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Original article

Interpreting the variations in xylem sap flux density within the trunk of maritime pine (*Pinus pinaster* Ait.): application of a model for calculating water flows at tree and stand levels

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Abstract – Sap flux density was measured throughout a whole growing season at different locations within a 25-year-old maritime pine trunk using a continuous constant-power heating method with the aim of 1) assessing the variability of the sap flux density within a horizontal plane of the stem section and 2) interpreting the time shift in sap flow at different heights over the course of a day. Measurements were made at five height levels, from 1.3 to 15 m above ground level. At two heights (i.e. 1.30 m and beneath the lower living whorl, respectively), sap flux density was also measured at four azimuth angles. Additionally, diurnal time courses of canopy transpiration, needle transpiration, needle and trunk water potential, and trunk volume variations were measured over 4 days with differing soil moisture contents. At the single tree level, the variability of sap flux density with respect to azimuth was higher at the base of the trunk than immediately beneath the live crown. This has important implications for sampling methodologies. The observed pattern suggests that the azimuth variations observed may be attributed to sapwood heterogeneity caused by anisotropic distribution of the sapwoods hydraulic properties rather than to a sectorisation of sap flux. At the stand level, we did not find any evidence of a relationship between the tree social status and its sap flux density, and this we attributed to the high degree of homogeneity within the stand and its low LAI. An unbranched three-compartment RC-analogue model of water transfer through the tree is proposed as a rational basis for interpreting the vertical variations in water flux along the soil–tree–atmosphere continuum. Methods for determining the parameters of the model in the field are described. The model outputs are evaluated through a comparison with tree transpiration and needle water potential collected in the field. (© Inra/Elsevier, Paris.)

sap flux / transpiration / water transfer model / *Pinus pinaster*

Résumé – Interprétation des variations de densité de flux de sève dans le tronc d'un pin maritime (*Pinus pinaster* Ait.) : application d'un modèle de calcul des flux aux niveaux arbre et peuplement. La densité de flux de sève brute d'un pin maritime de 25 ans a été mesurée en

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continu à différentes positions du tronc et durant une saison de croissance complète, par une méthode à flux de chaleur constant, dans le but a) d'étudier la variabilité de la densité de flux dans la section transversale du tronc et b) d'analyser le décalage de temps du signal entre différentes hauteurs au cours de la journée. Les mesures ont été effectuées à cinq hauteurs, de 1,3 à 15 m au dessus du sol. À deux niveaux (1,3 m et sous la couronne vivante, respectivement) la densité de flux a été mesurée suivant quatre azimuts. L'évolution journalière de la transpiration du couvert, de la transpiration des aiguilles, du potentiel hydrique du tronc et des aiguilles et des variations de volume du tronc a aussi été mesurée durant quatre journées couvrant une gamme de niveaux d'humidité du sol. Au niveau arbre, la variabilité de la densité de flux de sève dans la section horizontale de l'aubier était plus élevée à la base du tronc que sous la couronne. Ceci pourrait s'expliquer par l'anisotropie des propriétés mécaniques et hydrauliques du bois dans le plan horizontal, classique chez le pin maritime, plutôt que par une sectorisation du flux liée à l'architecture de la couronne. Au niveau peuplement, aucune relation entre la densité de flux de sève et le statut social de l'arbre n'a été mise en évidence, ce qui s'explique par l'homogénéité du peuplement et son faible indice foliaire. Nous avons utilisé un modèle de transfert RC à trois compartiments pour interpréter les variations de flux de sève le long du transfert sol-aiguille. Les méthodes de détermination des résistance et capacitance de chaque compartiment sont décrites. Les sorties du modèle ont été comparées avec les mesures de transpiration, flux de sève et de potentiel hydrique mesurées dans deux peuplements âgés de 25 et 65 ans respectivement.. Le modèle explique assez bien les variations de flux observées le long du continuum sol–aiguille. Au cours de la sécheresse, on observe une augmentation importante (× 10) de la résistance du compartiment racine–tronc. Cette augmentation est moins importante dans les branches (× 2). Les capacitances sont peu affectées par la sécheresse. (© Inra/Elsevier, Paris.)

***Pinus pinaster* Ait / transpiration / flux de sève / modèle de transfert hydrique**

1. INTRODUCTION

Sap flow measurement is a useful method for assessing the water use by forest trees; it does not require horizontally homogeneous stand structure and topography and therefore can be used in situations where methods such as eddy covariance cannot. Sap flow measurements allow one to partition the stand water flux between canopy sublayers or to discriminate between particular individuals in a stand. Sap flow data have been used for estimating hourly transpiration and canopy conductances in a range of forest stands [1, 10, 13, 19, 20]. The sap flow measurements can provide a useful investigative tool for a variety of purposes, providing the results can be properly upscaled to the stand level, which requires a description of the network of resistances and capacitances which characterise the pathway of water between the soil and the atmosphere [18, 26]. In order to do this, we need a scheme for quantitatively interpreting sap flow measurements on a rational basis. Until now, the methods used for extrapolating sap flow data to estimate stand transpiration have remained rather empirical, with the capacitances in the water transfer process within trees either being ignored [1, 7, 19] or extremely simplified, such as being reduced to a constant time shift between sap flux and transpiration [13]. Resistance and capacitance to water transfer within some forest trees have been determined for stem segments [9, 31] and for whole trees (using cut-tree experiments). However, the extent to which these measured values can be applied under natural conditions is questionable, since both methods rely on the analysis of pressure–flux relationships and water retention curves determined mainly under positive or slightly negative pressures [9]. Cohen et al. [4] proposed a method for estimating soil-to-leaf bulk resistance in the field based on sap flux measurement which avoided this 'artefact', and has been applied to different

forest species [1, 14, 23]. Using a resistance–capacitance analogue of the flow pathway, Wronski et al. [37] and Milne [25] derived values of stem resistance and capacitance from field measurements of water potential, stem shrinkage and transpiration on radiata pine and sitka spruce, respectively.

The aim of this paper is to present a simple RC analogue of water transfer within the soil–tree–atmosphere continuum in order to interpret diurnal variations of flux and water potential observed at different locations in the tree. Methods are described that allow the determination of both the resistance and capacitance of the tree, based on sap flux measurement in the field. In addition, we summarise the results obtained concerning the sap flux heterogeneity within a maritime pine stand in a horizontal plane and suggest methods for improving the accuracy of the estimation of water flux at tree and stand levels.

2. AN UNBRANCHED RC MODEL OF TREE WATER FLUX

The flow pathway along the soil–tree–atmosphere continuum is considered as a series of RC units. This sort of model was first applied by Landsberg et al. [22] on apple trees and solutions for estimating the water potential from transpiration measurements was given, e.g. by Powell and Thorpe [28]. The present model considers the tree as a three-compartment system: i) root and trunk, ii) branches and iii) needles. Such an approach has been applied to different coniferous trees, e.g. *Pinus radiata* [37], *Picea sitchensis* [25] and *Picea abies* [5]. *Figure 1* illustrates

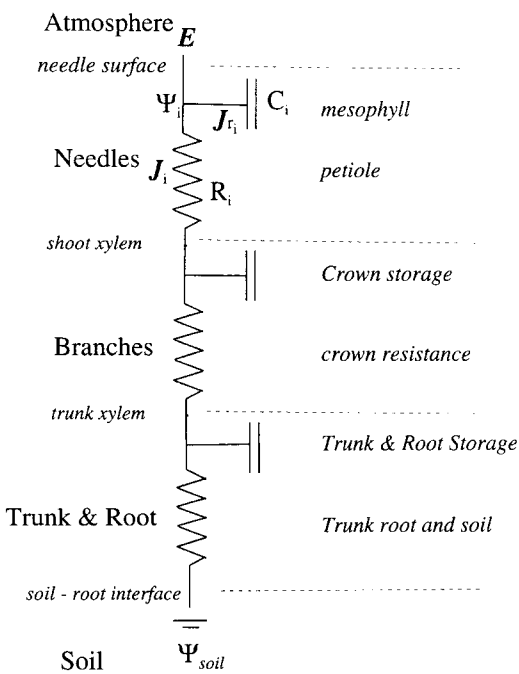

Figure 1. Electrical analogue of the model. Only the upper compartment is fully annotated.

the electrical analogue of the model. The main assumptions of our analysis can be summarised as follows:

– the crown is treated as a big leaf with a homogeneous temperature and transpiration rate;

– the resistance and capacitance of each compartment are independent of the flux or water potential of the compartment and remain constant during the day (but they can change between days);

– there is no storage resistance, that is the water potential gradient between the reservoir and the xylem can be neglected.

In the following, all the fluxes, resistances and capacitances are expressed on an all-sided needle area basis. The water potential values used in the present paper are corrected for the gravitational gradient. The basic equations for each compartment are as follows:

$$J_{i+1} = J_i + Jr_i \tag{1}$$

where

$$Jr_i = -C_i \cdot \frac{d\Psi_i}{dt} \tag{2}$$

$$J_i = \frac{\Psi_i - \Psi_{i-1}}{R_i} \tag{3}$$

where $\boldsymbol{J}_i$ is the liquid water flux expressed in $kg \cdot m^{-2} \cdot s^{-1}$, $\boldsymbol{J}r_i$ the storage flux, R_i ($MPa \cdot kg^{-1} \cdot m^2 \cdot s$) and C_i ($kg \cdot m^{-2} \cdot MPa^{-1}$) the resistance and capacitance of the compartment and Ψ_i its water potential (MPa). The subscript i denotes the compartment and can be either c for the branches of the crown, s for the stem and root, or n for the needles. If we assume that any change in the water potential of the lower compartment during each time step can be neglected, replacing Jr_i and J_i in equation (1) leads to the differential equation:

$$R_i \cdot C_i \cdot \frac{d\Psi_i}{dt} + \Psi_i = \Psi_{i-1} - J_{i+1} \cdot R_i \tag{4}$$

which can be solved for Ψ_i and $\boldsymbol{J}r_i$, giving the following expressions:

$$\Psi_i(t) = \Psi_{i-1}(t - \Delta t) - J_{i+1}(t) \cdot R_i + \left(\Psi_i(t - \Delta t) - \Psi_{i-1}(t - \Delta t) + J_{i+1}(t) \cdot R_i\right) \cdot \exp\left(\frac{-\Delta t}{R_i \cdot C_i}\right) \tag{5}$$

$$Jr_i(t) = \left(\frac{\Psi_i(t - \Delta t) - \Psi_{i-1}(t - \Delta t)}{R_i} + J_{i+1}(t)\right) \cdot \exp\left(\frac{-\Delta t}{R_i \cdot C_i}\right) \tag{6}$$

Equations (1), (5) and (6) allow us to estimate iteratively the time course of water flux and potential from the initial values of a given flux, J_i, and water potential, Ψ_i.

The parameters of the model can be derived as follows. The resistance of each compartment is given by the slope of the regression line relating the instantaneous sap flux within the compartment, $\boldsymbol{J}_i$, to the instantaneous difference between the water potentials at its upper and lower boundaries, i.e. $\Psi_i(t) - \Psi_{i-1}(t)$ [equation (3)]. A similar calculation has been applied previously for the whole tree, e.g. by Cohen et al. [4], Granier et al. [14] and Bréda et al. [1]. This analysis must be carried out with data covering the entire daily time course, where the final water content of the tree is equal to the initial. It does not necessarily require that measurements be made under steady-state conditions, i.e. $Jr_i(t)$ may take positive or negative values. In order to estimate the capacitance of the root + stem and branch compartments, we calculate the value of $\exp\left(\frac{-\Delta t}{R_i \cdot C_i}\right)$ as the slope of the regression line fitted between $Jr_i(t)$ and

$$\left(\frac{\Psi_i(t-\Delta t)-\Psi_{i-1}(t-\Delta t)}{R_i}+J_{i+1}(t)\right)$$

according to equation (6) and then extract the value of C_i using the value of R_i calculated previously. For the capacitance of the needle compartment, we used a value of 0.025 kg·MPa^{-1}·m^{-2}, assuming a bulk elastic modulus of 25 MPa [36] and a semi-cylindrical needle shape with an average diameter of 0.002 m.

3. MATERIALS AND METHODS

3.1. Sites

The model was parameterised and evaluated using data collected from two different experiments, at the Bray site in France (44°42N, 0°46W) and the Carrasqueira site in Portugal (38°50N, 8°51W) *(table I)*. Both sites were pure even-aged stands of maritime pine with an LAI ranging between 2.0 and 3.5. In both locations, the soil water retention capacity is rather low due to the coarse texture of the soil and a summer rainfall deficit that induces soil drought and subsequent tree water stress, this summer drought being far more severe at the Portuguese site. The sites were equipped with neutron probe access tubes and scaffolding towers, enabling monitoring of the soil moisture and micrometeorological variables. The Bray site has been extensively studied since 1987 and a detailed description can be found, e.g. in Diawara et al. [6]. The Carrasqueira site is also part of several Portuguese and European research projects and is described by Loustau et al. [24].

Determination of the model parameters was carried out for a single tree at the Bray site on 4 days (days 153, 159, 229 and 243) in 1995. *Table II* summarises the sampling procedure applied for each variable measured.

3.2. Azimuthal variability of sap flux density

Azimuthal variations in sap flux density across the sapwood horizontal section were assessed on three trees at the Bray site. Sensors were inserted at a height of 1.30 m in four azimuthal orientations. For one tree, sensors were inserted at 1.50 and 8.50 m, just below the last living whorl. Sap flux densities were monitored from May to August 1991 on two trees, and from May to September 1995 on the tree with two measurement heights. The trees were then cut and a cross section of stems at each measurement height was cut, rubbed down, polished and scanned with a high resolution scanner (Hewlett Packard Scanjet II cx). The number of rings crossed by each heating probe and the total conducting area were determined together with the ratio between the earlywood and latewood area crossed by the probe. We analysed only the data collected during clear days and considered only the normalised daily sums of sap flux density.

Table I. Main characteristics of the pine stand at the two experiment sites.

Site	Age (years)	Basal area at height of 1.3 m (m^2·ha^{-1})	Standing stock (stems·ha^{-1})	Leaf area index (m^2·m^{-2})	Mean height (m)	Mean cirumference at height of 1.3 m (m)	Sapwood basal area (m^2·ha^{-1})
Carrasqueira 1994	64	29.8	312	2.7	24.1	1.08	11.06± 0.62 (at 6 m high)
Bray 1995	25	35.9	660	3.0	15.8	0.81	10.86 ± 0.85 (at 8.5 m high)

Table II. Sampling scheme of the variables measured on the sample tree at the Bray site (1995).

Compartment	Height (m)	Number of replicates for each variable measured		
		Sap flux density, j (sap flow sensors)	Trunk shrinkage (displacement gauges)	Water potential Ψ_i (pressure chamber or soil psychrometer)
Needles	13	1		4 bare shaded needles (Ψ)
Branch	13	1		4 enclosed needles (Ψ_n)
	9		2	4 enclosed needles(Ψ_s)
	8.5	4		
	6.5	2	2	
Trunk	4.5	2	2	
	1.5	4	2	
	0.5	2	2	
Soil	0 to –0.5			15 psychrometric chambers Ψ_{soil}

In order to analyse the between-tree variability of sap flux density, we collected sap flux data from three different experiments, at the Bray Site in 1989 and in 1994 and at the Carrasqueira site in 1994. In each experiment, one sensor was inserted into the northern face of each stem and measurements were carried out as described above. The data were pooled and compared on a daily summation basis with respect to the average value of each site.

3.3. Flux measurement

The sap flux density of each compartment, j_i, was measured using the linear heating sensor designed by Granier [12] and applying the empirical relationship relating sap flux density to the thermal difference between the heated and reference probes. The measurements were carried out on a single tree, referred to here as the target tree *(table III)*. No attempt was made to take into account possible natural gradients of temperature between the two probes [11]. At the Bray site, the sap flux density at each measurement level was calculated as the arithmetic mean of the values measured by all the sensors at that height, one, two or four according to the height *(table II)*. At the Bray site, the whole tree water flux at $z = 8.5$ m, J_c, was calculated on a leaf area basis by:

$$J_c = j_c \cdot \frac{A_c}{L} \tag{7}$$

where A_c is the cross-sectional area of the conductive pathway and L the leaf area (all sided) of the tree. A_c was measured after the experiment on the slice of wood extracted from the trunk at a height of 8.5 m as described above. L was estimated using the sapwood area–leaf area relationship determined by Loustau (unpublished data) from a destructive sampling of 20 trees at the same site. At Carrasqueira, only one sensor was inserted at each level. In this case, the stem sap flux at a height of 1.5 m, J_s, and beneath the crown, J_n, was estimated by assuming that the daily total of water flow through the tree was conserved. This implies that the daily total of water flow at any location within the system is conserved and that the ratio between the respective values of the sapwood cross-sectional area and the daily sum of sap flux density at any pair of points of heights within the tree is constant. Thus, we

estimated the sapwood cross-sectional area of each compartment i ($i \neq c$), A_i, using the ratio between its daily sap flux density, $\sum_0^{24} j_i$, and the sap flux density beneath the crown, $\sum_0^{24} j_c$, as follows:

$$\frac{A_i}{A_c} = \frac{\sum_0^{24} j_c(t)}{\sum_0^{24} j_i(t)} \Leftrightarrow A_i = A_c \cdot \frac{\sum_0^{24} j_c(t)}{\sum_0^{24} j_i(t)} \quad (8)$$

3.4. Storage flux

The total storage flux of the crown and stem, J_{ri}, were calculated as the instantaneous difference between sap flux values measured above and beneath the compartment considered, according to equation (1), following Loustau et al. [24]. For the stem storage only, the elastic storage flux into the trunk was also estimated from trunk volume variations, assuming these variations were due only to the transfer of water from the phloem into the xylem. The dendrometers used were linear displacement transducers ('Colvern') regularly spaced along the stem *(table II)* and corrected for temperature variations. Each transducer was fixed to a PVC anchor which was attached to the opposite side of the trunk using 5-cm-long screws. Dead bark tissue was removed such that the sensor was directly in contact with external xylem.

3.5. Water potential measurements

Needle water potential was measured hourly using a pressure chamber. The branches and trunk water potential were estimated using non-transpiring needles attached at the appropriate locations *(table II)*. These needles were enclosed in waterproof aluminium-coated plastic bags after wetting the previous night, and it was assumed that their water potential came into thorough equilibrium with the branch or trunk xylem to which they were attached. The soil water potential was estimated as the average value of 15 soil psychrometric chambers used in dew-point mode (Wescor soil psychrometer) and buried at five depths from –10 to –50 cm.

3.6. Vapour flux measurements

The transpiration of pine canopy was estimated using eddy covariance measurements of the vapour flux at two levels, above the tree crowns and in the trunkspace between the tree crown and the understorey. Fluctuations in wind speed, temperature and in water vapour concentration were measured with a 3D or 1D sonic anemometer and a Krypton hygrometer, respectively. The difference between the vapour fluxes measured above and beneath the pine crowns was assumed to give the transpiration of the pine trees only. These measurements were available for 14 days at the Carrasqueira site in 1994, and for 10 days at the Bray site in 1995. The methods used, the corrections applied in order to take into account the density effects and the absorption of UV by oxygen, energy balance closure tests and sampling procedures are detailed by Berbigier et al. [2] for the Carrasqueira site and Lamaud et al. [21] for the Bray site.

4. RESULTS

4.1. Azimuthal variability of sap flux density in pine stands

Figure 2 shows the time course of the measured sap flux density at four azimuth angles and two heights in the trunk of the target tree at the Bray site throughout a typical spring day. There was very little, if any, variation in sap flux density with azimuth angle immediately beneath the crown, whilst considerable differences were found at the base of the trunk. This pattern was conserved throughout the whole measurement period, and was not affected by soil drought (data not shown). *Figure 3* summarises the results obtained concerning the variability of sap flux density at a height of 1.30 m for three trees

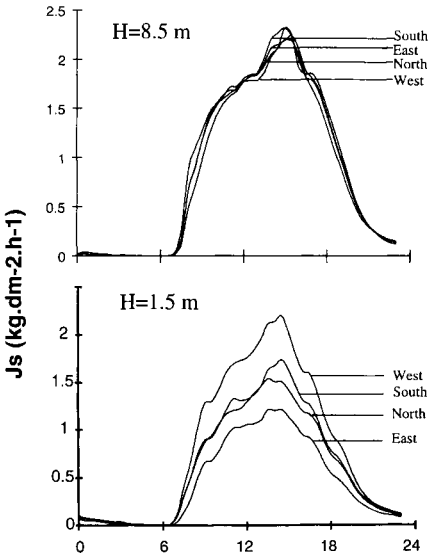

Figure 2. Azimuthal distribution of sap flux density at two heights for tree 2158, Bray site, 1995 (day of year 153).

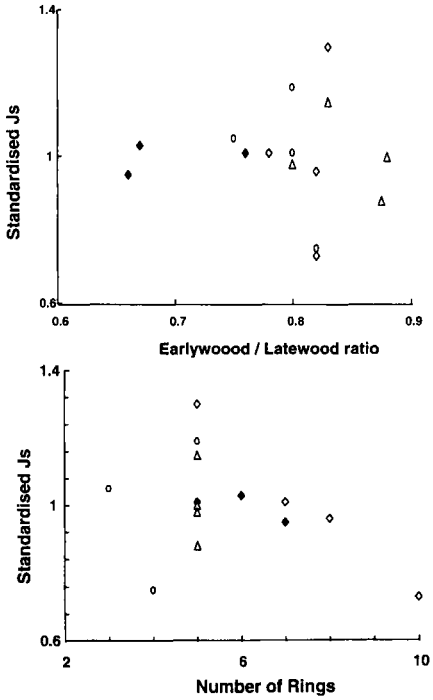

Figure 3. Relationship between the sapwood sap flux density and the ratio between earlywood and latewood (upper graph) and the number of rings (lower graph) crossed by the sensor. The measurements were made either at 8.5 m (closed symbols) or 1.3 m high (open symbols). (◆, ◇: tree 2158, ○: tree 2420, Δ: tree 2430.)

at the Bray site. The relationship between sap flux density and either the number of rings or the proportion of earlywood crossed by the probe was not significant, though there was a trend for the sap flow density to decrease as the number of tree rings measured increased in two out of four trees. Furthermore, there was no significant relationship between the variation in sap flux density and the stem basal inclination, even where the excentricity of heartwood and subsequent sapwood azimuthal anisotropy was obvious. No significant relationship was found between the sap flux density measured at 1.3 m high and tree size in either experiment *(figure 4)*.

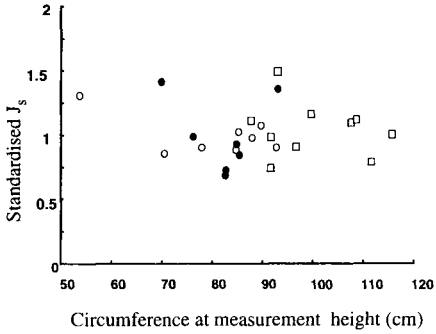

Figure 4. Relationship between normalised daily sap flux density and the circumference at breast height for three different experiments made at the Bray and Carrasqueira sites. (●: Bray site 1995, ○: Bray site 1994; □ : Carrasqueira site 1994.)

4.2. Determination of the parameters of the model

Figure 5 shows the flux–water potential gradient relationship used in calculating the resistance of the three compartments for 2 days of contrasting soil moisture. The corresponding values of the resistances are given in *table IV*. Soil moisture reached its lowest value on days 229 and 243 and the predawn water potential measured for these 2 days *(table IV)* are typical of those found during a severe drought in this area. There was a dramatic, 8-fold increase in the resistance of the root–trunk compartment under these drought conditions, which contrasted with a very slight increase in the resistance of the branch and needle compartments.

Figure 6 illustrates the procedure used for estimating the branch and stem capacitance for day 153. We did not observe any clear change in the stem or branch capacitance for the four sample days at the Bray site.

4.3. Model evaluation

Figure 7 compares the water potential values predicted by the model and the measured values, for day 153 at the Bray site. There is an acceptable agreement between the measured and predicted data, even if a difference is observed during the morning and late afternoon for the lower compartments. This figure also compares the storage flux for the stem predicted by

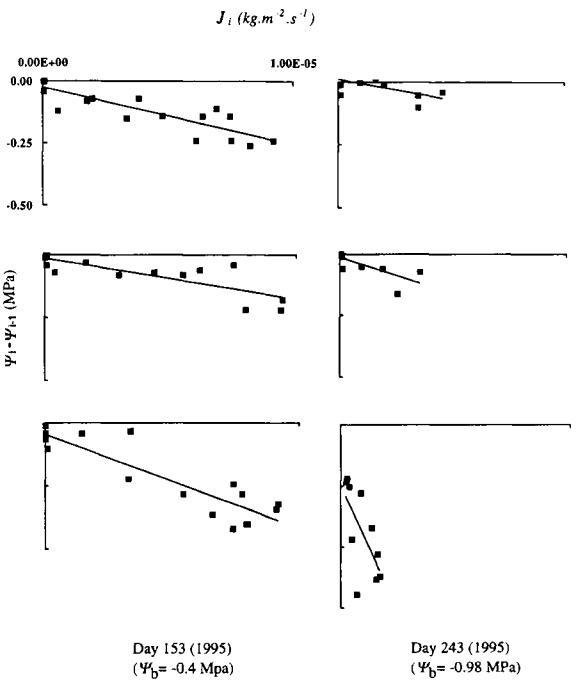

Figure 5. Relationship between the water potential difference measured ($\Psi_i - \Psi_{i-1}$) and the water flux measured, J_i, through each of the three compartments of the model, for two days of contrasting soil moisture. The predawn needle water potential, Ψ_b, is given. The slope of the regression line gives the value of the resistance of each compartment.

Table III. Cross-sectional areas of sapwood, heartwood and total stems at different measurement heights on the sample tree 2158 (Bray site 1995).

Height (m)	Total area ($10^{-4} \cdot m^2$)	Heartwood area (dm^2)	Sapwood area at the sensor location (measured) (dm^2)	Equivalent Sapwood area [estimated equation (9)] (dm^2)
1.3	2.70	0.321	2.379	2.87
4.5	2.478	0.338	2.132	2.32
6.5	2.04	0.252	1.783	1.84
8.5	1.57	0.069	1.503	(1.5)
14	0.24	0.006	0.230	1.51

Table IV. Resistance, capacitance and time constant values of the three compartments of tree 2158 at the Bray site and tree number 12 at the Carrasqueira site.

	Day of Year				
	153 (–0.40 Mpa)	159 (–0.40 MPa)	229 (–0.96 MPa)	243 (–0.98 MPa)	157–180 (–0.65 Mpa)
	Bray site (tree 2158)				Carrasqueira (tree 12)
Resistance (10^3 MPa·m^2·s·kg^{-1})					
Needles	24 ± 4	29 ± 6	38 ± 11	21 ± 14	30
Branches	16 ± 4	17 ± 5	12 ± 2	31 ± 12	40
Trunk+roots	38 ± 5	44 ± 6	205 ± 114	410 ± 32	150
Capacitance (kg·m^{-2}MPa^{-1})					
Needles	(0.025)	(0.025)	(0.025)	(0.025)	(0.025)
Branches	0.077 ± 0.016	0.095 ± 0.002	0.071 ± 0.020	—	0.025
Trunk + roots	0.036 ± 0.008	0.047 ± 0.010	0.043 ± 0.007	0.051 ± 0.010	0.030
Time constant $\tau = R \bullet C$ (min)					
Needles	10	12	16	9	12
Branches	20	27	14		17
Trunk + roots	23	35	147	348	75

Standard error on the estimate is also given. The value of predawn water potential is given in parentheses for each day. Values are expressed on a needle area basis.

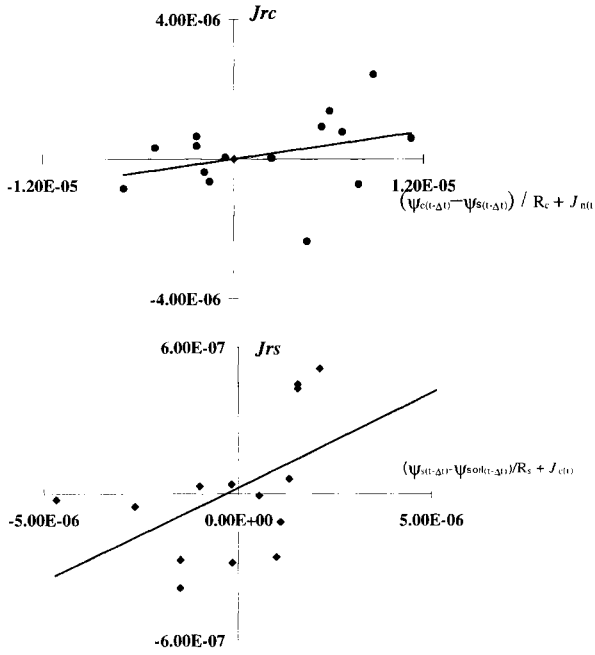

Figure 6. Plots used for the calculation of the capacitance of the trunk and branch compartments [see equation (6) in the text].

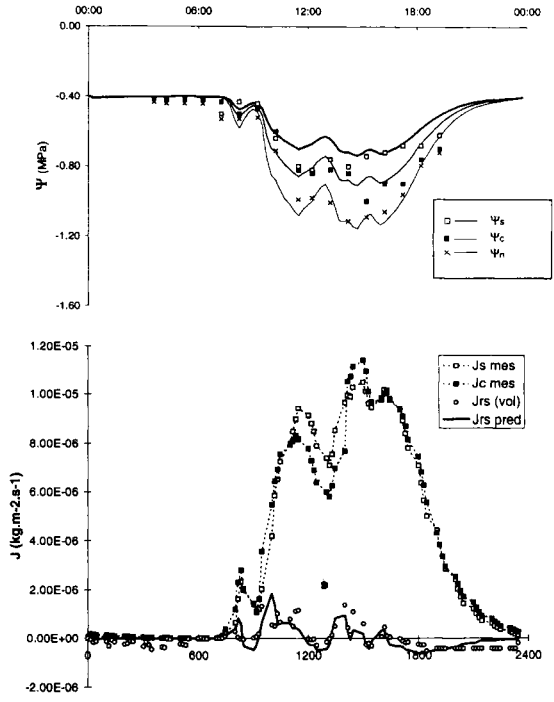

Figure 7. Comparison between the measured values of water potential and flux in the different compartments of the tree and their respective values as predicted by the model. The upper graph shows the comparison of water potential values for day 153. Each symbol corresponds to the average value of four measurements, the curves give the model predictions. The lower graph shows the time course of measured sap flux at the base (J_s) and the top (J_c) of the bole and the storage flux determined from trunk volume variations (J_{rs} vol) and predicted by the model (J_{rs} pred).

the model with the flux calculated from change in the stem volume. This comparison shows that predicted and observed data are the same order of magnitude but differences remain at certain times of the day. *Figures 8* and *9* show the model's outputs together with measured data for two representative days at the Carrasqueira and Bray sites, respectively. The parameter values used for implementing the model have been derived from measurements made at different heights [24] and are shown in *table IV*. The figures compare the values of vapour flux predicted from sap flow measurements at the base of the crown and at the base of the trunk with the evapotranspiration data measured by eddy covariance for 2 days on each site. We 'upscaled' the sap flux values from tree to stand using optically determined leaf area index values *(table I)*, assuming the needles had a semi-cylindrical shape, and calculating the sap flux as the average of the measurements made at a height of 6 m on a sample of ten trees at Carrasqueira and at a height of 8.5 m on seven trees at the Bray site. The time course of the predicted values of water potential are also shown and compared with measured data for the days 178 and 180 at the Carrasqueira site. The values measured by eddy covariance exhibited erratic variations, particularly when the weather regime was irregular, but the overall pat-

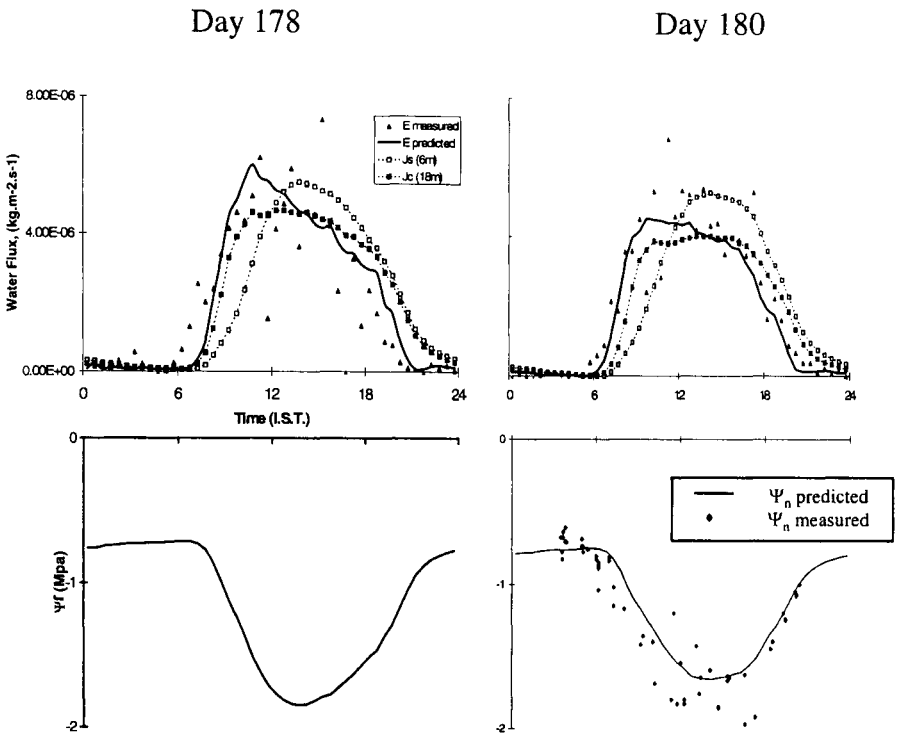

Figure 8. Comparison between the transpiration predicted by the model and the measured vapour flux from the pine canopy for 2 d at the Carrasqueira Site. The lower graphs show the predicted daily course of needle water potential, Ψ_n, and their measured values for day 180.

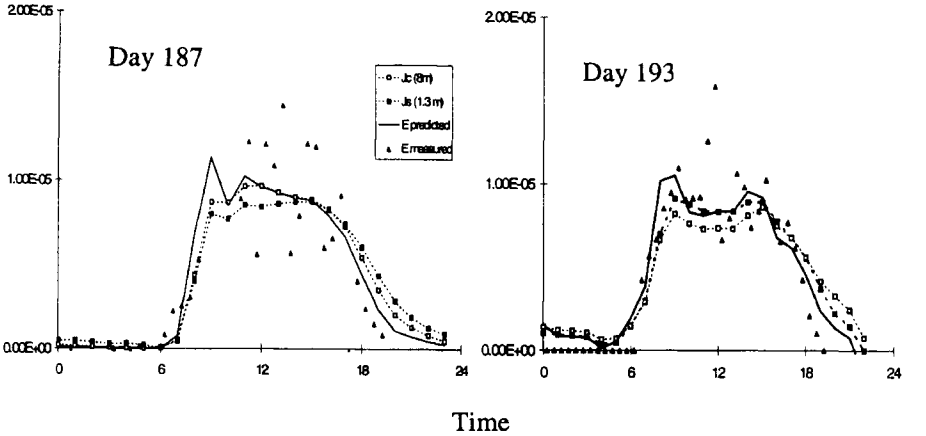

Figure 9. As in *figure 8* for 2 d at the Bray site in 1995.

tern showed acceptable agreement. Water potential values predicted by the model are also compared with measured data for 1 d (DOY 180 Carrasqueira site) and indicate that the model predicts the measured values reasonably well. *Figure 10* shows the relationship between the predicted and measured vapour flux values for both sites. Agreement is slightly better for the Carrasqueira where data were obtained on bright clear days than for the Bray where data were collected under changeable weather conditions.

DISCUSSION

An important methodological outcome of this work is that a lower sampling error for mean sap flux density of a homogeneous stand should be expected when the sap flux measurements are made immediately below the crown rather than at ground level. This is particularly true for trees exhibiting basal trunk curvature and subsequent wood excentricity and sapwood anisotropy. We did not find any literature concerning the pattern of azimuthal distribution of sap flux density according to the measurement height which could further support this conclusion. Since it is based on measurements made on only three trees, this conclusion deserves additional experimental support. Sap flux density variations could not be related significantly to the number of rings or the earlywood/latewood ratio of the sapwood crossed by the heating probe. We think, however, that such a relationship could occur within a tree but was not observed because of the low number of replicates. It may, nevertheless, play an important role since Dye et al. [8] showed that growth rings and compression wood created a radial heterogeneity in sap flux density within the sapwood of another pine species, *P. patula*, and that there was a subsequent heterogeneity in the azimuthal distribution of sap flux density. Additionally, it has long been established that the sap flux density varies radially within the sapwood cross-sectional area [3, 15, 16, 27] which could also affect the azimuthal distribution of sap flux in anisotropic stems. The between-tree variation of sap flux density was, therefore, unsurprising since the data presented in *figure 4* actually include the within-tree variability. In addi-

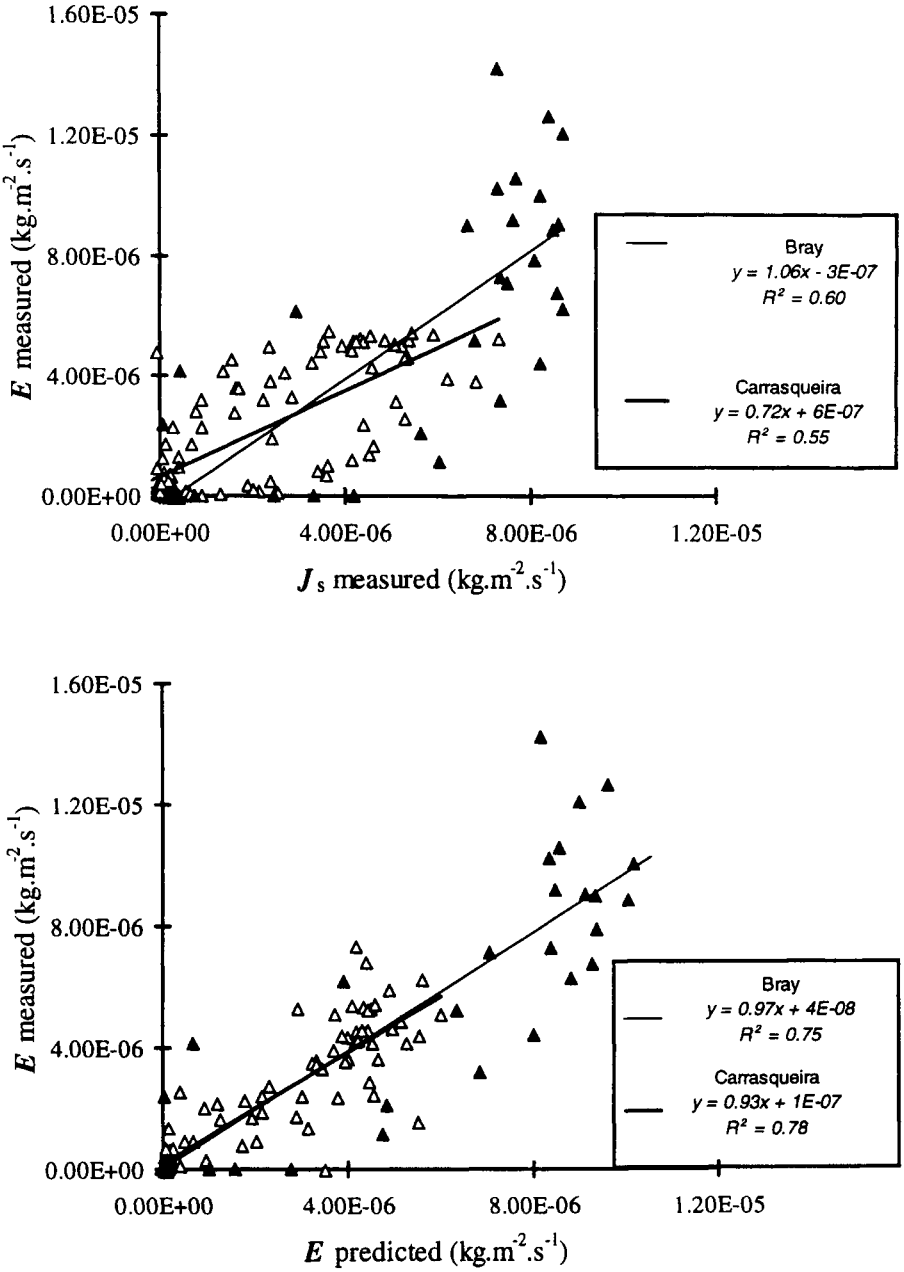

Figure 10. Relationships between observed and predicted values of transpiration (E) and sap flow measured at the base of the trunk (J_s) for the data presented in *figures 8* and *9*. (▲: Bray site, △: Carrasqueira site.)

tion, only a weak between-tree variation in sap flux density would be expected in these homogeneous pine stands where the leaf area index did not exceed a value of 3. This precludes any major differences between trees of differing social position.

Models based on a similar electrical analogue, with various degrees of sophistication in tree architecture representation were published by Powell and Thorpe [28], Landsberg [22], Wronski et al. [37], Milne [25] and Cruiziat et al. [5] following the pioneer work of Van den Honert [34], but their practical utilisation remains limited owing to the large numbers of parameters required. The merit of the present model is its simplicity, which could make it useful for routine transpiration calculations from sap flow measurements, provided that a proper parameterisation of the resistance and capacitance values is achieved. This would facilitate using sap flow measurements to estimate tree transpiration (and consequently surface conductance) when other techniques are impractical, and would allow partitioning of the vapour fluxes among canopy layers on a short term basis. From this point of view, the inadequacy of assuming that sap flow lags with a constant time shift behind transpiration should be highlighted. The constant time-lag hypothesis implies that the water storage flux in the tree would always correspond to a constant time fraction of the transpiration, which is obviously erroneous. The storage flux varies during the day and reaches its maximal absolute values in the morning and during the evening, and its minimal values, close to zero, at midday.

We observed a dramatic increase in the soil–trunk resistance under low soil moisture conditions, while the needle and crown resistances were nearly unaffected. This change in resistance observed during drought dramatically increased the time constant of the soil–trunk compartment, which was approximately 23 min with wet soil and reached 348 min with dry soil. Consequently, the estimation of hourly transpiration values from extrapolating sap flow measurements made at the base of the trunk becomes extremely difficult on dry soil since a very accurate measurement of the water potential at the soil–root interface becomes necessary. The major cause of this increase in the root–trunk compartment may be attributed to the decrease in soil hydraulic conductivity in the vicinity of the roots, since the trunk and root xylem of coniferous trees have not been reported as showing a substantial reduction in hydraulic conductivity caused by cavitation of tracheids at these levels of water potential [32]. Another important consequence of this increase in time constant under soil drought is that, under extremely dry conditions, trees might not have sufficient time overnight to restore their equilibrium water content. During a continuous period of drought, we can therefore hypothesise that trees having a large time constant, such as large coniferous trees, could experience a sort of 'runaway' dehydration resulting in them drying faster than the soil itself.

An interesting practical issue arising from the present paper is our method for estimating the values of the bulk resistance and capacitance of each compartment under natural conditions with minimum disturbance to the tree. These methods are consistent with the use of the parameter values in the model. Estimation of the bulk resistance of a transfer compartment through analysis of the flux–water potential relationship has been widely used by several authors, but has seldom been applied to subparts of trees in the field. Present methods rely on accurate determinations of the tree sap flow, which requires determination of sapwood area, mean sapflux density and needle area in a stand to a high degree of accuracy. Thus, application of this principle could

therefore be questionable in the case of a heterogeneous stand. Despite large scatter in the data, mainly caused by the rapid changes in evaporative demand during the measurement days, the estimated values of capacitance (0.078 and 0.038 kg $\cdot m^{-2} \cdot MPa^{-1}$) are within the expected range of magnitude for coniferous trees [30]. The capacitances found for the stem and branches are within the range of the values estimated from the measurements made by Edwards et al. [9] on two other coniferous species, *Pinus contorta* and *Picea sitchensis*. These capacitances were not affected during drought, a logical consequence of the conservation of water potential of each compartment resulting from stomatal closure and a subsequent drop in water flux.

We recognise that the parameterisation of the model relies on a small number of replicates at both sites. It would be necessary to enlarge the sample size of the measurements of flux and water potential to achieve more confidence in upscaling the model from the tree to the stand level. Despite this restriction, our approach allows us to investigate changes in water flux along the soil–tree–atmosphere continuum and has provided a method for predicting the water potentials and water fluxes at any point of the system which we have shown to be roughly consistent with data obtained from two different sites. Among the assumptions made a priori in the model, two of them may restrict its use and deserve therefore, some critical analysis.

1) The capacitances of the tree compartments were assumed to be constant over the range of water potential experienced. This assumption seems reasonable from the established relationship between needle water potential and water content but very little is known about the water relations of elastic tissues such as the stem phloem, which appears from *figure 7* to be the major component of the trunk and branch capacitances. In the longer term, the xylem of most coniferous trees is known to play a role as a water reservoir [35] but it appears to play an insignificant role on a daily basis [17, 37].

2) The tree is divided into homogeneous compartments characterised by a set of unique values of water potential, storage flux and main flux. This approximation is acceptable when the model includes a large number of small-size compartments and runs on a short-time resolution, typically seconds, which is not the case here. Nevertheless, we feel this assumption is still acceptable for the needle and branch compartments for which spatial variations in water potential values do not exceed 0.15 MPa (Loustau, unpublished results). This simplification is questionable for the lower compartment, which includes both the stem and root systems and may exhibit spatial differences in water potential as large as 0.5 MPa. Ignoring the resistance between storage tissues and xylem may also lead to underestimates of the time constant of the trunk and branch compartments, even if Milne (1989) found its value negligible when compared to the resistance of the main pathway.

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