the pines P1–5, the spruces S1–5 and for a weighted average for respective species

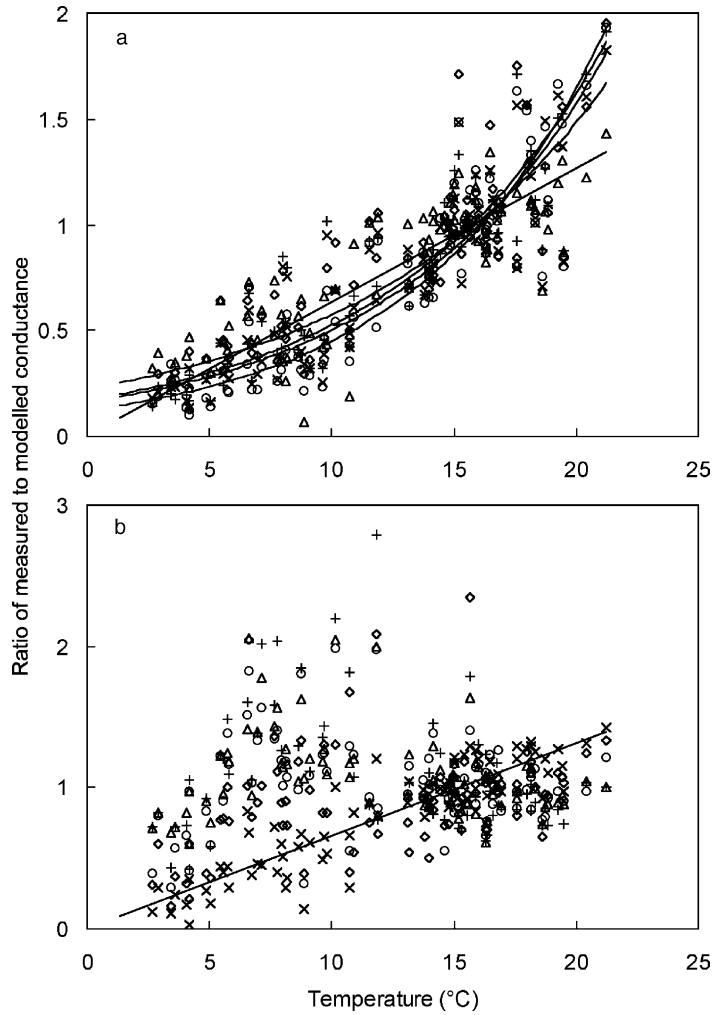|	P1	P2	P3	P4	P5	S1	S2	S3	S4	S5	Pine	Spruce
$f(T_{\text{day}})$	1	1	1	2	1	2	3	3	3	3	1	3
k	0.160	0.170	0.123	–	0.222	–	–	–	–	–	0.171	–
l	0.114	0.113	0.130	–	0.095	–	–	–	–	–	0.110	–
m	–	–	–	0.063	–	0.066	–	–	–	–	–	–

Fig. 5. The ratio of measured conductance to conductance modelled using radiance and vapour pressure deficit, plotted against temperature and regression lines. Data are from 16 April to 6 July and from 28 September to 27 October 1999. Days with Penman potential evaporation less than 1 mm were excluded. (a) Pines P1 ($\times$), P2 (+), P3 ($\bigcirc$), P4 ($\triangle$) and P5 ($\diamondsuit$). (b) Spruces S1 ($\times$), S2 (+), S3 ($\bigcirc$), S4 ($\triangle$) and S5 ($\diamondsuit$), the line is for S1, the only spruce with a temperature dependence.

Table 5
The values of the parameter x derived for the pines P1–5, the spruces S1–5 and for a weighted average for respective species

	P1	P2	P3	P4	P5	S1	S2	S3	S4	S5	Pine	Spruce
x_{0-20}	0.219	0.065	0.256	0.328	0.207	0.205	0.368	0.267	0.200	0.329	0.207	0.239
x_{0-50}	0.205	0.042	0.260	0.371	0.196	0.188	0.392	0.303	0.176	0.384	0.195	0.214

Above this value of relative extractable water (θ_{REW}), there is no restriction due to drought; below, there is a linear decrease down to zero at $0\theta_{REW}$. The parameter was calculated for θ_{REW} at both 0–20 and 0–50 cm depth.
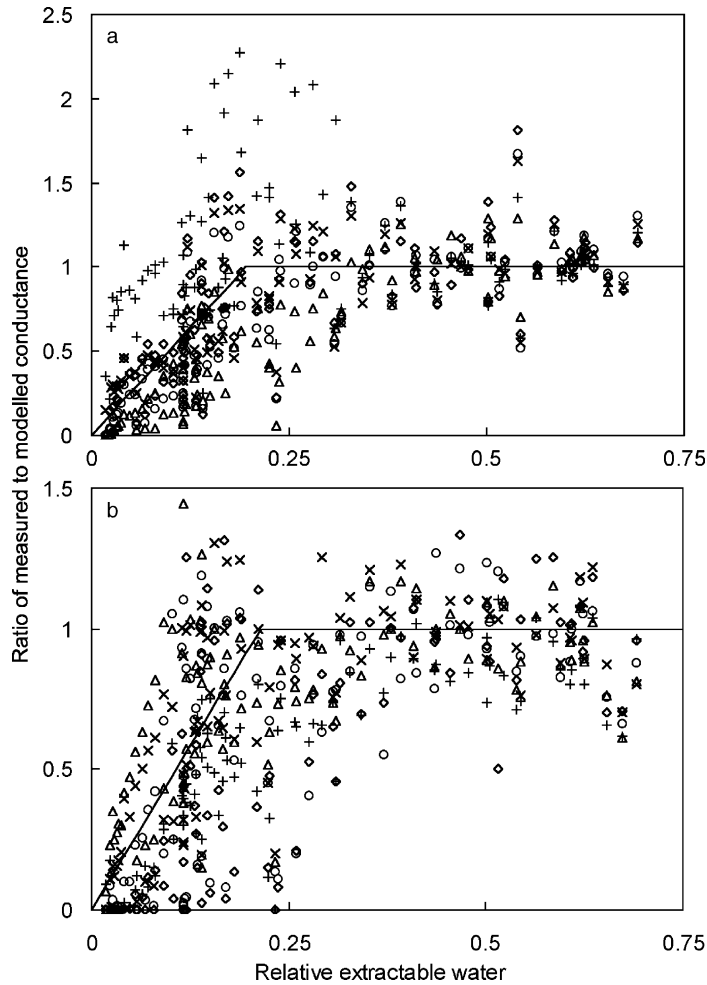
Fig. 6. The ratio of measured conductance to conductance modelled using radiance, vapour pressure deficit, and temperature, plotted against relative extractable water. The lines are the dependence for mean pine and spruce. Data are from 1 June to 15 September 1999. Four days with daytime vapour pressure deficit above 2000 Pa and 5 days with Penman potential evaporation less than 1 mm were excluded. (a) Pines P1 (×), P2 (+), P3 (○), P4 (△) and P5 (◇). (b) Spruces S1 (×), S2 (+), S3 (○), S4 (△) and S5 (◇).

The model was used to calculate the transpiration in 1999 and 2000. The modelled conductance for pine and spruce, respectively were used in Eq. (4) to calculate E_{day} (g m^{-2} s^{-1}), and in combination with daylength (s), total needle area ($\sum L_{treecor}$ (m^2)) and the area of the plot scaled to transpiration in millimetres per day. The measured E_{day} was scaled in the same way. In 1999, the model generally fitted the data well; the slope and r^2 for the regressions between measured and modelled transpiration forced through origin were 0.96 and 0.85, respectively for pine

($\theta_{REW\,0–50\,cm}$) and 0.94 and 0.86 for spruce (Fig. 7a and b). This is an important test, because it should reveal whether some extrapolations were made which would seriously have biased the results. In 2000, the spring and autumn were warm and dry while the summer was very wet. The soil water content was as high in the end of July as in the beginning of May; the lowest values of θ were found in the middle of June and in the end of September. There were only 7 days for pine and 11 days for spruce in the end of September that had $\theta_{REW\,0–50\,cm}$ below the threshold.
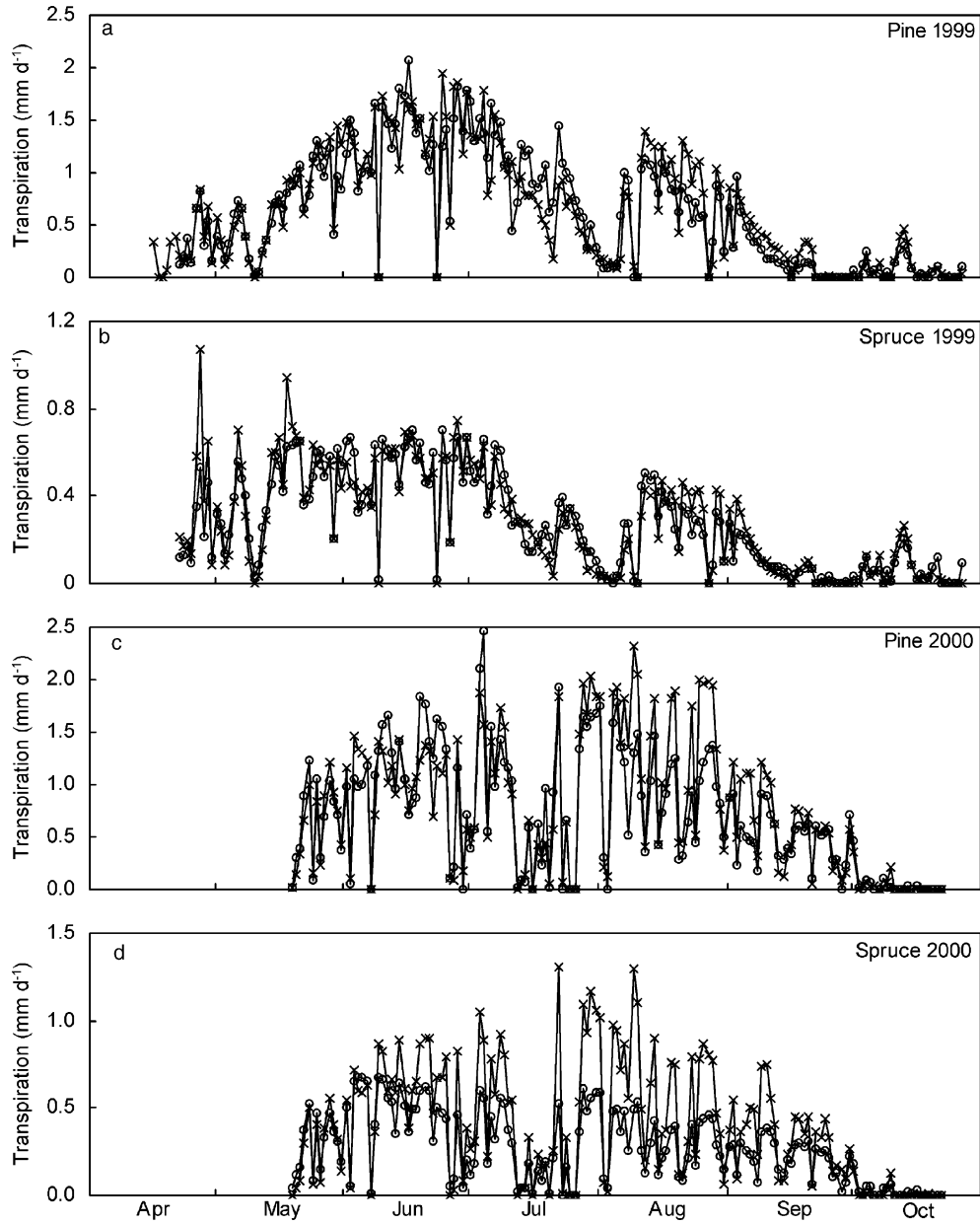
Fig. 7. Modelled daily stand level transpiration fitted to the measurements for the 1999 season and validated against the measurements for the 2000 season; measured transpiration ($\times$) and modelled transpiration ($\bigcirc$): (a) pine 1999, (b) spruce 1999, (c) pine 2000 and (d) spruce 2000.

In general, the model explained the variation in total transpiration well ($r^2 = 0.85$) but underestimated the transpiration by 26% (Fig. 8). This was due to an underestimation of the spruce transpiration by as much as 38% while that of the pine was 13% (Fig. 7c and d). There was, however, a shift in the performance of the model from the end of July when the weather became much drier. For the period before 26 July, the

Table 6

Slope and r^2 values for linear regressions, forced through origin, between measured and modelled conductance ($g_{tday\,measured} = slope(g_{tday\,modelled})$), for the pines P1–5, the spruces S1–5 and for a weighted average for respective species

	P1	P2	P3	P4	P5	S1	S2	S3	S4	S5	Pine	Spruce
Slope$_{0–20}$	0.969	0.855	0.998	0.923	0.950	0.961	0.899	0.870	0.581	0.966	0.978	0.911
$r^2_{0–20}$	0.64	0.46	0.69	0.74	0.63	0.62	0.56	0.48	0.23	0.52	0.68	0.58
Slope$_{0–20ex}$	0.993	0.864	1.003	0.915	0.963	0.967	0.940	0.937	0.982	1.005	0.985	0.984
$r^2_{0–20ex}$	0.66	0.39	0.70	0.82	0.65	0.71	0.80	0.68	0.73	0.59	0.68	0.74
Slope$_{0–50}$	0.974	0.857	0.987	0.902	0.947	0.962	0.903	0.846	0.574	0.941	0.976	0.918
$r^2_{0–50}$	0.64	0.44	0.70	0.74	0.62	0.58	0.50	0.45	0.22	0.53	0.67	0.52
Slope$_{0–50ex}$	0.998	0.866	0.992	0.893	0.96	0.969	0.943	0.905	0.987	0.975	0.983	0.993
$r^2_{0–50ex}$	0.67	0.36	0.71	0.81	0.64	0.66	0.8	0.62	0.67	0.58	0.67	0.68

The regressions were calculated for conductance modelled with soil water content (θ) at both 0–20 and 0–50 cm depth. The relationships restricted to the period 1 May to 30 September are also given ('ex' in subscript).
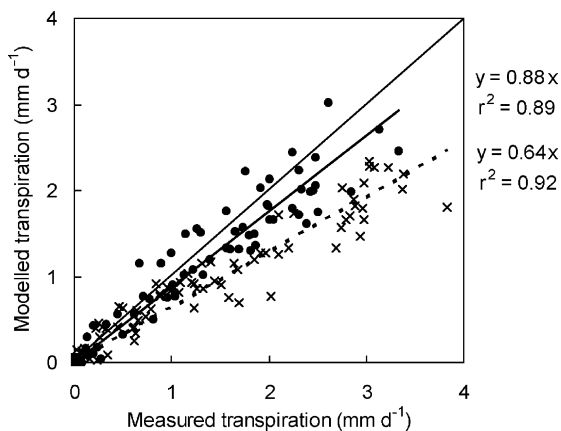

Fig. 8. Measured and modelled daily stand level transpiration for the 2000 season. The data were divided in two sets, before (●, solid regression line) and after (×, dashed regression line) 26 July. For the whole season the r^2 and slope was 0.85 and 0.74, respectively.

model underestimated the total transpiration by 12% but after that date it gave just 64% of the measured transpiration (Fig. 8).

4. Discussion

The levels of g_{tday} can be compared to studies of canopy conductance if g_{tday} is multiplied by the estimated leaf area index, assuming the stand to be monospecific (LAI: 3.7 for pine or 7.1 for spruce). This scaling-up to canopy conductance showed that the conductances for monospecific stands of pine and spruce, respectively were similar, with slightly greater scatter for spruce. This also indicates that mean transpiration for equally sized (diameter) pines and spruces was approximately equal, although there was some individual variation, which has previously been shown for a nearby stand (Cienciala et al., 1998). For spruce, the level of the canopy conductance was ca. 50% lower than in Cienciala et al. (1992), and for pine it was ca. 35% lower than that for a stand of *Pinus taeda* (Phillips and Oren, 1998). The level of g_{tmax} for spruce was close to what has been found by Cienciala et al. (1994), where also the daytime average and the same approach to modelling the response to D_{day} were used.

The spruces exhibited two distinct levels of conductance. Three trees had a much lower conductance than the others (Fig. 3b). It has previously been reported that spruces belonging to the comb or brush type, according to Dengler (1992), differed almost threefold in maximum conductance in a nearby stand (Morén, 1999). The branches of the brush type are more outspread and branched than those of the comb type which shoots are hanging. In the present study, however, all sapflow trees belonged to the brush type, although some of the comb type were present in the stand. A possible explanation may be that the three trees with the lower conductance were all growing closer than 3 m to a strip road of about 3 m width used in a thinning in 1990/1991 (Table 2). Soil compaction and root damage may have reduced their ability to extract water. The effect of strip roads on water flux has been little studied, but there are some contradictory

studies of their influence on tree growth: Kardell (1978) reported a negative and Kardell and Nilsson (1986) a positive effect on growth in studies of Norway spruce. In the estimates of leaf area, mainly based on the needle biomass according to Marklund (1988), there is also uncertainty. If their crown density had been lowered, the lower conductance of the trees close to the strip roads could have been caused by an overestimate of the needle area. In the most advanced form of Marklund's (1988) functions, the diameter increment for the last 5 years is included as the second most significant variable after diameter. Unpublished results from the stand of the present study indicate that the spruces close to strip roads do have reduced growth. The small variation in the conductance for the pines and the other two spruces, however, indicates that this simply calculated needle mass is correlated with transpiration, because the leaf area of the trees was based on the needle mass. The needle mass could therefore be regarded as a useful tool for scaling-up sapflow, as in Cienciala et al. (1998).

The parameter a, which describes how steep is the reduction in conductance with increasing D_{day}, was ca. 0.002 for the pines and 0.001 for the spruces. Where the same function for vapour pressure deficit has been used in other studies, the level has generally been lower. Cienciala et al. (1992, 1994) reported values of 0.00045 and 0.00070 for Norway spruce. Köstner et al. (1996) reported values for Scots pine between 0.00037 and 0.00051 and Grelle et al. (1999) a value of 0.00099 for a mixed pine and spruce forest. Of these studies, only those by Cienciala et al. (1992, 1994) were based on daily averages; the other studies used 30 min data. Variables such as radiation and vapour pressure deficit have different dynamics during the course of the day, and when daily averages are used, the effect of this is smoothed out. The values of the parameters can therefore not really be compared with those of parameters based on analyses with a shorter time step.

The difference in light response (Fig. 4a and b) between the pines and spruces may be a consequence of different light regimes. The radiation level was measured above the stand, and treated as identical for all trees in the modelling work. The pines had a much shorter crown length (Table 2), and their leaf area was distributed higher than the spruces (Morén et al., 2000). Spruce S5, which had values of the parameters a–c closer to the pines, had small opening in the stand on its southern side, hence might be expected to have been exposed to higher light levels.

In many studies, the temperature response function has been found to be non-significant and has been omitted (e.g. Grelle et al., 1999; Granier et al., 2000b). In others, a bell-shaped relationship using an optimum temperature (Stewart, 1988; Gash et al., 1989) has been used. In Granier et al. (2000a) a linear relationship between 10 and 17 °C was used, where the function took the value of 0 below the span and 1 above. In the present study, an exponential or linear relationship was found for the pines, while there was only one spruce that showed a linear response (Fig. 5a and b). For the spruces for which no dependence of temperature was used there was at tendency for lower conductance at the lowest temperatures (<7 °C). A temperature response function without an optimum or maximum level conflicts with the theory of the physical processes involved. The reason for the exponential behaviour for the pines could be that the parameter a was overestimated, i.e. the function of D_{day} was too steep. This could be explained if none of the data points in the right side of Fig. 3a reached the maximum level of the conductance for the respective D_{day}. Too low radiation might explain this, but all of those points belonged to high radiation levels ($R_{day} > 350$ W m^{-2} s^{-1}). Another explanation may be that the points in question belonged to the second half of May, and that the current year's shoots were not fully developed and the conductance therefore was lower. Pine exchanges more of its needles each year than spruce. Nevertheless, the final model showed no clear tendency to over- or underestimation when it was extrapolated above the range for which it was calibrated.

The effect of decreasing soil water content (θ) has been an issue in several studies. In Fig. 9, the results of some of them are presented together with the results from the present study. The results of the present study agree well with those of Stewart (1988), but are steeper than the findings by Ewers et al. (2001), Irvine et al. (1998) and Granier et al. (2000b). The most striking feature in the present study was the large variation between trees: for pine P2, there were 16 days below the threshold θ_{REW}, while for S2 there were as many as 95 days (Fig. 6a and b, Table 5). One explanation
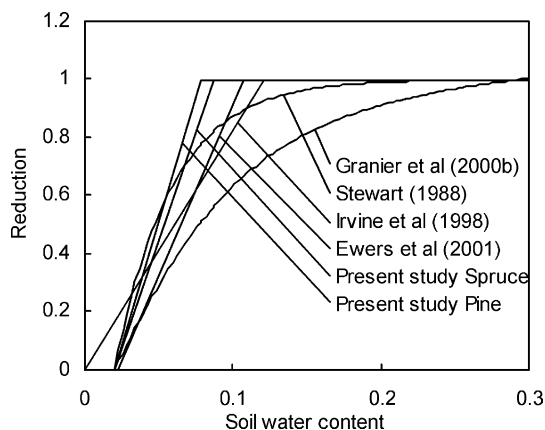
Fig. 9. The reduction of conductance/transpiration due to decreasing soil water content from a number of studies. Granier et al. (2000a,b) is a general study, Stewart (1988) is from a mixture of Scots pine and Corsican pine (*Pinus nigra* var. *miritima* (Ait.) Melv.), Irvine et al. (1998) is from Scots pine and Ewers et al. (2001) is from *Pinus taeda* (control treatment). The equations by Granier et al. and Stewart were converted from θ_{REW} to θ by their relationship in the present study.

for this behaviour could be the highly variable θ in the stand; the standard deviation was about 0.15 in May and 0.05 in July. There was a tendency for the spruces to be more affected by drought than the pines, although this was not significant. For the average pine and spruce, there were 63 and 75 days, respectively with drought restriction. During the dry summer of 1994, pine and spruce transpiration was reduced by 40 and 67%, respectively in an adjacent stand (Cienciala et al., 1998).

Soil water content was only measured down to 50 cm depth although during a drought it is likely that also deeper soil layers contribute to water uptake (e.g. VanSplunder et al., 1996). The relationship between soil moisture and soil tension was not determined for this particular soil, but measurements in a nearby pit (Stähli et al., 1995) shows that 20% θ_{REW} corresponds to about −2500 hPa. It should, however, be pointed out that the soil properties of the studied forest are very heterogeneous.

In 1999, the model fitted the measurements well (Fig. 7a and b). Much of the deviation occurred during periods when daily total sapflow and transpiration could not be expected to be the same (Waring et al., 1979; Zweifel and Häsler, 2001). Zweifel and Häsler

(2001) reported that the diurnal variation in stem radius can be as much as 1–2 mm in Norway spruce in winter and spring, which could explain some of the very high flow rates in the spruce trees on some days in April. The underestimate for some days in August could probably also be explained to some extent by the recharge of stored water after some rain events. Waring et al. (1979) reported that the change in water content of the sapwood could contribute to more than 1 mm per day of transpiration in a Scots pine plantation. The scatter of the model is also large during the warmest days in the middle of July, when the model was extrapolated far outside the temperature range for which it was calibrated. The performance of the model on the 2000 data changed drastically when the very rainy period ended. The reason could be that the trees adapts to the high soil moisture by decreasing the sensitivity of the stomatal conductance to increased VPD. The diurnal pattern in the transpiration and weather showed that although the radiation ended 1.5 h later in the end of August than in the beginning of June, the sapflow continued equally long (Fig. 10).

In Table 7, the correlations between the variables used in this study are listed. In addition to the high correlation between D_{day} and R_{day}, it is noteworthy that T_{day} and θ_{REW} are correlated. This behaviour is probably normal during moderately wet to dry growing seasons. As the driest periods normally are left out when the parameterisation is made, so are also the warmest. For this reason, it is difficult to distinguish the effect of temperature, vapour pressure deficit and soil moisture at the most extreme levels. LAI, which was not measured over the course of the season in the present study, is probably also correlated to temperature, especially in deciduous forests.

Table 7
The r^2 values for linear regressions between the variables (vapour pressure deficit (D_{day}), global radiation (r_{day}), temperature (T_{day}) and relative extractable water at two depths (θ_{REW})) used in the model

	D_{day}	R_{day}	T_{day}	$\theta_{REW\,0-20}$	$\theta_{REW\,0-50}$
D_{day}	1	0.65	0.62	−0.16	−0.05
R_{day}		1	0.34	−0.01	0.01
T_{day}			1	−0.48	−0.28
$\theta_{REW\,0-20}$				1	0.89

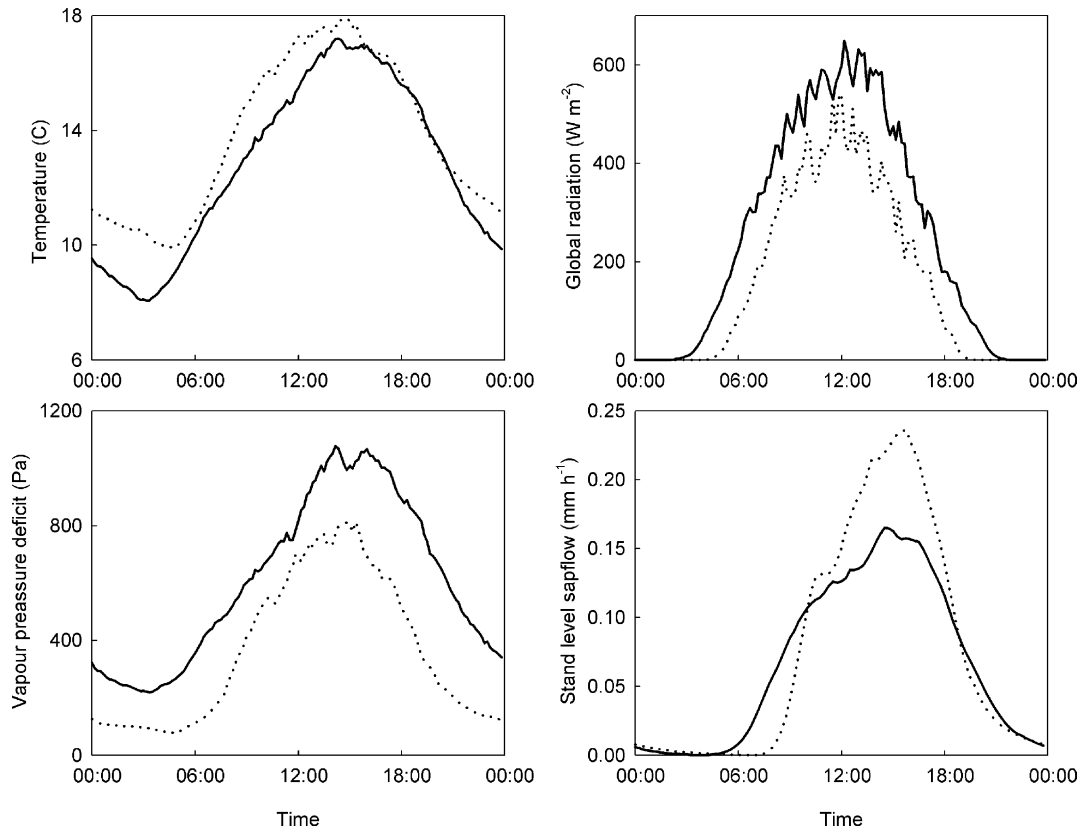Negative values indicate that the relationship was negative.

Fig. 10. Average diurnal pattern for 2 weeks of temperature (a), global radiation (b), vapour pressure deficit (c) and transpiration (d) for a period in the beginning of June (solid line) and in the end of August (dotted line) of 2000.

5. Conclusions

The main conclusions to be drawn from this paper are that on average, the reduction of conductance does not begin until 80% of the extractable amount of soil water has been depleted. We also found that the individual response to low soil water content varies greatly; spruce tended to be more affected by drought than was pine. It is also evident that the canopy conductance in Scots pine and Norway spruce trees shows slightly different responses to vapour pressure deficit and radiation when they are growing in a mixed stand. Pine shows a steeper response to both variables. In spring, and when the soil water content changes rapidly, there may be a poor connection between transpiration and sapflow, also when daily averages are used.

Validation of the model on data from the year after the calibration showed that after a sharp shift in weather conditions, from wet and rainy to warm and dry, the model underestimated the transpiration substantially.

For future studies, it is important to point out that the location of strip roads should be considered when selecting trees for sapflow measurements and when scaling-up to larger areas.

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