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## Simulated and measured water uptake by *Picea abies* under non-limiting soil water conditions

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### Abstract

A one-dimensional non-steady-state soil–plant–atmosphere continuum (SPAC) model was applied to a stand of *Picea abies* trees in southern Sweden. The simulated root water uptake was compared with measured sap flow under non-limiting soil water conditions. Sap flow was measured during the growing season using the tree-trunk heat balance method. The model included four resistances against water (soil–root, plant, stomatal and aerodynamic), one pool of easily available plant water and one compartment of intercepted water on the needle surface. The bulk stomatal resistance was estimated as the product of the combined effect of two independent variables—vapour pressure deficit and solar radiation. Good agreement between simulated and ‘measured’ water uptake was obtained both on short- and long-term scales, and the model explained 92–93% of the variation of measured uptake for both hourly and daily values. The pool of easily available water was found to be small (0.5 mm), i.e. of the same order as for agricultural crops.

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### 1. Introduction

The growing vulnerability of global climate as the consequence of industrialisation has dramatically increased demands for more reliable general circulation models. Such models have been found to be sensitive to how the available energy is partitioned between sensible and latent heat fluxes at the vegetation–atmosphere interface, and there is a great need to improve this part of the models. So-called

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## List of symbols

All areas given in the units refer to the unit ground surface unless otherwise noted.

$a_L, b_L, c_L$	Coefficients of the Lohammar equation (Eq. (8)) (24.5 s m <sup>-1</sup> , 0.5 kPa, 547 W m <sup>-2</sup> , respectively)
$A$	Average cross-sectional area of trees (m <sup>2</sup> )
$A_{ij}$	Leaf area per unit ground surface (leaf area index (LAI), nine)
$A_{\min}$	Cross-sectional area of a hypothetical tree, representing the size of the smallest, most suppressed, but still living trees on the plot (m <sup>2</sup> )
$A_R$	Cross-sectional area for a measured tree R (m <sup>2</sup> )
$c_p$	Specific heat of air at constant pressure (1005 J kg <sup>-1</sup> K <sup>-1</sup> )
$e_a$	Vapour pressure of the air above canopy (kPa)
$e_d$	Saturated vapour pressure of the air above canopy (kPa)
$e_s$	Saturated vapour pressure of the air inside the stomata cavities (kPa)
$E$	Transpiration rate (mm h <sup>-1</sup> )
$E_0$	Penman open-water evaporation (mm h <sup>-1</sup> )
$E_G$	Flow of water to the ground (mm h <sup>-1</sup> )
$E_I$	Evaporation rate of intercepted water (mm h <sup>-1</sup> )
$E_P$	Precipitation rate (mm h <sup>-1</sup> )
$E_Q$	Water uptake by roots (mm h <sup>-1</sup> )
$E'_Q$	$E_Q$ shifted so as to mimic transpiration (mm h <sup>-1</sup> )
$E_Q$	Water uptake by roots (simulated) (mm h <sup>-1</sup> )
$g_c$	Canopy conductance ( $g_c = 1/r_c$ ) (m s <sup>-1</sup> )
$g'_c$	Canopy conductance estimated using $E'_Q$ in inverse of Eq. (8) (m s <sup>-1</sup> )
$H$	Sensible heat flux from canopy to the air (W m <sup>-2</sup> )
$k$	Radiation extinction coefficient related to leaf area (0.5)
$k$	Von Kármán's constant (0.41)
$k_p$	Rain interception coefficient related to leaf area (0.3)
$Q_{wt}$	Sap flow rate (kg per tree h <sup>-1</sup> )
$r_a$	Aerodynamic resistance (s m <sup>-1</sup> )
$r_c$	Canopy resistance (s m <sup>-1</sup> )
$r_{c\text{Max}}$	Maximum canopy resistance (200 s m <sup>-1</sup> )
$r_{c\text{Min}}$	Minimum canopy resistance (30 s m <sup>-1</sup> )
$r_p$	Plant resistance (11.5 MPa s m <sup>2</sup> g <sup>-1</sup> )
$r_r$	Soil–root resistance (MPa s m <sup>2</sup> g <sup>-1</sup> )
$R_n$	Canopy net radiation (W m <sup>-2</sup> )
$R_{no}$	Net radiation above canopy (W m <sup>-2</sup> )
$R_s$	Incident radiation intensity (0.3–3 μm) on a horizontal surface (W m <sup>-2</sup> )
$S$	Scaling factor (Eq. (13))
$t$	Time (s)
$T_a$	Air temperature (°C)
$T_s$	Canopy surface temperature (°C)
$u$	Wind speed above canopy (m s <sup>-1</sup> )
$V$	Easily exchangeable water in the plant (mm or g m <sup>-2</sup> )
$V_I$	Water intercepted on the canopy surface (g m <sup>-2</sup> )
$V_{I\text{Max}}$	Maximum water intercepted on the canopy surface (100 g m <sup>-2</sup> (leaf))
$V_{\text{Max}}$	Maximum easily exchangeable water in the plant (0.5 mm, or 0.55 g m <sup>-2</sup> (leaf))
$z_d$	Displacement height (9 m)
$z_h$	Height of reference measurements above canopy (15.5 m)
$z_0$	Roughness length (1.35 m)
$\beta$	Tree number per unit area
$\gamma$	Psychrometric constant (67 Pa K <sup>-1</sup> )
$\delta e$	Air vapour pressure deficit (kPa)
$\delta t$	Generally used for a difference during a time step

$\Delta_{\text{Max}}$	Maximum allowed deviation in canopy energy balance ( $\text{W m}^{-2}$ )
$\lambda$	Latent heat of water vaporisation ( $2.45 \times 10^6 \text{ J kg}^{-1}$ )
$\rho$	Density of dry air ( $1.2 \text{ kg m}^{-3}$ )
$\psi_c$	Canopy water potential (MPa)
$\psi_{c\text{Max}}$	Maximum canopy water potential ( $-1.7 \text{ MPa}$ )
$\psi_{c\text{Min}}$	Minimum canopy water potential ( $-0.1 \text{ MPa}$ )
$\psi_s$	Soil water potential ( $< -0.025 \text{ MPa}$ )

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SVAT (soil–vegetation–atmosphere–transfer) models have been proposed as suitable sub-models for solving this particular problem. SVAT models must give a realistic description of the properties of a surface, especially in respect to changes in weather, yet they must not be over-complex, to permit easy extrapolation and modification. A suitable compromise for these requirements seems to be offered by the single-layer models. They usually work with easily available input data, which makes it possible to apply them extensively to various types of vegetation surfaces. On the other hand, questions remain about the accuracy of model estimations. To judge their performance, a sound verification of the particular model outputs is necessary.

The main aim of this study was to evaluate the applicability of a single-layer ('big-leaf') model to simulate diurnal water uptake for a homogeneous spruce stand. In this first step, the analysis was made for non-limiting soil water conditions only, to minimise the effect of variation in soil factors. The model used here is based on the soil–plant–atmosphere continuum (SPAC) concept, and simulates the flow of water from soil through the plant to the atmosphere. The basic version of the model was described and tested by Kowalik and Turner (1983) for water potential of soybean, and by Kowalik and Eckersten (1984) for evapotranspiration from a willow stand. Kowalik and Eckersten (1989) used the model for leaf–air temperature differences on willow. The new version of the model (Eckersten, 1991a,b) includes several further developments on linking the water model to a growth model (not used here) and the possibility of including alternative resistance functions. This single pool model does not have the potential to describe water uptake and transport in trees in the detailed branched models presented by Edwards et al. (1986) and Tyree (1988). However, its simplicity permits an application to homogeneous forest areas. Kowalik et al. (1988) used the model on Douglas fir forest and, verified on 4 days, found satisfactory agreement between simulated and measured twig water potential and bulk stomatal resistance. However, the simulated water uptake was compared only with the output of another model (SWATRE) and agreed only in cumulative values.

Here, as we have a fairly extensive set of measured data, we could parametrise the SPAC model for a homogeneous even-aged spruce stand growing under non-limiting soil water conditions. The components of the model were optimised on two small ( $n = 3$  and  $n = 4$ ) sets of days for determination of stomatal response function, the amount of easily rechargeable water and some other parameters. By comparing the dynamics of the simulated and measured water uptake, conclusions could be drawn on the suitability of the proposed mechanisms and the necessary parameters could be quantified. The goals of this study were to evaluate the applicability of the model to estimate diurnal water uptake for the homogeneous spruce stand, and to increase our

understanding of how water flow through the plant is regulated. The parametrisation will also later be used for the conditions of soil water deficit.

## 2. Materials and methods

### 2.1. SPAC model description

The model consists of only two compartments, one for easily available water located in the plant and one for intercepted water on the canopy surface. The stand concerned is treated by the model as horizontally uniform with evenly distributed leaf surfaces. The time step is 1 min and input data are minute values for global radiation, air temperature, air relative humidity, wind speed and precipitation, registered above the canopy, and daily values on soil water potential.

#### Plant water

There is a reservoir of easily available water in the plant ( $V$ ) which is supplied through root uptake ( $E_U$ ) and consumed by transpiration ( $E$ ). The volumetric change of the reservoir during one time step ( $\delta t$ ) is the difference between these flows. The integration is made according to the Euler method (see Eckersten, 1991a):

$$\delta V = \int_{t-\delta t}^t (E_U - E) dt \quad (1)$$

The canopy water potential ( $\psi_c$ ) is related to  $V$  as

$$\psi_c = \psi_{cMax} - (\psi_{cMax} - \psi_{cMin})[1 - (V/V_{Max})] \quad (2)$$

where  $\psi_{cMax}$  and  $\psi_{cMin}$  are maximum and minimum values of  $\psi_c$  and  $V_{Max}$  is the maximum size of the capacitance  $V$ . The difference between soil water potential ( $\psi_s$ ) and  $\psi_c$  constitutes the potential for uptake of water across the resistances of the soil ( $r_r$ ) and the plant ( $r_p$ ):

$$E_U = (\psi_s - \psi_c)/(r_r + r_p) \quad (3)$$

#### Canopy energy balance

The net radiation ( $R_n$ ) absorbed by the canopy is partitioned between latent ( $\lambda E$ ) and sensible ( $H$ ) heat fluxes, and storage of heat in plant tissues is assumed to be negligible. The surface temperature ( $T_s$ ) is determined by iteratively changing its value until the sum of all three fluxes in the energy balance is below a certain limit ( $\Delta_{Max} = 0.1 \text{ W m}^{-2}$ ):

$$R_n - H - \lambda E \leq \Delta_{Max} \quad (4)$$

The canopy is treated as one unit and needs one value for radiative energy available for the heat fluxes. For the spruce stand with a leaf area index ( $A_{li}$ ) of nine,  $R_n$  is almost equal  $R_{no}$ . Hence, we do not use a complex radiative model (e.g. Grace et al., 1987; Wang and Jarvis, 1990). Instead, a simple model (Beers' law) is used to predict the fraction of the net radiation above canopy ( $R_{no}$ ) that is absorbed by the canopy

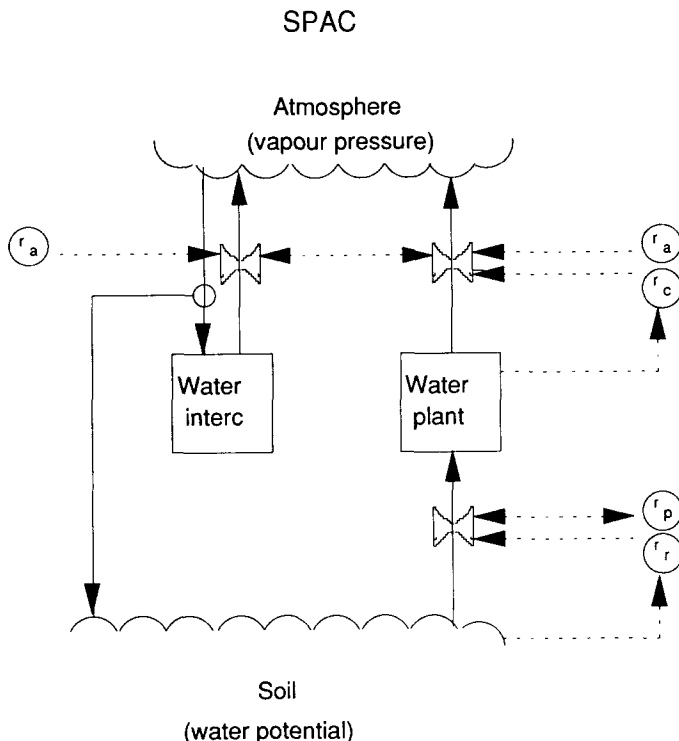


Fig. 1. Schematic description of the SPAC model. Solid lines are flows of water and dotted lines are flows of information.

( $R_n$ ). With  $k$  as the radiation extinction coefficient, we obtain

$$R_n = R_{no}[1 - \exp(-kA_{li})] \tag{5}$$

The partitioning of net radiation between the latent and sensible heat fluxes depends on atmospheric and plant conditions. The latent heat flux is driven by the difference in vapour pressure between that inside the stomatal cavities and that of the air above the canopy. The air in stomatal cavities is assumed to be saturated and of temperature  $T_s$ . The latent heat flux is estimated as

$$\lambda E = \frac{\rho c_p (e_s - e_a)}{\gamma (r_c + r_a)} \tag{6}$$

where  $r_c$  is the canopy resistance (total stomatal resistance per unit of ground area) and  $r_a$  is the bulk aerodynamic resistance between the stand and reference level above the canopy. The sensible heat flux ( $H$ ) is proportional to the difference between the surface temperature ( $T_s$ ) and the air temperature ( $T_a$ ) divided by  $r_a$ , assumed equal for sensible and latent heat:

$$H = \rho c_p (T_s - T_a) / r_a \tag{7}$$

### Resistances

The pathway for water flow from the bulk soil to the atmosphere is represented by four resistances: the soil-root resistance ( $r_r$ ) from the soil (where water potential is  $\psi_s$ ) to the root surface, the plant resistance ( $r_p$ ) from the root surface to the mesophyll of leaves where the water potential is  $\psi_c$ , the canopy resistance ( $r_c$ ) from the leaf-mesophyll to the air of the leaf surface, and finally, the aerodynamic resistance ( $r_a$ ) from the leaf surface to the air above the canopy, where the vapour pressure is  $e_a$  (see Fig. 1). The resistances vary with environmental conditions of the air and the soil as well as with plant conditions.

The soil-root resistance ( $r_r$ ) is a function of root distribution and soil water conditions. In this study, the model was applied on material under non-limiting soil water conditions and thus  $r_r$  was assumed to be zero. The plant resistance ( $r_p$ ) was kept constant. The canopy resistance ( $r_c$ ) decreases with radiation and increases with vapour pressure deficit of the atmosphere ( $e_d - e_a$ ), according to an equation originally derived for pine (Lohammar et al., 1980):

$$r_c = a_L [1 + b_L (e_d - e_a)] (c_L + R_s) / R_s \quad (8)$$

where  $r_{cMin} \leq r_c \leq r_{cMax}$ . The aerodynamic resistance ( $r_a$ ) is estimated from the logarithmic wind profile law in neutral conditions as

$$r_a = \frac{\ln^2 [(z_h - z_d) / z_o]}{k^2} \quad (9)$$

where  $z_h$  is reference height,  $z_d$  is zero plane displacement,  $z_o$  is roughness length,  $k$  is Von Kármán's constant and  $u$  is the wind speed at height  $z_h$ . No correction is made for stability. The estimated maximum error associated with this assumption was less than 4%.

### Rain interception

A fraction of the rain falling on the canopy ( $E_p$ ) is intercepted on the vegetative surfaces and thereafter evaporated to the air ( $E_I$ ). The rest ( $E_G$ ) falls to the ground and is no longer included in the calculations of the model (the soil water potential is input to the model). The change of water stored on the vegetative surfaces ( $\delta V_I$ ) during a time step ( $\delta t$ ) is the net sum of these flows, although limited by the maximum water interception capacity ( $V_{IMax}$ ), which is assumed to be proportional to the leaf area:

$$\delta V_I = (E_p - E_G - E_I) \delta t \quad (10)$$

The rain is assumed to be intercepted by the canopy in a similar way as the radiation. Hence Beers' law is used but instead of the radiation extinction coefficient we use the rain interception coefficient ( $k_p$ ):

$$E_G = E_p \exp(-k_p A_{li}) \quad (11)$$

The intercepted water evaporates ( $E_I$ ) in a way similar to that for the transpired water ( $E$ ) except that the site of evaporation is outside of the stomata. Hence,  $E_I$  is calculated using the same equations as for  $E$  but with the canopy resistance ( $r_c$ ) equal to

zero (Eq. (6)). This gives  $E_1$  much higher than rates of  $E$  (Shuttleworth and Calder, 1979). When there is intercepted water on the vegetative surfaces, the transpiration is assumed to continue from those parts which are still dry. The net radiation of the whole canopy ( $R_n$ ) is shared among the wet and dry surfaces in relation to the resistances against the flows (the fraction for  $E$  was  $r_a/(2r_a + r_c)$ ).

## 2.2. Measurements of sap flow

Sap flow was measured continuously during the growing season by the thermal heat balance (THB) method, with internal heating of xylem tissues using the eight-channel sap flow meter made at the Institute of Forest Ecology, Brno, Czechoslovakia (nowadays commercially available from Ecological Measuring Systems, Brno, Czech Republic). Heat was applied to a stem segment using 3–5 electrodes inserted into conductive xylem tissues (Čermák et al., 1973, 1982; Kučera et al., 1977). The monitoring unit consisted of a battery of four copper–constantan thermocouples in eight stainless steel hypodermic needles with an external diameter of 1 mm (Čermák and Kučera, 1981). Output from the thermocouples was recorded using a data-logger and the mass flow of water obtained from calculations based on the differential heat balance equation (Kučera et al., 1977). There were usually two measuring points on opposite sides of the trunk at breast height, to take account of possible variation of sap flow within the stem. The sap flow measurements were performed in 1990. The validation data set included measurements of three co-dominant trees with diameters at breast height of 15–18 cm and heights of 12.5–15.9 m.

## 2.3. Expressing tree sap flow in ground-surface unit

Sap flow ( $Q_{wt}$ ) measured by the THB method on individual sample trees was recalculated into flow of water ( $E_Q$ ) expressed per unit of ground surface by a procedure based on the approach of Čermák et al. (1980).  $E_Q$  is calculated from  $Q_{wt}$  using a linear relationship (with non-zero intercept) between basal area and sap flow. The intercept of this relationship is given by a basal area ( $A_{min}$ ) of a hypothetical sample tree, i.e. a tree with definite size but practically no measurable sap flow (thus transpiration can be assumed with minimal error to be zero). This tree represented the smallest, most suppressed, but still living, tree of the experimental stand. The calculation can be expressed as

$$E_Q = SQ_{wt} \quad (12)$$

where the scaling factor  $S$  is

$$S = [(A - A_{min})/(A_R - A_{min})] \times \beta \quad (13)$$

and where  $A$  is the average cross-sectional area of trees on the plot,  $A_R$  is the cross-sectional area for the measured tree  $R$  and  $\beta$  is tree number per unit area.

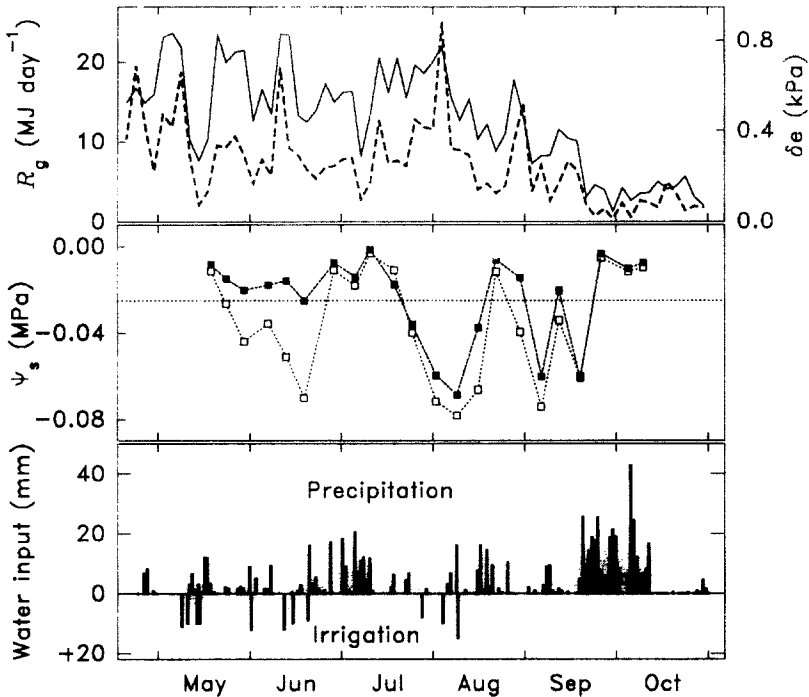


Fig. 2. Upper part: climatic characteristics of the growing season at the site; global radiation ( $R_g$ ; upper left, solid line) and vapour pressure deficit ( $\delta e$ ; upper right, dashed line) data shown are 3-day mean values. Middle part: soil water potential ( $\psi_s$ ) at a depth of 15 cm on Plot A (filled symbols) and Plot B (open symbols); the level of  $\psi_s = -0.025$  MPa (dotted line) determines the periods included in validation data set for Plots A and B. Lower part: water input by daily precipitation and irrigation for Plot A.

#### 2.4. Site description and climate

The site is located in Skogaby, south-west Sweden, 30 km south-east of Halmstad ( $56^{\circ}33.5'N$ ,  $13^{\circ}13.5'E$ ) at an altitude of about 100 m. The sandy till topsoil has a pH of 4.0 and the subsoil 4.5. The soil temperature (5 cm) was lower than  $10^{\circ}C$  for only a few days and was never below  $8^{\circ}C$ . The climate is rather humid, with annual precipitation around 1100 mm (Fig. 2). The mean (1931–1960) annual air temperature is about  $7^{\circ}C$ . The investigated stand was a Norway spruce (*Picea abies* L. Karst.) monoculture that was 24 years old (in 1990). It is a second-generation coniferous forest. The basic stand characteristics were: stem basal area  $34\text{ m}^2\text{ ha}^{-1}$ ; mean height 13.5 m; tree density 2400 trees  $\text{ha}^{-1}$ . There was no understorey vegetation and there were no other tree species. The canopy was closed and leaf area index (LAI) on the investigated site was, on average, nine during the growing season (L.-O. Nilsson and K. Wiklund, personal communication, 1992). The stand included an irrigated part (Plot A), and an undisturbed part (Plot B). On Plot A, a sprinkler system was used to provide an even distribution of water. The irrigation regime was determined by the SOIL model (Jansson and Halldin, 1979) aimed at keeping the soil water deficit below



20 mm of water during the growing season. The irrigation was not sufficient during certain periods.

The soil water potential ( $\psi_s$ ) was measured at a depth of 15 cm by tensiometers about 2 m from the measured trees. Air temperature, air humidity, wind speed, solar radiation and precipitation were measured in an open area (50 m by 50 m, surrounded by forest) about 400 m from the study trees. Wind speed ( $u$ ) was measured at a height of 2 m above ground. A comparative wind speed measurement was made 1 year later (in 1991), when an anemometer was placed 2 m above the top of the canopy. Using this,  $u$  was corrected to represent the conditions above the canopy.

### 2.5. Application of the model

The model was applied to the spruce stand for the period of the growing season, from April to October 1990. The model was tested for non-limiting water conditions. The only criterion for choosing the validation data set was soil water potential ( $\psi_s$ ): the spells with values of  $\psi_s$  less than  $-0.025$  MPa were excluded. Therefore the measurements on two representative trees in Plot A were mostly used, complemented by a third tree from Plot B, including all the periods with  $\psi_s$  within the limit mentioned above. Apart from this, one continuous period of 15 days (28 July–12 August) in Plot A was excluded, when the performance of the sap flow measurement technique was considered doubtful. The simultaneous measurements on Plots A and B (30 cases) were averaged, because of practically identical soil water conditions and stand characteristics. In this way, the sets of 120 daily cases and 2896 hourly cases suitable for validation procedure were obtained.

The measured sap flow ( $Q_{wt}$ ) was converted to units per ground surface area (see above) and considered as measured root uptake,  $E_Q$ , i.e. we define the root uptake as being equivalent to the water flow at the position of the thermocouples in the tree trunk (1.3 m above the ground). It means that, in the model, the pool of easily available water is considered to be situated above the location of sap flow measurement. In this way, the simulated root uptake  $E_U$  could be compared with the measured uptake  $E_Q$ .

### 2.6. Parametrisation

A continuous period of 4 days (12–15 June) was used for detailed determination of the parameters of the canopy resistance function ( $r_c$ ; Eq. (8)), which was used in inverse form to avoid high values in the fitting procedure, thus estimating canopy conductance ( $g_c = 1/r_c$ ) rather than  $r_c$ . The period included two clear and two overcast days. The criteria for parametrisation procedures were  $r^2$  and the slope parameter for the resulting relationship was between  $E_U$  and  $E_Q$ , but the coefficient of variation for the individual parameters was also considered.

The procedure for obtaining the actual canopy conductance values ( $g'_c$ ) involved cross-correlation between the time series of  $E_Q$  and standard Penman (1948) open water evaporation ( $E_0$ ) to detect the mutual time shift between  $E_0$  and  $E_Q$  (resolution

of 15 min). Accordingly,  $E_Q$  was shifted ( $E'_Q$ ) by a specific number of minutes to represent transpiration rate; any other discrepancies in diurnal courses between  $E'_Q$  and actual transpiration apart from time lag were neglected. Then  $g'_c$  values were calculated in a rearranged form of the Penman–Monteith equation. The fitting was made on these values to estimate the parameters  $a_L$ ,  $b_L$  and  $c_L$  of Eq. (8).

The values of plant resistance ( $r_p$ ) and the pool of the easily available water ( $V_{Max}$ ) were estimated by means of the model from a continuous period of 3 days (29–31 May), which included a day with a rain event around noon, followed by one clear and one overcast day (see also Results).

The maximum canopy water potential ( $\psi_{cMax} = -0.1$  MPa) represents a tension that was expected to balance the weight of a water column of 10 m (the height representing the middle of the green canopy); this water potential was also measured in this stand under wet conditions. (For other parameters, see the list of symbols.)

### 2.7. *Input variables*

The input variables were hourly values of relative air humidity, air temperature, precipitation, wind speed and global radiation. Net radiation above the canopy was estimated as a linear function of global radiation ( $R_n = -35 + 0.8R_g$ ), where the slope of 0.8 was taken as the mean of the reported values for a coniferous stand (see Jarvis et al., 1976). The projected LAI ( $A_{ij}$ ) was given a constant value of nine as a mean value of monthly measurements (L.-O. Nilsson and K. Wiklund, personal communication, 1992).

## 3. Results and discussion

### 3.1. *Sensitivity of water uptake to changes in model components*

The simulated water uptake ( $E_U$ ) was most sensitive to canopy resistance ( $r_c$ ) and to a lesser degree to plant resistance ( $r_p$ ), size of the pool (easily exchangeable water,  $V_{Max}$ ), and aerodynamic resistance ( $r_a$ ), respectively. Using a continuous period of 1 month (21 June–20 July) as a test period, a positive change of  $r_c$ ,  $r_p$ ,  $V_{Max}$  and  $r_a$  by 25% resulted, in each case, in significantly different  $E_U$  ( $P < 0.001$ ). The effects expressed by the sum of residuals (absolute value of changed minus original  $E_U$ ) were 21.8 mm, 6.7 mm, 6.6 mm and 0.8 mm for  $r_c$ ,  $r_p$ ,  $V_{Max}$  and  $r_a$ , respectively. Relative to  $r_c$  (100%), these values are 30.8%, 30.5% and 3.8% for  $r_p$ ,  $V_{Max}$  and  $r_a$ , respectively.

The pattern of the influence of the particular model parameters for estimating  $E_U$  may differ substantially for other types of vegetation. This can be expected mostly for parameters  $r_p$  and  $V_{max}$ , which are dependent on the physical size of a plant and properties of the conductive system. For low crops, a larger sensitivity to  $r_a$  can also be expected.

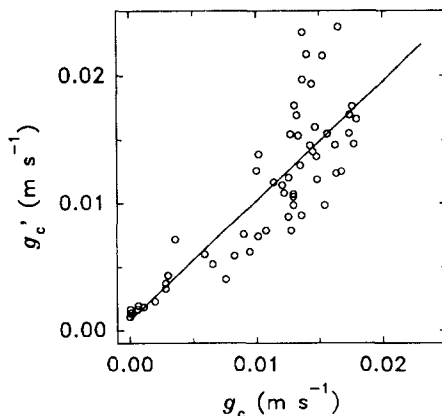


Fig. 3. Parametrisation of the Lohammar function for  $g_c$ : the hourly 'actual' values of  $g_c'$  (obtained by the inverse of the Penman–Monteith equation with  $E$  being mimicked by  $E'_0$ ) against the simulated conductance ( $g_c$ ) for 12–15 June.

### 3.2. Parametrisation of the canopy conductance function

The parameters of the canopy conductance function ( $g_c = 1/r_c$ ; see Eq. (8)) were  $0.041 \text{ m s}^{-1}$ ,  $0.5 \text{ kPa}$  and  $547 \text{ W m}^{-2}$  for  $1/a_L$ ,  $b_L$  and  $c_L$ , respectively. The  $r^2$  value for fitting the derived  $g_c'$  (see above) to the equation was 0.70, using a period of 4 days (12–15 June); the coefficients of variation were 31%, 41% and 46% for the parameters  $a_L$ ,  $b_L$  and  $c_L$ , respectively.

The coefficients of variation of the parameters are high. This is caused by using a limited data set and probably also by the difference in the diurnal dynamics of transpiration ( $E$ ) and sap flow ( $Q_{wt}$ ) rates. As  $g_c'$  was basically derived using  $Q_{wt}$  and the correction could only be made for time delay between sap flow and transpiration, the conductances may be biased by a remaining elastic discrepancy between  $E$  and  $Q_{wt}$ , caused by the pool in a tree. This is reflected by a slightly non-linear pattern in the scatter between derived and estimated conductance (Fig. 3):  $g_c$ , predicted by the inverse of the Lohammar function, diverges mainly in the morning hours, when the difference between fluxes of  $E$  and  $Q_{wt}$  can be expected to be largest. The prediction is good for the periods in the middle of the day, when  $E$  and  $Q_{wt}$  are supposedly well balanced. Massman and Kaufmann (1991) performed a thorough test of five models of  $g_c$ . The Lohammar function performed well compared with the other models. Verified on transpiration and conductance measurements with cuvettes, Massman and Kaufmann reported  $r^2 = 0.73$  for fitting the observed  $g_c$  with the model (for Engelmann spruce), using photosynthetic photon flux density and leaf-to-air vapour pressure difference as driving variables. With respect to those results, the parametrisation of canopy conductance with the Lohammar model was considered of acceptable accuracy. The parametrised model is shown in Fig. 4, where it can be observed that  $g_c$  is strongly dependent on both  $R_g$  and  $\delta e$ . Examples of diurnal pattern of  $g_c$  during one clear day (30 May) and one overcast day (24 May) are shown in Fig. 5.

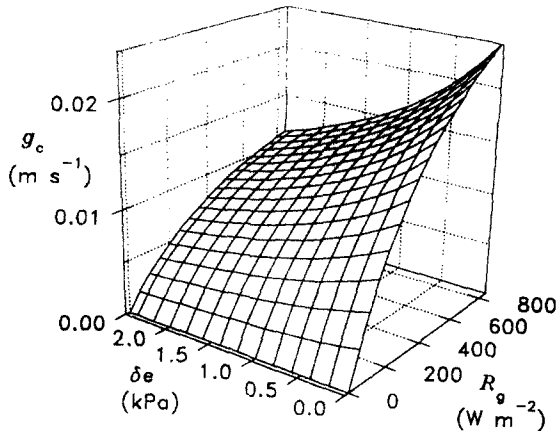


Fig. 4. Modelled canopy conductance ( $g_c$ ): the inverse of the Lohammar function (Eq. (9)) with global radiation ( $R_g$ ) and vapour pressure deficit ( $\delta_e$ ) as driving variables (see text for the parameter values).

The simulations showed that there were relatively small differences between transpiration and sap flow rates. The differences were mainly characterised by a time lag (Fig. 5). This indicates that the approach used here to estimate canopy conductance on the basis of time-adjusted sap flow gives acceptable results. It is also evident that this approach fulfils most of the basic requirements for the top-down determination of canopy conductance as described by Baldocchi et al. (1991): a dry, fully developed, horizontally homogeneous canopy situated on level terrain; identical sink-source levels for transfer of water vapour, heat and momentum; negligible cuticular transpiration and soil evaporation.

All attempts to include canopy water potential ( $\psi_c$ ) as an additional modifier for estimating  $g_c$  failed. The effect of  $\psi_c$  was a limitation of water uptake during times of high rates, which did not correspond to the measured values of sap flow. In their review of models for predicting water fluxes through canopies, Whitehead and Hinckley (1991) noted that the role of  $\psi_c$  as either an indicator or predictor of various processes has not yet been fully developed, although it is often an important component of a model, or the output of a model. It could be expected that for the conditions of soil water deficit,  $\psi_c$  might become of major importance, as shown by the logic of Eqs. (1), (3) and (6). However, our experience, as above, supports the suggestions by Bates and Hall (1981) on soil water potential in the respect that the driving variable is not  $\psi_c$ .

### 3.3. Calibration of plant resistance and capacitance

Total plant resistance ( $r_p$ ) was treated as a constant.  $r_p$  was initially estimated from the measured variables  $\psi$  and  $Q_{wt}$  during 2 days, using Eq. (3) and replacing  $F_U$  by  $Q_{wt}$  ( $r_r$  and  $\psi_s$  were zero).  $r_p$  was 12.7 and 14.1  $\text{MPa s m}^2 \text{g}^{-1}$  during early afternoon hours for two trees under non-limiting soil water conditions (data not shown). However, a slightly lower plant resistance, 11.5  $\text{MPa s m}^2 \text{g}^{-1}$ , gave a better fit between measured and simulated water uptake for a 3 day period in May (Fig. 6).

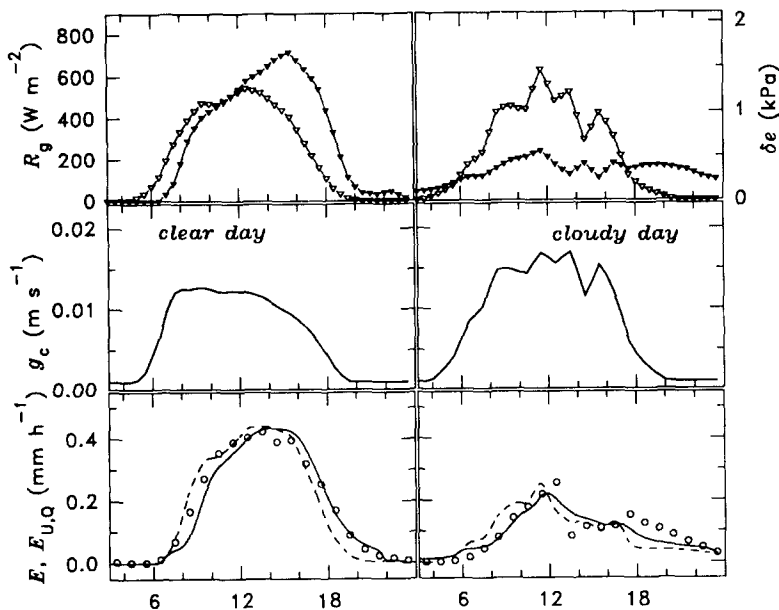


Fig. 5. The diurnal course of the modelled canopy conductance ( $g_c$ ) during a clear day (13 August; middle left) and a cloudy day (24 May; middle right). Lower part: the modelled transpiration ( $E$ ; dashed line) and water uptake ( $E_U$ ; solid line) as compared with 'measured uptake' ( $E_Q$ ; open symbols). Upper part: the global radiation ( $R_g$ ; open symbols) and vapour pressure deficit ( $\delta e$ ; filled symbols) for these days.

A higher value of  $r_p$ , e.g.  $16 \text{ MPa s m}^2 \text{ g}^{-1}$ , decreases water uptake (dotted line in Fig. 6) at a given potential difference (Eq. (3)). This causes two major discrepancies compared with measured data. At high transpiration rates the pool of easily available water is emptied and the canopy water potential decreases to its minimum value ( $\psi_{\min}$ ), and this limits  $E_U$  (30 May; Fig. 6). The other effect is a prolonged uptake during the evenings, caused by slower filling up of  $V$  by  $E_U$ . This makes  $E_U$  deviate more with respect to  $E_Q$ .

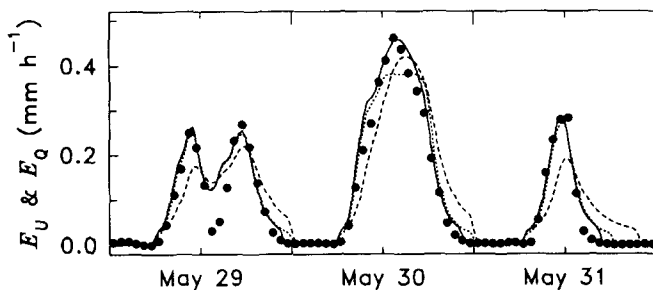


Fig. 6. The effects of plant resistance ( $r_p$ ) and of the capacitance ( $V_{\text{Max}}$ ) for the simulated water uptake ( $E_U$ ) demonstrated on the period 29–31 May:  $E_U$  with  $r_p = 11.5 \text{ MPa s m}^2 \text{ g}^{-1}$  and  $V_{\text{Max}} = 0.5 \text{ mm}$  (solid line) as compared with  $E_U$  for  $r_p = 16 \text{ MPa s m}^2 \text{ g}^{-1}$  (dotted line) or with  $E_U$  for  $V_{\text{Max}} = 1.5 \text{ mm}$  (dashed line); the 'measured' uptake  $E_Q$  is shown by filled symbols.

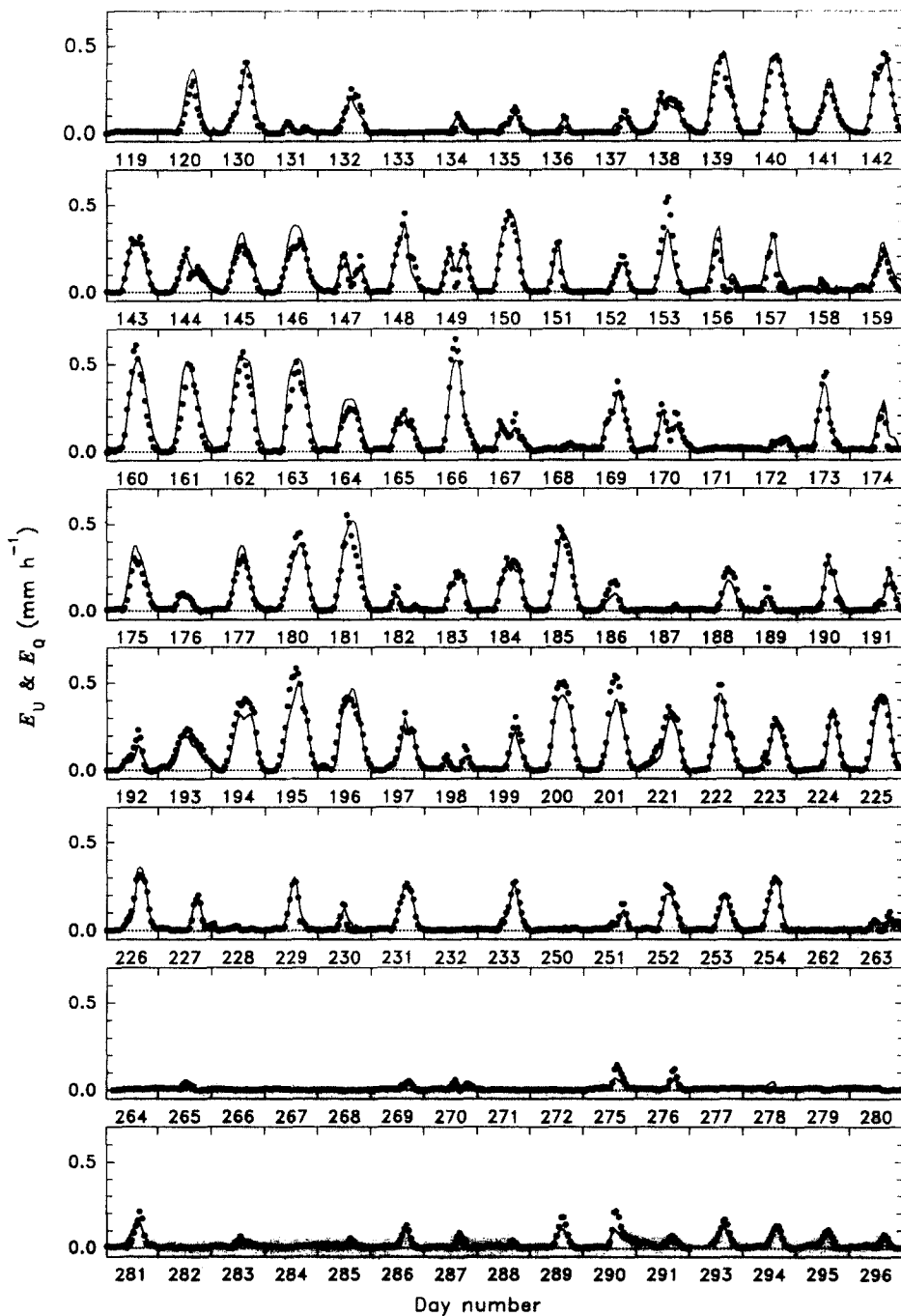


Fig. 7. Modelled ( $E_U$ ; solid line) and 'measured' ( $E_Q$ ; filled symbols) water uptake (in hourly values for the validation period (April–October). It should be noted that the day numbers on the x-axis are not consecutive.

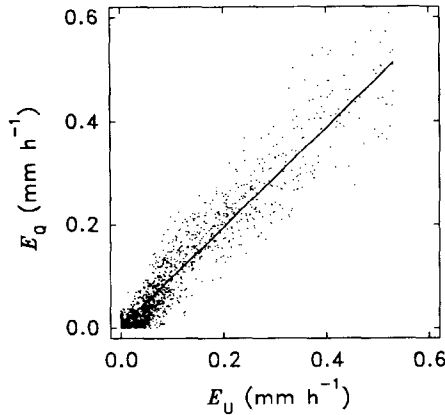


Fig. 8. Scatter view on the relationship between  $E_U$  and  $E_Q$  in hourly values ( $r^2 = 0.92$ ).

Nevertheless,  $r_p$  is still considered as one of the most uncertain factors in the model. There is both experimental and theoretical evidence that the branches of most tree species are to a high degree hydraulically isolated from the stem, owing to the presence of constriction zones between stem and branches or between primary and secondary branches (see Sprugel et al., 1991). This makes the pattern of hydraulic conductivity in a tree very complex. This situation was neglected in the model by assuming that, above the level of stem flow measurement, the plant was represented by only one capacitance with uniform water potential. Also, several studies (Feddes and Rijtema, 1972; Hansen, 1974) have indicated that  $r_p$  for crops varies with transpiration rate. We tested  $r_p$  as a decreasing function of uptake rate, but this way the agreement between simulated and measured hourly uptake was not improved.

The size of the pool of easily available water ( $V_{Max}$ ) was found to be 0.5 mm. The sensitivity of the simulated uptake ( $E_U$ ) on  $V_{Max}$  is demonstrated for the period 29–31 May.  $E_U$  is shown for  $V_{Max} = 0.5$  mm and for  $V_{Max} = 1.5$  mm (Fig. 6; solid and dashed line, respectively). The latter value of  $V_{Max}$  caused a considerable discrepancy between  $E_Q$  and  $E_U$ , thus indicating an unrealistic size of  $V_{Max}$ . The quantity of 0.5 mm represents roughly a quarter of the average daily water uptake on the site. Schulze et al. (1985) found the amount of available water storage to be 24% and 14% of the daily transpiration rate in *Larix* and *Picea* trees, respectively. Carlson and Lynn (1991) estimated the magnitude of the capacitance effect in large plants in their model to be no larger than 20–50  $W m^{-2}$  (in transpiration per unit of leaf area); this corresponds well to our value of 0.5 mm, which, when expressed in transpiration per unit of leaf area (LAI 9), is 40  $W m^{-2}$ .

### 3.4. Validation of the modelled water uptake

Hourly values of measured and simulated water uptake ( $E_Q$  and  $E_U$ ) for the complete data set are presented in Fig. 7. The simulated diurnal course of  $E_U$  was

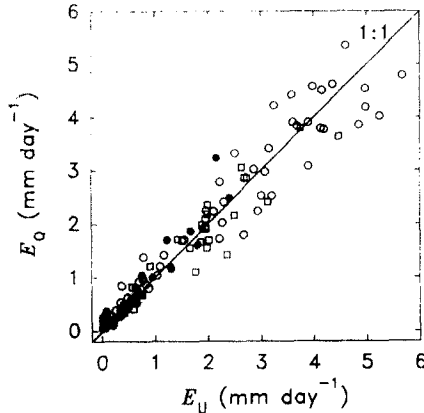


Fig. 9. Scatter view on the relationship between  $E_U$  and  $E_Q$  in daily integrals ( $r^2 = 0.93$ ). The subsets of dry, wet and intermediate days are shown by open circles, filled circles and open squares, respectively.

in good agreement with measured  $E_Q$  for all kinds of weather conditions (Fig. 7): sunny days (e.g. Days 140 and 150), days with a rain shower (e.g. Days 131 and 149), rainy days (e.g. Days 158 and 228), days with flow during night/dark hours (e.g. Days 144, 193 and 221). The highest discrepancy was found for days with sharp peaks during midday (e.g. Days 153 and 173). In total, the model explained 92% of the variation of  $E_Q$  in hourly values ( $r^2 = 0.92$ ). It may be observed on the scatter plot (Fig. 8) that the points are not distributed equally along the regression line, but form a slight S-shaped pattern. This probably is an effect of the simplifications made here, namely, ignoring the complex hydraulic architecture of a tree by using one capacitance only and considering the sap flow in a stem at height of 1.3 m as the water uptake by roots.

The linear regression between the daily integrals of  $E_U$  and  $E_Q$  had  $r^2 = 0.93$  ( $n = 120$  cases), with the intercept and slope parameters 0.15 ( $SE = 0.052$ ) and 0.92 ( $SE = 0.023$ ), respectively. The sums of daily  $E_U$  and  $E_Q$  were 199 mm and 200 mm, respectively, with an equal average value of 1.7 mm (all for  $n = 120$ ). The regression analysis performed on subsets of dry or nearly dry days ( $n = 52$ ; daily precipitation less than  $0.6 \text{ mm day}^{-1}$ ) and wet days ( $n = 38$ ; daily precipitation  $4.5 \text{ mm day}^{-1}$  and more) had  $r^2$  values of 0.91 and 0.92 for dry and wet subsets, respectively (Fig. 9). The slope parameters of these regressions were 0.9 and 1.1 for dry and wet sets, respectively; this is, however, biased by different distributions of the data, with wet cases mostly close to zero. The regressions limited by  $E_U = 2 \text{ mm}$  give the slope parameter of 1.0 for both wet and dry cases. As seen in Fig. 9, the simulated wet cases follow the pattern of simulated dry cases fairly well. This demonstrates that the model performs well for both wet and dry conditions, although we used an approximate model for how transpiration occurs in the case of intercepted water on the leaves.

It should be emphasised that the parametrisation was made only for seven selected days, i.e. about 5% of the whole data set. The correspondence between simulated and measured uptake was equally good throughout the season and under different weather conditions, and therefore the overall model performance must be judged



as good. Future work with the model will address water limiting conditions in the stand. This would include the behaviour of  $r_r$  (set to zero here), and we also expect the water storage in plants and  $r_p$  to behave differently.

#### 4. Conclusions

(1) The simple 'big-leaf' model explained 92–93% of the variation in water uptake of spruce trees growing under non-limiting soil water conditions for both hourly values and daily integrals.

(2) The model performed well for both dry and wet weather conditions.

(3) The modelled water uptake is most sensitive to canopy resistance (conductance). It is also sensitive to the size of the capacitance and the plant resistance, especially considering the accuracy with which they can be determined.

(4) The pool of easily available water in spruce trees was estimated to be 0.5 mm, which is roughly one-quarter of the average daily water output by transpiration.

#### 5. Acknowledgements

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