

Stored water use and transpiration in Scots pine: a modeling analysis with ANAFORE

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Summary We estimated daily use of stored water by Scots pine (*Pinus sylvestris* L.) trees growing in a temperate climate with the ANAFORE model (ANALYSIS of FOREst Ecosystems) and compared the simulation results with sap flow measurements. The original model was expanded with a dynamic water flow and storage model that simulates sap flow dynamics in an individual tree. ANAFORE was able to accurately simulate diurnal patterns of measured sap flow under microclimatic conditions that differ from those of the calibration period. Strong relationships were found between stored water use and several tree characteristics (diameter at breast height, sapwood area, leaf area), but not with tree height. Relative to transpiration, stored water use varied over time (between less than 1% and 44% of daily transpiration). On days when transpiration was high, trees were more dependent on stored water, indicating that the contribution of internal water to transpiration is not a constant in the water budget of trees.

Keywords: nighttime transpiration, *Pinus sylvestris*, sap flow, stomatal conductance.

Introduction

A thorough understanding of the interactions between a forest and the atmosphere requires the quantification of all components of the water balance of the forest ecosystem. Tree transpiration is a crucial component in this balance. The effects of leaf microclimate on stomatal regulation of transpiration are well described in the literature, although the underlying mechanisms are not fully understood (Whitehead 1998, Buckley et al. 2003, Buckley 2005). There are two groups of empirical models that describe the responses of stomatal conductance (g_s) to the leaf environment. (1) One group of models describes g_s as a product of multiplicative functions of environmental variables (e.g., Jarvis 1976). (2) A second group of

models is based on the close link between g_s and the rate of photosynthesis (e.g., Ball et al. 1987, Leuning 1995). These latter models are typically coupled with the biochemical model of photosynthesis described by Farquhar et al. (1980) and are the most widely used (Whitehead 1998).

There is considerable evidence that g_s is affected not only by the leaf environment but also by root-sourced hydraulic and chemical signals (Whitehead 1998). These signals of soil water deficit have been described in partly mechanistic models. For example, Tardieu and Davies (1992, 1993) developed an interactive model that incorporates both hydraulic and chemical (abscisic acid; ABA) signals. The combined effects of the leaf and root environments on g_s were initially described empirically (Tenhunen et al. 1994). Later, both effects were combined in more mechanistic models (e.g., Dewar 2002, Buckley et al. 2003, Buckley 2005). Models that combine both effects have been tested against measurements of g_s (e.g., Gutschick and Simoneau 2002, Bauerle et al. 2004) but, to our knowledge, have not been incorporated in process-based, mature tree to ecosystem-scale models. In this study, we tested the performance of the ANAFORE (ANALYSIS of FOREst Ecosystems) model (Deckmyn et al. 2006, Op de Beeck et al. 2007), which incorporates an improved version of the Dewar (2002) model for g_s , on a diurnal scale for individual trees.

Many efforts have been made to quantify water fluxes in terrestrial ecosystems. Verstraeten et al. (2005) give a good overview of available measurement techniques and models for determining water fluxes at different scales. To estimate water fluxes in Scots pine (*Pinus sylvestris* L.) in Brasschaat (Belgium), we combined process-based modeling (ANAFORE) and sap flow measurements.

A common problem for process-based gas exchange models working on the scale of mature trees to ecosystems, is the need for large calibration and validation datasets. The growing availability of eddy covariance data provides the opportunity

to compare forest ecosystem models with long-term (multi-year) datasets. However, eddy covariance assesses the total water vapor flux, which contains not only transpiration by the trees, but also soil and canopy evaporation and understory transpiration. In contrast, sap flow measurements allow the calibration and testing of models of transpiration only. Several SVAT (Soil Vegetation Atmosphere Transfer) models have previously been calibrated or validated using sap flow data on a diurnal scale (Chiesi et al. 2002, Oltchev et al. 2002, Meiresonne et al. 2003).

When comparing diurnal patterns of modeled transpiration and sap flow measurements, water storage should be taken into account. The voluminous sapwood of the secondary xylem of large trees can provide a significant storage component of the tree water budget (Čermák et al. 1982, 2007, Meinzer et al. 2001). Water storage in tree stems and canopies causes a time lag between the onset of transpiration measured (or modeled) at the leaf or canopy level and the onset of sap flow measured at breast height. The larger the tree, the larger the storage capacity and the longer the time lag (Goldstein et al. 1998). The transpiration of stored water during the day causes diurnal stem diameter fluctuations, as previously reported for several deciduous and coniferous tree species (e.g., Tatarinov and Čermák 1999, Zweifel and Häslner 2001, Sevanto et al. 2002, Steppe and Lemeur 2004). When storage is included in a process-based model, sap flow can be estimated from modeled transpiration and stored water use can be estimated. This is important because there is limited information on the contribution of internal water stores to total daily water use (Čermák et al. 1982, 2007, Meinzer et al. 2001).

The goals of our study were to: (1) estimate the use of stored water of individual pine trees using the ANAFORE model and sap flow measurements; and (2) relate stored water use to tree size (e.g., stem diameter, height, sapwood area).

Materials and methods

Site description

The forest under investigation is “De Inslag”, a mixed forest located in Brasschaat (51°18′33″ N, 4°31′14″ E), in the Belgian Campine region, about 20 km north-east of Antwerp. The site is part of the European Carboeurope-IP network and is a Level-II observation plot (ICP-II forests) for intensive monitoring of forest ecosystems (EC-UN/ECE 1996), managed by the Flemish Research Institute for Nature and Forest (INBO). The landscape is a coastal plain, nearly flat (slope < 0.3%) and at a mean elevation of 16 m. The climate is temperate maritime with a mean annual temperature of 9.8 °C and 750 mm of annual precipitation. The site is located in an area with high nitrogen deposition (30–40 kg ha⁻¹ year⁻¹; Neiryneck et al. 2002).

This relatively small (150 ha) forest consists of many patches of different coniferous and deciduous species, with a variety of understory species. We focused on the Scots pine stand, described by Curiel Yuste et al. (2005). This even-aged stand was planted in 1929, and tree density was 556 trees ha⁻¹ in 1997. In November 1999, the stand was thinned to 377 trees

ha⁻¹. In winter 2000, mean diameter at breast height (DBH) was 29.4 cm and mean height was 21.4 m.

The soil is loamy sand, moderately wet, with a distinct humus and iron B-horizon and is classified as an Umbric Regosol (FAO classification; Roskams et al. 1997). Below the sandy layer, at a depth of 1 to 3 m, is a clay layer, causing poor drainage. The groundwater depth is usually 1.2 to 1.5 m. The soil is typically moist, but rarely saturated because of the high hydraulic conductivity of the upper sandy layers. A detailed description of the physical and chemical properties of the soil is available (Janssens et al. 1999, Neiryneck et al. 2002).

Sap flow measurements

Sap flow data were obtained during the growing season of 2000. From May 26 to October 18, 2000, sap flow was measured on 14 sample trees (two groups of seven trees located in the vicinity of the soil water sensors). The main attributes of the sampled trees are given in Table 1. Leaf area of the sample trees was determined as described by Čermák et al. (1998), based on destructive measurements on a series of sample trees from the same stand. Sapwood area was estimated from radial sap flow profiles: the border between sapwood and heartwood was defined as where sap flow reached zero.

Sap flow in the sample trees was measured by the heat field deformation (HFD) method, based on observed changes of an artificial heat field around a linear heater in stems, which depends on sap flow rate and xylem tissue properties (Nadezhdina and Čermák 2000, Nadezhdina et al. 2004, 2006). Deformation of the heat field generated by the linear heater in a certain tangential section of the stem is characterized by the ratio of temperature gradients measured around the heater in the axial and tangential directions. This ratio is the basis for sap flow calculation.

Sap flow in sample trees was measured with two types of sensors: small, single-point sensors for routine sap flow measurements during the entire growing season and long multi-point sensors for determination of the variable flow pattern along the xylem radius in the tree stem. Each sap flow sensor consisted of two sets of differential thermocouples and a linear heater. Needles of the multi-point sensor contained six thermocouples, 10 or 16 mm apart. Four multi-point sensors were employed, providing 24 measurement points. By moving the needles along the radius half of the distance between the thermocouples (5 or 8 mm), 24 additional measuring points were obtained. The conducting system of stems at breast height was therefore characterized by 48 measuring points per sample tree. The radial pattern was used to scale-up sap flow from routine single-point measurements to the whole-tree level, according to the procedure described by Nadezhdina et al. (2002). The temperature data (temperature differences) were measured every minute and recorded as 15-min means by data loggers (EMS-12, Unilog & Environmental Measuring Systems Inc., Brno, Czech Republic).

Supporting measurements

Meteorological parameters, including global radiation (pyranometer, Kipp and Zonen CM6B, The Netherlands), net radi-

Table 1. Main attributes of the 14 sampled Scots pine (*Pinus sylvestris*) trees in the year 2000 in the experimental plot in Brasschaat, Belgium. All values are given for individual trees. Abbreviation: DBH = diameter at breast height.

Tree No.	DBH (cm)	Height (m)	Sapwood area (cm ²)	Leaf area (m ²)	Leaf-to-sapwood area (m ² cm ⁻²)
11	36.0	18.2	564	90.5	0.16
12	32.5	18.1	494	75.1	0.15
13	31.2	19.0	511	69.3	0.14
14	29.9	16.3	428	65.3	0.15
15	27.9	15.2	393	56.7	0.14
16	26.7	15.9	320	53.7	0.17
17	30.6	15.5	430	66.1	0.15
21	34.4	23.1	563	82.7	0.15
22	32.2	22.0	424	74.3	0.18
23	29.6	16.7	425	63.3	0.15
24	28.2	19.2	423	58.6	0.14
25	26.7	19.9	420	53.3	0.13
26	23.7	16.0	297	41.9	0.14
27	27.7	18.4	434	57.1	0.13

tion (REBS 07, Seattle, WA), photosynthetically active radiation (PAR, JYP-1000 sensor, SDEC, Tours, France), air temperature and relative humidity (DTS-5A Decot Instrument Co Ltd, Abingdon, U.K.), wind speed (Decot DWR-250G) and precipitation (Decot DRG-51) were continuously measured at the top of a 40-m tower located within the Scots pine stand, and recorded half hourly by a data logger (Campbell CR10, CSI, Logan, UT). More details about the instruments and methods (e.g., gap filling) used can be found in Kowalski et al. (2000) and Carrara et al. (2003).

Soil water content was measured twice a week at two locations in the Scots pine stand with a series of time domain reflectometry (TDR) sensors placed every 25 cm down to a depth of 175 cm (cabletester: Tektonix 1502B, Redmond, WA). Volumetric soil water content measurements were linearly interpolated to obtain estimates for the entire measurement period. Soil water potential was calculated from the volumetric soil water content based on the power function model of van Genuchten (1980). Parameters for the soil water retention curve were determined at the site by Meiresonne et al. (2003).

Model description

The ANAFORE model is operative over a range of temporal (half hours, days, years) and spatial (leaf, single tree, forest stand) scales. The model simulates carbon and water fluxes, tree growth and wood tissue development from incoming solar irradiance, air temperature, air vapor pressure deficit, wind speed and precipitation. ANAFORE follows a bottom-up approach: leaf-level processes (half-hourly photosynthesis and transpiration) are implemented into a daily operating single tree architecture and allocation module. Light interception is modeled based on the approach proposed by de Pury and Farquhar (1997). The leaves are distributed over multiple horizontal crown layers, and the leaf-level simulations are conducted for the sunlit and shaded fraction of each layer separately. Moreover, the crown is further subdivided into vertical

sections, to allow differentiation between the more sunlit periphery and the shaded interior of the crown. Stomatal aperture, sap flow, photosynthesis (Farquhar 1980) and transpiration (Penman 1948, Monteith 1965) are simulated on a half-hourly basis.

From the net photosynthesis and the daily maintenance respiration of the tissues, daily C gain of a tree is calculated. This net gained C is distributed over the different biomass pools, following basic allocation rules and phenological allocation patterns. Allocation of the cumulated carbon gain to woody tissues is calculated on a daily basis, using the improved pipe theory (Deckmyn et al. 2006). Because of the mesic climate and the maturity of the study trees, the annual production of new xylem vessels is of relatively minor importance. Hence, intra-annual changes in stem resistance were not taken into account in the water storage module.

ANAFORE simulates fundamental processes such as photosynthesis, respiration, stomatal conductance and transpiration in detail at the single tree level, which makes this model a suitable tool for diurnal simulations of water fluxes in individual trees. Nevertheless, the descriptions of sap flow dynamics and the internal water storage in individual trees are missing from the original model. For our study, ANAFORE was expanded by the addition of a dynamic water flow and storage model. The key processes relevant to our study—stomatal conductance, transpiration and sap flow in the tree—are described below.

Stomatal conductance The stomatal conductance model is derived from the formula of Dewar (2002):

$$g_s = \frac{a_1 (A_n + R_d)}{c_i \left(1 + \frac{VPD}{D_0} \right)} e^{-[ABA] \beta e^{\delta V_{leaf}}} \quad (1)$$

where g_s is stomatal conductance to CO₂ (mol m⁻² s⁻¹), A_n is

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net leaf CO₂ assimilation rate (mol m⁻² s⁻¹), R_d is dark respiration rate (mol m⁻² s⁻¹), c_i is intercellular CO₂ concentration (mol mol⁻¹ air), VPD is atmospheric vapor pressure deficit (kPa), a_1 (dimensionless) and D_0 (kPa) are empirical constants that are parameter combinations, [ABA] is leaf xylem concentration of abscisic acid (ABA) (mol m⁻³), Ψ_{leaf} is leaf water potential (MPa), β is basal sensitivity of stomata to ABA (m³ mol⁻¹) and δ (MPa⁻¹) is a factor relating stomatal ABA sensitivity to Ψ_{leaf} . According to Dewar (2002), leaf xylem concentration of ABA can be calculated as:

$$[\text{ABA}] = \frac{-\lambda_{\text{root}} \Psi_{\text{root}} - \lambda_{\text{leaf}} \Psi_{\text{leaf}}}{V_w (E + a)} \quad (2)$$

where Ψ_{root} and Ψ_{leaf} are root and leaf water potentials, respectively, λ_{root} and λ_{leaf} are root and leaf ABA synthesis coefficients, respectively, V_w is molal volume of H₂O, E is transpiration rate and a is the ABA sequestration rate. To improve the model simulations, we adapted the original formula (Equation 1) of Dewar (2002) as follows:

$$g_s = \frac{a_1 (A_n + R_d) + b}{c_i \left(1 + \frac{\text{VPD}^2}{D_0} \right)} e^{-[\text{ABA}] \beta e^{\delta \Psi_{\text{leaf}}}} \quad (3)$$

The first improvement is the introduction of an empirical constant b (mol m⁻² s⁻¹) to allow for variable stomatal conductance during nighttime when gross photosynthesis becomes zero. Transpiration is generally assumed to be insignificant at night when stomata close; however, there is increasing evidence that stomata of some species do not fully close at night, allowing for nighttime transpiration if there is a sufficient driving force (Daley and Phillips 2006). Nighttime stomatal opening and transpiration have been observed in several woody species (Čermák et al. 1982, Hogg and Hurdle 1997, Oren et al. 1999, Steppe and Lemeur 2004, Daley and Phillips 2006) including Scots pine (Skärby et al. 1987, Musselman and Minnick 2000, Nadezhkina et al. 2002).

Nighttime sap flow does not necessarily imply nighttime transpiration, because refilling of storage pools can also cause sap flow. Moreover, even if stomata are closed at night, some water loss may occur from the leaves by cuticular transpiration (Benyon 1999). However, a positive correlation between nighttime sap flow and VPD suggests that sap flow can be attributed to nighttime transpiration (Benyon 1999, Daley and Phillips 2006). In our study, the mean measured nighttime sap flow for the 14 pine trees was clearly correlated with VPD (Figure 1). These results suggest that we can attribute at least a part of the nighttime sap flow to stomatal transpiration when VPD is high during the night. We believe that it is incorrect to assume a constant stomatal conductance at night (e.g., Uddling et al. 2005), because g_s may be limited by signals from the roots or by VPD during nighttime. Hence we introduced the constant b in the stomatal model, in such a way that it allows for variable stomatal opening during the night.

Because b is a new parameter, there are no published values. Daley and Phillips (2006) conducted an analysis to partition nighttime sap flux between refilling of internal water stores and transpiration. They found that nighttime sap flux frequently exceeded recharge estimates, and that 10% of the daily water flux could be attributed to nighttime transpiration in paper birch. Benyon (1999) found a value of 5% for *Eucalyptus grandis*. We were unable to partition nighttime sap flow, because no measured estimates of leaf-level transpiration were available. A value of 5.0×10^{-6} mol m⁻² s⁻¹ was assumed for b , which resulted in nighttime transpiration estimates ranging between 5 and 15% of the daytime transpiration rates.

The second improvement to Equation 3 is the introduction of VPD² in the denominator of the equation. Without this improvement, large overestimates (up to 90%) of measured sap flow occurred on days with high VPD. With this improvement, Equation 3 simulates greater stomatal closure at high VPDs, which improved the model fit considerably (e.g., the r^2 for Scots pine No. 21 improved from 0.49 to 0.81). Because of this alteration, we could not use literature values for D_0 , and assumed this empirical constant equaled 1 kPa² (the units of D_0 have changed because of the different formulation).

Through a series of equations, Equation 3 can be coupled with the photosynthesis model of Farquhar et al. (1980) to calculate A_n and R_d . This equation series is solved according to Op de Beeck et al. (2007).

Transpiration Actual transpiration at the leaf level is calculated according to the Penman-Monteith approach (Penman 1948, Monteith 1965):

$$\lambda E = \frac{s(R_n - G) + \rho_a c_p g_b \text{VPD}}{s + \gamma \frac{g_b}{g_w}} \quad (4)$$

where E is canopy transpiration (kg m⁻² s⁻¹), λ is latent heat of

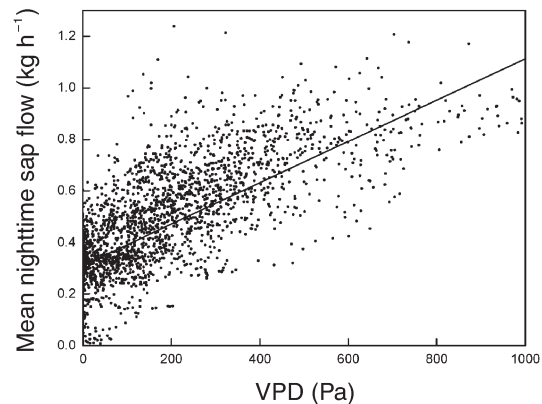


Figure 1. Correlation between mean half-hourly nighttime sap flow and mean half-hourly vapor pressure deficit (VPD), measured on 14 Scots pine (*Pinus sylvestris*) trees from May 26 to October 18, 2000. Explained variance (R^2) of the regression line is 0.55 ($P < 0.0001$). Nighttime was defined as having zero incoming radiation.

vaporization (J kg^{-1}), s is the slope of the saturated water vapor pressure curve ($\text{Pa } ^\circ\text{C}^{-1}$), R_n is net radiation above the canopy layer (W m^{-2}), G is sensible heat storage (W m^{-2}), ρ_a is air density (kg m^{-3}), c_p is specific heat of dry air ($\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$), g_b is boundary layer conductance for H_2O (m s^{-1}), VPD is vapor pressure deficit (Pa), γ is the psychrometric constant ($\text{Pa } ^\circ\text{C}^{-1}$), and g_w is total conductance for H_2O (m s^{-1}) between the evaporating site and the bulk air (i.e., the series sum of the stomatal and boundary layer conductances) (Jones 1992). The sunlit and shaded leaf areas of each canopy layer were used to scale up from leaf-level transpiration to transpiration of the entire tree.

Sap flow To estimate sap flow at the stem level from simulated transpiration rates, ANAFORE was expanded with a module that simulates sap flow dynamics for an individual tree, taking into account water storage. The sap flow model used in ANAFORE is based on the electrical analog approach and is a simplified version of the water transport submodel of the RCGro model (Steppe et al. 2006). A diagram of the model is given in Figure 2. To model diurnal variations in water flow through plants, non-steady state models, which use both water flow resistances and capacitances, must be used (Hunt et al. 1991). This simplified dynamic flow and storage model has three flow resistances and one capacitance. Transpiration of an individual tree and soil water potential are the model inputs. The model assumes that water potential in the root xylem is equal to soil water potential.

Vertical water transport in the xylem can be described by Ohm's law:

$$E = \frac{\Psi_{\text{stem}} - \Psi_{\text{leaf}}}{R_x} \quad (5)$$

$$F_{\text{tree}} = \frac{\Psi_{\text{soil}} - \Psi_{\text{stem}}}{R_x} \quad (6)$$

where E is transpiration rate (mg s^{-1}), F_{tree} is stem sap flow (mg s^{-1}), Ψ_{soil} is soil water potential (MPa), Ψ_{stem} is water potential in the stem xylem, Ψ_{leaf} is leaf water potential (MPa) and R_x is xylem flow resistance (MPa s mg^{-1}). Both xylem flow resistances are assumed equal. This assumption ignores variation in xylem hydraulic resistance within a tree, which might be a limitation of the model. Besides vertical water transport, internally stored water can contribute to the daily transpiration loss because of the hydraulic connection between the xylem and the storage pools. This contribution depends on the magnitude of the hydraulic exchange resistance (R_s ; MPa s mg^{-1}) that must be overcome when water flows from the storage compartments to the xylem to equilibrate the imbalance between water supply and demand during the day (Lhomme et al. 2001). Water flow to or from the storage pools f_{storage} (mg s^{-1}) can be expressed as:

$$f_{\text{storage}} = \frac{\Psi_{\text{stem}} - \Psi_{\text{storage}}}{R_s} \quad (7)$$

where Ψ_{storage} is water potential in the storage compartment (MPa). Values of f_{storage} are negative when water is withdrawn from the storage pool. Flow rates out of the xylem compartments can be derived from Kirchhoff's electric current law (Figure 2):

$$E = F_{\text{tree}} - f_{\text{storage}} \quad (8)$$

The capacitance C of the storage tissue (mg MPa^{-1}) can be defined as the ratio between the change in amount of water in the storage tissue and the change in water potential of the tissue (e.g., Hunt 1991, Phillips et al. 2003).

$$C = \frac{\Delta W}{\Delta \Psi_{\text{storage}}} \quad (9)$$

where W is water content of the storage compartment (mg), corresponding to the total charge on the capacitor of an electrical circuit. The capacitance is considered here as a constant parameter per tree (Steppe et al. 2006).

The flow rate to or from the storage pool f_{storage} described in Equation 7 is equivalent to the change in water content of the storage pool:

$$f_{\text{storage}} = \frac{dW}{dt} \quad (10)$$

Our sap flow model combines the above set of algebraic and differential Equations (5–10). As initial conditions, the water potential of the storage tissue is considered to be zero when the

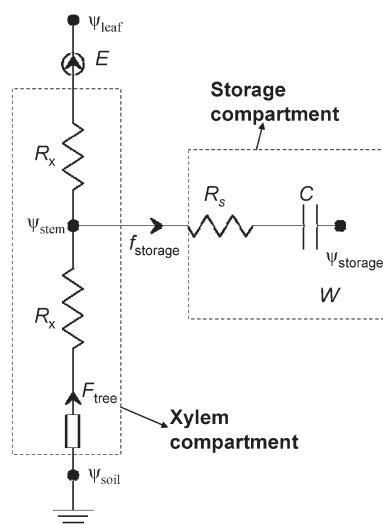


Figure 2. Diagram of the water storage model. Xylem and storage compartments are shown. Abbreviations: Ψ_{soil} , soil water potential; Ψ_{stem} , water potential of stem xylem; Ψ_{leaf} leaf water potential; Ψ_{storage} , water potential in storage compartment; f_{storage} , water exchange between xylem and storage compartment; F_{tree} , stem water flow; R_s , exchange resistance between xylem and storage compartment; R_x , xylem flow resistance; C , capacitance of storage compartment; E , transpiration rate; and W , water content of storage compartment.

water content is maximal.

The whole set of equations of the stomatal, photosynthesis, transpiration and sap flow model is solved numerically by an iteration procedure that converges to an equilibrium leaf water potential using the “golden section search” procedure (Press et al. 1996) for each time step and the leaf water potential of the previous time step as an initial estimate.

Storage calculation

The diurnal patterns of modeled transpiration and measured sap flow indicate that transpiration exceeds daytime sap flow and is less than nighttime sap flow (Figure 3a). The effect of taking account of nighttime transpiration is especially clear during nights with high VPD, when transpiration is considerable. The difference between measured sap flow and modeled transpiration is given in Figure 3b. Positive values indicate that water storage is being recharged. Negative values indicate that stored water is being used to fulfill the transpiration needs of the leaves. Each day, the use of stored water was estimated as the integrated area below the zero line. A similar storage use calculation was performed based on the modeled sap flow instead of the measured sap flow.

Model parameterization

Parameter values for the stomatal and storage model are listed in Table 2. Other parameter values (photosynthesis parameters, leaf area, stand structure) taken from Sampson et al. (2006), which are based on measurements at the Brasschaat site, were adopted where possible, otherwise values from the literature were used. The stomatal parameters describing the ABA response were taken from Tardieu and Davies (1993). Three parameters from the stomatal model (a_1 , D_0 , b) and three parameters of the storage model (C , R_s , R_x) were calibrated in this study. The variability in these parameters among different individual trees can be investigated by calibrating them separately for the individual Scots pine trees. To calibrate these parameters successfully, all fitted parameters must be identifiable.

To be identifiable, a parameter must fulfill two conditions: (1) the model output must be sufficiently sensitive to changes in the parameter value and (2) the parameters must not be highly correlated (Dochain and Vanrolleghem 2001, Brun et al. 2002). To test this identifiability, a sensitivity analysis was conducted on the six parameters. Based on a perturbation of 10%, a sensitivity measure of the model output for each of the six parameters and their correlations was determined, as described by Steppe et al. (2006). In case of highly correlated parameters, one of the parameters was given a fixed value, facilitating estimation of the other.

The sensitivity analysis resulted in the following ranking from high to low sensitivity: $R_s(49.92) > C(48.80) > R_x(48.29) > D_0(48.27) > a_1(47.42) > b(47.16)$. The values in parentheses measure the sensitivity of the model output to a change in a parameter. A high value indicates that the parameter has an important influence, a value of zero means that the simulation result does not depend on the parameter (Brun et al. 2002). The model was sufficiently sensitive to all six parameters, but there was considerable correlation between most parameters. Because of its relatively lower sensitivity, b was given an assumed value (Table 2). The highest correlations were found between a_1 and D_0 , between a_1 and R_s and between R_s and R_x (Table 3). In agreement with previous studies, C and R_x were correlated to some degree (Meinzer et al. 2003, Domec et al. 2005). Therefore assumed values were used for D_0 and R_s (Table 2). As explained in the model description, we assumed D_0 equaled 1. For R_s , only two literature values for conifers could be found: 0.0093 (*Picea sitchensis*; Milne and Young 1985) and 0.025 MPa s mg⁻¹ (general value for conifers; Hunt et al. 1991). Preliminary model tests indicated that these values did not result in satisfactory parameterizations of ANAFORE. Therefore, we assumed a lower value of 0.0013 MPa s mg⁻¹ for R_s . To calibrate parameters a_1 , C and R_x , the simplex method (Nelder and Mead 1965) was used to minimize the sum of squared errors for the variable F_{tree} .

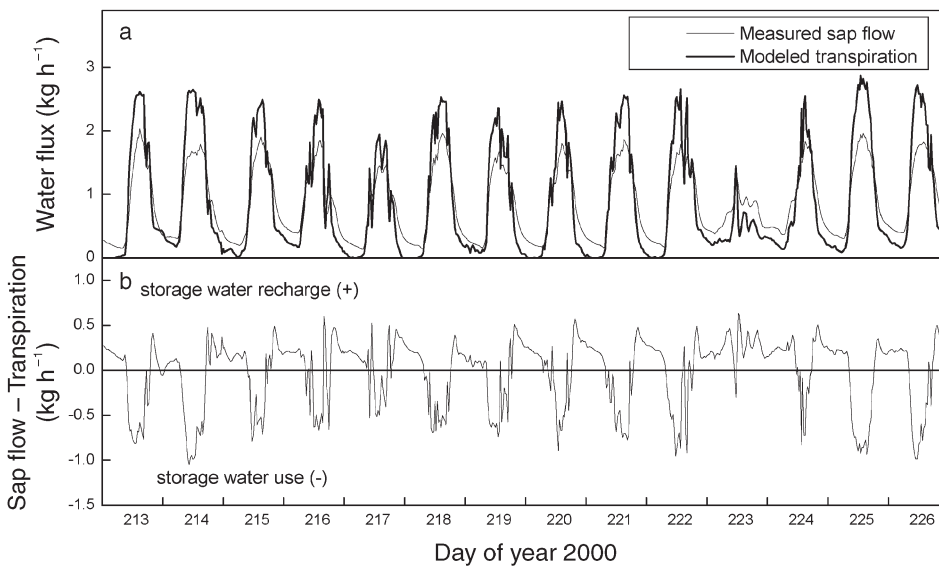


Figure 3. (a) Diurnal pattern of measured sap flow and modeled transpiration of an individual pine tree (No. 24) from August 1 to August 14, 2000. (b) Diurnal pattern of the difference between measured sap flow and modeled transpiration. The surface area between the negative values and the x-axis represents the daily use of stored water of the tree.

Table 2. Parameter values used for the stomatal and water storage models.

Parameter	Description	Value
a (mol H ₂ O m ⁻² s ⁻¹)	ABA sequestration rate	10 ⁻⁴ (Tardieu and Davies 1993)
a_1 (dimensionless)	Empirical constant (parameter combination)	Calibrated
C (mg MPa ⁻¹)	Capacitance of storage compartment	Calibrated
D_0 (kPa ²)	Empirical constant (parameter combination)	1.0 (assumed)
b (mol m ⁻² s ⁻¹)	Empirical constant	5.0 × 10 ⁻⁶ (assumed)
R_s (MPa s mg ⁻¹)	Hydraulic exchange resistance between xylem and storage compartment	0.0013 (assumed)
R_x (MPa s mg ⁻¹)	Xylem flow resistance	Calibrated
V_w (m ³ mol ⁻¹ H ₂ O)	Partial molal volume of water	18 × 10 ⁻⁶
β (m ³ mol ⁻¹ ABA)	ABA sensitivity parameter	1.48 × 10 ⁻⁴ (Tardieu & Davies, 1993)
δ (MPa ⁻¹)	ABA sensitivity parameter	-2 (Tardieu and Davies 1993)
λ_{root} (μmol MPa ⁻¹ m ⁻² s ⁻¹)	ABA synthesis constant of roots	4.0 × 10 ⁻⁶ (R. Dewar, INRA, Bordeaux, France, pers. comm.)
λ_{leaf} (μmol MPa ⁻¹ m ⁻² s ⁻¹)	ABA synthesis constant of leaves	1.0 × 10 ⁻⁶ (R. Dewar, INRA, Bordeaux, France, pers. comm.)

Sap flow data were available at a 15-min time step, but meteorological model inputs were available only at a 30-min time step. Therefore, the model parameters were estimated based on half-hourly sap flow data. The first two weeks of the dataset were chosen as the parameterization dataset (May 27–June 9). The rest of the dataset (June 10–October 18) was used to test the model performance.

Model performance

Goodness-of-fit of the model was evaluated first by comparing half-hourly values of modeled and measured sap flow and then by comparing modeled daily values of stored water use with stored water use calculated from modeled transpiration and measured sap flow. Both estimates of stored water use are not partially related, but as independent measurements of stored water use were unavailable for the measurement period, this approach provides an indication of the accuracy of the storage estimates. The explained variance (r^2), systematic and unsystematic mean squared errors (MSE_s and MSE_u) and the index of agreement (d) were calculated (Kramer et al. 2002, Müller et al. 2005). The model was evaluated based on these parameters because Wallach and Goffinet (1987, 1989) concluded that evaluation of models should not be based on R^2 values alone, but also on the analysis of mean squared errors (MSE). The use of MSE makes it possible to discriminate between

systematic MSE_s and MSE_u. Another parameter used for model evaluation was the index of agreement d (Willmott 1981). Values of the index range from $d = 1$ for perfect agreement, to $d = 0$ for no agreement between predicted and observed values.

Results

Model performance

Modeled sap flow could be fitted closely to the measured sap flow during the calibration period (Figure 4). The fitted parameter values for each tree are given in Table 4. The model simulated measured sap flow well under microclimatic conditions that differ from the calibration period (Figure 5). Overall, the model results were in good agreement with the sap flow measurements for all sample trees (Figure 6, Table 5). The regression line between modeled and measured sap flow for each tree was always close to the 1:1 line, and the explained variance (R^2) ranged from 0.76 to 0.88. The MSE_s values were low compared with the MSE_u values (Table 5). Low MSE_s values indicate that our model simulations of sap flow were not biased in a systematic way and, thus, probably did not lead to large discrepancies between measured and modeled water fluxes. An index of agreement (d) of 0.93 or more (Table 5)

Table 3. Correlation matrix of the six parameters that were taken into consideration for calibration: a_1 , D_0 , b (empirical constants of stomatal model), C (capacitance of storage compartment), R_s (storage resistance) and R_x (xylem flow resistance).

	a_1	D_0	b	C	R_s	R_x
a_1	1	0.62	0	0	0.44	0.26
D_0	0.62	1	0.16	0.02	0.18	0.10
B	0	0.16	1	0.05	0.01	0.05
C	0	0.02	0.05	1	0.10	0.27
R_s	0.44	0.18	0.01	0.10	1	0.38
R_x	0.26	0.10	0.05	0.27	0.38	1

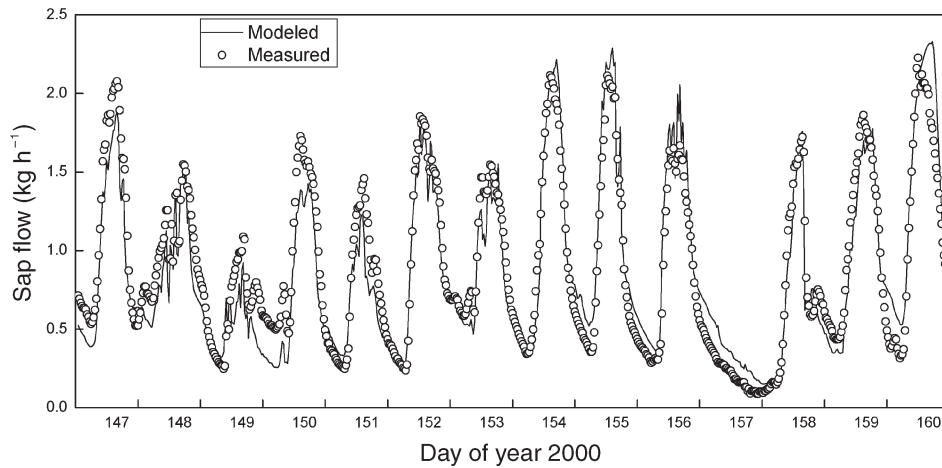


Figure 4. Measured and modeled sap flow rates of an individual pine tree (No. 16) for the parameterization period from May 27 to June 9, 2000.

indicates a high agreement between the model and the data (d can be interpreted as an improved version of r^2 ; Willmott 1981).

Simulated daily stored water use was compared with stored water use calculated from the modeled transpiration and the measured sap flow (Figure 6, Table 5). Although the explained variances (R^2 range: 0.65–0.85) were lower and errors were significantly higher than the variances obtained for the sap flow simulations, we found a substantial agreement between the two approaches for estimating stored water use (d range: 0.84–0.94). Moreover, the MSE_s values were low compared with the MSE_u values (Table 5). Nevertheless, Figure 6b indicates that the high modeled stored water use values are underestimated, which points to a systematic bias between measured and modeled sap flow on days with high stored water use, possibly caused by inaccuracies in the diurnal patterns of modeled transpiration. Unfortunately, the diurnal patterns of transpiration could not be validated, because of the lack of in-

dependent measurements of leaf-level transpiration. We can conclude, however, that the extreme values of water storage use should be interpreted with care.

The seasonal pattern of the daily sums of measured sap flow and modeled transpiration show close agreement (Figure 7a), although differences occurred on some days. It is evident that modeled daily sap flow is closely related to modeled transpiration ($r^2 = 0.98$) (Figure 7 inset). Moreover, the close relationship between measured daily sap flow and modeled daily transpiration ($r^2 = 0.85$) is a strong indication that the daily transpiration estimates are reliable. Absolute stored water use (Figure 7a) was higher in summer and lower in winter, whereas relative stored water use (Figure 7b) did not show any seasonality.

Stored water use versus tree size

We analyzed stored water use calculated from the difference between measured sap flow and modeled transpiration in detail. In absolute terms, daily transpiration and stored water use are determined by tree size (Figure 8). Maximum use of stored water during the study period ranged from 6 kg day⁻¹ for the smallest trees to 16 kg day⁻¹ for the largest trees.

Across all trees, the use of stored water ranged between less than 1% and 44% of their daily transpiration. All trees showed the same pattern: the higher the transpiration rate, the more water a tree used from the storage pools. Although we predicted that the use of stored water would reach a maximum at a certain point, this was not observed (Figure 8). In absolute terms, larger trees had a higher maximum stored water use than smaller trees because of a higher absolute transpiration rate as a result of a higher leaf area. The onset of substantial use of stored water occurred at higher transpiration rates in larger trees than in smaller trees. The finding that larger trees can transpire more without using stored water, may reflect a larger water uptake capacity of the root system. At the tree level, smaller trees need more stored water to transpire as much as a large tree. Expressed per unit leaf area, however, we observed no differences in maximum daily transpiration among trees (Figure 9), nor did we observe differences in

Table 4. Calibrated values for parameters a_1 (empirical constant of stomatal model), C (capacitance of storage compartment) and R_x (xylem flow resistance) for different trees based on two weeks of sap flow data (May 27–June 9, 2000).

Tree No.	a_1	C (10^6 mg MPa ⁻¹)	R_x (MPa s mg ⁻¹)
11	3.73	23.7	0.00150
12	4.38	32.9	0.00129
13	4.45	50.5	0.00172
14	3.89	43.5	0.00167
15	2.17	69.0	0.00139
16	2.24	37.8	0.00147
17	3.25	46.5	0.00178
21	3.13	48.6	0.00156
22	3.07	34.4	0.00182
23	2.04	51.7	0.00090
24	1.34	38.4	0.00097
25	1.42	54.5	0.00099
26	1.59	49.1	0.00083
27	2.63	55.6	0.00179

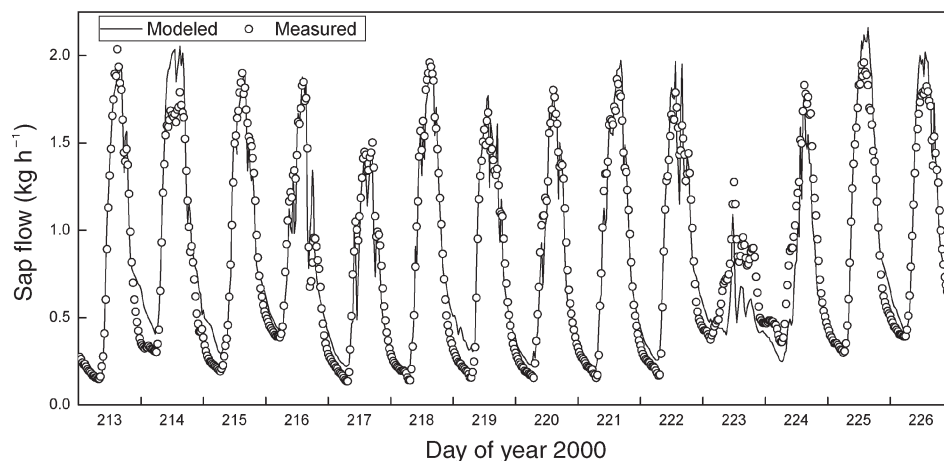


Figure 5. Measured and modeled sap flow rates of an individual pine tree (No. 24) from August 1 to August 14, 2000 during the validation period.

stored water use per unit leaf area between the smaller and larger trees.

To illustrate the relationship between stored water use and tree size, we compared the 14 sample trees on four days exhibiting a large range in daily transpiration. For all trees, more stored water was used on days with higher transpiration. Di-

ameter at breast height, sapwood area and leaf area were significantly correlated with stored water use (Figures 10a, 10c and 10d). The slope of the linear relationships between stored water use and these tree characteristics became steeper on days with higher transpiration, suggesting greater stored water use in larger trees (Figure 10a). In contrast, no significant relationship between stored water use and tree height was observed (Figure 10b).

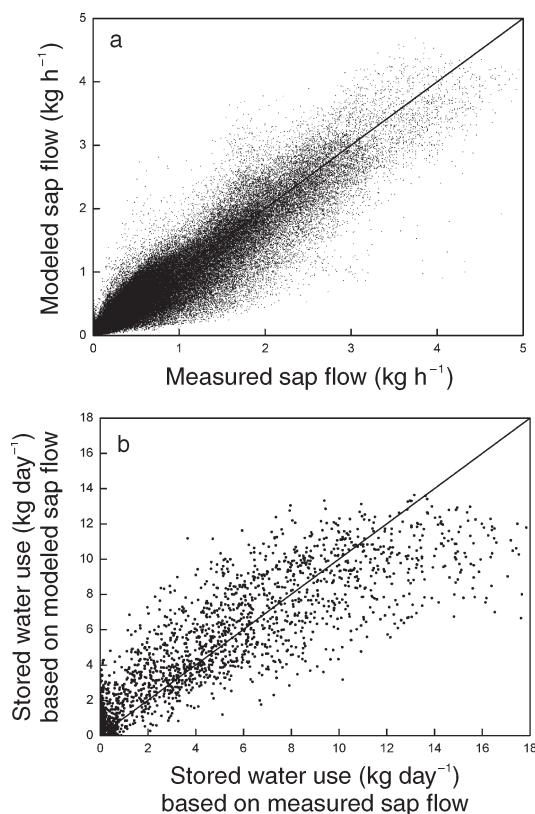


Figure 6. Scatter plots for 14 pine trees for the validation period from June 10 to October 18, 2000. The solid line represents the 1:1 line. Explained variances (r^2) for each tree are given in Table 5. (a) Scatter plot of measured and modeled half-hourly sap flow. (b) Scatter plot of calculated daily stored water use based on measured and modeled sap flow.

Discussion

Model performance

Our results show that the incorporation of a water flow model in ANAFORE made it possible to simulate diurnal patterns of sap flow in individual trees quite precisely, and demonstrates the usefulness of coupling a process-based transpiration model to a sap flow model. Diurnal modeled transpiration simulations could not be compared with independent transpiration measurements at the tree scale. Nonetheless, on longer time scales, sap flow becomes a good validation for transpiration and, on a daily scale, simulated transpiration and measured sap flow were in good agreement.

When evaluating a model, it is important to check if the estimated parameter values are realistic. The fitted parameter a_1 of the stomatal model ranged from 1.34 to 4.45 for different individual trees. Literature values with which to compare these values are scarce. Uddling et al. (2005) reported a value of 7.99 for birch and Dewar (2002) reported a value of 6. Although this estimated parameter value falls within the expected range, we cannot learn much from this parameter, because it is a combination of unknown factors (related to turgor pressure and mechanical influence of the guard cells and leaf epidermis) and has no physiological meaning (Dewar 2002).

The estimated values of R_x ranged from 0.00083 to 0.00182 MPa s mg^{-1} . The xylem resistance of the entire tree (ranging from 0.00166 to 0.00364 MPa s mg^{-1}) is twice the value of R_x , because two resistances in series were considered in the water flow model (Figure 2). A wide range of published values of xylem resistance or conductance can be found in dif-

Table 5. Performance of the ANAFORE model in predicting sap flow and stored water use for 14 individual pine trees from June 10 to October 18, 2000. Statistical criteria of the regression of modeled versus measured values: coefficient of determination (r^2), systematic (MSE_s), unsystematic (MSE_u) and total (MSE) mean square error, and the agreement index (d). All r^2 values are significant ($P < 0.0001$).

Tree No.	Half-hourly simulations of sap flow ($n = 6960$)					Daily simulations of storage water use ($n = 145$)				
	r^2	MSE_s	MSE_u	MSE	d	r^2	MSE_s	MSE_u	MSE	d
11	0.85	0.056	0.152	0.208	0.95	0.70	1.55	10.38	11.93	0.89
12	0.87	0.017	0.150	0.167	0.97	0.72	1.94	10.90	12.84	0.90
13	0.76	0.025	0.153	0.179	0.93	0.69	4.92	32.35	37.27	0.84
14	0.82	0.025	0.118	0.142	0.95	0.76	1.65	9.61	11.26	0.92
15	0.79	0.002	0.078	0.081	0.94	0.79	2.09	14.26	16.35	0.87
16	0.86	0.000	0.049	0.050	0.96	0.81	1.04	6.39	7.43	0.91
17	0.82	0.005	0.098	0.103	0.95	0.85	1.23	7.17	8.40	0.94
21	0.81	0.050	0.117	0.167	0.97	0.74	1.99	11.67	13.65	0.90
22	0.81	0.011	0.091	0.101	0.95	0.75	1.31	7.52	8.83	0.91
23	0.85	0.004	0.076	0.080	0.96	0.71	1.02	6.30	7.32	0.87
24	0.85	0.003	0.041	0.044	0.96	0.65	0.56	3.44	4.00	0.85
25	0.86	0.001	0.037	0.037	0.96	0.73	0.62	3.92	4.54	0.87
26	0.88	0.000	0.028	0.028	0.97	0.70	0.48	3.29	3.77	0.84
27	0.82	0.012	0.066	0.078	0.95	0.78	1.00	5.97	6.97	0.92

ferent units. Recalculated to MPa s mg^{-1} , reported values for different tree species range from 0.00016 to 0.6 MPa s mg^{-1} (0.001 to 0.6 MPa s mg^{-1} for Scots pine) (Milne and Young 1985, Hunt et al. 1991, Mencuccini and Grace 1994, Becker et al. 1999, Domec et al. 2005, 2006, Meinzer et al. 2006, Steppe et al. 2006). Thus, our estimated values for R_x fall well within this range.

Fitted parameter values for C ranged from 23.7×10^6 to $69.0 \times 10^6 \text{ mg MPa}^{-1}$ (Table 4). Comparison with literature values is difficult because there is little agreement about the units of C (Aumann and Ford 2002). Reported values for coniferous species range from 0.17×10^6 to $2.1 \times 10^6 \text{ mg MPa}^{-1}$ (Milne and Young 1985, Wronski et al. 1985, Hunt et al. 1991, Kobayashi and Tanaka 2001). Compared with these values, all our esti-

mated values for Scots pine are an order of magnitude higher. This discrepancy might be caused by different approaches for measuring capacitance. Most literature values give the capacitance of the stored water pool in the stem, whereas our modeling approach determines the overall capacitance of a storage pool that includes water storage in the xylem and phloem of the stem as well as the water storage in twigs and needles.

For ecological models, the need to represent mechanisms implies that over-parameterization and poor identifiability are common (Medlyn et al. 2005). In general, fitted parameter values are uncertain to some degree. The fitted parameters in Table 4 can be considered as the optimal fit using the available data, but different parameterizations may lead to an equally good fit. In our study, the capacitance was a typical example of

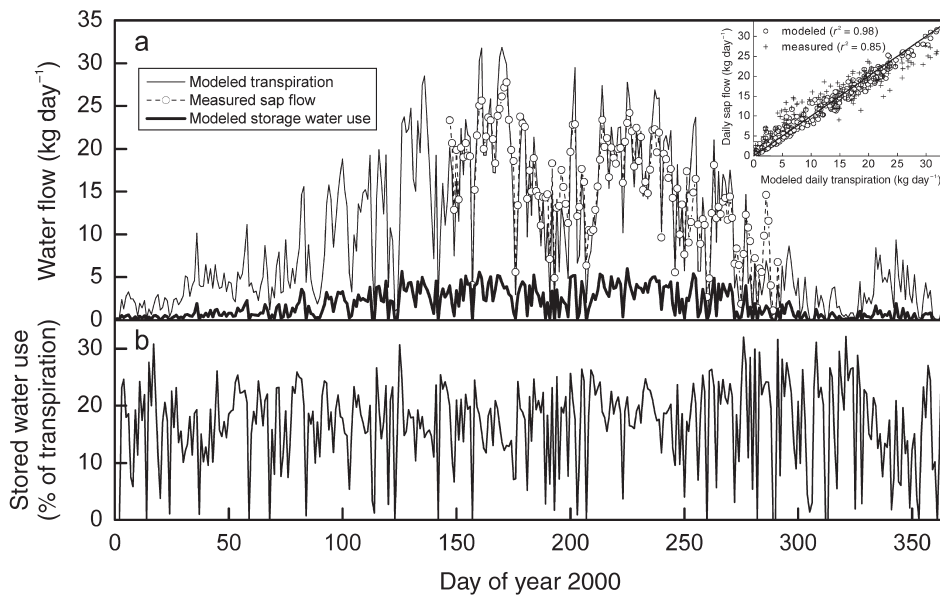


Figure 7. (a) Seasonal pattern of modeled transpiration, measured sap flow and the modeled stored water use of an individual pine tree (No. 25). The inserted scatter plot shows a close correspondence between measured daily sap flow and modeled daily transpiration ($r^2 = 0.85$). The scatter of the modeled sap flow versus modeled transpiration is even closer to the 1:1 line ($r^2 = 0.98$). Differences between daily transpiration and daily sap flow occur when there is a net depletion or refilling of the stored pool during that day. (b) Seasonal pattern of the modeled daily stored water use relative to the transpiration (Tree No. 25).

such an equifinality problem. Whole stem or tree capacitance varies with time, space and water tension (Jarvis et al. 1981, Čermák et al. 1982) and is difficult to measure (Holbrook 1995). Therefore, no firm conclusions about capacitance could be derived. Soil-to-leaf hydraulic resistance varies among trees and seasons (Fisher et al. 2006). Modeling these dynamics is a challenge and is well beyond the scope of this paper.

Stored water use

Use of stored water minimizes temporal imbalances between water supply and demand in trees (Goldstein 1998). Our results show that stored water use is concentrated during the day when conditions are most favorable for photosynthesis. The clear pattern of higher transpiration than sap flow during the day and lower transpiration during the night (Figure 3a) indicates that water flow through the stem rarely reached steady state conditions. This means that there were no periods when transpiration and sap flow were equal.

Nocturnal transpiration may prevent complete recharge of internal water storage pools and, consequently, limit the supply of water at the beginning of the next day (Donovan et al. 2003). Moreover, nighttime stomatal opening may result in negative effects such as ozone damage (Musselman and Minnick 2000). Nonetheless, despite these potential negative effects of nighttime transpiration, it may also provide trees with an ecological advantage by enabling them to maximize photosynthesis early in the morning when VPD is still low, increasing their water-use efficiency (Daley and Phillips 2006). The occurrence of substantial nighttime transpiration may thus play an important role and should be included in stomatal models.

Throughout simulation period, relative stored water use of

the Scots pine trees ranged from less than 1% up to 44% of the daily transpiration. On several days when simulated transpiration did not exceed sap flow, stored water use was close to zero. On these days, storage pools were refilled. For pine trees, it was reported that stored water contributes from 10 to 50% to daily transpiration (Waring et al. 1979; Loustau et al. 1996). Literature values for other coniferous trees range from 2 to 65% (Tyree 1988, Tyree and Yang 1990, Kobayashi and Tanaka 2001, Zweifel and Häsler 2001, Meinzer et al. 2001, Zweifel et al. 2001). Most of these studies consider water stored in the stem tissues only. However, at the tree level, the contribution of stored water is even higher because twigs and needles can also act as storage organs. In our study, the water storage compartment comprised the stem, the twigs and the needles.

The finding that the relative use of stored water varied significantly over time for a single tree is an important indication that the contribution of the internal water storage is not a fixed parameter in the water budget of trees. Loustau et al. (1996) previously reported that stored water in *Pinus pinaster* accounted for 12% of the daily water loss when soil water was abundant, but this amount increased to 25% during a period of drought. On days with higher transpiration, our study trees were more dependent on stored water. Thus, not only drought (Loustau et al. 1996, Phillips et al. 2003), but also a high atmospheric demand increases the dependence on stored water on a diurnal time scale.

There was a clear relationship, which was stronger on days with high transpiration rates, between absolute stored water use (Figure 10) and several tree dimensions (DBH, sapwood area, leaf area), as previously observed by Goldstein et al. (1998) in a study on five tropical tree species. In that study, water storage use increased exponentially with tree height for five

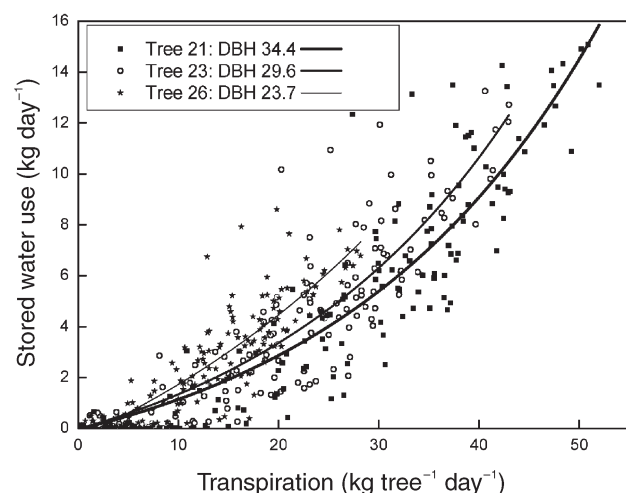


Figure 8. Daily stored water use as a function of the total daily transpiration. Three examples are shown for individual pine trees, covering the entire range of DBH (diameter at breast height) of all sample trees. Other trees showed similar patterns (data not shown for clarity). The thickness of the fitted curves corresponds to the DBH. The explained variance (r^2) for the fitted curves is 0.84 (Tree 21), 0.80 (Tree 23) and 0.75 (Tree 26).

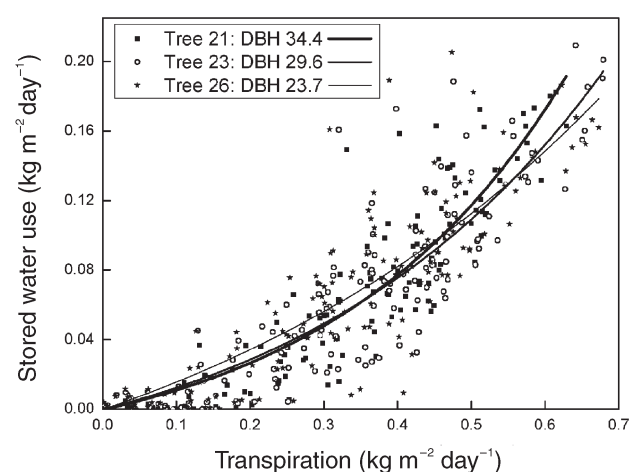


Figure 9. Daily stored water use as a function of the total daily transpiration, both on a leaf area basis. Three examples are shown for individual pine trees, covering the range of diameter at breast height (DBH) of all sample trees. Other trees showed similar patterns (data not shown for clarity). The thickness of the fitted curves corresponds to the DBH. The explained variance (r^2) for the fitted curves is 0.84 (Tree 21), 0.80 (Tree 23) and 0.75 (Tree 26).

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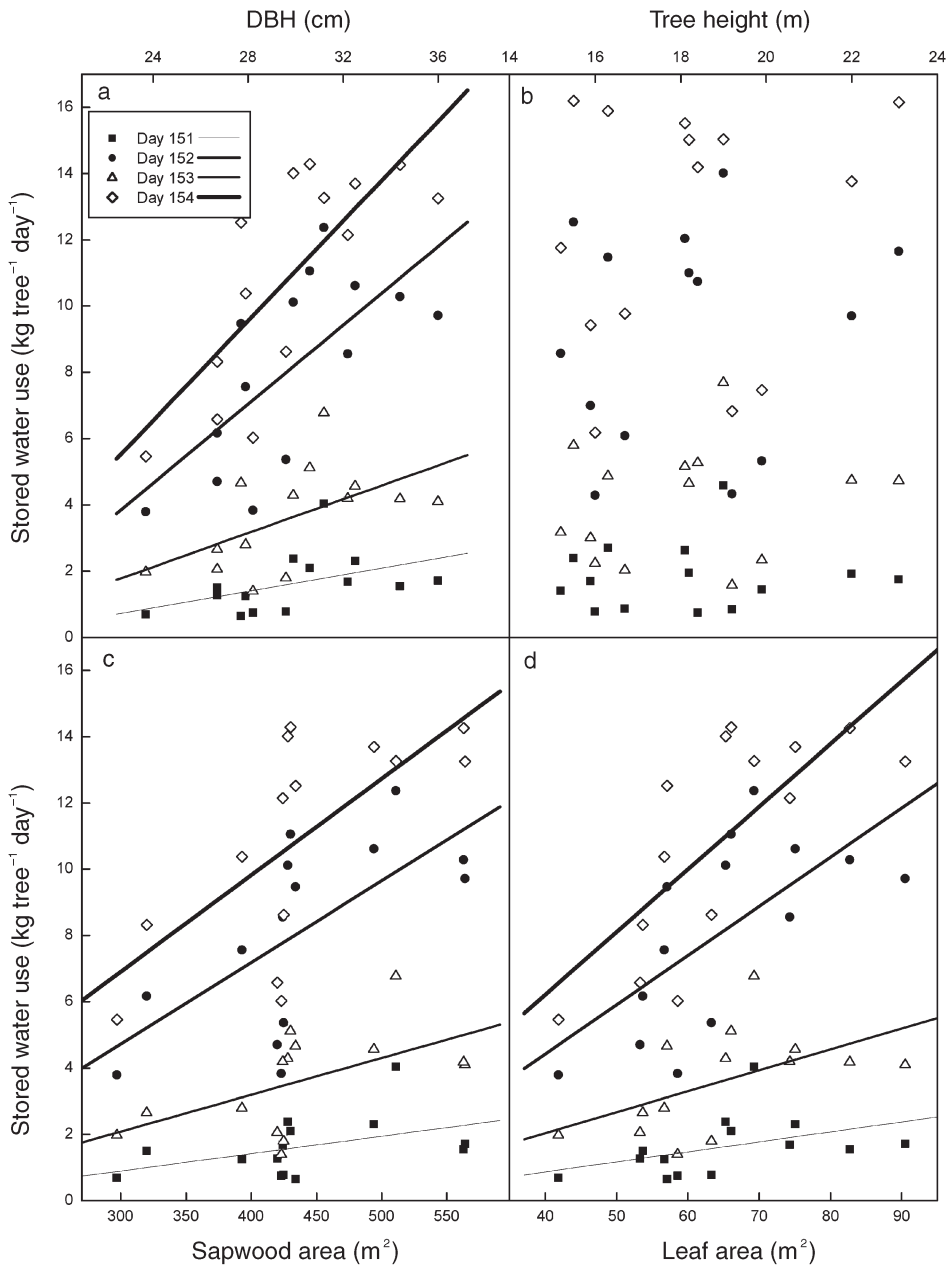


Figure 10. Daily stored water use as a function of tree size: (a) diameter at breast height (DBH); (b) height; (c) sapwood area; and (d) leaf area; plotted for 14 individual pine trees on 4 days varying in transpiration rate. Other days showed similar relationships (data not shown for clarity). The thickness of the fitted curves corresponds to the total daily transpiration rate. Fitted curves showed a significant ($P < 0.05$) relationship with DBH, sapwood area and leaf area. No significant linear relationships were observed between stored water use and tree height ($P > 0.05$).

tropical tree species, with stored water use ranging from 4 kg day⁻¹ in a 0.20-m diameter *Cecropia longipes* to 54 kg day⁻¹ in a 1.02-m diameter *Anacardium exelsum*, representing 9–15% of the total daily water loss. Goldstein et al. (1998) concluded that tree size rather than species was the most important determinant of diurnal water storage. Similarly, Perämäki et al. (2005) concluded that tree size, especially tree height, is the main factor explaining the time lag between water flux at the leaf level and water flux at breast height. In contrast, we found no clear effect of tree height of the Scots pines on their stored water use, although we found correlations with DBH, sapwood volume and leaf area (storage in twigs and needles). Because the stand we studied is even-aged, the small range in tree height (15–23 m) probably precluded a clear

height effect. Phillips et al. (2003) calculated stored water use for several tree species with a much greater height range and found a clear influence of height: e.g., a Douglas fir of 15 m had a mean storage use of 7%, whereas a Douglas fir of 60 m used 25% on average.

The differences in stored water use by individual trees might influence the variation in leaf-level measurements of transpiration and stomatal conductance in different trees. Goldstein et al. (1998) concluded that water storage capacity must be taken into account when comparing the behavior among individuals of different and even the same species, because differences in stomatal regulation of transpiration may reflect differences in water storage rather than other traits.

To conclude, the incorporation of a water flow model in

ANAFORÉ resulted in accurate model predictions of diurnal patterns and one seasonal pattern of sap flow. The next step in the development of the model will be a more detailed analysis of the seasonal pattern of stored water use and of the water flow model parameters. Such an analysis can reveal the effects of microclimate and drought on the model parameters. Taking into account seasonal changes in the storage parameters could further improve the estimates of stored water use. Inclusion of nighttime stomatal conductance proved to have an important influence on stored water recharge during the night and is thus useful to take into account in models. The combination of ANAFORÉ with sap flow measurements provides interesting possibilities for calculating water storage in individual trees. Stored water use was found to vary among trees and over time (up to 44% of daily transpiration). Among trees, stored water use increases with DBH, sapwood area and leaf area of the individual tree.

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