

# Modeling water transportation and storage in sapwood — model development and validation

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## Abstract

I have described a single tree water flux model that combines the stomatal conductance model based on plant physiological knowledge with the concept of fluid mechanics used to describe water transportation and storage in sapwood. The model was parameterized and validated using field data of the water budget of *Cryptomeria japonica* [J. Jpn. For. Soc. 78 (1996) 66] determined by weighing a suspended cut tree. In their experiment, water transportation and storage in the sapwood and leaves and the sapwood potential were examined under ordinary conditions and extreme conditions where water uptake was stopped by sealing the cut stem surface. Numerical experiments show the information to reproduce the observed results: low intensity of stomatal response to decreasing leaf water potential and lower hydraulic conductance of the crown sapwood than the conductance of the trunk sapwood. The model reproduced the observed results under both ordinary and extreme conditions using only information of observed physical size and hydraulic properties, except for the information on low values of hydraulic conductance of the crown sapwood. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Numerical model; Water budget of single tree; Transpiration; Sap flow; Uptake; Water storage

## 1. Introduction

A reliable representation of air–land processes is necessary to increase the understanding of global and regional environmental changes caused by land use and climate change. How the available energy is partitioned between sensible and latent heat fluxes at the air–land interface is an important problem. Vegetation, in particular, covers a major part of the land surface and promotes latent heat exchange as a result of transpiration. Therefore, investigating the energy exchange over a vegetated surface is essential because vegetation exerts a large influence on global and regional climate.

So-called soil–plant–atmosphere continuum (SPAC) models have been used to solve the problem. “Plant” in these models has often been regarded as a simple pathway of water flow. However, the contributions of stored water in plants to transpiration have gradually been recognized and have been considered in the surface energy balance (e.g. Carlson and Lynn, 1991; Hunt et al., 1991; Cienciala et al., 1994; Kravka et al., 1999). The sapwood in Douglas-fir serves as a major reservoir of water and contributes about 17% to the daily transpiration stream (Waring and Running, 1978). Waring et al. (1979) suggested that 30–50% of the transpired water is extracted from water stored in the stem sapwood in Scots pine. The total amount of available water storage is 24 and 14% of the total daily transpiration in larch and spruce, respectively (Schulze et al., 1985). The ecophysiological

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importance of the water storage capacity of trees is that it may influence the ability of the plant to continue photosynthesis and growth despite temporary drought conditions (Ewers and Cruiziat, 1991). Plants use the stored water to keep stomata open and maintain transpiration when soil moisture is limited or atmospheric demand increases. The amount of water stored in the trunk includes 12% of the daily transpiration in spring, but the trunk storage increases to 25% of the daily transpiration at the end of summer under drought conditions (Loustau et al., 1996). Stored water modifies transpiration fluxes and has a marked effect on the surface energy budget during periods of plant water stress, and the water storage capacity has little effect in small plants (Carlson and Lynn, 1991).

The plant has a reservoir of easily available water that is supplied through uptake and is consumed by transpiration. The water potential in the plant depends on the relationships between the capacitance and the easily available water stored in the plant. The fundamental driving force of water uptake and transportation in the plant is the water potential; accordingly, to represent easily available water stored in the plant the water transportation and storage in the plant should be described in terms of the water potential.

As the equation of water flow through the SPAC resembles that of electrical flow in a conducting system, it is often termed the Ohm's law analogy. This model, which is composed of a series of resistances, can be applied to plants with negative and positive water potential. Although very convenient for analyzing the way in which various factors affect water flow through the SPAC, Ohm's law analogy is an oversimplification because it assumes steady-state flow and constant resistance, conditions that seldom exist (Kramer and Boyer, 1995). Trees, in particular, can store a large volume of water because of their physical size and differences exist in the water flow out of and into a plant organ. Therefore, a non-steady-state model must be used to predict diurnal variations of water uptake and water potential, and a physically based model should be used to analyze the internal process in the plant of uptake and transpiration.

In this study, I described a single tree water flux model that combines the stomatal conductance model based on plant physiology with the concept of fluid mechanics that is used to describe water transportation and storage in sapwood. Non-steady-state diffusivity

equations are valuable because they describe the relationship between three quantities: (1) volume flow, (2) time lag between transpiration stream and uptake, and (3) pressure gradient. Therefore, I used diffusivity equations to represent water flow through the tree stem. Some studies have made models using diffusivity equations that include the water flow from uptake to transpiration (Ishida, 1985; Kanda and Hino, 1990). However, they chose small plants as the subject of study and the model that they made was insufficient to describe the mechanism of water storage in sapwood. Also, some studies validate the model describing water budget in a single plant body, especially in a single tree body. This study aimed to describe a model that may be used as a submodel in the SPAC model for forests and to show its validity and its response to the changes in model parameters having physical meaning in relation to water flow through sapwood.

## 2. Numerical model

### 2.1. Concept

I used the tree examined by Takizawa et al. (1996) as the tree model in this study. The trunk of the tree was cut under water and was placed in a container of water. Hence, uptake resistance of the root system did not exist. Johnson et al. (1991) pointed out that a principal objection to using leaf water potential as an index of control of stomata is that leaves can detect root water stress when the leaf water potential is less negative (i.e. close to 0), and close their stomata accordingly. Therefore, as the roots of the sample tree were excised, the leaf water potential would have influenced their stomatal aperture. Water flux in the system can be represented as an integration of four components: (1) the atmospheric demand and stomatal behavior, (2) the controls upon the water flow rate from one part of the system to another, (3) uptake and (4) internal storage.

The rate of transpiration depends on the leaf boundary layer conductance, mainly influenced by wind speed, and the stomatal conductance determined by stomatal aperture, which is influenced by many environmental factors, such as radiation, temperature, humidity and water status in the plant. A water deficit in the leaf caused by the transpiration lowers its water potential, causing water to move from the xylem

to the evaporating cells in the leaf. This reduces the tension or pressure in the xylem sap and produces a water potential gradient in the cohesive hydraulic system of the tree. This pressure is transmitted to the bottom of the trunk where water uptake occurs. In this model, the wood trunk was treated as a porous or a capillary-tube medium, and water flow through the sapwood was represented as the movement through a capillary-tube according to the gradient of pressure and the hydraulic conductivity.

The difference in the water flow out of and into a plant organ must come from or go into internal plant storage. Zimmermann (1983) proposed that mechanisms involved in water storage in trees are capillarity, cavitation and elasticity of tissues. However, Brough et al. (1986) pointed out that in the above mechanisms capillarity determines the greater part of diurnal change of water storage in sapwood. In my model, according to Brough et al. (1986), tiny spaces in the wood of trees that are intercellular spaces and spaces inside non-living fibers can be filled with water because of capillary action.

## 2.2. Model description

The flow equation governing the unsteady water flow through a tree stem with absorption is expressed by the following equation:

$$\left[ \int_z^{z+\Delta z} S_p(z) dz \right] C_p \frac{\partial \psi_p}{\partial t} = -\frac{\partial q}{\partial z} \Delta z - Q(z) \quad (1)$$

where  $z$  is the height from water surface (m),  $t$  the time (s),  $\psi_p$  the water potential in the sapwood (m),  $S_p(z)$  the cross-sectional area (m<sup>2</sup>) of the stem at the height of  $z$ ,  $C_p$  the capacitance of sapwood (m<sup>-1</sup>),  $q$  the flow rate (m<sup>3</sup> s<sup>-1</sup>) of sap and  $Q(z)$  is the sap flow rate (m<sup>3</sup> s<sup>-1</sup>) from trunk to branch.  $S_p(z)$  is expressed as

$$S_p(z) = \pi d^2 \left(1 - \frac{z}{h}\right)^2 \quad (2)$$

where  $d$  is the radius of the stem (m) at water surface and  $h$  is the tree height (m). Eq. (2) indicates that the shape of stem is assumed to be a cone. Volumetric water content  $\theta_p$  in the stem (m<sup>3</sup> m<sup>-3</sup>) is given by

$$\theta_p = a - b \ln(-\psi_p) \quad (3)$$

as given by Takizawa et al. (1996), where  $a$  and  $b$  are the fitted parameters. Therefore, the capacitance of sapwood  $C_p$  can be obtained as follows:

$$C_p = \frac{d\theta_p}{d\psi_p} = -\frac{b}{\psi_p} \quad (4)$$

The flow rate of sap  $q$  is assumed to flow in all cross-sectional areas of the stem:

$$q = -K_p S_p(z) \left( \frac{\partial \psi_p}{\partial z} + 1 \right) \quad (5)$$

where  $K_p$  is the hydraulic conductivity in sapwood (m s<sup>-1</sup>) when sap is assumed to flow in all cross-sectional areas of the stem. Because sap only really flows through tracheids or vessels, the real hydraulic conductivity  $K'_p$  (m s<sup>-1</sup>) is expressed by

$$K'_p = K_p \frac{S_p(z)}{S_t(z)} \quad (5')$$

where  $S_t(z)$  is the cross-sectional area (m<sup>2</sup>) of the tracheid or vessel at the height of  $z$ . As  $Q(z)$  is 0 at the height where neither foliage nor branch exist, it is expressed by the following functions with respect to clear length  $l_c$  (m):

$$Q(z) = \begin{cases} \frac{S_b(z)(\psi_p - \psi_1)}{r_f}, & \text{for } z \geq l_c \\ 0, & \text{for } z < l_c \end{cases} \quad (6)$$

where  $S_b(z)$  is the total cross-sectional area (m<sup>2</sup>) of the branch at height  $z$ ,  $\psi_1$  the leaf water potential (m) and  $r_f$  is the xylem resistance (s) for a branch.

Water balance in the foliage is expressed by the following equation, which is the top boundary condition for water flow:

$$S \Delta z \alpha(z) k C_l \frac{\partial \psi_1}{\partial t} = Q(z) - \frac{1}{\rho_w} S \Delta z \alpha(z) E(z) \quad (7)$$

where  $S$  is the projected crown area (m<sup>2</sup>),  $\alpha(z)$  the leaf area density (m<sup>2</sup> m<sup>-3</sup>) at height  $z$ ,  $k$  the leaf thickness (m),  $C_l$  the capacitance of a leaf (m<sup>-1</sup>) and  $\rho_w$  is the density of liquid water (kg m<sup>-3</sup>).  $E(z)$ , the transpiration rate (kg m<sup>-2</sup> s<sup>-1</sup>) for a leaf area at height  $z$ , can be expressed by a bulk transfer equation as follows:

$$E(z) = \rho_a c_e(z) u(z) \{q_s(T_1(z)) - q_a(z)\} \quad (8)$$

where  $\rho_a$ ,  $c_e(z)$ ,  $u(z)$ ,  $T_1(z)$  and  $q_a(z)$  are the density of air (kg m<sup>-3</sup>), the bulk transfer coefficient for latent

heat, wind speed ( $\text{m s}^{-1}$ ), leaf temperature (K) and specific humidity ( $\text{kg kg}^{-1}$ ), respectively.  $q_s(T_1)$  is the saturation specific humidity ( $\text{kg kg}^{-1}$ ) at temperature  $T_1$ .  $c_e(z)$  can be expressed by the following function for the bulk transfer coefficient for sensible heat  $c_h$  and the stomatal conductance  $g_{\text{sw}}$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ):

$$c_e(z) = \frac{c_h}{1 + c_h(\rho'_a/g_{\text{sw}})u(z)} \quad (9)$$

where  $\rho'_a$  is the density of air ( $\text{mol m}^{-3}$ ). Based on an improved version of the model proposed by Jarvis (1976),  $g_{\text{sw}}$  can be described by the following multiplication form of each individual function of PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), leaf temperature  $T_1$  (K), vapor pressure deficit VPD (kPa) and leaf water potential  $\psi_1$  (m) (Kosugi et al., 1995; Yu et al., 1996):

$$g_{\text{sw}} = g_{\text{sw max}} f_1(\text{PAR}) f_2(T_1) f_3(\text{VPD}) f_4(\psi_1) \quad (10)$$

where  $f_1$ ,  $f_2$ ,  $f_3$  and  $f_4$  all have the value from 0 to 1.  $g_{\text{sw max}} f_1(\text{PAR})$  and  $f_2(T_1)$  are expressed by the following functions proposed by Jarvis (1976):

$$g_{\text{sw max}} f_1(\text{PAR}) = \frac{g_{\text{sw max}} \text{PAR}}{\text{PAR} + g_{\text{sw max}}/a_s} \quad (11)$$

$$f_2(T_1) = \left( \frac{T - T_n}{T_o - T_n} \right) \left( \frac{T_x - T}{T_x - T_o} \right)^{(T_x - T_o)/(T_o - T_x)} \quad (12)$$

where  $g_{\text{sw max}}$  is the maximum stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  $a_s$  is the parameter representing the efficiency of opening stomata by the energy of light.  $T_x$ ,  $T_n$  and  $T_o$  are the maximum temperature, the minimum temperature and the optimum temperature for opening stomata, respectively.  $f_3(\text{VPD})$  is expressed by the following function proposed by Kosugi et al. (1995):

$$f_3(\text{VPD}) = \frac{1}{1 + b_d \text{VPD}} \quad (13)$$

where  $b_d$  is the parameter representing the response of closing stomata to increasing vapor pressure deficit.  $f_4(\psi_1)$  is expressed by the following function proposed by Mascart et al. (1991):

$$f_4(\psi_1) = \frac{1}{1 + (\psi_1/\psi_c)^2} \quad (14)$$

where  $\psi_c$  is the parameter representing the intensity of the response of closing stomata to decline in leaf water potential.

In this study a value-specified boundary condition was used for the bottom boundary condition for water flow. As  $z = 0$  represents water surface, the following equation can be obtained:

$$\psi_p|_{z=0} = 0 \quad (15)$$

The governing Eq. (1) is solved using Eqs. (2)–(15) and the water potential in the sapwood  $\psi_p$  is obtained. During the calculations, water uptake rate, sap flow rate, transpiration rate and leaf water potential also can be obtained. A finite difference method was used for the numerical calculations. With space steps and time steps, the control volume method (Patankar, 1980), where the infinitesimal control volume is defined at each node, and the implicit difference method that uses a modified Picard method (Celia et al., 1990) as an iteration method were used, respectively.

### 3. The data

To validate the model, I used the data set of the water budget of *Cryptomeria japonica* measured by Takizawa et al. (1996). They cut the trunk of the tree under water and placed the bases of the trunk in a container of water while the tree top was supported in its normal position in the canopy. The whole tree without roots was suspended and was weighed continually, and water uptake was measured by decreasing water in the container. The water potential of the leaf at the tree top and in the sapwood at the height of a clear length were measured continually using a pressure chamber (e.g. Kramer and Boyer, 1995). The sapwood water potential was obtained by measuring the leaf water potential of the lowest branch in that tree. Because that branch was covered by a black bag that stopped its transpiration, the water potential of its leaf was the same as the water potential of the sapwood stuck by that branch (e.g. Landsberg et al., 1976). Takizawa et al. (1996) intensively observed the distribution of the leaf water potential, and found a relationship between the water potential of the leaf at the tree top and at other positions and the relationship at each leaf position between the leaf water potential and the relative water content in the leaf. As a result, they were able to estimate the distribution of leaf water potential and the stored water in the foliage, which means all leaves in the canopy, from the leaf water potential at the tree top.

Table 1  
Dimensions of sample tree used in the model

Height $h$ (m)	9.0
Diameter of the bottom of trunk $2d$ (m)	0.1
Projected crown area $S$ (m <sup>2</sup> )	4.0
Total leaf area (m <sup>2</sup> )	28.0
Clear length $l_c$ (m)	4.5

Therefore, Takizawa et al. (1996) made useful measurements of time courses of transpiration, which is the difference between the change of weight of the tree and the water uptake, the uptake, the water storage in the sapwood and foliage and the leaf and the sapwood water potential. Table 1 shows the dimensions of the tree examined by them. Moreover, they examined the sapwood sample of the tree at the laboratory and measured the volume of sapwood and porosity. Therefore, they obtained the relationships between the water potential and the relative water content in the sapwood.

Fig. 1 shows the diurnal variations of leaf and sapwood water potential, transpiration and uptake rate and stored water of the foliage and sapwood measured by Takizawa et al. (1996). On the first day of their experiment, transpiration started 1 h earlier than the water uptake, decreased at noon before the maximum uptake, and stopped in the evening, while the uptake was prolonged during the evening. Water deficit in the foliage by transpiration decreased the leaf water potential and the sapwood water potential. Differences between the leaf and the sapwood water potential

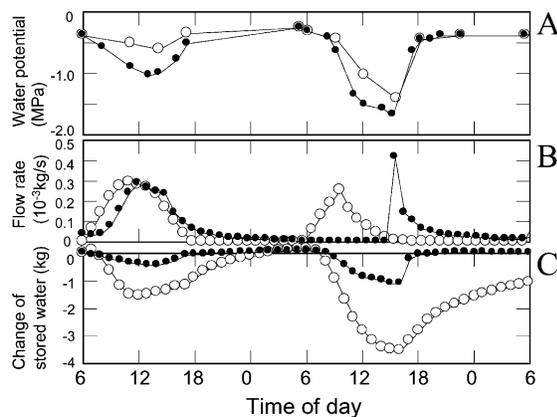


Fig. 1. Diurnal variations of (A) leaf (●) and sapwood (○) water potential, (B) transpiration (○) and uptake (●) rate, and (C) stored water of the foliage (●) and sapwood (○) (Takizawa et al., 1996).

increased from morning to noon, but decreased in the afternoon, and were little in the evening and early morning. The time of the minimum leaf water potential did not correspond to that of the maximum transpiration. Changes in stored water in the sapwood were much larger than in the foliage. Stored water took 6 h to restore in the sapwood after the restoration of stored water in the foliage. On the second day, transpiration of the sample tree continued with its cut stem surface sealed by vaseline. Then, the water uptake stopped and stored water in the sapwood extremely decreased. The minimum water potential of the leaf and sapwood decreased from  $-0.99$  MPa on the first day to  $-1.68$  MPa and from  $-0.53$  MPa on the first day to  $-1.36$  MPa, respectively. The transpiration suddenly decreased before noon from the effect of its decreasing leaf water potential. The maximum change in stored water in the leaf and sapwood was twice as much as before the cut stem surface was sealed. When transpiration stopped on the second day, the base of the trunk was recut under water and the restoration process of the stored water by water uptake was examined. The moment the base of the trunk was recut, water uptake suddenly occurred and the leaf and sapwood potential suddenly increased. Then, the stored water in the foliage was restored immediately, but the stored water in the sapwood was not restored until the next morning.

#### 4. Numerical experiments

To obtain the information needed to reproduce the results from the observations of the sample tree (Fig. 1), seven numerical experiments were made. Case 1 was the basic case. Tables 2 and 3 show the parameters used in Case 1. Model parameters describing the properties of water transportation and storage

Table 2  
Model parameters describing water transportation and storage in sapwood

Symbol	Value	Description
$K_p$ (m s <sup>-1</sup> )	$4.0 \times 10^{-5}$	Eq. (3)
$a$	0.88	Eq. (4)
$b$	0.073	Eq. (4)
$r_f$ (s)	$7.2 \times 10^3$	Eq. (6)
$C_1$ (m <sup>-1</sup> )	$1.67 \times 10^{-3}$	Eq. (7)
$k$ (m)	$5.0 \times 10^{-4}$	Eq. (7)

Table 3  
Model parameters describing transpiration

Symbol	Value	Description
$C_h$	0.05	Eq. (9)
$g_{sw \max}$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	0.8	Eq. (11)
$a_s$	0.003	Eq. (11)
$T_n$ (K)	278	Eq. (12)
$T_o$ (K)	313	Eq. (12)
$T_x$ (K)	318	Eq. (12)
$b_d$	0.2	Eq. (13)
$\psi_c$ (m)	-250	Eq. (14)

in the sapwood were estimated using the sample tree data of Kobayashi et al. (1993) and Takizawa et al. (1996) (Table 2). Here, the properties of water storage in the sapwood were represented as the relationships between volumetric water content in the whole trunk of the sample tree and sapwood water potential at the height of a clear length, and the hydraulic conductivity in the sapwood was explained from the water flow resistance of the whole sample tree in Ohm's law analogy. Table 3 shows model parameters describing transpiration through stomata. The meteorological data as inputs for calculations were estimated using sinusoidal functions (e.g. Leuning et al., 1995) taking the place where the experiment was made and its season into consideration. The parameters describing transpiration were arbitrarily determined so that the transpiration as a calculation result may fit the observation results, because the control of transpiration resulting from relationships between meteorological factors and stomatal conductance was not so important in this study, but those parameters were reasonable (e.g. Kondo and Watanabe, 1992; Kosugi et al., 1995; Yu et al., 1996). As stomatal conductance is described as Eq. (10), it is influenced by many environmental factors. Here, I attempted to examine the relationship between the leaf water potential and the transpiration by considering influence of the leaf water potential on stomatal conductance, because the properties of water transportation and storage in sapwood reflect the leaf water potential.

In Cases 2 and 3,  $\psi_c$  in Eq. (14) was altered.  $\psi_c$  represents the intensity of stomatal response to decreasing water potential.  $\psi_c$  of -100 and -50 were used for Cases 2 and 3, respectively, while  $\psi_c$  of -250 was used for Case 1. The relationship between transpiration and water potential was examined from Cases 1 to 3.

In Cases 4 and 5,  $b$  in Eq. (4) was altered.  $b$  represents the intensity of the capacitance of sapwood. As the capacitance of the crown sapwood was larger than that of the trunk sapwood (e.g. Schulze et al., 1985; Takizawa et al., 1996),  $b$  of the trunk sapwood was varied and examined.  $b$  of 0.04 and 0.01 were used for Cases 4 and 5, respectively, while  $b$  of 0.073 was used for Case 1.

In Cases 6 and 7,  $K_p$  in Eq. (5) was altered. The resistance to water movement is especially high at the junction of branches with the trunk (e.g. Kramer and Boyer, 1995). The resistance of crown sapwood is larger than that of trunk sapwood in this sample tree (Kobayashi et al., 1993). Therefore,  $K_p$  of the crown sapwood was varied and examined.  $K_p$  of  $2.0 \times 10^{-5}$  and  $1.0 \times 10^{-5}$  were used for Cases 6 and 7, respectively, while  $K_p$  of  $4.0 \times 10^{-5}$  was used for Case 1.

The numerical experiments provide much information on the response of the calculations to the change in parameters,  $\psi_c$ ,  $b$  and  $K_p$ . Finally, the numerical simulation to reproduce the observation results (Fig. 1) was made using this information.

## 5. Model results and discussion

I used the meter (m) for water potential in numerical calculations, but mega Pascal (MPa) in the following model results, because "MPa" is used in the data of references to be compared with the model results.

### 5.1. Model response to stomatal conductance

The simulation period was 2 days. On the second day of this simulation, water uptake was stopped when the transpiration rates were positive (see Fig. 1).

Fig. 2 shows the shape of a partial function  $f_4(\psi_1)$  with several values of  $\psi_c$  in Cases 1–3. Fig. 3 shows the time variations of leaf water potential and transpiration with variable values of  $\psi_c$  in Cases 1–3. When  $\psi_c$  is less negative,  $f_4(\psi_1)$  is low (Fig. 2), and then transpiration is reduced. Fig. 4 shows the relationships between transpiration and leaf water potential described by using the first day simulation results. Hysteresis is evident there because leaf water potential tends to peak later in the day than transpiration and is associated with capacitance. Hysteresis

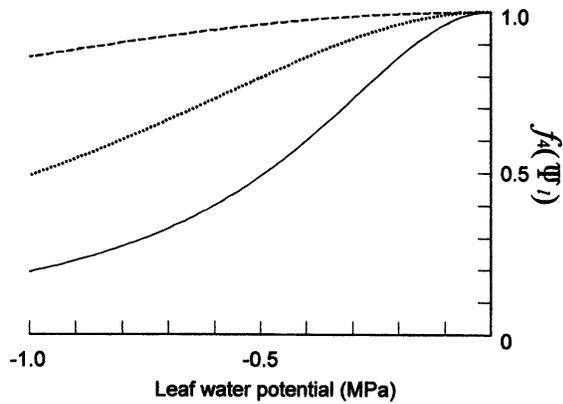


Fig. 2. Relationships between leaf water potential  $\psi_l$  and partial function  $f_4(\psi_l)$ . Case 1:  $\psi_c = -250$  (---); Case 2:  $\psi_c = -100$  (···); Case 3:  $\psi_c = -50$  (—).

curves in this simulation resemble those of Jarvis (1976), Schulze et al. (1985) and Carlson and Lynn (1991). When  $\psi_c$  is less negative, the size of the curve decreases; that is,  $\psi_c$  controls the transpiration rate and leaf water potential simultaneously (Fig. 4). When  $\psi_c$  is less negative, as  $f_4(\psi_l)$  is low with a low leaf water potential and transpiration is reduced, the leaf water potential can remain high (Figs. 2 and 3).

Therefore, when  $\psi_c$  was less negative ( $\psi_c = -50, -100$ ), as the leaf water potential did not decrease even though the water uptake stopped, the minimum leaf water potential of each day was almost the same during the 2-day simulation. However, when  $\psi_c$  was

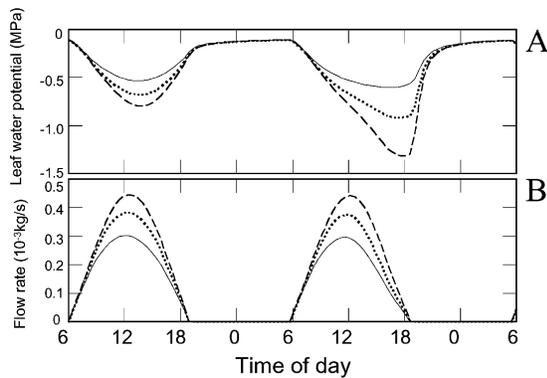


Fig. 3. Relationships between the value of  $\psi_c$  and the leaf water potential (A) and the transpiration rate (B). Case 1:  $\psi_c = -250$  (---); Case 2:  $\psi_c = -100$  (···); Case 3:  $\psi_c = -50$  (—).

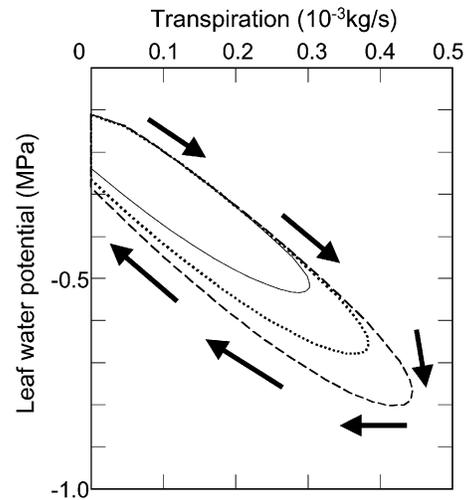


Fig. 4. Relationships between transpiration and leaf water potential. Case 1:  $\psi_c = -250$  (---); Case 2:  $\psi_c = -100$  (···); Case 3:  $\psi_c = -50$  (—).

more negative ( $\psi_c = -250$ ), while the water uptake stopped, the minimum leaf water potential was much more negative, about  $-1.3$  MPa (Fig. 3), because  $f_4(\psi_l)$  did not reduce the transpiration. Therefore, a more negative value of  $\psi_c$  is needed to reproduce the shape of the leaf water potential curve (Fig. 1). Fig. 1 shows a much more negative value of leaf water potential while the water uptake stopped than while it was positive.

### 5.2. Model response to capacitance

The 1-day simulation was made. Note that the decrease in  $b$  means a decrease in capacitance of the sapwood. Fig. 5 compares the predicted transpiration, water uptake and leaf water potential in Cases 1, 4 and 5. The leaf water potential in each case was almost the same because the capacitance  $C_p$  in Eq. (1) is insensitive to the production of the gradient of the water potential in sapwood. Therefore, as in each case the stomatal conductance did not change, the transpiration was also almost the same. A decrease in the capacitance of the trunk sapwood due to decreasing  $b$  made the peak of water uptake lower and later. The water uptake that peaked lower during the daytime was higher during the evening.

From the observation results, the peak of transpiration was a little higher and a little earlier than that of

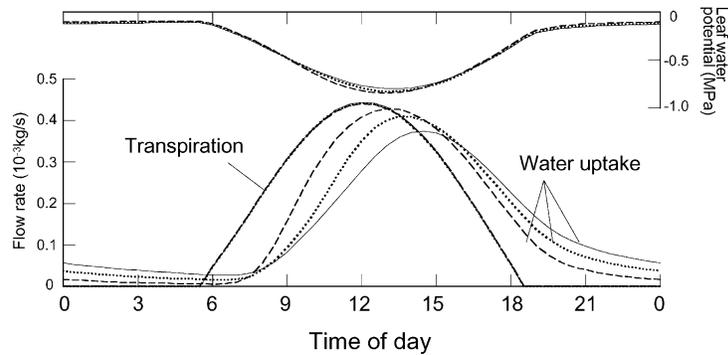


Fig. 5. Simulated transpiration, water uptake and leaf water potential with various values of  $b$ . Case 1:  $b = 0.073$  (---); Case 4:  $b = 0.04$  (···); Case 5:  $b = 0.01$  (—).

the uptake, showing that in this sample tree the capacitance of the trunk sapwood was not so different from that of the crown sapwood. Also, by examining the relationships between the volumetric water content in the whole trunk of the sample tree and the sapwood water potential at only one point, the height of a clear length, the capacitance of the sapwood was sufficient to simulate the water budget of this sample tree.

### 5.3. Model response to hydraulic conductance

Fig. 6 compares the predicted transpiration, water uptake and leaf water potential in Cases 1, 6 and 7. The leaf water potential decreased together with decreasing  $K_p$  in the crown sapwood. Consequently, when

$K_p$  was low, the stomatal conductance was reduced, and the transpiration peak was lower. During the day, when  $K_p$  was low, water uptake peaked lower, but it increased during the evening. Here, as a decreasing peak of transpiration corresponds to a decreasing peak of water uptake, the difference between the peak of transpiration and the peak of water uptake did not vary with  $K_p$ . However, the difference between the timing of the peak of transpiration and the peak of water uptake increased with decreasing  $K_p$ . If a large resistance of the root system existed, the difference in the timing of those peaks would increase more.

With the calculation results, except for increasing delay of the peaks between transpiration and uptake, regulating  $K_p$  is necessary to control only the leaf

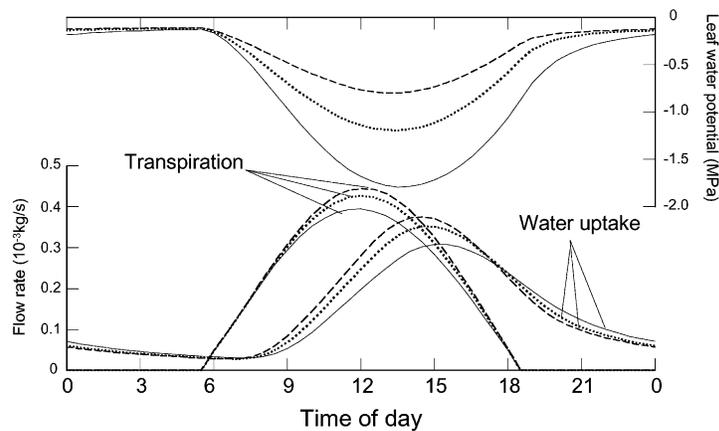


Fig. 6. Simulated transpiration, water uptake and leaf water potential with various values of  $K_p$ . Case 1:  $K_p = 4.0 \times 10^{-5}$  (---); Case 6:  $K_p = 2.0 \times 10^{-5}$  (···); Case 7:  $K_p = 1.0 \times 10^{-5}$  (—).

water potential when a simulation is made to reproduce the observation results.

#### 5.4. Reproduction of observation results

The 2-day simulation when the water uptake was stopped when the transpiration rates were positive on the second day was made to reproduce the observation results shown in Fig. 1. The information obtained from the above numerical experiments and the observed results in Fig. 1 are as follows:

1. A more negative  $\psi_c$  is needed to make a difference between the leaf water potential on the second day and on other days, and so that the simulated transpiration rate agrees with the observed value  $g_{sw\ max}$  should be tuned because  $g_{sw\ max}$  controls the transpiration rate regardless of leaf water potential.
2. In this simulation, the difference between capacitance of the trunk sapwood and that of the crown sapwood is not necessary.
3. As a low transpiration rate affected by low  $g_{sw\ max}$  produces a high leaf water potential, a low  $K_p$  in the crown sapwood is needed to reduce the high leaf water potential so that the simulated leaf water potential may correspond with the observed leaf water potential.

In this simulation  $g_{sw\ max}$  of 0.5 and  $K_p$  in the crown sapwood of  $2.0 \times 10^{-5}$  were used with other parameters in Case 1 that was maintained according to the above-mentioned information 1–3. Fig. 7 shows simulated diurnal variations of leaf and sapwood water potential, transpiration and uptake rate and changes in stored water in the foliage and sapwood. Their simulated diurnal variations agreed well qualitatively with the measured variations of many kinds of features of the observation results: time lag between the peak of transpiration and peak of uptake, water uptake prolonged during the evening, severe reduction in water potential when uptake stopped, and a sudden increase in uptake and stored water when the uptake restarted (Figs. 1 and 7).

The largest discrepancies between the observed and the calculated results were the sudden decreasing transpiration before noon and the change in stored water in the foliage when uptake stopped (Fig. 1). According to Eq. (4) proposed by Takizawa et al. (1996), as the volumetric water content in the stem  $\theta_p$  decreases,

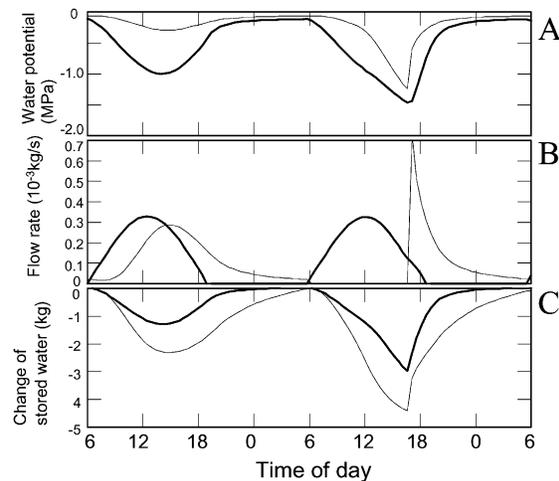


Fig. 7. Simulated diurnal variations of (A) leaf (—) and sapwood (---) water potential, (B) transpiration (—) and uptake (---) rate, and (C) stored water of the foliage (—) and sapwood (---).

water potential in sapwood  $\psi_p$  approaches constant (e.g. when  $\theta_p = 0$ ,  $\psi_p = -\exp(a/b)$ ). However, the residual water content in sapwood  $\theta_{pr}$ , defined as the water content at which  $\psi_p$  is infinitely small, likely exists in  $\theta_p$ . As  $\theta_{pr}$  was not measured in their observations, I did not assume  $\theta_{pr}$  in this model. If I use  $\theta_{pr}$  in this model, the above discrepancies should not occur. Because  $\psi_p$  becomes infinitely small and  $f_4(\psi_1)$  becomes low when  $\theta_p$  becomes close to  $\theta_{pr}$ , the sudden decreasing transpiration before noon should occur. Consequently, the change in stored water in the foliage becomes small. In other words, as  $f_4(\psi_1)$  responds to a much smaller leaf water potential, if the roots exist, stomata might have closed and the transpiration might have decrease without realizing a much smaller leaf water potential on the second day (Figs. 1 and 7) as mentioned by Johnson et al. (1991) (see Section 2.1).

Fig. 8 compares the simulated profiles of the leaf water potential with the profiles measured by Takizawa et al. (1996). The simulated profiles were made at various times, while the observed profiles were measured at 12.00–13.30 h of each observation day. The profile simulated for 14.00 h agreed well with the measured profiles. In this simulation, profiles of the leaf water potential at the other times, that is, diurnal variation of the profiles, were predicted. Here, the fact should be noted that diurnal variation of profiles of water potential is very difficult to measure. In the morning

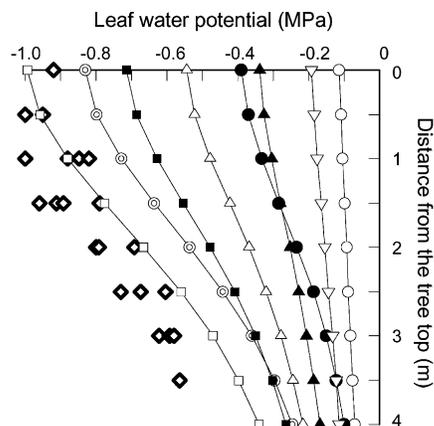


Fig. 8. Comparison between simulated profiles of leaf water potential at (○) 5.00 h, (●) 8.00 h, (⊙) 11.00 h, (□) 14.00 h, (■) 17.00 h, (△) 18.00 h, (▲) 19.00 h and (▽) 21.00 h, and profiles of the leaf water potential at (◇) 12.00–13.30 h measured by Takizawa et al. (1996).

leaf water potentials were high at all heights and their gradient was gentle. During the day the leaf water potential of the upper part decreased and the gradient was steep. After sunset the leaf water potential of the upper part increased and the gradient was gentle.

This model can synthetically simulate transpiration, distribution of water potential, uptake and water storage in a single tree, using almost only physical properties observed in the sample tree such as its size and the hydraulic properties of its sapwood. Consequently, to reproduce the observed results of leaf water potential profiles, the hydraulic conductivity of the crown sapwood must be lower than the conductivity of the trunk sapwood. The measurement of the hydraulic conductivity of the crown sapwood should be distinguished from that of the trunk sapwood.

## 6. Conclusions

I have described a model showing quantitatively and qualitatively the water balance in a single tree without a root component. In this model, in response to atmospheric demand, transpiration occurs and the water potential is distributed in the tree. Water uptake occurs by this distribution as a driving force, and the difference between transpiration and water uptake is water storage in sapwood. As detailed climatic data,

that is, time courses of solar radiation, wind speed, etc. were not used, a detailed fitting of the simulated results to the observed results was not made. Moreover, I assumed that vessels and tracheary elements are ideal (i.e. perfectly smooth capillaries of constant diameter throughout their length), and I ignored embolism, air-filled vessels and tracheids that result in increased resistance to water flow in this model. However, the model parameters used did have clear physical meanings. Even water potential in a plant, which causes the water uptake, is a kind of parameter in a number of SPAC models (e.g. Cienciala et al., 1994). In this model, water potential in a plant has a clear physical meaning and can be compared with real water potential observed in a sample plant. The simulated results, such as transpiration, water uptake, water potential and water storage change in sapwood, agreed well qualitatively with the observed results, even though for extreme conditions (Figs. 1 and 7). Therefore, this model can examine the influence of various parameters representing the moisture characteristics of various tree species on the transpiration and uptake.

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