

## Diurnal water relations of beech (*Fagus Sylvatica* L.) trees in the mountains of Italy

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### Abstract

Trees live in oscillating environments. Daytime light and warm periods alternate with night darkness and cooler temperatures. The adaptation of a tree is explained by its accommodation to such diurnal cycles. These diurnal pulses were monitored and simulated on computer. Summer measurements in Abetone (1230 m above sea level) included continuous registration of air temperature, relative humidity, wind speed, solar radiation and precipitation. Soil water contents were approximated from water balance. The response of a beech tree was measured as diurnal cycles of the twig water potential, stomatal conductance and sap water flow reflecting transpiration rate. All these measured output variables were simulated by a soil–plant–atmosphere–continuum (SPAC) model. Additional diurnal responses of the tree were calculated, such as leaf to air temperature difference, Bowen ratio and pool of water content in the tree. The evaluation of the adaptation was related to the recurrent cycles in diurnal loops, as the time-dependent relationship between the twig water potential and the sap water flow. The daily value of transpiration was 1.3 mm at the end of August. Results from simulation indicate that the model behaves correctly and can be used as a research tool for generating new scientific hypotheses.

*Keywords:* Beech; Italy; Transpiration; Modelling; *Fagus Sylvatica* L.

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### 1. Introduction

Tree growth is limited by water availability. Even under adequate soil moisture, water deficits frequently develop which can impair such processes as photosynthesis, translocation, protein synthesis and cell elongation.

A quantitative estimation of transpiration in a deciduous forest required an investigation of water potential gradients and pathway resistances in the soil, roots, stems, branches, stomata and atmosphere (Nizinski and Saugier, 1989). The component potentials and resistances are subjected to temporal and spacial variations determined by climatic parameters and plant properties (Passioura, 1982). Our paper follows the research of Ladefoged (1963), who first measured the transpiration of *Fagus sylvatica*, using the heat pulse velocity method. He found the rate of transpiration of a beech stand to be between 0.6 and

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$1.5 \text{ l m}^{-2} \text{ day}^{-1}$ , which equals 0.6 to 1.5 mm day<sup>-1</sup>. Heimann and Stickan (1993) reported the heat pulse velocity in a single beech tree (*Fagus sylvatica*) as well, looking for the correlation between heat pulse velocity and weather conditions during the vegetation period. Our measurements give similar daily values to those of Ladefoged (1963), but we concentrate mainly on the diurnal course of the fluxes instead of seasonal values.

The main aim of this study is to evaluate the applicability of a soil–plant–atmosphere–continuum model (SPAC, see Philip, 1966; D'Hollander and Impens, 1975) to simulate water relations of beech trees. The model used here is based on the concept of the flow of water from soil through the plant to the atmosphere and includes four resistances against water flow (soil–root, plant, stomatal and aerodynamic) and a pool of easily available plant water. Diurnal patterns of water uptake by roots, transpiration rate, plant water content of easily available water, twig water potential, stomatal resistance, leaf to air temperature difference and the ratio between sensible and latent heat flux (Bowen ratio) are the simulation outputs.

The basic computer version of the SPAC model was described and tested by Kowalik and Turner (1983) for plant water potential of soybean in Australia and by Kowalik and Eckersten (1984) for evapotranspiration from a willow stand in Sweden. Eckersten and Kowalik (1985) and Kowalik and Eckersten (1989) applied the model to simulate leaf–air temperature difference on willow. Olszta (1989) simulated water relations of grasslands in Poland using this model, and Kowalik et al. (1988) used the model on a Douglas fir forest in Italy for predicting twig water potential and bulk stomatal resistance. A similar study was made by Florax et al. (1990) for water relations in Douglas fir stands influenced by acid rain in the Netherlands. A listing of the program has been published by Kowalik and Eckersten (1989), Florax et al. (1990) and Eckersten (1991a,b). A recent review of the model of the plant water dynamics was published by Kowalik (1994).

This model presents transpiration governed mainly by a relationship between the stomatal resistance and leaf or twig water potential. Low stomatal resistance determines high transpiration rates and results in more negative water potentials (Jones, 1992).

The diurnal changes in wood tissue water content provide an internal storage for water. It appears that both elastic (dimensional change of stem contraction often exhibited) and inelastic tissues (cavitation often exhibited) are involved as internal storage areas for water (Hinckley et al., 1978). In this paper we do not discuss the location of the internal pool of easily available water. From the research of Magnani and Borghetti (1995) the inelastic tissue storage related to xylem cavitation can play a role in our beech stand in Abetone (Italy). It is related to relatively high pathway resistance for the liquid water flow in xylem of roots, stem and branches.

## 2. Material and methods

### 2.1. Experimental site

The experiment was carried out in a 35-year-old even-aged beech stand (present height 15–20 m), growing on a North–East facing slope of the Abetone forest (Pian di Novello, Northern Apennines, Italy, 44°07'N, 10°40'E, 1230 m a.s.l.).

The climate is characterized by long, cold winters and cool, rainy summers. The mean annual temperature is 5.9°C; the temperature of the coldest month (January) is –3.3°C, while that of the warmest is +15.7°C. The mean (1971–1980) annual precipitation amounts to 2608 mm, mostly concentrated in the fall, winter and spring; October and November are the rainiest months. Snowfall is common during winter and even in the late spring.

The vegetation is dominated by beech (*Fagus sylvatica*), a native species, while silver fir (*Abies alba*) has been planted for economic reasons. The soils of Pian di Novello forest are Inceptisols and Spodosols, acid silt loam soils with the podzolization processes differently expressed. The humification processes are very active but, lacking the reworking of organic and mineral fractions by microfauna, the profile presents Oe and Oa horizons, rich in hyphae and sharply separated from the lower A or AE horizon. Root density seems high in all soil profiles. The B horizons show evidence of accumulation of Fe, Al and organic matter eluviated from the overlying A and E horizons (Ugolini et al., 1993). Soil forming processes, as deduced from the combination

soil solution and solid phase studies, indicate that the Pian di Novello forest soils are subjected to a leaching process, but the weak Al concentration in solution and the relatively high pH values of the solution indicate the low intensity of the actual process of podzolization (Carnicelli et al., 1996).

## 2.2. Plant material – trees

Three trees were selected for the experiment, called: Tree 1, Tree 2 and Tree 3. Projected areas on the ground were: F1 = 15.5 m<sup>2</sup>, F2 = 9.1 m<sup>2</sup>, F3 = 5.5 m<sup>2</sup>. Most of the results were collected on 26 August 1992. Measurement of twig water potential, sap flow and stomatal conductances were made on the same three trees. Daily courses of twig water potential ( $\psi_t$ , MPa), stomatal conductance ( $g^*$ , cm s<sup>-1</sup>) and sap flow ( $J$ , l h<sup>-1</sup> per tree) were determined.

## 3. Measurement of meteorological variables

Air temperature, air relative humidity, wind speed and short-wave solar radiation were measured 2 m above the canopy, using a tower of 20 m height. The data were recorded every 30 min and stored on a data logger.

Wind participates in the transport of water and heat from the surface of the leaves to the free atmosphere. Wind speed together with the height of the plants and the reaction of the plants to the action of wind determines the coefficient  $r_a$ , the aerodynamic resistance of the canopy (Monteith and Unsworth, 1990).

According to data of Grace (1983) for small leaf dimensions and for low wind speed the resistance may be 10 s m<sup>-1</sup>. The simulation was made for  $r_a = 10$  s m<sup>-1</sup> because the measured wind speed was low, between 0.5 and 1.5 m s<sup>-1</sup>.

## 4. Measurement of ecophysiological variables

### 4.1. Plant water content

Throughout the season four wood cores, 30 mm long and 3 mm in diameter, were extracted with an increment borer at breast height from the main stem

of three trees, other than the above-mentioned 1, 2, 3 beech trees. Cores were extracted at dawn from four directions at right angles and immediately sealed with parafilm. In the laboratory, the fresh weight ( $W_f$ ) and the dry weight ( $W_d$ , after 48 h in an oven at 80°C) of wood cores were determined to the nearest 0.1 mg. The fresh volume ( $V_f$ ) of each sample was determined as the weight of water displaced. The volume fraction of water in the wood, also called the relative water content (RWC), was calculated (see Borghetti et al., 1991):

$$\text{RWC} = (W_f - W_d) / (\rho_w \cdot V_f) \quad (1)$$

where  $\rho_w$  is the density of water. This volume fraction of water in the wood was directly related to the measured twig water potential.

### 4.2. Measurement of plant water potential and stomatal conductance

At regular intervals through the season, pre-dawn xylem water potential ( $\psi_t$ ) was measured with a pressure chamber (Scholander et al., 1965) on three to six apical twigs per tree. Roughly at the same dates, xylem water potential was measured at dawn on several (up to six) basal branches, which had been enclosed overnight in black polyethylene bags. Acting as tensiometers inserted into the stem wood, these branches provided an estimate of the xylem water potential ( $\psi_t$ ) at the base of the stem (Hellkvist et al., 1974). Twig water potentials were registered on several days, for example on August 26, 1992, as a diurnal course. Stomatal conductance was measured on apical leaves with a null-balance steady state porometer (L-1600 Li-Cor, Lincoln, Nebraska).

### 4.3. Sap flow

We measured the sap flow velocity in the beech tree. The principle of measurement is based on the process where a small pulse of heat is injected in the stem of a tree by means of an electric current through a resistor which is implanted in the xylem. The temperature sensors are mounted above and below the place of heat input. The injected heat will move through the xylem by diffusion and by water flow. From the measured increase of temperature, the velocity of water flow in a tree can be calculated.

In our beech trees of Abetone forest sap flow was measured by the thermoelectric ‘heat pulse method’, with a custom heat pulse velocity recorder (Soil Conservation Centre, Palmerston North, New Zealand) (see Borghetti et al., 1993, and Magnani and Borghetti, 1995, for a detailed description of the method).

## 5. Model used

### 5.1. Brief description of the model

A detailed description of the model has already been published. Computer software was given by Kowalik and Eckersten (1989), Florax et al. (1990) and Eckersten (1991a,b). In this paper the description is restricted to the main assumptions.

The pathway for water flow from the bulk soil to the atmosphere is represented by four resistances (Fig. 1): the soil–root interface resistance ( $r_t$ , MPa m<sup>2</sup> s g<sup>-1</sup>) from the soil (where the liquid water

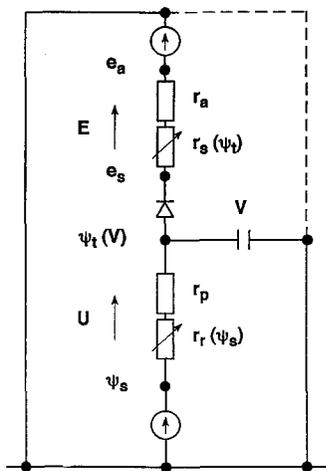


Fig. 1. Catenary model of the plant hydraulic system as a linear series with the hydraulic resistances in the soil–root interface ( $r_t$ ), xylematic tissues of roots, stem, branches and leaves ( $r_p$ ), surface of mesophyll, substomatal cavities and stomata at the leaf surface ( $r_s$ ), air between leaf surface and bulk atmosphere ( $r_a$ ), each being represented by a single regulated resistor ( $r_r(\psi_s)$ ,  $r_p$ ,  $r_s(\psi_t)$ ,  $r_a$ ). Capacitance of the appropriate tissues is described as  $V$ . The liquid inflow  $U$  is driven by the potentials between soil ( $\psi_s$ ) and twig or leaf ( $\psi_t$ ); the water vapour outflow  $E$  is driven by the difference between saturated vapour pressure in substomatal cavities ( $e_s$ ) and in bulk air ( $e_a$ ).

potential is  $\psi_s$ ) to the root surface; the xylematic plant resistance ( $r_p$ , MPa m<sup>2</sup> s g<sup>-1</sup>) from the root surface to the mesophyll of leaves where the liquid water potential is  $\psi_t$  (MPa); the canopy stomatal resistance ( $r_s$ , s m<sup>-1</sup>) from the leaf–mesophyll surface of evaporating water to the air of the leaf surface (for flow of vapour) and finally, the aerodynamic resistance ( $r_a$ , s m<sup>-1</sup>) from the leaf surface to the air above the canopy, where the vapour pressure is  $e_a$  (hPa). The model consists of one compartment for easily available liquid water located in the plant. The stand concerned is treated by the model as horizontally uniform.

The time step of simulation is 1 min and input data are minute values of global radiation  $R_s$ , air temperature  $T_a$ , air relative humidity  $h_a$ , wind speed  $u$ , registered above the canopy, and daily values of soil water potential  $\psi_s$ . Precipitation and interception can be included, but the model was run for a clear day without any rain.

The initial step of calculation is to obtain net solar radiation  $R_n$  from  $R_s$ , as  $R_n(R_s)$ ;  $e_a$  from  $T_a$  and  $h_a$ , as  $e_a(T_a, h_a)$ ;  $r_s$  from  $R_s$ , as  $r_s(R_s)$ ;  $r_s$  from  $\psi_t$ , as  $r_s(\psi_t)$  and  $r_t$  from  $\psi_s$ , as  $r_t(\psi_s)$ .

The net radiation above the canopy ( $R_n$ , W m<sup>-2</sup>) should be an input variable and it can be estimated from the global radiation above the canopy ( $R_s$ , W m<sup>-2</sup>). We measured this relationship, but as a first approximation it was taken as:

$$R_n = a_R \cdot R_s - b_R \quad (2)$$

where  $a_R = 0.649$ ,  $b_R = 23$  (Feddes, 1971).

The actual water vapour pressure in the atmosphere above the canopy  $e_a$  (hPa) is calculated from the equation:

$$e_a = h_a \cdot e_d / 100 \quad (3)$$

where  $h_a$  is the relative humidity of the air (%) and  $e_d$  is the partial pressure of the saturated water vapour of the air above the canopy, calculated from the actual air temperature ( $T_a$ , °C) using the standard Tetens (1930) equation (see Monteith and Unsworth, 1990) or the approximated function  $e_d(T_a)$  introduced by Feddes et al. (1978).

Stomatal resistance  $r_s$  is affected by the incoming short-wave radiation  $R_s$  as a function  $r_s(R_s)$ , given by several authors. The stomatal resistance for light levels below 25 W m<sup>-2</sup> is set equal to cuticular resistance and below 250 W m<sup>-2</sup> a linear correlation

is assumed for the relationship between intensity of solar radiation and stomatal resistance (Jarvis et al., 1976). For  $R_s > 250 \text{ W m}^{-2}$ , the stomatal resistance is assumed to depend entirely on the leaf (or twig) water potential,  $r_s(\psi_t)$  and not on the solar radiation (Florax et al., 1990). Relation  $r_s^*(R_s)$  can be illustrated by the values (valid for different plants and partly confirmed by our own experimental data) as:

$R_s$ ( $\text{W m}^{-2}$ )	< 25	100	150	200	250	> 250
$r_s^*$ ( $\text{s m}^{-1}$ )	5000	760	500	380	300	300

where  $r_s^*$  is a single leaf stomatal resistance, related to the canopy stomatal resistance by the relation:

$$r_s = r_s^* / L_{ai} \quad (4)$$

where  $L_{ai}$  (or LAI) is the leaf area index ( $\text{m}^2 \text{m}^{-2}$ ). The relation between leaf (or twig) water potential  $\psi_t$  (MPa) and single leaf stomatal resistance can be illustrated by the values for Douglas fir (Florax et al., 1990):

$\psi_t$ (MPa)	< -2.0	-2.0	-1.5	-1.3	0.0
$r_s^*$ ( $\text{s m}^{-1}$ )	5000	5000	1200	865	300

where Eq. (4) holds as well. Similar values were obtained for willow (Kowalik and Eckersten, 1984). We took the same characteristics for beech (see discussion below), but this relationship was not a subject of our experiment.

The resistance to water flow through the soil to the roots,  $r_r$  ( $\text{MPa m}^2 \text{s g}^{-1}$ ), will vary with soil water content, root density  $L_v$  ( $\text{cm cm}^{-3}$ ) and effective rooting depth  $L$  (cm). Soil hydraulic resistance for flow of liquid water from the soil into the root hair's surface is the series-linked resistances to flow of water:

$$r_r = b / (a \cdot |\psi_s|^{-n}) \quad (5)$$

where  $\psi_s$  (MPa) is the soil water potential in the root zone,  $a$  and  $n$  are parameters determining the shape of the unsaturated conductivity curve  $K(\psi_s)$ ,  $b$  is the root density resistance factor (MPa), which considers the length and geometry of the root system (Feddes, 1981):

$$b = \ln(r_2/r_1) / (2 \cdot \pi \cdot L_v \cdot L) \quad (6)$$

where  $r_1$  is the root radius (cm);  $r_2$  is the mean distance between roots in the soil (cm);  $L$  is the effective rooting depth in the soil profile (cm);  $L_v$  is the length of the roots in the unit volume of soil ( $\text{cm}$

$\text{cm}^{-3}$ ) and, according to De Willigen and van Noordwijk (1987):

$$r_2 = 1 / \sqrt{(\pi \cdot L_v)} \quad (7)$$

In our simulation we assumed (from literature and soil survey data) for roots:  $L_v = 5 \text{ cm cm}^{-3}$ ; and for soil water:  $\psi_s = -0.007 \text{ MPa}$  ( $\text{pF} = 1.85$ ), resulting in  $r_r = 2.5 \text{ MPa m}^2 \text{s g}^{-1}$ , as a constant value for daily simulations.

In the model the transpiration is governed mainly by a relationship between the stomatal resistance ( $r_s$ ) and a leaf or twig water potential ( $\psi_t$ ). As regards pathway resistance to water flow, the total resistance for the liquid water flow ( $r_r + r_p$ ) was considered constant, while the stomatal resistance ( $r_s$ ) was considered to respond to changing conditions.

A reservoir of easily available water in the plant ( $V$ ,  $\text{g m}^{-2}$ ) is considered in the model, which is supplied through root uptake ( $U$ ,  $\text{g m}^{-2} \text{s}^{-1}$ ) and consumed by transpiration ( $E$ ,  $\text{g m}^{-2} \text{s}^{-1}$ ). The volumetric change of the reservoir ( $dV$ ) during one time step ( $d\tau$ ) is the difference between these flows:

$$dV = \int (U - E) d\tau \quad (8)$$

or using the Euler method of integration:

$$V_{i+1} = V_i + \Delta\tau \cdot (U - E) \quad (9)$$

where  $\Delta\tau$  is the time step of calculations ( $\Delta\tau = 1$  min here), and  $i$  and  $i+1$  are indexes of time ( $t_{i+1} - t_i = \Delta\tau$ ).

The canopy water potential ( $\psi_t$ , MPa) is related to  $V$  as  $\psi_t(V)$ :

$$\psi_t = \psi_{tm} \cdot (1 - V/V_0) \quad (10)$$

where  $\psi_{tm}$  and  $\psi_t$  are minimum and actual values of the potentials (MPa), and  $V_0$  and  $V$  are the maximum and actual size of the capacitance ( $\text{g m}^{-2}$ ).

The difference between soil water potential ( $\psi_s$ , MPa) and leaf or twig water potential ( $\psi_t(V)$ , MPa) constitutes the driving force for uptake of water across the resistances of the soil–root interface ( $r_r$ ,  $\text{MPa m}^2 \text{s g}^{-1}$ ) and the plant xylematic resistance ( $r_p$ ,  $\text{MPa m}^2 \text{s g}^{-1}$ ):

$$U = (\psi_s - \psi_t) / (r_r + r_p) \quad (11)$$

The latent heat flux is driven by the vapour pressure difference between stomatal cavities ( $e_s$ , hPa) and the air above the canopy ( $e_a$ , hPa). The air in stomatal cavities is assumed to be saturated and of

temperature  $T_s$  ( $^{\circ}\text{C}$ ). The latent heat flux is estimated as:

$$\lambda \cdot E = (\rho \cdot c_p / \gamma) \cdot (e_s - e_a) / (r_s + r_a) \quad (12)$$

where  $r_s$  ( $\text{s m}^{-1}$ ) is the canopy resistance (total stomatal resistance per unit of ground area) and  $r_a$  is the bulk aerodynamic resistance between the stand and reference level above the canopy (it was taken as  $10 \text{ s m}^{-1}$ ).  $\lambda$  is latent heat of vaporization of water ( $= 2.4518 \times 10^6 \text{ J kg}^{-1}$ ),  $\rho$  is the density of the air ( $= 1.2 \text{ kg m}^{-3}$ ),  $c_p$  is the specific heat of air at constant pressure ( $= 1005 \text{ J kg}^{-1} \text{ K}^{-1}$ ),  $\gamma$  is a psychrometric constant ( $= 67 \text{ Pa K}^{-1}$ ).

The sensible heat flux ( $H$ ,  $\text{W m}^{-2}$ ) is proportional to the difference between the surface temperature ( $T_s$ ,  $^{\circ}\text{C}$ ) and the air temperature ( $T_a$ ) divided by  $r_a$  ( $\text{s m}^{-1}$ ) assumed equal for sensible and latent heat:

$$H = \rho \cdot c_p \cdot (T_s - T_a) / r_a \quad (13)$$

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

$$R_n - H - \lambda \cdot E \leq 0.1 \text{ W m}^{-2} \quad (14)$$

The canopy is treated as one unit and needs one value for radiative energy available for the heat fluxes. The partitioning of net radiation between the latent and sensible heat fluxes depends on atmospheric and plant conditions.

The values of  $U$  and  $E$  are calculated for time  $i$  and for time  $i + 1$  ( $U_i$ ,  $E_i$ , and  $U_{i+1}$ ,  $E_{i+1}$ ). Similarly, the values of  $V$  are calculated as  $V_i$  and  $V_{i+1}$ . The solution of  $V_{i+1}$  is possible only by an iterative method which is stopped by a criterion when canopy water potentials  $\psi_t$  in the two consecutive iteration steps are not too different. This potential  $\psi_t$  is determined by changing iteratively its value until the differences are not too large ( $< 40 \text{ kPa}$ , taken arbitrarily) for the considered  $V_{i+1}$ .

It means that having the initial value of  $r_s$  we calculate the rate of transpiration  $E$  (Eq. (12)), next we calculate easily exchangeable water in the plant

$V$  (Eq. (9)), next the twig water potential  $\psi_t(V)$  (Eq. (10)) and again stomatal resistance from the function  $r_s(\psi_t)$ .

After getting the situation that the values of  $T_s$  and  $V$  do not need more iterations, we can calculate and print the results (i.e.  $r_s$ ,  $\psi_t$ ,  $E$ ,  $H$ ,  $U$ ,  $T_s$ ,  $T_s - T_a$ ,  $H/(\lambda \cdot E)$ ) for the respective time steps.

## 6. Time invariant inputs

### 6.1. Time invariant data for SPAC

Time invariant data for the SPAC model contain:

- the relationship between twig water potential  $\psi_t$  and wood relative water content (RWC) and easily available water  $V$ ;
- the relationship between twig water potential  $\psi_t$  and leaf stomatal conductance  $g^*$ ;
- soil-root hydraulic resistance  $r_r(\psi_s)$ ;
- plant water xylematic resistance  $r_p$ .

### 6.2. Relation $\psi_t(V)$

Twig water potential  $\psi_t$  (MPa) and the relative water content RWC (%) of twig xylem were measured on the studied beech trees (Fig. 2). The readily exchangeable twig water content  $V$  ( $\text{g m}^{-2}$ ) was estimated in accordance with literature data.

For these data of RWC,  $V$  and  $\psi_t$ , the linear relation can be applied to Eq. (10), where  $\psi_t$  is a linear function of  $V/V_0$ , according to:  $\psi_t = \psi_{tm} \cdot (1$

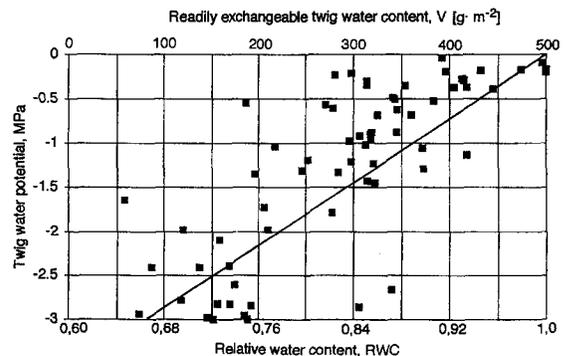


Fig. 2. Relationship between wood relative water content (RWC) and twig water potential ( $\psi_t$ ). On the upper axis the readily exchangeable twig water content ( $V$ ) was estimated in accordance with literature data.

–  $V/V_0$ ), where  $V$  ( $\text{g m}^{-2}$ ) is the amount of easily exchangeable water in the plant per unit area of the soil at a certain time,  $V_0$  is the maximum value for  $V$  (for relative water content  $\text{RWC} = 100\%$ ),  $\psi_{\text{tm}}$  (MPa) is the minimum value of  $\psi_t$  when  $V$  is equal to zero.

The maximum storage of easily exchangeable water when no water stress is present was estimated to  $V_0 = 500 \text{ g m}^{-2}$  or 0.5 mm (see Kowalik and Turner, 1983; Florax et al., 1990). It is not clear whether this plant capacitance is located either in leaves or in wood. It was assumed that if  $V = 250 \text{ g m}^{-2}$  then  $\text{RWC} = 80\%$  and if  $V = 0$  then  $\text{RWC} = 60\%$  (Fig. 2). All functional living cells in a tree must remain turgid with relative water content above 75% (Bradford and Hsiao, 1982), but it depends on the specific pressure–volume curve. It is obvious that the values of  $\psi_t$  at 80% of RWC provide a measure of the decrease in water potential which has occurred with a 20% loss of water. The value of  $\psi_t = -1.9 \text{ MPa}$  for  $\text{RWC} = 80\%$  was reported for *Betula pendula* by Jarvis and Jarvis (1963) and for Douglas fir by Kowalik et al. (1988).

For  $V = 0$ ,  $\psi_t$  is equal to  $-3.6 \text{ MPa}$  from extrapolation of data from Fig. 2. The size of the pool of easily available water ( $V_0$ ) was estimated by Cienciala et al. (1994) to be 0.5 mm for spruce (*Picea abies*), but by Kowalik et al. (1988) to be 1 mm for Douglas fir (*Pseudotsuga menziesii*). Cienciala et al. (1994) indicate that the quantity of 0.5 mm represents roughly one quarter of the average daily water uptake on the site. Schulze et al. (1985) found the amount of available water storage to be 24% and 14% of the daily transpiration rate in *Larix* and *Picea* trees, respectively. Carlson and Lynn (1991) estimated the magnitude of the capacitance effect in large plants to be about 0.5 mm as well, recalculated from the transpiration rate (about 20–50  $\text{W m}^{-2}$  per unit of leaf area in their model). Waring and Schlesinger (1985) found that water removed from sapwood during the day may provide one-third of the daily requirements for transpiration.

### 6.3. Relation $g^*(\psi_t)$

A relationship was needed between twig water potential  $\psi_t$  and stomatal leaf conductance  $g^*$  during branch dehydration on the sunny day of August 26, 1992 (Fig. 3).

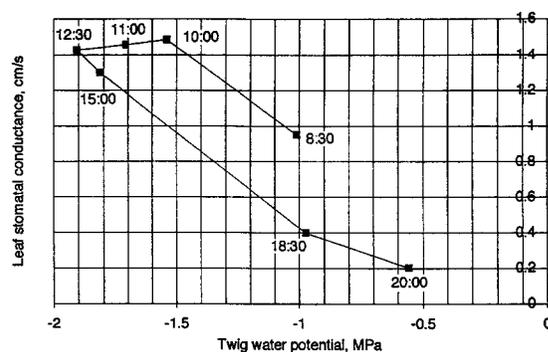


Fig. 3. Leaf stomatal conductance  $g^*$  ( $\text{cm s}^{-1}$ ) as a function of the twig water potential (MPa), measured during the sunny day of August 26, 1992, in Abetone beech forest. From these data one can separate the limited light effects in the morning (8:30) and evening (18:30 and 20:00) from the effects of sunny hours (10:00; 11:00; 12:30; 15:00).

The control of stomatal closure under water stress by decrease of turgor pressure of stomatal cells, caused by decrease of leaf water potential, is well recognized (Jones, 1992), but the link between leaf and turgor pressure of stomatal cells is not so straightforward. Grace (1983) indicates: “the observations showed that stomata shut when the plant suffers water stress” (p. 51) and “stomatal conductance in the field is often found to depend upon the leaf water potential” (p. 52). Dixon and Johnson (1993) showed that the relationship between stem water potential and stomatal conductance in red ash indicated that partial stomatal closure was induced when the water stress dropped to about  $-1.0 \text{ MPa}$ . We have a similar situation in beech trees. The leaf stomatal resistance  $r_s^*$  equals the reciprocal value of the conductance ( $r_s^* = 1/g^*$ ). Stomatal resistance  $r_s$  is taken as the resistance of an imaginary single leaf layer  $r_s^*$  and the number of layers is set equal to the leaf area index ( $L_{\text{ai}}$ ). This gives the equation:

$$r_s = 1/(g^* \cdot L_{\text{ai}}) \quad (15)$$

where  $r_s$  is canopy stomatal resistance ( $\text{s m}^{-1}$ ),  $L_{\text{ai}}$  is the leaf area index ( $\text{m}^2 \text{ m}^{-2}$ ) estimated to be 3.85 for the beech stand in Abetone,  $g^*$  is leaf stomatal conductance. Measured canopy stomatal resistances  $r_s$  can be related to the measured twig water potential, for better estimation of the functional relationship  $r_s(\psi_t)$ . This function is depicted in Fig. 4, where the line of filled points indicates a shape of the function  $r_s(\psi_t)$  used in simulation model for  $L_{\text{ai}} =$

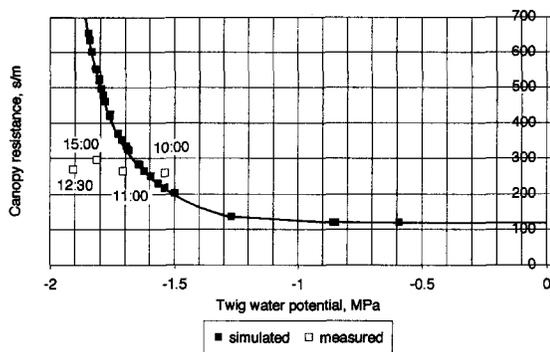


Fig. 4. Canopy stomatal resistance  $r_s$  ( $\text{s m}^{-1}$ ) as a function of the twig water potential (MPa). Open squares as measured points during the day on August 26, 1992 (at 10:00; 11:00; 12:30; 15:00), black squares and solid line are simulated for August 24–26, 1992.

3.85 and open points are the values measured at midday of the sunny day of August 26, 1992. It is a rather poor accordance between experimental and simulated data. In principle a negative threshold of  $\psi_t$  for stomatal closure was not reached in the very few field measurements.

The change of stomatal conductance with water potential is given in Fig. 4, and it shows that the threshold value of  $\psi_t$  was reached only for the very beginning of the partial stomatal closure. The variations of  $g^*$  are driven by solar radiation as well (in the mornings and evenings). The relationship between  $r_s$  and  $\psi_t$  in the model was taken as a line drawn through the points:  $1/r_s = 0.00000001 \text{ m s}^{-1}$  for  $\psi_t = -10 \text{ MPa}$ ;  $1/r_s = 0.00000001 \text{ m s}^{-1}$  for  $\psi_t = -2 \text{ MPa}$ ;  $1/r_s = 0.0033 \text{ m s}^{-1}$  for  $\psi_t = 0.0 \text{ MPa}$ . It is important to note that this relationship has not been experimentally derived for beech yet, but was assumed from the literature (Florax et al., 1990).

#### 6.4. Values of $r_p$ and $r_r$

Daily courses of xylematic water potential in apical twigs ( $\psi_t$ ) and sap flow ( $J$ ) were measured on July 29 and August 26 in three beech trees. Values of water potential were plotted against the corresponding values of sap flow (see Fig. 8). At several moments during the day we attempted to estimate plant resistance ( $r_p$ ) as the proportionality constant between water potential differential and sap flow ( $J = \Delta\psi/r_p$  or  $r_p = \Delta\psi/J$ ). Total xylematic plant

resistance was estimated considering as driving variable for water flow the difference in water potentials between the soil and apical twigs.

Here the value  $r_p = 60 \text{ MPa m}^2 \text{ s g}^{-1}$  was measured in beech and applied to the simulation. Some simulations were performed with  $r_p = 45$  as well. It was much higher than for willow ( $= 16$ , Kowalik and Eckersten, 1984), Douglas fir ( $= 16$ , Kowalik et al., 1988) or spruce ( $= 11.5$ , Cienciala et al., 1994). As indicated by Cienciala et al. (1994), a higher value of  $r_p$  decreases water uptake by the tree. Consequently, at high transpiration rates the pool of easily available water is emptied and the twig water potential decreases, and this limits  $E$ . The other effect is a prolonged uptake during the evenings, caused by slower filling up of reservoir  $V$  by inflow  $U$ . Nevertheless,  $r_p$  is still considered as one of the most uncertain factors in the model and the modelled water uptake is very sensitive to the plant resistance  $r_p$  (it was indicated as well by Kowalik and Eckersten, 1984), especially considering the accuracy with which it can be determined (Cienciala et al., 1994). The beech tree shows a very high plant resistance  $r_p$ , at least in comparison with willow or Douglas fir. If we assume that plant capacitance is located in the leaves then the hydraulic resistance may be constant, but if the capacitance is in the xylem, the resistance  $r_p$  may be variable.

It is an open question as to whether different species growing in the same environment may have differences in wood permeability. We can refer here to the research of Whitehead et al. (1984). They found that spruce (*Picea sitchensis*) has twice the wood permeability of pine (*Pinus contorta*) with equivalent leaf area in plantations in Scotland. Our results indicate that Douglas fir (*Pseudotsuga mezesii*) has four times higher water permeability than beech (*Fagus sylvatica*) in the mountain conditions of the Apennines, Italy, but Douglas fir is not a native species of the Apennines.

## 7. Results and discussion

### 7.1. Comparison between measured and simulated values

Hourly values of measured sap flow  $J$  (changing the unit from  $1 \text{ h}^{-1}$  per tree $^{-1}$  to  $\text{g m}^{-2} \text{ s}^{-1}$ ),

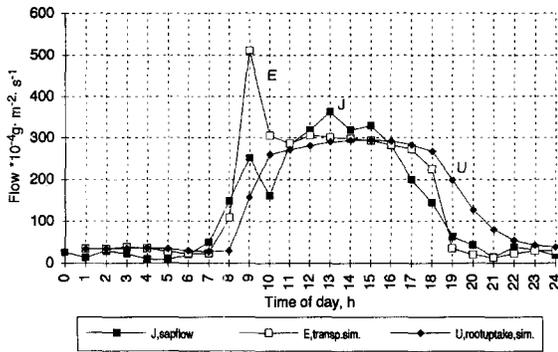


Fig. 5. Measured sap flow  $J$ , simulated transpiration rate  $E$  and root water uptake  $U$ , during the sunny day of August 26, 1992, in Abetone.

simulated water uptake  $U$  ( $\text{g m}^{-2} \text{s}^{-1}$ ) and transpiration rate  $E$  ( $\text{g m}^{-2} \text{s}^{-1}$ ) are presented in Fig. 5. This demonstrates that the model performs well for a sunny day and wet soil conditions, and the correspondence between simulated and measured water uptake was good.

Twig water potential  $\psi_t$  changes throughout the day (Fig. 6). It is apparent that the plants, even under optimum soil moisture conditions, undergo diurnal variations in water status, which is given by the amplitude of daily fluctuations of twig water potential. For the sunny day of August 26 there is a large drop in the values of  $\psi_t$ . It is necessary to remember, however, that the water potential in a wide variety of forest trees and shrubs rarely drops below  $-2.0$  MPa, irrespective of the size or amount of canopy (Scholander et al., 1965).

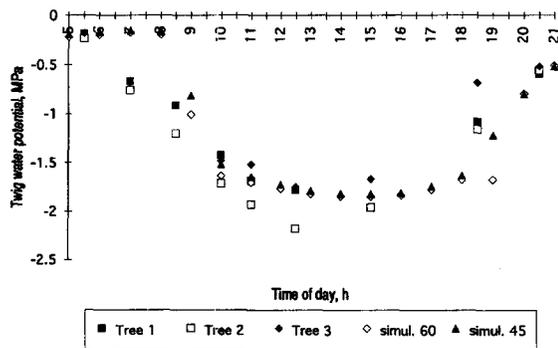


Fig. 6. Measured and simulated twig water potential in the beech stand, August 26, 1992, in Abetone. Simul. 60 means  $r_p = 60 \text{ MPa m}^2 \text{ s g}^{-1}$ ; simul. 45 means  $r_p = 45 \text{ MPa m}^2 \text{ s g}^{-1}$ .

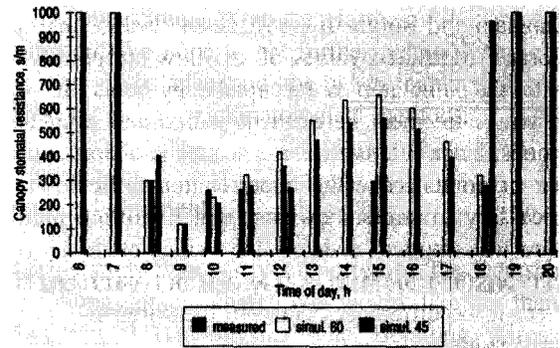


Fig. 7. Measured and simulated canopy stomatal resistance ( $\text{s m}^{-1}$ ) in the beech stand, August 26, 1992, in Abetone. Simul. 60 means  $r_p = 60 \text{ MPa m}^2 \text{ s g}^{-1}$ ; simul. 45 means  $r_p = 45 \text{ MPa m}^2 \text{ s g}^{-1}$ .

Fig. 7 shows the diurnal distribution of canopy stomatal resistance  $r_s$  ( $\text{MPa m}^2 \text{ s g}^{-1}$ ) indicating the influence of light (sunrise 7:00 and sunset 19:00) on the opening of stomata. The scale of the  $r_s$  figures makes the daytime values appear nearly constant, but actually there is an important variation.

Fig. 8 shows the comparison between measured and simulated loop of the diurnal relation between twig water potential and water uptake. In the measurements the sap flow was taken, whereas in the simulation it was the water uptake by roots. The hysteresis response is very limited in measured data and it is not visible at all in the simulation. The very high xylematic resistance of beech may be a reason for the lack of such hysteresis, recognized in many other trees. Lack of hysteresis was attributed by

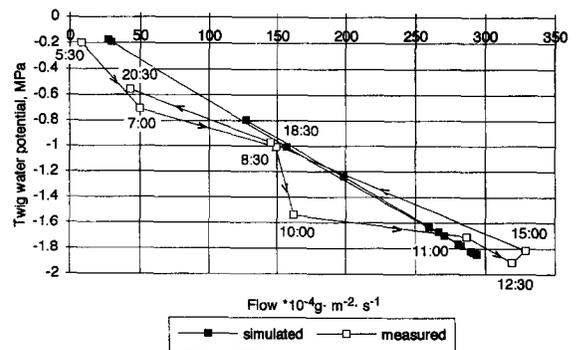


Fig. 8. Twig water potential versus sap water flow of water per square metre of soil below the tree (measured as sap flow and simulated as water uptake by roots), August 26, 1992, in Abetone.

Magnani and Borghetti (1995) to the lack of internal storage. Measured values of sap flow are correlated with the simulated water uptake by roots. It is a general agreement between measured and simulated values, but a relatively large scatter and small number of points make the interpretation difficult. It is necessary to stress, however, that no fitting procedure was applied to determine values of model parameters and for such a case it is not surprising for there to be differences between measured and simulated values.

### 7.2. Simulation of additional relations

Fig. 9 shows the diurnal course of the simulated leaf to air temperature difference ( $^{\circ}\text{C}$ ) during the clear day of August 26, 1992. Simulated values of  $\Delta T$ , the difference between leaf and air temperature, were most often higher than  $2^{\circ}\text{C}$  (up to  $3.2^{\circ}\text{C}$ ). It indicates a weak cooling effect of evaporating water in the beech stand.

The trees are transpiring a relatively small amount of water and this is reflected not only by overheating of leaves, but also in the simulated Bowen ratio (Fig. 10), the relation between sensible and latent heat outflow. Low values of Bowen ratio (between 0 to 0.6) indicate an evaporating ecosystem, but higher values of Bowen ratio are related to the strong convective conditions. The beech stand seems to save water and the participation of the sensible heat flow is high, when the participation of latent heat flow (evaporative heat outflow) is low. The small number of data is not sufficient for better evaluation

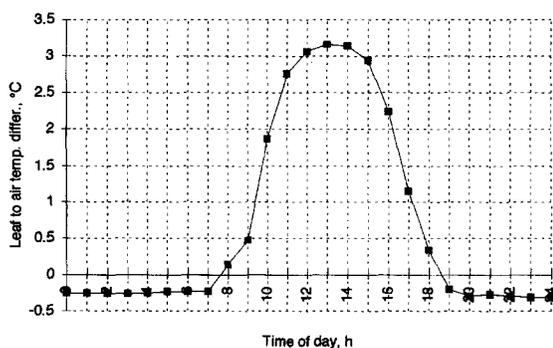


Fig. 9. The diurnal course of the simulated leaf to air temperature difference ( $^{\circ}\text{C}$ ) during a clear day August 26, 1992, in Abetone.

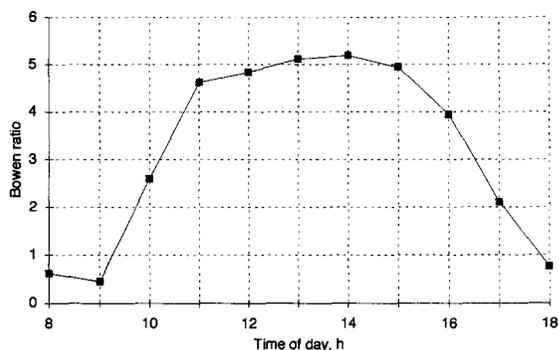


Fig. 10. The diurnal course of the simulated Bowen ratio during a clear day August 26, 1992, in Abetone.

of the climatic conditions in the beech stand in Abetone.

The diurnal course of the simulated readily exchangeable water content  $V$  for the beech stand is depicted in Fig. 11. It is clear, that the pool of water is recovered during the night and that the plant is well adapted to the actual evaporative demand of the environment.

Fig. 11 shows the changes in tissue water content and the changes in an internal storage of water in the beech stand. It is not possible to answer the question of which tissues are involved as internal storage for water. On the one hand, they could be elastic tissues, and in this case the dimensional change of the stem should be visible (stem shrinkage during daytime hours). On the other hand, they could be inelastic tissues, supplying tree in water. In this case the

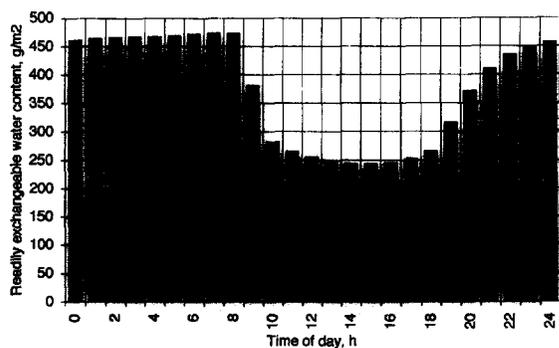


Fig. 11. The diurnal course of the simulated readily exchangeable water content  $V$  ( $\text{g m}^{-2}$ ) for the beech stand in Abetone during the clear day of August 26, 1992.

cavitation can be exhibited, without stem contraction.

## 8. Conclusions

The feedback relationship between leaf canopy temperature, transpiration, stomatal resistance, twig water potential and amount of water stored in the plant have been described, formulated and solved numerically for a beech stand in Abetone, Italy.

The results of the calculations agree well with diurnal experimental data for sap flow, twig water potential and stomatal resistance, but the research results are limited here to one representative sunny day, August 26, 1992.

The model provides diurnal distribution not only for transpiration rate, twig water potential and stomatal resistance, but also for leaf canopy temperature, Bowen ratio above the stand and plant water contents.

Different realistic input values can be introduced, mainly lower soil water potentials, lower root densities and new diurnal values of meteorological driving variables (solar radiation, air temperature, air relative humidity, wind speed, precipitation and interception of water).

The modelled water uptake is sensitive to the size of the capacitance and the plant resistance. The pool of the easily available water in beech trees was estimated to be 0.5 mm, and the plant xylematic resistance as high as 60 MPa m<sup>2</sup> s g<sup>-1</sup>. The daily value of transpiration was 1.3 mm, a surprisingly low value for a clear sunny day at the end of August in Italy, but in agreement with results published by Ladefoged (1963) for *Fagus sylvatica*. For lower xylematic resistance (taking 16 instead of 60 for example) and fully open stomata, the transpiration was 2.3 mm day<sup>-1</sup>, for the same clear day conditions.

Tree water status may determine morphological relationships between root-conducting and foliar-transpiring tissue, for example the allocation strategy to develop higher root density or to develop higher leaf area index. The general impression is that the plant community of the beech stand in Abetone is reducing community leaf area and developing high root density. This can be related to the poor nitrogen

supply, not only to the water status of the trees. This problem is open for future research. Results from simulation indicate that the model behaves correctly and can be used as a research tool for generating new scientific hypotheses.

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