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A MODEL OF TRANSPIRATION AND SOIL–WATER BALANCE FOR A MATURE OAK FOREST

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ABSTRACT

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A hydrological model for the development of the soil-water content in a 120-year-old oak stand (*Quercus petraea*) is presented with a 1-day time resolution. The model was conceived for working with daily potential evapotranspiration, throughfall and leaf area index data. It predicts transpiration from the dry canopy and soil-water content. The canopy is considered as a single leaf (the Penman–Monteith equation) which entails measurements of the physiological control of vapour flow from the leaf such as stomatal resistance (porometer), leaf water potential (pressure chamber), leaf area index, root distribution and soil-water potential (tensiometers). The model estimates the daily leaf water potential that controls the opening of the stomata which in turn regulate the transpiration flow by equating soil moisture abstraction and transpiration. The model was tested using data for the growing seasons of the Fontainebleu forest near Paris (France) in 1981, 1982 and 1983. Simulated transpiration and soil-water content correlated well with neutron probe measurements of the soil-water content. The model can be used for the quantification of tree water stress, which has numerous applications such as assessing stand productivity, disease and insect epidemic susceptibility, fire danger rating and nutrient cycling.

INTRODUCTION

Transpiration in a deciduous forest is a continuous process during the foliated phase and is quantitatively important amounting to 75% of precipitation during that period ($E_t = 333$ mm year^{-1} for average European tree species; Roberts, 1983). A quantitative estimate of transpiration flux required an investigation of water potential gradients and pathway resistances, as indicators of differential energy involved in the movement of liquid water (through the

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soil, roots, stems, branches and the stomatal cavity) as well as that of water vapour (from the stomatal cavities into the air). The component potentials and resistances are subjected to temporal and spatial variations determined by climatic parameters and plant properties (Passioura, 1982). Deciduous forest transpiration seems essentially to be governed by foliage development and stomatal regulation (Stewart, 1983; Morton, 1984; Halldin et al., 1984). Although it is easy to model the prediction of the leaf area index (Nizinski and Saugier, 1988b), it is not so for stomatal aperture which is affected by environmental factors such as light, CO_2 concentration, leaf water status, air humidity, temperature or other factors such as leaf age, nutrition, disease and gaseous polutants (O_3, SO_2, NO_x, etc.). The effect of these factors is difficult to quantify in the natural environment (Jones, 1983). The approach widely used in published forest transpiration models (Jarvis, 1976; Calder, 1977; Federer, 1979; Bringfelt, 1982; Halldin et al., 1984; Kowalik and Eckersten, 1984) is the regression of stomatal resistance against leaf water potential and/or specific humidity deficit and/or irradiance. The present paper presents a soil-water balance where transpiration is governed by a relationship between the stomatal resistance (r_s) and leaf water potential (ψ_1), the relationship changing with leaf age. The model is derived from the work of Saugier (1974), inspired by Cowan's study (1965), in which the so-called self-regulation of the plant water balance is brought about by capillary flow in the soil–plant–atmosphere continuum. Thus the model estimates the daily leaf water potential by equating transpiration and water uptake by roots. In Saugier's (1974) model developed for a natural grassland (*Agropyrum dasystachyum*), the empirical ratio of r_s to ψ_1 is constant for different values of the leaf-area index. In contrast to grassland where the leaf turnover is continuous, leaf production and senescence in deciduous tree species occur at different times of year. There is a given production of leaves (LAI_{max}) which is stable during the entire vegetative season and then decreases as senescence sets in. Therefore the ratio r_s/ψ_1 is related to leaf age.

MODEL DESCRIPTION

Soil-water content

Figure 1 presents a schematic plan of the model, whose output is the daily soil-water content (S). It is based on the water balance equation where the water balance of the root zone is the difference between the input, i.e. throughfall (P_n) and the output, i.e. drainage from the root zone (D) and water uptake by roots (U). According to Fardjah and Lemée (1980), the litter has a protective function (self-mulching), thus in the model, evaporation occurred in the litter only. The soil profile is supplied only by throughfall, the daily value of which was calculated from the interception model of Nizinski and Saugier

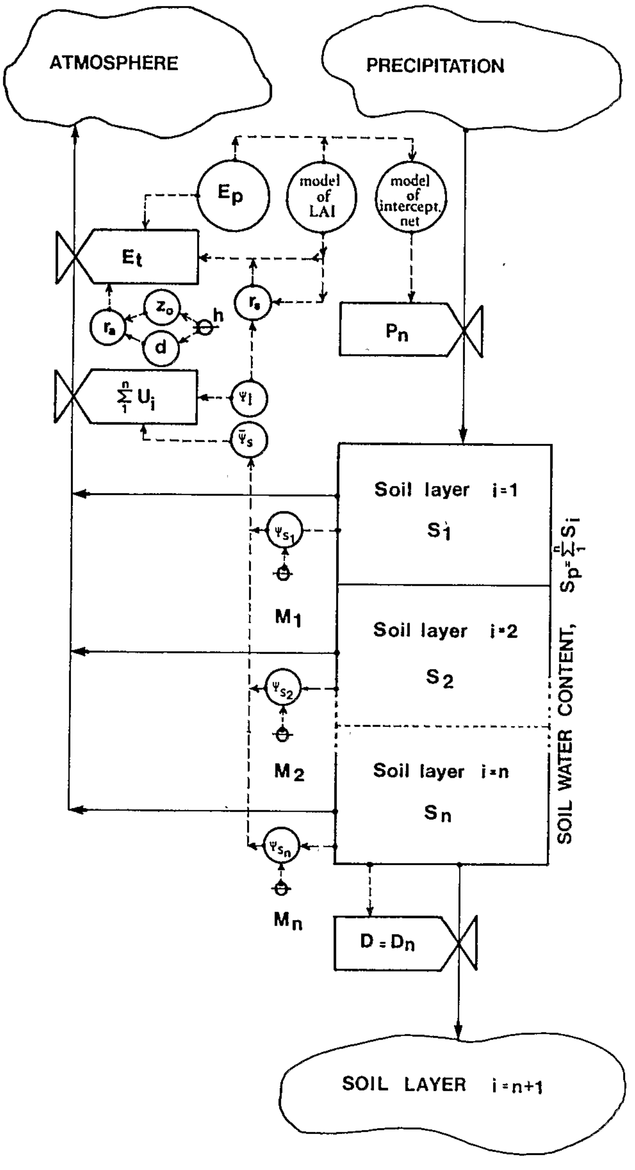

Fig. 1. Functional scheme of the soil-water content model (U_i: water uptake by roots in layer i; D_i: drainage from layer i; E_p: potential evaporation; E_t: transpiration; *LAI*: leaf area index; P_n: throughfall; M_i: length of the roots in layer i; S_i: soil-water content of layer i; *d*: zero plane displacement height; *h*: height of the forest; *i*: index of the soil layer; *n*: number of the soil layers; r_s: stomatal resistance; r_a: aerodynamic resistance; z_0: roughness height; ψ_l: leaf water potential; ψ_{si}: water potential of soil layer i).

(1988a). As the maximum daily precipitation at Fontainebleau was 71 mm day^{-1} (30 July 1947 and 1 August 1981), it is assumed that the soil at this site never attained saturated hydraulic conductivity and that run-off did not therefore exist (estimated by Fardjah (1978), the in situ saturated hydraulic conductivity of soils in Fontainebleau forest for the less-permeable pedologic horizon B is equal to $k_s = 6.1 \times 10^{-6}$ m s^{-1} or 527 mm day^{-1}). The soil profile is composed of n layers (i) with each layer being characterized by its soil-water retention thresholds, i.e. the maximum at field capacity (S_{FCi}) and the minimum at wilting point (S_{WPi}). The soil layers are seen as n tanks in series. Each layer drains to the layer below when the volume of water drained from the preceding layer ($D_{(\mathrm{i}-1)}$) added to the volume already present ($S_{\mathrm{i}(\mathrm{d}-1)}$) and reduced by the water volume taken up by roots (U_{i}) is greater than the field capacity of this layer (S_{FCi}). When the soil-water content of the last layer (n) exceeds its field capacity, there is water drainage from the root zone, thus $D = D_n$. Simulation starts on the first day of the year (day d = 1) and the initial condition was assumed: soil-water content of each layer equals field capacity ($S_{\mathrm{i}(1)} = S_{\mathrm{FCi}}$. The inputs for the model, expressed daily were: potential evapotranspiration (E_{p}), throughfall (P_{n}) and leaf area index (LAI). Four main parameters were used: the ratio of stomatal resistance to leaf water potential ($r_{\mathrm{s}}/\psi_{\mathrm{l}}$), distribution of root length (M_{i}), field capacity and wilting point of each soil layer (S_{FCi} and S_{WPi}).

Transpiration

In the model, the water uptake by roots is equal to transpiration (conservation of water flow from soil to the stomatal cavities) and water flow through all the roots, the stem, all the branches, all the leaves (liquid water flow) and the water vapour through the stomata into the air (water vapour phase) are equal and make up the transpiration flow.

Liquid water flow — water uptake by roots

Each layer (i) which is considered homogeneous has its characteristic soil-water retention and root distribution. This implies that the water uptake by roots is regular and equal over the whole depth of each layer. The total water uptake by roots over the whole soil profile was calculated using the mean soil-water potential (ψ_{s}) obtained from the soil-water potentials of the n layers (ψ_{si}) weighted by the coefficient (C_{i}) which is expressed as the ratio of root lengths in the soil layer i (M_{i}) to the total root lengths in the root zone (M) (Van Bavel and Ahmed, 1976). Thus, the water uptake by roots in the soil layer i can be described as

$$U_{\mathrm{i}} = ((\psi_{\mathrm{si}} - \psi_{\mathrm{l}})/R)\ C_{\mathrm{i}} \qquad (\mathrm{mm\ day^{-1}}) \qquad (1)$$

where ψ_{si} = soil-water potential of layer i (bar); ψ_{l} = leaf water potential (bar);

R = total resistance along the soil–plant pathway and the whole equal to: (a) soil hydraulic resistance for water flow in the soil, from soil to root surface hairs; (b) hydraulic resistance of the plant to waterflow, i.e. root epidermis, xylem and mesophyll hydraulic resistances (bar $\mathrm{day^{-1}\ mm^{-1}}$). The value for the resistance to liquid water flow in the plant, taken from the literature, is constant and of the magnitude $R=0.5$ bars $\mathrm{day^{-1}\ mm^{-1}}$ (Saugier, 1974); C_i = fraction of the total root length found in the soil layer i. The water uptake by roots in the total soil profile is therefore

$$U=\sum_{1}^{n} U_i=(\psi_s-\psi_l)/R \qquad (\mathrm{mm\ day^{-1}}) \tag{2}$$

where $\psi_s=\sum \psi_{si}C_i$ = average soil-water potential (bar); U = water uptake by roots in the whole soil profile ($\mathrm{mm\ day^{-1}}$); n = number of layers in the soil profile. For equal soil-water potentials the soil-water uptake by roots will be linearly proportional to the root length.

Soil-water potential

The soil-water potential for each soil layer i, on day d, ψ_{si}, was calculated from the soil-water content of the layer on day d−1, $S_{i(d-1)}$, expressed as a volumetric water content

$$\Theta_{i(d-1)}=(S_{i(d-1)}/h_i)\ 1000 \qquad (\mathrm{cm^3\ cm^{-3}}) \tag{3}$$

where $\Theta_{i(d-1)}$ = volumetric water content of the soil layer i, day d−1 ($\mathrm{cm^3\ cm^{-3}}$); h_i = layer thickness (m). The soil-water potential of layer i is given by Gardner (1960) as

$$\psi_{si}=A_i(\Theta_{i(d-1)})^{B_i} \qquad (\mathrm{bar}) \tag{4}$$

where A_i and B_i = coefficients dependent on the hydraulic characteristics of the soil layer i.

Water vapour flow — transpiration

The water vapour flow through the stomata is equal to the water vapour pressure gradient divided by the resistance to vapour transport through the stomata, cuticle and leaf boundary layer. For this simulation, Monteith's (1965) method was adopted, where the evaporative surface was considered as a single layer in which the mean stomatal resistance of the canopy is equal to the sum of the stomatal resistance of all the leaves. Thus the transpiration, E_t, rate from a forest canopy can be quantitatively expressed as follows

$$E_t=E_p(1+(\gamma/(\Delta+\gamma))(r_s/(LAI\ r_a))) \qquad (\mathrm{mm\ day^{-1}}) \tag{5}$$

where γ = psychrometric constant ($\mathrm{mb\ K^{-1}}$); Δ = slope of the saturation vapour pressure vs. temperature curve ($\mathrm{bar\ K^{-1}}$); r_s = stomatal resistance ($\mathrm{s\ m^{-1}}$); LAI = leaf area index; r_a = aerodynamic resistance ($\mathrm{s\ m^{-1}}$); E_p = potential evapotranspiration calculated by Penman's (1948) formula (mm day^{-1}) modified by van Bavel (1966)

$$E_p = (\Delta R_n + \rho c_p \delta e / r_a) / L(\Delta + \gamma) \qquad (\text{mm day}^{-1}) \qquad (6)$$

where R_n = net radiation (W m^{-2}); ρc_p = heat capacity of air at constant pressure (J m^{-3} K^{-1}); δe = saturation pressure deficit of air (mb); L = latent heat of vapourization of water (J kg^{-1}; 2.46×10^6).

Aerodynamic resistance

The turbulent diffusion resistance for heat and water vapour flow from the leaf boundary layer into the atmosphere (r_a) is related to wind speed and forest height. Under neutral stability conditions r_a is given by Monteith (1965) as

$$r_a = (1/(k^2 u))(\ln(z-d)/z_0)^2 \qquad (\text{s m}^{-1}) \qquad (7)$$

where k = von Karman constant (0.39); u = wind speed (m s^{-1}); z = height above ground (m); z_0 = roughness height (m); d = zero plane displacement height (m). In the absence of wind profile data, d and z_0, the surface roughness parameters, were estimated according to an empirical formula which relates both parameters to mean tree height (Thom, 1971)

$$d = 0.75h \qquad (\text{m}) \qquad (8)$$

$$z_0 = 0.10h \qquad (\text{m}) \qquad (9)$$

Stomatal resistance

Decrease in plant water content causes a decrease in leaf water potential (ψ_l). If the leaf water potential reaches a given threshold, i.e. the critical leaf water potential $\psi_{l\text{crit}}$, then tree water status begins to affect the stomatal resistance and stomatal closure begins. Different trees appear to have different thresholds for stomatal closure (Hsiao, 1973) but threshold values in deciduous trees generally range from -13 to -25 bar (Federer, 1977) (for *Q. petraea* $\psi_{l\text{crit}} = -15.7$ bar was calculated). Field measurements in the *Q. petraea* stand (Fig. 2b), suggested an empirical model for stomatal resistance in terms of leaf water potential and leaf age (Nizinski and Saugier, 1989)

(1) when $\psi_l > -25.5$ bar with $r^*_{\text{smax}} = 1.58$ s mm^{-1}

$$r_s = ((r^*_{\text{smax}} - r_{\text{smin}}) / \psi_{l\text{max}} - \psi_{l\text{crit}}))(\psi_l - \psi_{l\text{crit}}) + r_{\text{smin}} \qquad (\text{s mm}^{-1}) \qquad (10)$$

(2) when $\psi_l \leqslant -25.5$ bar

$$r_s = r_{\text{smax}} = 2.27 \text{ s mm}^{-1}$$

where r_s = mean stomatal resistance (s mm^{-1}); r^*_{smax} = theoretical maximal stomatal resistance (s mm^{-1}); r_{smin} = minimal stomatal resistance (s mm^{-1}); $\psi_{l\text{max}}$ = maximum leaf water potential (bar) and $\psi_{l\text{crit}}$ = critical leaf water potential (bar).

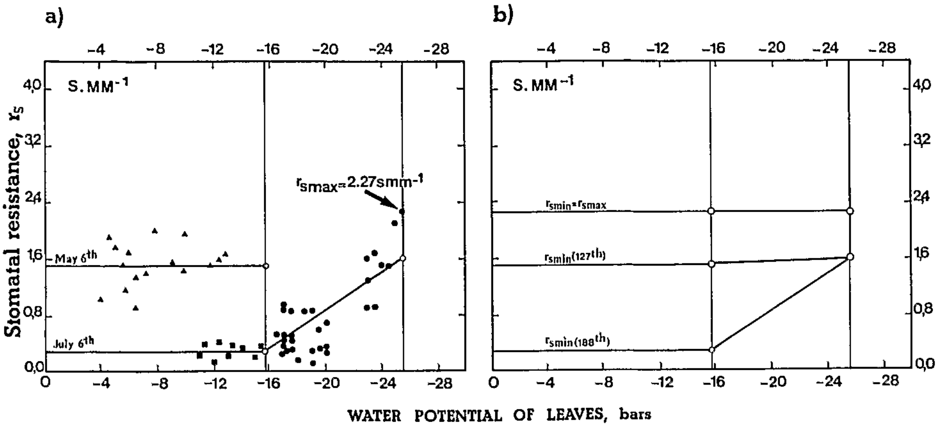

Fig. 2. Variations in the mean leaf stomatal resistance of the forest (r_s) with the mean leaf water potential of the canopy (ψ_l) for *Quercus petraea*. (a) Field measurements on different days during the 1983 growing season; (b) model (see eq. 10).

Leaf water potential

According to eq. 2, if the leaf water potential is less than or equal to the soil-water potential then water uptake by roots is nonexistent

$$\text{if } \psi_l \leqslant \psi_s \text{ then } \sum_1^n U_i \simeq 0 \qquad (\text{mm day}^{-1})$$

Otherwise, the water uptake by roots is equal to canopy transpiration

$$\sum_1^n U_i \simeq E_t \qquad (\text{mm day}^{-1}) \tag{11}$$

Then using eqs. 2 and 5, eq. 11 becomes

$$(\psi_s - \psi_l)/R \simeq E_p/(1 + (\gamma/(\Delta+\gamma))(r_s/(LAI\, r_a))) \qquad (\text{mm day}^{-1})$$

Upon rearrangement the actual leaf water potential (ψ_l) is given by

$$\psi_l = R(E_p/(1+\gamma/(\Delta+\gamma))(r_s/(LAI\, r_a))) + \psi_s \qquad (\text{bar}) \tag{12}$$

This is an implicit equation, because r_s depends on ψ_l (eq. 10). Thus, to estimate the actual leaf water potential an iterative technique has to be employed (Rose et al., 1976). The steps of the iteration are as follows (Fig. 3): take $\psi_l \geq \psi_{lcrit}$ so $r_s = r_{smin}$, if $U > E_t$ then take $\psi_l \leqslant \psi_{lcrit}$ so $r_s = r_{smax}$, if $U < E_t$ then $\psi_{lcrit} > \psi_l > \psi_{lmax}$ and $r_{smin} < r_s < r_{smax}$. Thus, the solution ($U \simeq E_t$) is between ψ_{lcrit} and ψ_{lmax}. The next step is to take $\psi_l = (\psi_{lcrit} + \psi_{lmax})/2$. The calculations are repeated to obtain a final value of ψ_l until the difference between calculated value of water uptake and transpiration is smaller than initial accuracy α (taken arbitrarily).

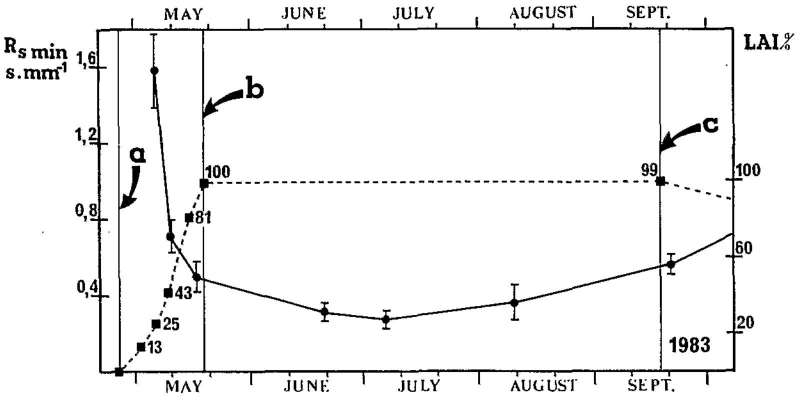

Fig. 3. Changes in minimal stomatal resistance with leaf age in *Quercus petraea* at Fontainebleau forest during the 1983 growing season (r_{smin} (●) = minimal stomatal resistance; *LAI* (■) = leaf area index; *a* = budburst day; *b* = first day of fully leaved phase; *c* = leaf fall).

SITE DESCRIPTION AND MEASUREMENTS

Study site

Field work was carried out on plot No. 267 ("Gros-Fouteau"), situated on a rise in the centre of the 22 000-ha Fontainebleau Forest near Paris (48°26′N, 2°41′E) at 136 m altitude. The limestone bedrock is covered with silicious, quaternary wind-blown sand. The depth of the sandy layer has determined the characteristics of the plot's soils: these are leached or podzolic. The climate of the region is partly maritime, partly subcontinental. The mean annual precipitation (1883–1983) is 720 mm, being fairly evenly distributed throughout the year (with a maximum of 72 mm in January and December and a minimum of 48 mm in March and 46 mm in April). The mean annual temperature is 10.2°C (average of monthly means of 18.2°C in July and 2.2°C in January). The overstory canopy is exclusively 120-year-old oaks (*Q. petraea*). The mean tree height is 30 m, stand density is 182 trees ha^{-1} and the total basal area is 33.8 m^2 ha^{-1}. The understory consists mainly of seedlings and beech saplings (*Fagus silvatica*). According to Lemée (1966), the vegetation of the sample site is characteristic of an oak stand on acid soils.

Material and methods

Morpho-physiological parameter measurements

During the growing seasons of 1982 and 1983 three main model parameters were measured in situ.

Stomatal resistance

The stomatal resistance measurements were made using a portable porometer "MK II" from "Delta T Devices" (Monteith and Bull, 1970) on randomly-selected leaf samples in the tree canopy; in total 50 sampled leaves day^{-1}.

Leaf water potential

After stomatal resistance measurements, the leaf was separated from the branch with a razor blade at the leafstalk base and inserted into a pressure chamber (PMS Inst. Co., Corvallis, Oregon, U.S.A.; error range ±0.5 bars). The technique for estimating the plant water status using a pressure chamber is described in detail by Ritchie and Hinckley (1975).

Root distribution

The roots were harvested on 18 February 1983, from a pit reaching the limestone slab (limit of the soil profile), at a depth from 0.7 to 1.0 m, between two mature trees, 8 m apart. The roots were extracted from 1-dm^3 cubes of soil taken from three pedological horizons; in total 24 samples. The roots were graded by size: (a) "small roots" having a diameter equal or smaller than 1 mm, and regarded as absorptive roots; (b) "large roots" with a diameter larger than 1 mm and regarded as non-absorptive roots. For each layer the total length of the small roots was estimated using the line intersection method described by Newman (1966).

Soil-moisture measurements

Soil-water content

The neutron probe "Solo" made at the Centre d'Etudes Nucléaires in Cadarache was used. The neutron probe calibration was established by Fardjah (1978) using the gravimetric technique. The measurement device is composed of nine permanent access tubes that reach down to the limestone slab. Measurements were made in each tube every 10 cm from the soil surface (from 29 January 1981 to 21 December 1983) every 20–30 days during the non-foliated phase and weekly during the foliated phase. The soil-water content sum (expressed in mm) of each layer of the tube makes up the tube (profile) soil-water content. For each layer of each tube, the mean soil-water content measured during the non-foliated phase (transpiration nonexistent) was considered as the field capacity value and the lowest value of the soil-water content measured at the research plot during the 3-year study period was used as the permanent wilting point. The difference between the field capacity value and the permanent wilting point value made up the "available water" content of each soil layer and the sum of the layer's "available water" content made up the "available water" of the soil profile.

Volume-potential curves

The volumetric water content was plotted relative to the soil-water potential for all the layers in the nine access tubes on the following basis: (1) the volumetric soil-water content measurements ($cm^3\,cm^{-3}$); (2) soil-water potential: (a) at the field capacity (S_{FC}) of $\psi_{SFC} = -0.1$ bars and at permanent wilting point (S_{WP}) of $\psi_{SWP} = -16$ bars for sandy soils (Rutter, 1975); (b) obtained from measurements at the study site for the soil-water potential range within -0.1 and -0.8 bars, using "soil moisture" tensiometers.

RESULTS AND DISCUSSION

Morpho-physiologic parameters

Stomatal resistance/leaf water potential

The response of stomata to the development of leaf water potential has three distinguishable curve phases (Fig. 2a) according to eq. 10.

(1) First phase. If the leaf water potential is greater than or equal to the critical leaf water potential ($\psi_{1crit} = -15.7$ bars) then the stomatal resistance is constant and a minimum for the given leaf age (minimal stomatal resistance changes with leaf age). Figure 3 illustrates this development during the 1983 growing season, from budburst day (26 April) to leaf senescence (26 October). Eleven days after budburst, stomatal resistance closed to 1.58 ± 0.19 s mm^{-1} for the leaf area index equal to 21% of the maximum leaf area index ($LAI_{max} = 4.38$). The leaf surface increase corresponded to the rapid decrease of minimal stomatal resistance (r_{smin}), with r_{smin} being equal to 0.5 ± 0.08 s mm^{-1} when the leaf area index is maximal (18 May). This decrease continued until its lowest minimum value of 0.29 ± 0.03 s mm^{-1} on 6 July, after which the value of r_{smin} increased from 0.29 to 0.56 ± 0.02 s mm^{-1} (21 September). On 21 September, leaf senescence began ($LAI = 99\%$ of LAI_{max}), reaching 0.74 ± 0.12 s mm^{-1} on 26 October ($LAI = 75\%$ of LAI_{max}). This first phase is represented by the straight line series $r_{smin} = \text{constant}$ for $\psi_1 \geqslant \psi_{1crit}$.

(2) Second and third phases, i.e. the stomatal regulation phase. According to the measurements, the relationship between leaf water potential and stomatal resistance is an exponential function (Ritchie and Hinckley, 1975) for a given leaf age. This stomatal regulation phase can be expressed by the exponential curve series, but in view of scattered experimental points and the fact that the numerical resolution of Rose et al. (1976) to estimate the leaf water potential was used (Figs. 2b and 4), each exponential function was reduced to two linear functions.

(a) The first linear function is expressed by eq. 13. This is the second phase.

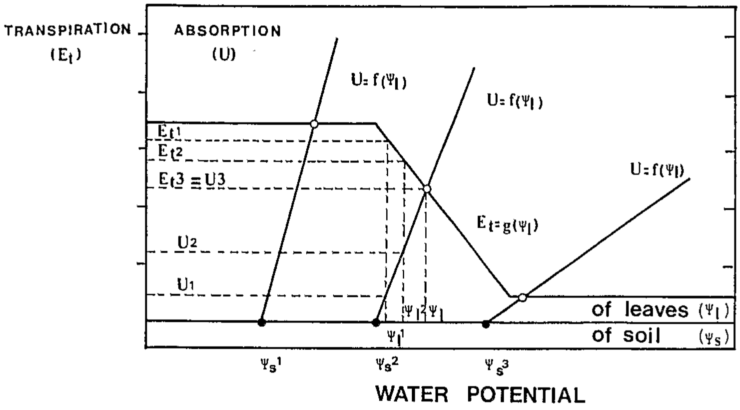

Fig. 4. Scheme of leaf water potential estimation (see "Leaf water potential").

$$r_s = b - a\,|\psi_l| \quad (\text{for } \psi_{l\mathrm{crit}} > \psi_l > \psi_{l\mathrm{max}}) \qquad (\mathrm{s\ mm^{-1}}) \qquad (13)$$

With leaf age increasing until the beginning of July, a increases and b decreases, after which the trend is reversed. Thus this relationship expressed for 20 July 1983 is: $r_s = 0.132|\psi_l| - 1.778$ (s mm^{-1}). The critical leaf water potential value was −15.7 bars, which is similar to the value obtained by Aussenac and Levy (1983) for *Q. pedunculata* (−14 bars).

(b) The second linear function expressed by $1.58 < r_s < 2.27$ (s mm^{-1}) for $\psi_l > -25.5$ bars is valid for all leaf age. This is the third phase. The value of $r^*_{\mathrm{smax}} = 1.58$ s mm^{-1} (theoretical maximal stomatal resistance) is the calculated value representing the intersection point between the eq. 12 series and this function, the values of $r_s = 2.27$ s mm^{-1} and $\psi_l = -25.5$ bars being the maximal measured values for stomatal resistance and leaf water potential (20 July 1983). The maximum stomatal resistance value of $r_s = 2.27$ s mm^{-1} used in the model compares with the $r_s = 3$ s mm^{-1} value obtained for *Q. pedunculata* by Aussenac and Levy (1983).

Root distribution

The root system of *Q. petraea* has one or more taproots which ramify on contact with the limestone slab located between 0.5 and 1.5 m of depth. The root lengths per unit soil volume change with soil depth: they are long in horizon A_1 (1.23 ± 0.22 m dm^{-3}), decrease on A_2 (0.38 ± 0.14 m dm^{-3}) and increase again on horizon B (0.9 ± 0.33 m dm^{-3}), the increase being greater for small roots. The root lengths per unit soil volume are similar for the four analysed soil profiles. The distribution of the root lengths per unit soil volume depends on the amount of available water (S_{AW}) in the soil, with maximum rooting observed on A_1 ($S_{\mathrm{AW}} = 13.2$ mm and $M = 1.23$ m dm^{-3}), minimum rooting in A_2 ($S_{\mathrm{AW}} = 8.8$ mm and $M = 0.38$ m dm^{-3}), and average rooting in B

($S_{AW}=10$ mm and $M=0.9$ m dm^{-3}). Thus, the trees seem to equilibrate hydraulically with "wet" areas in the soil profile (observed at Fontainebleau Forest in *Fagus silvatica* by Fardjah and Lemée (1980)).

SOIL-WATER CONTENT — DISCUSSION AND CONCLUSION

A simulation of the soil-water content development was made for the 1981, 1982 and 1983 growing seasons (from budburst to leaf fall at 50% of LAI_{max}) for nine neutron access tube sites. The simulated values for soil-water content and those measured in situ were compared (Fig. 5). To avoid ambiguity when testing the model against the average value of the stand tube No. 21 was used as a representative of the study plot. The quantitative importance of transpiration was confirmed. The mean value was 288.4 mm year^{-1} (339.8, 241.1, 284.2 mm year^{-1}) (76.4% of precipitation) or 1.63–2.15 mm day^{-1} (mean growing season, 154 days duration; 158, 148, 156 days). These results correspond to those found by Ambros (1978) for *Q. pedunculata* (250–320 mm year^{-1}), by Aussenac and Granier (1979) for *Q. petraea* (254–300 mm year^{-1}) and by Roberts (1983) for *Q. petraea* (320–327 mm year^{-1}). The simulated soil-water content corresponded well with the in situ measurements, although the study period covered climatically different years (with precipitation in 1981 being 1085 mm, which is 51% more than the mean annual value for 103 years (720.4 mm); the annual values for 1982 of 791 mm and for 1983 of 744.4 mm were close to the yearly mean value. The simulated soil-water content for 1982 was good, but for 1981 and 1983 it was sometimes under- or overestimated. There is a tendency to underestimate for the periods when the soil-water content nears field capacity (May, June, July, August of 1981 and at the beginning of May, 1983), and to overestimate for the "dry" periods (June, July, August, October of 1983). There are several explanations for the differences between the simulated and measured values. The net interception model (Nizinski and Saugier, 1988a) underestimated throughfall during the foliated phase in 1981. From 24 April to 6 November, the throughfall was underestimated by -9.9 mm, which can explain the underestimation of the soil-water content in May, June, July and August of 1981. The hydraulic properties of the soil were not studied experimentally. As the relationship between the soil-water potential and the soil-water content was largely based on data in the literature, the soil-water content corresponding to the given soil-water potential could be too low or too high due to hysteresis. It is possible that the *Q. petraea* roots penetrated the limestone slab cracks. In this case, the actual water uptake by roots would have been in the soil profile as well as in the limestone slab cracks. The given simulated transpiration took into account the water uptake of roots in the soil profile only, which would result in an overestimation of water uptake by the roots and consequently, an underestimation of the soil-water content. In the model, drainage occurs during a day of precipitation and in the next step of

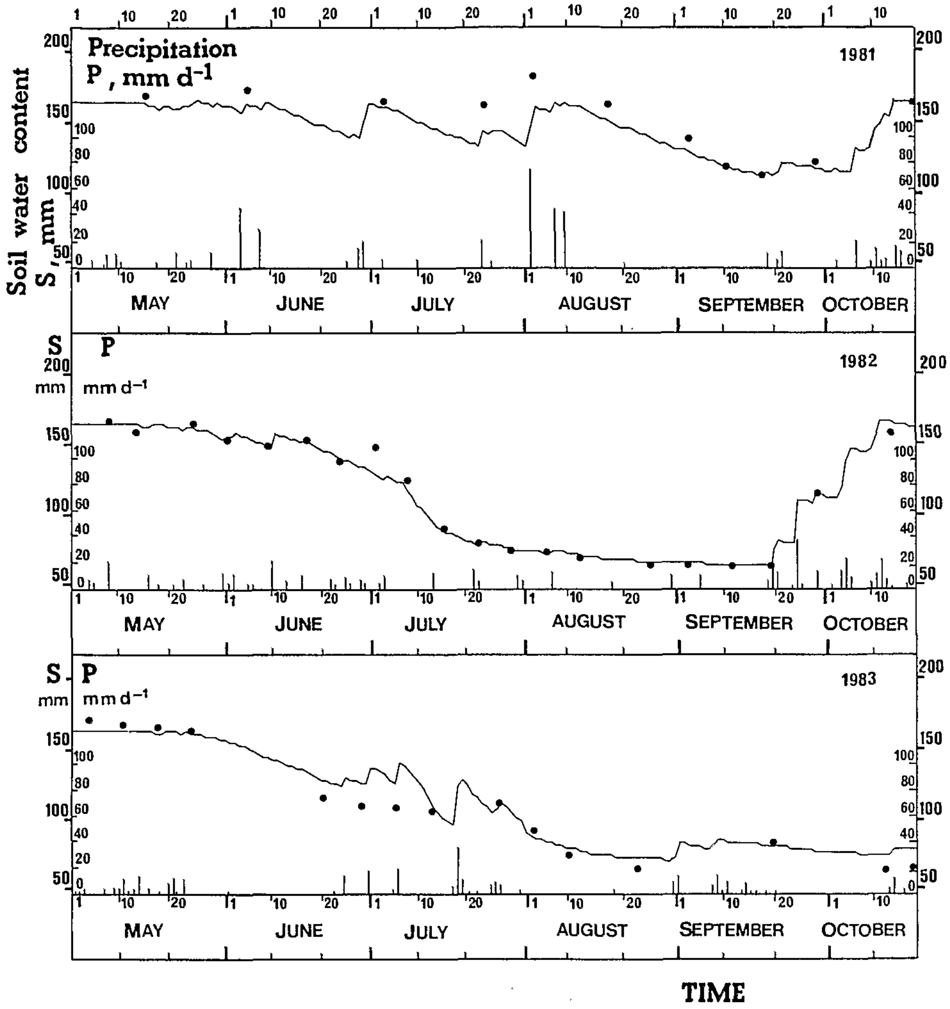

Fig. 5. Simulated (——) and measured (●) total soil-water content during the 1981, 1982 and 1983 growing seasons. Tube No. 21 (field capacity: $S_{FC}=166.6$ mm; permanent wilting point; $S_{WP}=63.2$ mm).

simulation (day d+1) the actual soil-water content is equal to the field capacity. However, it seems that the actual drainage is slower. So after precipitation which causes drainage, the actual water content is above field capacity and can remain so for only 1 more day. Two examples can be given to illustrate this: (a) on 1 August 1981, after precipitation of 70.4 mm the measurement indicated $S=188.5$ mm (2 August 1981), which is 22 mm more than field capacity; (b) after 2 days of precipitation on 15 March 1982 ($P=9.4$ mm) and 16 March 1982 ($P=3.5$ mm), the soil-water content measured on 17 March 1982 was

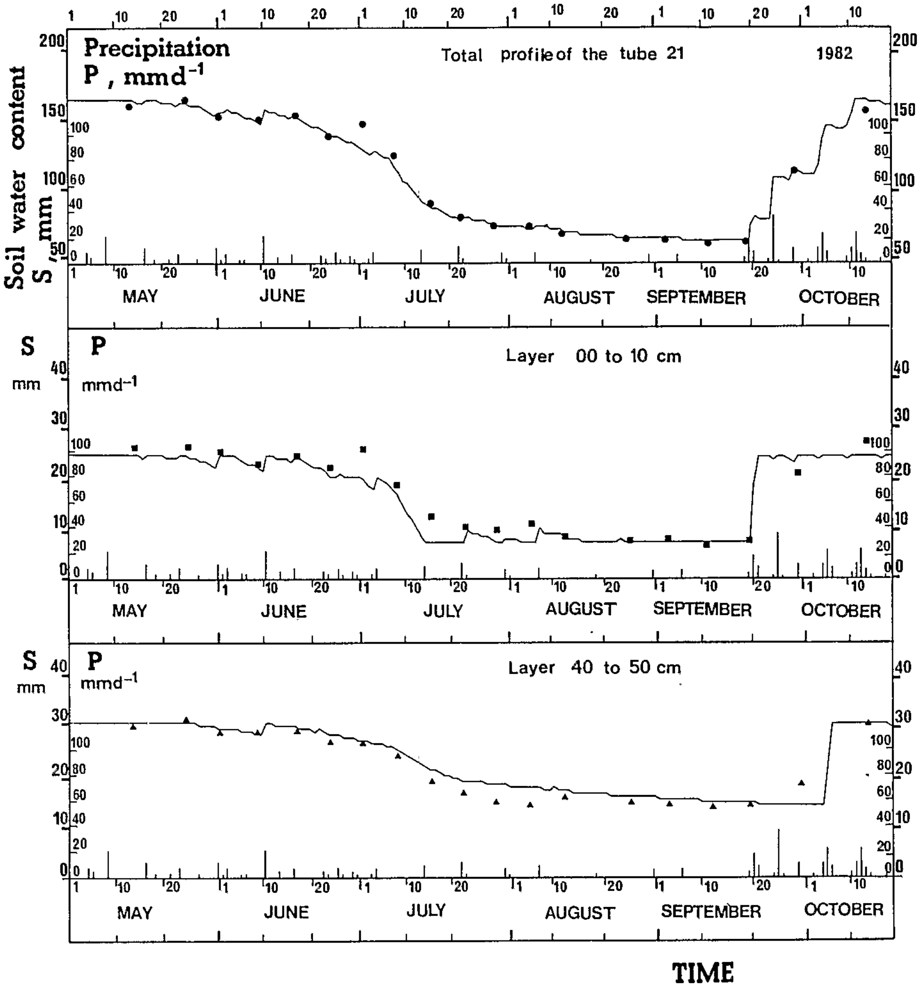

Fig. 6. Simulated (——) and measured (● ■ ▲) values for the total soil-water content in tube No. 21, for the soil layers 0–0.10 m ($S_{\mathrm{FC}(1)}=23.9$ mm; $S_{\mathrm{WP}(1)}=7.2$ mm) and 0.40–0.50 m ($S_{\mathrm{FC}(5)}=30.2$ mm; $S_{\mathrm{WP}(5)}=14.0$ mm) during the 1982 growing season.

$S=180.3$ mm, which is 13.7 mm above field capacity. In the model, rapid drainage may well lead to an underestimation of the actual soil-water content when S approaches field capacity, i.e. at the beginning or end of the vegetative season or after heavy precipitation (e.g. on 1 August 1981). In addition, the water uptake by the roots of understory trees ($LAI_{\mathrm{max}}=0.95$; height of 1–4 m) was not taken into account. This probably caused an overestimation of the simulated soil-water content.

Moreover, it seems that there is compensation between two or more of the model outputs. For example, in the 3 years of study the simulations of the soil-water content in the total soil profile for 1982 were closest to the in situ measurements (Fig. 6), because an overestimation of the soil-water content in the 0–10 cm layer (horizon A_1) was compensated for by an underestimation in the 40–50 cm layer (B horizon). This type of compensation becomes progressively more marked from May to September. Computation of water uptake in the soil layers implies that the root lengths per unit soil volume are constant in time. In fact, according to Reich et al. (1980) for *Q. alba* and to Johnson et al. (1984) for *Q. rubra* root lengths and absorption capacity show spatial and temporal variation. Future studies of the water uptake by roots in the soil profile need to emphasize dynamic and spatial aspects. Here, stomatal resistance was considered in relation to temporal variations (leaf ageing) and to spatial variations (leaf position within the tree crown). Introducing the leaf ageing parameter into the r_s/ψ_1 ratio (eq. 10) improved the accuracy of the predicted transpiration, which consequently correlated well with the measured soil-water content. Leaf sampling within the crown ought to be possible to extrapolate the stomatal resistance results to the rest of the crown. Branch position, distance above ground, distance from trunk, aspect of leaves, etc. are additional complications that require careful planning prior to sampling (Nizinski, 1986). As regards pathway resistance to water flow through the soil–plant–atmosphere continuum, the total resistance for the liquid water flow (R) was considered constant, while the stomatal resistance (r_s) was considered to respond to changing conditions. Future models ought to integrate variations in the total resistance of liquid water flow by taking into account the development of the root lengths (or of the absorbant surfaces of roots) in the temporal perspective, as was done for the leaf area index development. Variations in stomatal resistance expressed as a function of leaf area index and leaf age for a given condition, describe the morphologic development of the leaves; progressive increase in the number of stomata per leaf surface unit, reduction of leaf hairiness, wax-filling of the stomatal pores, etc. — this has been observed for *Castanea sativa* and *Q. petraea* (Nizinski and Saugier, 1989).

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ABSTRACT

Nizinski, J. and Saugier, B. (1988). A model of transpiration and soil-water balance for a mature oak forest. Agricultural and Forest Meteorology.

A hydrologic model for the development of the soil-water content in a 120 year-old oak stand *(Quercus petraea)* is presented with a one day time resolution. The model was conceived for working with daily potential evapotranspiration, throughfall and leaf area index data. It predicts transpiration from the dry canopy and soil-water content. The canopy is considered as a single leaf (the PENMAN-MONTEITH's equation) which entailed measurements of the physiological control of vapour flow from the leaf such as stomatal resistance (porometer), leaf water potential (pressure chamber), leaf area index, root distribution and soil-water potential (tensiometers). The model estimates the daily leaf water potential equalizing absorption and transpiration, that controls the opening of the stomatas which in turn regulate the transpiration flow. The model was tested during the growing seasons of 1981, 1982 and 1983 in the Fontainebleau forest (22000 ha) near Paris (France). Simulated transpiration and soil-water content correlated well with measurements of the soil-water content (neutron probe). The model can be used for the quantification of tree water stress, which has numerous applications such as assessing stand productivity, disease and insect epidemic susceptibility, fire danger rating and nutrient cycling.

Key words: Forest, water balance, *Quercus petraea*, modelling, stomatal resistance.