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Original article

Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests

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Abstract – To partition evapotranspiration between canopy and subcanopy components in a 12-m-tall *Pinus taeda* forest and to assess certain aspects of environmental regulation of canopy transpiration, we quantified water flux in a forest using three approaches: 1) measuring water flux in xylem of trees, and scaling to stand transpiration of canopy trees (E_C); 2) measuring soil water content and saturated conductivity, and modeling drainage to estimate total evapotranspiration (E_T) during rainless days based on a local water balance (LWB); and 3) using an eddy correlation approach to estimate total E_T. We calculated variances for each estimate, and proposed an approach to test for differences between estimates of E_C and E_T. Diurnal 'patterns' in water uptake were similar using direct measurements in stem xylem and LWB. However, LWB was found to be inappropriate for estimating 'absolute' E_T diurnally when changes in soil moisture between consecutive measurements were small. Eddy correlation estimates of E_T are of a higher temporal resolution than xylem flux measurements made in branches. Diurnal flux patterns in branches are more similar to the pattern generated by eddy correlation than those in stems. However, differences between the patterns indicate that patchiness in branch transpiration may preclude using branch xylem flux measurements to estimate canopy conductance. In one stand, daily E_C accounted for ca 70 % of total E_T estimated by either LWB (in a separate study) or the eddy correlation approach; the difference between E_T and E_C was significant based on variances calculated to account for spatial variation in each. Regardless of the vapor pressure deficit, E_C decreased linearly with soil moisture from 2.5 to 1.5 mm d^{-1} over a 9-d drying cycle, as soil moisture in the rooting zone (ca 0.35 m depth) declined by 23 mm. (© Inra/Elsevier, Paris.)

canopy transpiration / subcanopy evapotranspiration / sap flux / soil water balance / variability

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Résumé – Une méthode pour séparer les flux hydriques en forêt basée sur l'extrapolation des mesures de flux de sève, le bilan hydrique et le calcul des variances. Dans le but de séparer, dans l'évapotranspiration d'une forêt de *Pinus taeda* de 12 m de hauteur, la participation des arbres de celle du sous-étage, et d'évaluer les caractéristiques de la régulation de la transpiration des arbres, les flux hydriques ont été quantifiés à partir de trois approches complémentaires : a) la mesure du flux de sève brute dans les arbres, permettant de calculer la transpiration du peuplement (E_{C}) ; b) le bilan hydrique local (LWB), à partir de la mesure de la teneur en eau du sol, de la conductivité hydraulique du sol à saturation, et de la modélisation du drainage pour estimer l'évapotranspiration totale (E_{T}) pendant des périodes sans pluie ; c) la mesure, d'E_{T} au moyen de la méthode des corrélations turbulentes. Les variances de chaque estimation ont été calculées, et une approche pour tester les différences entre E_{C} et E_{T} a été proposée. Les variations journalières de consommation en eau à partir du flux de sève étaient similaires à celles obtenues à partir du bilan hydrique. Néanmoins, la méthode LWB s'est montrée inadéquate pour estimer les variations absolues d'E_{T} lorsque les variations de teneur en eau du sol étaient faibles. L'estimation de E_{T} au moyen des corrélations turbulentes a montré une plus forte résolution temporelle que celle basée sur la mesure de flux de sève dans les branches. Une plus grande similitude des variations journalières d'E_{T} a été montrée entre les méthodes des corrélations turbulentes et du flux de sève dans les branches qu'avec le flux de sève mesuré dans les troncs. Toutefois, des différences dans les allures de courbes semblent indiquer qu'il existe une hétérogénéité de la transpiration des branches, ce qui exclut l'utilisation de cette méthode pour évaluer la conductance du couvert. Dans une des parcelles, E_{C} journalier a atteint environ 70 % d'E_{T} estimé par la méthode LWB (cf. une autre étude), ou par les corrélations turbulentes. À partir du calcul des variances, pour prendre en compte la variabilité spatiale des différentes estimations, on a pu montrer que la différence entre E_{T} et E_{C} était significative. En dehors de l'effet du déficit de saturation de l'air, E_{C} a montré une diminution linéaire avec l'humidité du sol, pour passer de 2,5 à 1,5 mm/j, sur une période de 9 j de dessèchement, tandis que l'humidité du sol dans la sphère racinaire (qui s'étend sur environ 0,35 m de profondeur) diminuait de 23 mm. (© Inra/Elsevier, Paris.)

transpiration du couvert / transpiration du sous-étage / flux de sève / bilan hydrique / variabilité

Nomenclature

A_{G}	ground area
A_{Si}	sapwood area (i = category)
b	empirical constant
D	vapor pressure deficit
E_{Ci}	stand transpiration by canopy trees
E_{SC}	subcanopy stand evapotranspiration
E_{T}	total evapotranspiration
J_{Si}	xylem water flux
J_{out}	flux in xylem outer 20 mm
J_{in}	flux in xylem, inner 20–40 mm
H	matric potential
$K(\theta)$	hydraulic conductivity
K_{S}	saturated hydraulic conductivity
L	leaf area index
LE	latent heat flux
L_{V}	latent heat of vaporization
LWB	local water balance
P_{T}	throughfall precipitation
q	Darcian flux
q'	water vapor concentration fluctuation
r	correlation coefficient
ΔS_{W}	changes in soil moisture
TDR	time domain reflectometer
w'	vertical velocity turbulent fluctuation
σ^2	variance
θ	soil moisture content
θ_{S}	saturated soil moisture content
∇	gradient operator
<>	temporal average
$\bar{\ }$	spatial average

1. INTRODUCTION

In a series of publications beginning with an introduction to water balance dynamics, Eagleson [18] stated that modeled land–atmosphere interactions must retain both the underlying physical determinism and the uncertainty that plays a large role in nature. Thus, any approach to modeling or estimating water balance must rely on probability distributions, which apply to the values of model parameters and independent variables, and to the information, or observations, used to evaluate the system's behavior.

In recent years, a rapidly increasing number of papers on water flux in tree xylem reflects the introduction of affordable, easy-to-use instruments. Most users consider some of the variability in the measured water flux when values are extrapolated to the stand. However, generally less attention is paid to calculating the uncertainties about the estimated stand transpiration, which is based on sensors often representing less than 1 % of the leaf area of monitored trees. Several authors have suggested methods to improve scaling measurements to stand-level [13, 17, 26, 28, 48]. Thus far, stand-level transpiration estimates based on xylem water flux (J_S) measurements have been assumed to vary mostly with time, implicitly assuming that the variation in space is captured in the variability in J_S among measured trees. As a result, differences between canopy transpiration (E_C) values obtained by this method and, e.g. eddy correlation estimates of total evapotranspiration (E_T) have been attributed, under certain conditions, to the subcanopy contribution to stand transpiration and evaporation (E_{SC}; [2, 17].

In order to account for some variability in J_S, sample trees have been chosen to represent different size classes [2, 17]. Based on this approach, E_C is calculated as the product of J_S in each tree diameter class, or of water flow per unit of circumference, and the area of xylem in each class, or the total circumference of all trees in the class, respectively. E_C is calculated by summing over all classes. The motivation behind this scaling approach is that trees of different size classes have different flow rates per unit of xylem area or tree circumference. However, while in some situations J_S may be affected by the intensity of competition around measured trees [2], or by spatial variation in rooting volume and soil moisture availability [27, 28], this is not always the case [54].

Here we suggest a method for incorporating the variability in both J_S and hydroactive xylem area (A_S) per unit of ground area (A_G; sapwood area index) to estimate the variance about the calculated E_C. The result is an interval of values within which E_C is likely to occur at a selected probability level. This approach is useful for two lines of investigations: 1) comparison of estimated E_C based on xylem water flux measurements with other E_C estimates based on modeling [64] or mass balance (e.g. eddy correlation, water budget; [2, 10]; and 2) partitioning of transpiration between canopy and subcanopy in forests [17, 40]. When subtracting E_C obtained with scaled xylem water flux measurements from E_T obtained, for example, by eddy correlation in order to estimate E_{SC}, it is necessary to account for the sources of, and sinks for, water unique to each method. The sources and sinks are likely to differ, not only in the vertical axis, but also horizontally. Thus, for eddy correlation measurements they are determined by the footprint size and direction, and for J_S measurements they are affected by the sampling design. In this study, we address only the variability associated with estimated E_C.

In most situations, J_S measurements represent water uptake rate rather than transpiration. When comparing E_T with E_C estimated diurnally, the resulting time-lag may introduce large errors into the partitioning of fluxes between canopy and subcanopy [27, 43]. Using Granier-Type xylem flux sensors inserted in the main stem of trees and in branches, we compared diurnal patterns of water uptake and transpiration, respectively, to the source of water in the canopy, estimated with eddy correlation flux measurements above the canopy combined with measurements of water vapor concentration within the canopy volume. A companion paper [50] describes the lag effect in terms of potential errors in estimating canopy conductance.

2. MATERIALS AND METHODS

The study was undertaken in a 12-year-old, uniform plantation of loblolly pine (*Pinus taeda* L.; 1000 m x 300 m) located near Durham, NC, USA, in the Blackwood Division of Duke Forest (32°52'N, 79°59'W), a transitional zone between the coastal plain and the Piedmont plateau. One-year-old seedlings were planted in 1983 at 2.4 m spacing, and at the time of the study, formed the main canopy, reaching a height of 12 m. Below, occasionally reaching into the main canopy, were naturally seeded loblolly pines, a small number of individuals of other species, including *Liquidambar styraciflua* L., *Juniperus virginiana* L. and *Quercus phellos* L., as well as herbaceous, grass and vine species. The natural regeneration increased the density of individuals in the stand from the planted 1 736 ha^{-1} to over 5 200 ha^{-1}, with most of the natural regeneration in the subcanopy, small diameter classes. The stand is located on soils of the Enon Series, moderate-fertility, acidic Hapludalfs of low potential for erosion due to less than 2 % slope. Soil moisture is extracted mostly from the top 35 cm (ca 90 %; Oren et al. [49]) and maximum extractable water to this depth is ca 120 mm.

In the summer of 1994, 66 circular plots of 44.5 m^2 were positioned in the stand, and the diameter at 1.3 m above ground for all individuals with a diameter greater than 20 mm was measured. In addition, three plots were established in 1993 and 1994 as part of a long-term study of water flux in forests, one plot on a portion (111 m^2) of the stand encircled by the free air CO_2 enrichment (FACE) prototype, and the others as reference plots (Ref. 1 and Ref. 2) nearby (53 and 117 m^2, respectively), and diameters were measured as above. Individual tree and plot characteristics are shown in *table I*.

2.1. Overstory transpiration – scaled xylem flux measurements

Overstory transpiration was estimated using measurements of xylem water flux in the outer

Table I. Stand parameters in September 1994 for the three sites in Duke Forest, representing the mid-point of the study performed from March 1993 to May 1996.

	Ref. 1	Ref. 2	FACE
Stand characteristics			
age (years)	13	13	13
density (stems ha^{-1})	5 240	5 220	3 700
basal area (m^2 ha^{-1})	14.9	16.9	15.8
sapwood area (m^2 ha^{-1})	12.7	14.4	13.4
leaf-area index (m^{2}m^{-2})	1.6	1.8	1.7
Average tree			
DBH (mm)	97 (9)	136 (9)	137 (8)
height (m)	7.1	7.4	7.8

Leaf-area index values represent the seasonal minimum in May 1994, and can nearly double in the seasonal maximum. One standard error of diameter breast height, DBH.

20 mm of the xylem in trees of two plots, FACE and Ref. 1, taken with Granier-Type sensors [22]; and at two depths (0–20 mm from the cambium and 20–40 mm) in trees of Ref. 2, using modified sensors, as described in detail in Phillips et al. [51]. Ten individuals were measured in each plot; here we report on data collected between June 1993 and September 1996. Measurements of J_S provide values in units of $g_{H2O}\ m^{-2}{}_{xylem}s^{-1}$, which must be converted to units of flux for the stand using the hydroactive xylem area (sapwood) per unit of ground area (A_S:A_G, unitless) as a scaling variable. Scaling was based on measured J_S in outer xylem only (J_{out}), while J_S in the inner xylem (J_{in}) was estimated based on J_{out} and a correction factor obtained by comparing J_{in} with J_{out} in Ref. 2. The flux in each xylem region was scaled using its respective A_S:A_G to obtain plot-level E_C for comparison with 1) total evapotranspiration (E_T) obtained with the local water balance (LWB) calculation in that plot. The flux in each xylem region was also scaled using average inner and outer sapwood in the 66 plots to a stand-level E_C for comparison with 2) E_T obtained with the eddy correlation calculation in the whole stand. Due to the young age of the stand, sapwood comprised all the cross-sectional area inside bark [51]; bark thickness was estimated from a relationship developed on site with outside bark diameter.

Vapor pressure deficit (D) was calculated from relative humidity and temperature monitored with sensors (RHA1, Delta-T Devices Ltd., Cambridge, UK) positioned in both FACE and Ref plots 7 m above ground, a point corresponding to the peak in the stand leaf area index (L) profile as estimated with a canopy area analyzer (LAI 2000, Li-Cor., Lincoln, NE, USA). Temperature, relative humidity and the Granier-Type sensors were interrogated every 30 s, and half-hour means were stored in a data-logger (DL2, Delta-T Devices). On 19 September 1994, Granier-Type sensors were monitored in six branches, originating 5, 7 and 9 m above ground in each of two trees, and data were stored every 20 min for further comparison with eddy correlation estimates. During the study, photosynthetically active quantum flux (LI-193SA spherical quantum sensor, Li-Cor) and shortwave radiation (LI-200SA pyranometer) were also measured above the canopy using the same logging procedure.

2.2. Evapotranspiration – local water balance (LWB) approach

The LWB method, shown to produce reasonable estimates of E_T over a large portion of one growing season [35, 59], was evaluated for use in conjunction with xylem flux measurements to partition evapotranspiration between canopy and subcanopy components over short periods of time, such as portions of a single day. The method is based on measurements of throughfall precipitation (P_T, mm), and volumetric soil moisture content (θ) in the rooting volume. Volumetric soil moisture measurements are used to calculate changes in soil moisture, ΔS_W, between measurement times, and estimate drainage from the soil below the rooting zone. Evapotranspiration is calculated as the balance between P_T, ΔS_W and drainage. The method assumes negligible evaporation from wet surfaces and soil. The experiment was conducted over a single rainless day (see below for details on instruments and calculations). We chose a day without precipitation, several days after the last rain event, to avoid all errors associated with estimates of P_T, one of the three components in the LWB approach, as well as to strengthen the assumption that little evaporation occurs.

Estimates of ΔS_W with respect to time, dS_W/dt, and drainage (see below), were obtained from measurements of θ [12, 45, 60]. At five locations along a radial transect in the 30 m diameter FACE plot, metallic time domain reflectometer (TDR; Tektronix 1502-B, Redmond, Oregon, USA) rod pairs, 0.10, 0.20, 0.35 and 0.70 m in length, were installed vertically from the surface to four depths. Time domain reflectometer measurements were taken at 1-h intervals throughout 29 September 1994.

An empirical relationship is typically derived to convert κ measurements to θ. Topp et al. [61] derived a general relationship for different mineral soils which was found to be suitable for soils with low clay content. The soil in this study was a clay loam in the upper horizons, and Topp's equation was tested and found to quantify θ accurately [59]. Soil moisture content was calculated for each interval by subtracting total moisture estimated from two rod pairs of consecutive length and dividing by the difference in length.

The drainage can be estimated as a Darcian flux $q = K(\theta)\nabla H$, where $K(\theta)$ is hydraulic conductivity at θ, H is the matric potential and ∇

is the gradient operator. For deeper layers, the moisture content depth variation is not large and in a first order analysis the drainage is strictly gravitational so that $\nabla H \cong 1$ (see, e.g. [33, 66]). Hence $q = K(\theta)$, and an equation developed by Clapp and Hornberger [16] may be used to calculate drainage. Thus, the drainage flux is

$$K(\theta) = K_S\,[\theta/\theta_S]^{2b+3} \qquad (1)$$

where K_S is saturated hydraulic conductivity, and θ_S is the saturated moisture content. The exponent b is empirical, and must be estimated based on the soil type. We estimated b using a root exclusion monolith over a large part of one growing season (nearly 5 months), measuring P_T and ΔS_W, and calculating drainage by difference (assuming evapotranspiration and lateral flow to be negligible; see Todd [59] for a full description of the process). Calculated drainage from the monolith was made to equal $K(\theta)$ in the monolith by changing b iteratively.

Saturated conductivity, K_S, necessary for estimating drainage [equation (3)], was measured with a compact constant head permeameter (Amoozemeter, Ksat, Inc., Raleigh, North Carolina) which quantifies the steady state flow of water through soil [1]. Measurements of K_S were made at 0.20–0.35 m and 0.55–0.70 m soil depths at four of the five positions where TDR values were collected and averaged.

Saturated soil moisture, θ_S, also necessary to estimate drainage [equation (1)], was estimated in different soil levels based on the following procedure: a trench was excavated in a stepwise fashion, representing 0.1-m incremental intervals from the ground surface to 0.6 m in depth. At each step, 0.1-m TDR rods were installed and θ was measured after the soil was brought to saturation. The value of θ_S was similar, 54 % (SE = 2 %) in all layers.

2.3. Evapotranspiration – micrometeorological approach

In a uniform and extensive canopy, under steady-state conditions, the mean source of water vapor from the stand, E_T, can be estimated from the flux above the canopy, accounting for changes in absolute humidity in the canopy volume. Total evapotranspiration can then be compared to E_C estimated using the Granier-Type sensors. During the summer of 1994, water vapor flux was measured on 9 days in the FACE plot using an eddy correlation system positioned above the canopy [34]. The measurements at z/h = 1 (where z and h are the instrument and canopy height, respectively) were made with a Gill triaxial sonic anemometer (Gill Instruments, Hampshire, UK) mounted 0.25 m from a Campbell Scientific krypton hygrometer (Campbell Scientific, Logan, Utah, USA). The velocity, temperature and water vapor concentration measurements from these instruments were sampled at 10 Hz (21X Campbell Scientifc micrologger). The raw measurements were then fragmented into 27.5-min runs, with each run comprising 16 384 ($= 2^{14}$) measurements per variable per run. The friction velocity (u_*), latent heat flux (*LE*) was then computed as described in Katul et al. [34]. In brief, $LE = L_V\langle w'q'\rangle$, where L_V is the latent heat of vaporization, w' is the vertical velocity turbulent fluctuation, and q' is the water vapor concentration fluctuation, and <> denotes time averaging. The FACE prototype was not enriched with CO_2 in four of the days, and atmospheric CO_2 in the canopy was maintained at an average of 55 Pa for five of the days.

3. RESULTS

3.1. Canopy transpiration

To estimate E_C, information on J_S and A_S:A_G is combined [26, 65]. In measuring J_S, we quantified the effects of two sources of variability: 1) depth in the xylem, and 2) competition.

Within-tree variability in J_S is apparent in *figure 1,* where diurnal J_S in the outer xylem was more than twice that in the inner xylem (compare J_{in} and J_{out} in Ref 2) during most of the day. Inner xylem also required a longer night-time period to recharge its storage. The standard error bars displayed in *figure 1* demonstrate the large between-tree variability in J_{out}. The variability among individuals is shown in detail in the inset in *figure 1,* where diurnal average J_{out} of the 30 trees in the stand displays a non-normal distribution; the dis-

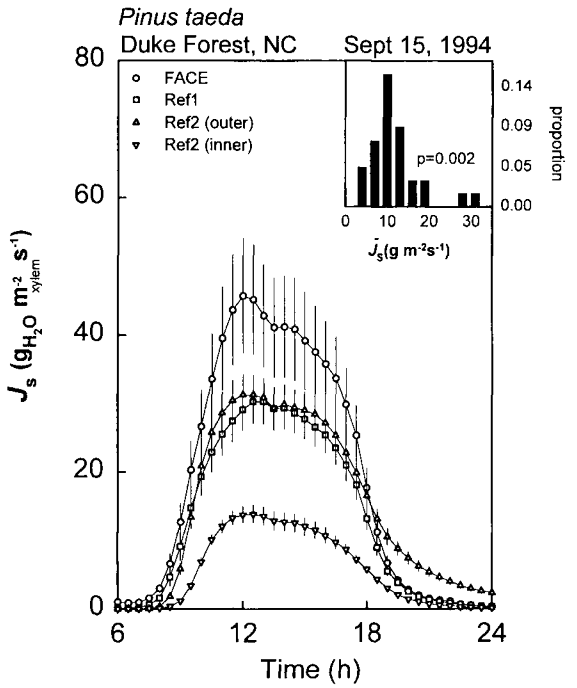

Figure 1. Diurnal pattern of water flux in the xylem (J_S) in three clusters of trees in the outer 20 mm of the xylem, and the next 20 mm of the xylem (Ref 2 cluster only). Vertical lines represent 1 SE. Inset: frequency distribution of average diurnal outer J_S combined from the three clusters shows a departure from normality.

tribution of the natural log transform of the data is not different from normal ($P > 0.7$). Between-tree variability in J_S is, in part, explained by competition, indicated as A_S:A_G in a 3-m-radius plot surrounding and including a monitored tree (*figure 2*), but was uncorrelated with tree height or diameter ($P > 0.1$). The negative correlation between J_S and A_S:A_G is used in the calculations of the variance of E_C, according to equations (4) and (6) below. Differences among plots potentially incorporated a small effect of elevated CO_2 at FACE. However, direct responses of stomates to elevated CO_2 in this site were found to be weak (~ 5 % reduction in stomatal aperture with double ambient CO_2; [19]).

When measurements of J_S are made at different xylem depths, canopy transpiration is estimated based on $\bar{J}_S$ in each depth, $\bar{J}_{S_i}$ ($g_{H_2O} m^{-2}_{sapwood} s^{-1}$) and the sapwood area index for a given xylem depth in a plot, including the measured individuals, A_{S_i}:A_G ($m^2_{sapwood} m^{-2}_{ground}$):

$$\bar{E}_{C_i} = \bar{J}_{S_i} A_{S_i}:A_G \qquad (2)$$

Average canopy transpiration in the stand, E_C, is the sum of $\bar{E}_{C_i}$ for all categories (e.g. depth, azimuth, size class, species).

The variance around the estimate for each category, $\sigma^2_{\bar{E}_{C_i}}$, is given by

$$\sigma^2_{\bar{E}_{C_i}} = \sigma^2_{\bar{J}_i} \cdot (A_{S_i}:A_G)^2 \qquad (3)$$

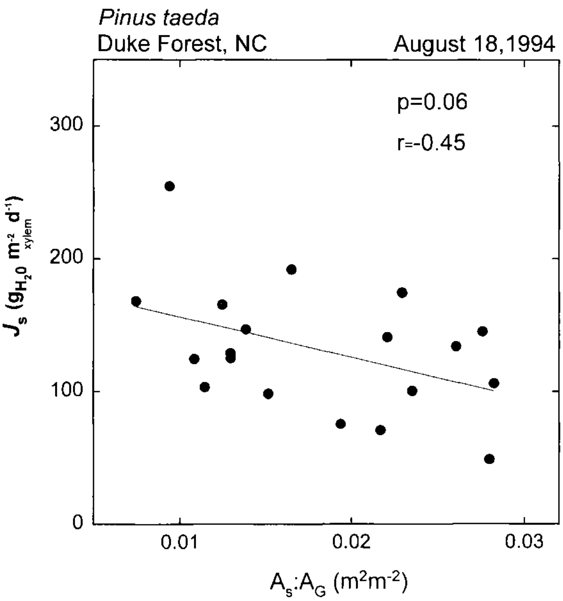

Figure 2. Relationship between water flux in the xylem, J_S, and the competition for soil water, as indicated by the xylem area of all trees, including the tree monitored for xylem flux, per m^{-2} ground, in a 3-m-radius area around each monitored individual, $A_S{:}A_G$.

where $\sigma^2_{J_i}$ is the variance of J_{S_i} (i.e. variance of flux in a given depth) and $A_S{:}A_G$ has zero variance for a single plot case. The combined variance of two categories (or more), such as the variance of the flux in inner ($\sigma^2_{E_{C_{in}}}$) and outer ($\sigma^2_{E_{C_{out}}}$) xylem, about E_C is

$$\sigma^2_{E_C} = \sigma^2_{E_{C_{in}}} + \sigma^2_{E_{C_{out}}} + 2r_{E_{C_{in}}E_{C_{out}}} \qquad (4)$$

where $r_{E_{C_{in}}E_{C_{out}}}$ is the correlation coefficient between the two categories. This estimate of E_C and its variance on a plot level is suitable for comparison with estimates of E_T based on the LWB approach in the same plot. Using equations (2)–(4), E_C and $\sigma^2_{E_C}$ were calculated. E_C and $\sigma^2_{E_C}$, the latter converted to standard error, are shown in *figure 3*, both without accounting for the radial pattern with depth in J_S, and with correction *(figure 3)*. It is clear that not accounting for categorical differences in J_S causes a large over-estimation of E_C, a discrepancy that becomes more significant as E_C decreases (uncorrected $E_C = -0.10 + 0.83\, E_C$ corrected; $r^2 = 0.99$).

3.2. Evapotranspiration – LWB method

In order to compare estimates of E_C to those of E_T based on the LWB approach at a high temporal resolution, measurements were conducted in the FACE plot from 0830 to 2030 EST on 29 September 1994, a cloudless day with a maximum air temperature of 25.5 °C and a minimum of 11.1 °C. Throughout the day, θ in the top soil layer (0–0.1 m) changed from 11.65 to 10.52 % (one-way ANOVA, $P < 0.0001$; SAS, Cary, NC, USA), while in the other

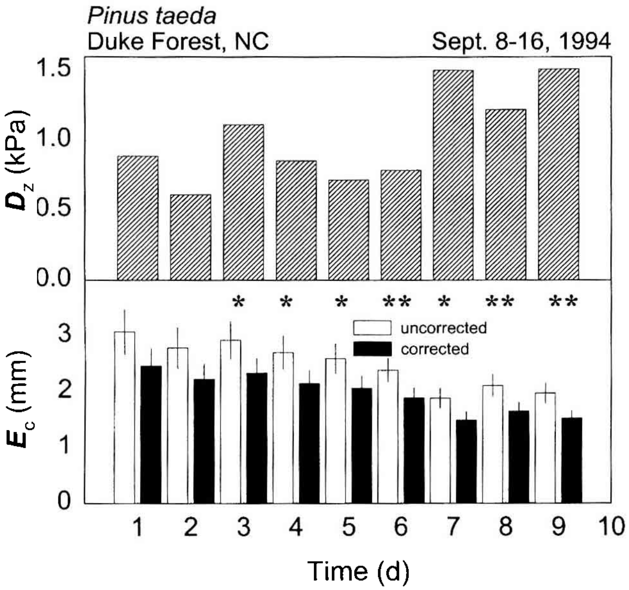

Figure 3. Daytime mean vapor pressure deficit, standardized by day length (number of hours with measurable light over 24 h), D_Z, and daily transpiration by canopy trees, E_C, corrected and uncorrected for the difference in flux between inner and outer xylem. Vertical lines represent 1 SE, and asterisks indicate that the two estimates of E_C differ (* $P < 0.05$; ** $P < 0.01$). The data represent a 9-d drying period. D_Z does not explain the variability in E_C ($P > 0.3$).

three layers to a depth of 0.7 m, θ remained constant ($P > 0.05$; *figure 4a*). Converting θ at the top layer to ΔS_W, and testing for the difference between the means (LSD) identified four distinctly different means ($P < 0.05$; *figure 4b*). These were used to construct the diurnal pattern in soil moisture and E_T (based on Vogt et al. [63]). The diurnal pattern in ΔS_W reflected a reduction of 1.13 % in θ. Cumulative drainage, calculated with equation (1), was very low (0.058 mm), reflecting the low drainage rate in these soils under unsaturated conditions *(figure 4c)*. A diurnal pattern in E_C was compared to E_T estimates based on the LWB approach. After calculating drainage [equation (1)], diurnal E_T was estimated from ΔS_W and drainage *(figure 4b, c)*, and is depicted in *figure 4d*, along with diurnal E_C, calculated with its variance as described before. The variance estimate for E_T was restricted to the variance in measurements among TDR rods, carried through the calculations. (Variance estimates for a longer measurement period must also include the spatial variance in P_T.) The estimates of diurnal E_T were indistinguishable from those of E_C, indicating that E_{SC} was negligible, or that the sensitivity of TDR (ca 1 % measurement error) is insufficient to detect small changes in soil moisture between frequent measurements in zones from which 1) drainage is low, and 2) soil moisture is not taken up by roots at high rates.

Daily E_C during the study day, based on the scaled measurements of J_S, was 1.28 mm, while the estimate of E_T, based on the LWB, was 1.25 mm. This reflects the insensitivity of the TDR to small changes in θ, which can translate to a large

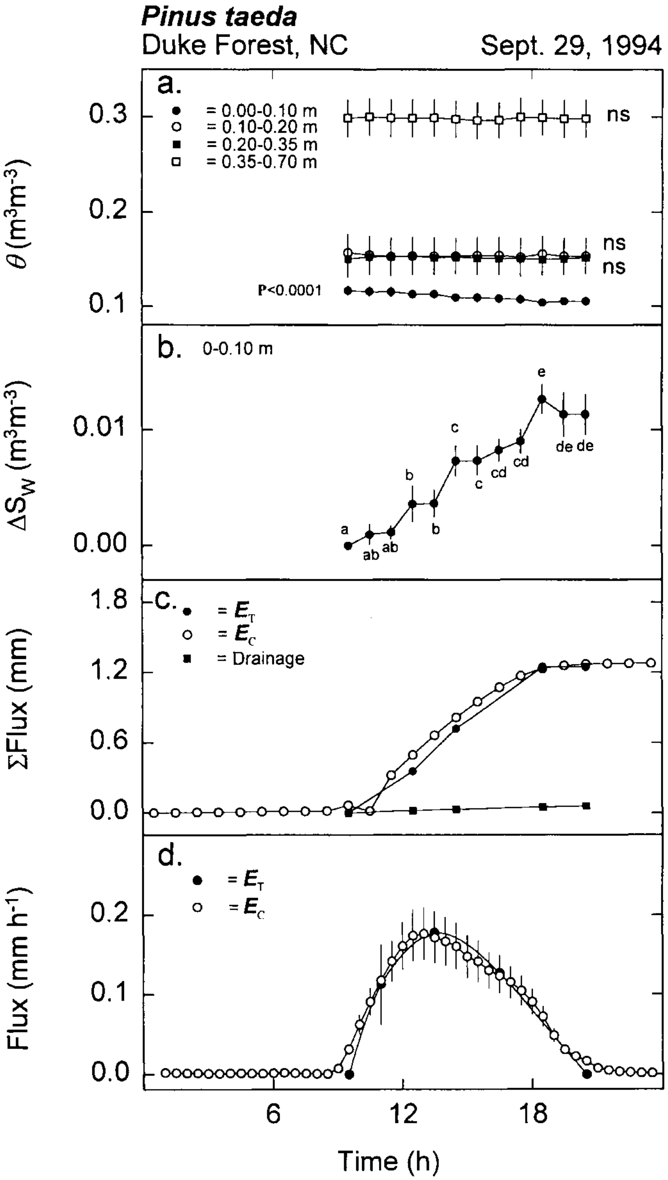

Figure 4. Throughout the day, volumetric soil water content, θ, in the top soil layer (0–0.1 m; measured with a time domain reflectometer, TDR) changed from 11.65 to 10.52 %, while in the other three layers, to a depth of 0.7 m, θ remained constant (a). Converting θ at the top layer to changes in stored water, ΔS_W and testing for the difference between the means, identified four distinct means ($P < 0.05$; b). Cumulative drainage [calculated using equation (3) in text] was very low (0.058 mm; c). A diurnal pattern in canopy transpiration, E_C, was compared as cumulative values (c) or periodic values (d) to total evapotranspiration, E_T, estimated from ΔS_W and drainage. Vertical bars represent 1 SE, calculated for E_C as described in the text, and for E_T based on the variance between individual TDR rod-pairs.

amount of soil moisture depletion when integrated over a thick rooting zone. If the requirement that only significantly different measurements of θ are used for estimating $\boldsymbol{E}_{\mathrm{T}}$ is relaxed so that changes in θ are considered regardless of their statistical significance, daily $\boldsymbol{E}_{\mathrm{T}}$ becomes 1.74 mm, of which $\boldsymbol{E}_{\mathrm{C}}$ accounts for ca 76 %.

3.3. Evapotranspiration – micrometeorological approach

Comparisons of $\boldsymbol{E}_{\mathrm{C}}$ to $\boldsymbol{E}_{\mathrm{T}}$, the latter estimate based on eddy correlation measurements, must scale $\boldsymbol{J}_{\mathrm{S}}$ measurements to a larger footprint than a single plot of 30 m radius or less. Optimally, $\boldsymbol{J}_{\mathrm{S}}$ measurements should be made in trees selected randomly in an area large enough to represent the footprint of the eddy correlation measurement point, and $\mathrm{A_S{:}A_G}$ should be estimated in plots positioned around the selected trees. In practice, factors such as the number of data-loggers available and the maximum sensor-to-logger distance, which maintains signal integrity, confounds the number of $\boldsymbol{J}_{\mathrm{S}}$ measurements that can be made and their spatial distribution. Then, a few clusters for $\boldsymbol{J}_{\mathrm{S}}$ measurements are established, $\mathrm{A_S{:}A_G}$ is measured around each of the randomly selected trees to assess the correlation between the two variables, and additional plots selected randomly in the stand are used to capture the variability in the scaling variable, $\mathrm{A_S{:}A_G}$. (In species and situations where there is evidence for a relationship between $\boldsymbol{J}_{\mathrm{S}}$ and tree size, stratification by size classes may also be necessary; Phillips et al. [51] demonstrated that there was no relationship between $\boldsymbol{J}_{\mathrm{S}}$ and size class in our stand.) Because of the experimental nature of our stand, the clusters and plots were not selected randomly, however, between cluster variability in $\boldsymbol{J}_{\mathrm{S}}$ is illustrated in *figure 1*.

Because scaling measurements based on Granier-Type sensors to the stand involve two variables, equation (2) changes so that the means of $\boldsymbol{J}_{\mathrm{S}}$ and $\mathrm{A_S{:}A_G}$ in each category (e.g. xylem depth) are used

$$\overline{\boldsymbol{E}}_{\mathrm{C_i}} = \overline{\boldsymbol{J}}_{\mathrm{S_i}} \cdot \overline{\mathrm{A_{S_i}{:}A_G}} \qquad (5)$$

and $\boldsymbol{E}_{\mathrm{C}}$ is the sum of $\boldsymbol{E}_{\mathrm{C_i}}$. The variance about $\boldsymbol{E}_{\mathrm{C_i}}$ is calculated as

$$\begin{aligned}
\sigma^2_{\boldsymbol{E}_{\mathrm{C_i}}} &= \overline{\boldsymbol{J}^2_{\mathrm{S_i}}} \cdot \overline{\left(\mathrm{A_{S_i}{:}A_G}\right)^2} \\
&+ \left(\mathrm{r}_{\boldsymbol{J}^2_{\mathrm{S_i}}\left(\mathrm{A_{S_i}:A_G}\right)^2} \cdot \sigma_{\boldsymbol{J}^2_{\mathrm{S_i}}} \cdot \sigma_{\left(\mathrm{A_{S_i}:A_G}\right)^2} \right) \\
&- \overline{\boldsymbol{J}}^2_{\mathrm{S_i}} \cdot \overline{\left(\mathrm{A_{S_i}{:}A_G}\right)}^2 - \left(\mathrm{r}_{\boldsymbol{J}^2_{\mathrm{S_i}}\left(\mathrm{A_{S_i}:A_G}\right)} \cdot \sigma^2_{\boldsymbol{J}^2_{\mathrm{S_i}}} \cdot \sigma^2_{\left(\mathrm{A_{S_i}:A_G}\right)} \right) \\
&- 2\overline{\boldsymbol{J}}_{\mathrm{S_i}} \cdot \overline{\left(\mathrm{A_{S_i}{:}A_G}\right)} \cdot \mathrm{r}_{\boldsymbol{J}_{\mathrm{S_i}}\left(\mathrm{A_{S_i}:A_G}\right)} \cdot \sigma_{\boldsymbol{J}_{\mathrm{S_i}}} \cdot \sigma_{\left(\mathrm{A_{S_i}:A_G}\right)}
\end{aligned} \qquad (6)$$

where $\mathrm{r}_{\boldsymbol{J}_{\mathrm{S_i}}(\mathrm{A_{S_i}:A_G})}$ is the correlation coefficient between $\boldsymbol{J}_{\mathrm{S_i}}$ and $\mathrm{A_{S_i}{:}A_G}$ (e.g. *figure 2*). The variance of canopy transpiration in each category, $\sigma^2_{\boldsymbol{E}_{\mathrm{C_i}}}$, can be combined to variance about $\boldsymbol{E}_{\mathrm{C}}$, $\sigma^2_{\boldsymbol{E}_{\mathrm{C}}}$, using equation (4). In general, we use the covariance term when two variables (A and B) satisfy the condition $(\mathrm{r_{AB}} \cdot \sigma^2_{\mathrm{A}} \cdot \sigma^2_{\mathrm{B}})/(\overline{\mathrm{A}} \cdot \overline{\mathrm{B}}) > 0.1$.

The contribution of the variability in $\mathrm{A_{S_i}{:}A_G}$ to $\sigma^2_{\boldsymbol{E}_{\mathrm{C_i}}}$ can be seen in *figure 5*, which shows wide ranges in both inner and outer xylem area index. Although the study was performed in a stand planted uniformly to ca 1 800 trees $\mathrm{ha^{-1}}$, establishment of natural regeneration increased the density to over 5 200 trees $\mathrm{ha^{-1}}$ in some plots, and natural variability in resources within the apparently uniform site (e.g. depth to a clay pan), resulted in variation in growth rate. Combined, these

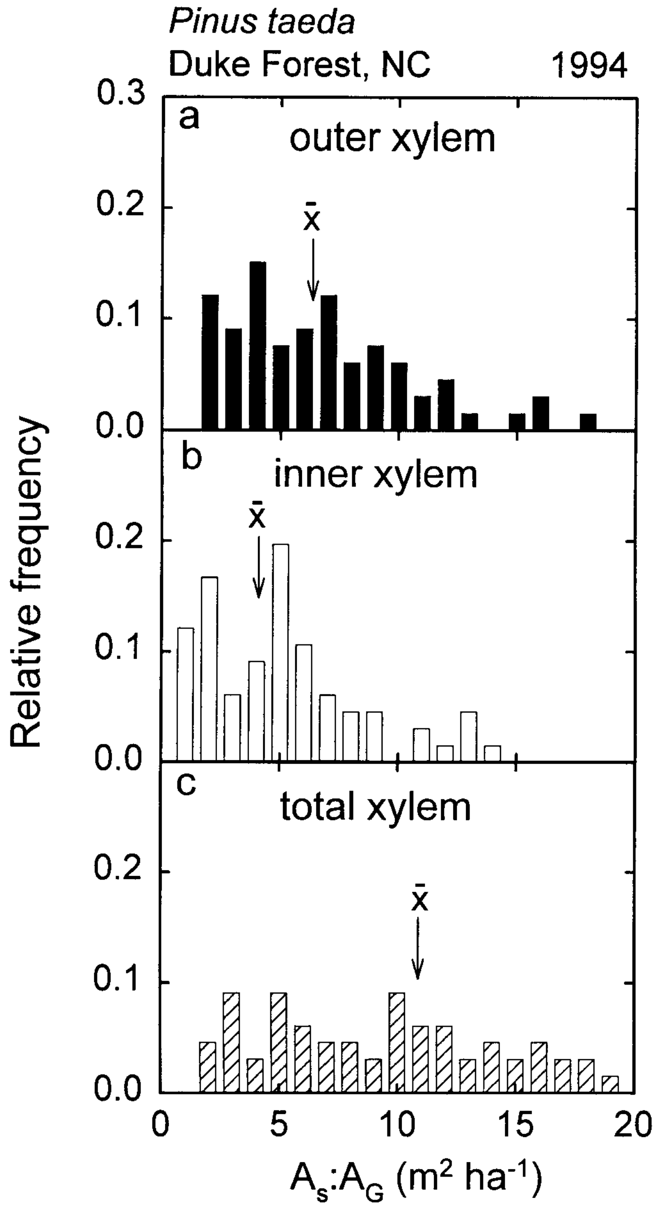

Figure 5. A wide range in both outer (a) and inner (b) xylem area index (A_S:A_G) can be seen in data from 66 plots established in a 12-year-old stand planted uniformly to ca 1 800 trees ha^{-1}. Establishment of natural regeneration and natural variability in resources within the apparently uniform site resulted in a total xylem area (roughly 90 % of basal area) that is almost evenly distributed from 2 to 19 m^2 ha^{-1} (c).

factors result in a total xylem area (roughly 90 % of basal area) that is relatively evenly distributed from 2 to 19 $m^2 ha^{-1}$ (*figure 5c*).

Using the information in *figures 2* and *5*, and J_{S_i} measured over 9 d in which eddy correlation measurements were made above the canopy, E_C and its variance were calculated. E_C and its standard error are shown in *figure 6* in comparison to E_T estimated based on eddy correlation measurements. Over 9 d, eddy correlation based estimates of E_T ranged from 0.6 to 3.8 mm d^{-1}. The relationship between the estimates based on the two methods was linear ($R^2 = 0.89$; $P < 0.0001$), with a zero intercept ($P > 0.1$), and was not affected by atmospheric CO_2 concentration. The estimated E_C accounted for 69 % of E_T. It is possible that not all the difference between E_T and E_C can be attributed to evapotranspiration from the subcanopy; we did not attempt to match the footprint of the eddy correlation system with the corresponding A_S:A_G plots at each point in time during the 9-d comparison, and, thus, the sources of water vapor may not have been exactly the same for the two methods. Such a detailed analysis would refine the comparison between E_T and E_C.

A major assumption in using J_S to infer transpiration is that water flux at the sensor reflects water transpired by leaves, an assumption which may be correct only for branch level measurements. By comparing diurnal E_C patterns, obtained using Granier-Type sensors to measure J_S in stems and branches, with diurnal E_T patterns obtained using eddy correlation, it is possible to evaluate the utility of xylem flux measurements for estimating tran-

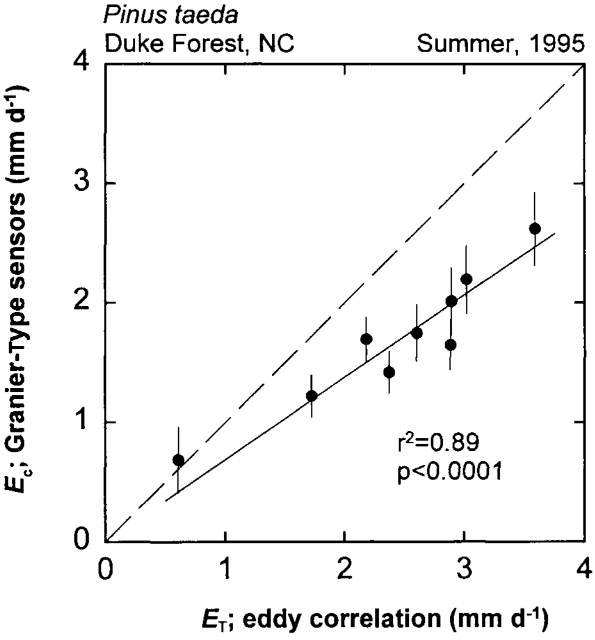

Figure 6. Canopy transpiration, E_C (vertical bars are 1 SE) is compared to total evapotranspiration, E_T, estimated based on eddy correlation measurements. The relationship between the estimates based on the two methods was linear, with a zero intercept ($P > 0.1$), and was not affected by atmospheric CO_2 concentration. The relationship was $E_C = 0.69E_T$.

spiration. The comparison is based on the assumption that flux of water vapor above the canopy can be converted to the source of water vapor in the canopy by accounting for changes in absolute humidity in the canopy volume (using data on temperature and relative humidity collected at 7 m, and assuming that there is no vertical profile; [64]). Moreover, it is assumed that the behavior of canopy trees is similar to the behavior of all the vegetation in the stand; thus, while E_C may account for only ca 70 % of ***LE*** at any time, the pattern in both is assumed to be similar. This assumption is supported by the high correlation between flux measurements made using eddy correlation systems at two canopy levels (above the canopy and at 0.7 canopy height; $R^2 = 0.72$; $P < 0.001$; N = 133 during 8 d, each datum representing a 27.3-min sum; P intercept > 0.1), but may not be valid both early and late in the day.

On a clear day (19 September 1994), shortwave radiation showed a nearly symmetric pattern, while the pattern in ***D*** was lagged relative to radiation *(figure 7a)*.

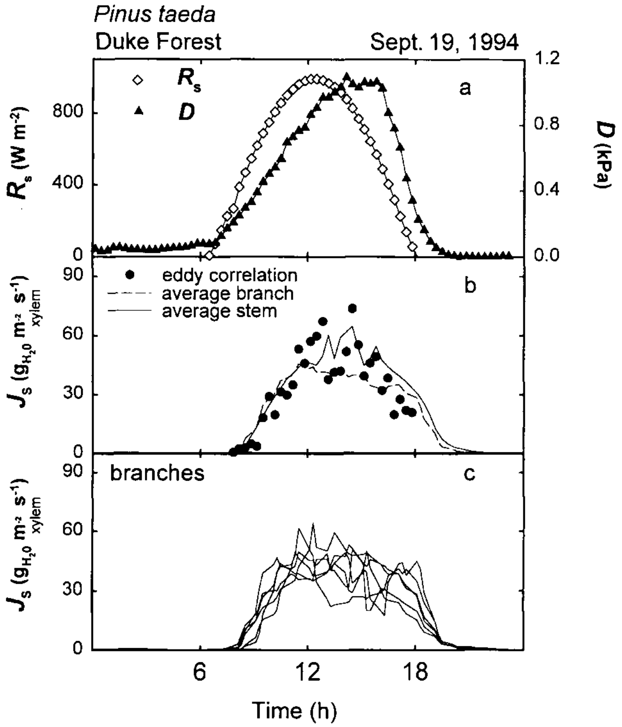

Figure 7. On a clear day, shortwave radiation (R_S) showed a nearly symmetrical pattern, while the pattern in vapor pressure deficit, ***D***, lagged relative to the radiation (a). Latent heat flux, ***LE***, obtained with eddy correlation above the canopy, was converted for convenience of comparison with xylem flux, J_S, into similar units (b). The J_S of two trees adjacent to the tower, and their six branches, were compared to ***LE*** (b). Individual branches may display large high frequency variation (c), more similar to that measured with eddy correlation.

Latent heat flux was converted to J_S using the average A_S:A_G in the stand (see *figure 5c*), and summed over 20-min intervals. (A conservative thermal equilibrium response time of the Granier-Type sensor is ca 30 s.) Eddy correlation measurements were made at the canopy–atmosphere interface, and, based on the previous findings *(figure 6),* were not expected to produce similar values. Thus, comparison of values from eddy correlation measurements, stems and branches were made only to assess whether the high frequency variation in these measurements are similar. For this purpose, only J_S of two trees adjacent to the tower, and their six branches, were compared to ***LE***. In *figure 7b,* it is apparent that the three diurnal patterns are similar, but that the high frequency fluctuations are smoothed in the mean J_S of the two stems; the pattern is even smoother when more trees are averaged. Even the average diurnal pattern in branch J_S is smooth, although branches are certainly less affected by the storage component in the xylem relative to stems. Thus, although certain branches may display large variation on time scales of 5–20 min, more similar to that measured with eddy correlation *(figure 7c),* it is difficult to identify the branches whose behavior might reflect that of the whole canopy.

4. DISCUSSION

Difficulties in scaling fluxes arise when variables that exhibit both high spatial and temporal variability are sampled [31, 42]. For this reason, there is an increased tendency to use methods that integrate over 'either' spatial or temporal variability. Micro-meteorological methods provide a foot-print level of spatial integration [3, 23], but their utility for assessing the effect of forest structure on flux is limited, and they are unsuitable to study different physiological responses of co-occurring species [40]. Therefore, when the purpose of an investigation is to assess the effect of variation in environmental conditions on different sources and sinks within the canopy, or to calculate canopy stomatal conductance of different components in the forest [3], other approaches must be employed. Sapflow measurements allow evaluation of spatial variability and, in combination with local water balance or micro-meteorological flux estimates, can partition fluxes amongst distinct sources. These sources may represent strata within the canopy, or patches of different species within a strata. Partitioning water flux into strata may also be accomplished by positioning eddy correlation instruments at a desired number of levels within the canopy [17, 24], however, the compatibility of foot-prints (i.e. similarity in the spatial variation within source areas) must be assured before measurements from a pair of instrument at different heights are compared [39].

4.1. Scaling sap flux and local water balance

Scaling of sapflow to the stand level has often been carried out by first scaling flux measurements to the tree using tree circumference (Cermák-Type sensors; [2, 38]), tree sapwood area (heat pulse velocity and Granier-Type sensors; [5, 28, 30, 41, 43, 62]), or projected crown area [48]. In each of these studies, a relationship was shown between tree transpiration and one or more variables describing a measure of tree size, e.g. stem circumference, diameter, basal area, sapwood area, projected crown area or tree leaf area. This, of course, is to be expected, because all of these measures are strongly auto-correlated. Because one of these measures is used to scale heat flux or pulse measurements to tree sapflow, they are, in turn, auto-correlated with tree transpiration. The apparently good relationship between a measure of tree size and tree transpiration, especially convincing when the range in tree size is large, has been used to justify calculating stand flux by combining the number of individuals per hectare in each size category with the flux density in a representative individual(s) [10, 17, 26]. However, this may mask potentially known and accountable sources of variability in the original sap flux data.

Many investigations have found that, after standardizing tree sapflow by a conducting or transpiring surface area (i.e. sapwood or leaf area), or an index of these areas (e.g. projected crown area), differences in flow among individual trees decrease, and become generally unrelated to a measure of tree size [2, 17, 43, 54, 58]. In closed stands, some of the residual variability originated from emergent [40, 62] or very suppressed [10, 17] positions in the canopy, position in relation to neighboring crowns [2] and competition *(figure 2)*. Here we demonstrate that, even in a so-called homogeneous plantation of pine, a patchy distribution in sapwood area index *(figure 5)* causes high variation in competition among patches, and, in turn, a large variability in sap flux density among individuals *(figure 1)*. Large variability in sapwood area index has been reported in other, apparently homogeneous stands [27]. The standardized flow, or flux, may not be distributed normally, reflecting forest structure ([2]; inset *figure 1*).

To account for a proportion of the variability associated with canopy positions of individual crowns, Granier et al. [26] recommended using a proportional sampling procedure, whereby trees to be sampled are allocated into categories (e.g. diameter classes) of a scaling variable (e.g. tree sapwood area) in proportion to the ratio of the sum of the values in the category (e.g. total sapwood area in a class) to the sum of values in the stand. This, or a similar procedure has been used by many investigators [10, 13, 15, 40, 54, 62]. Its main weakness is that it implies that variation in $\boldsymbol{J}_S$ is related to tree size, although it has been shown that $\boldsymbol{J}_S$ (unlike $\boldsymbol{J}_S A_S$ of individual trees) is rarely related to size, but is related to exposure and competition. Thus, Cermák [13] showed that $\boldsymbol{E}_C$ estimates had appreciably lower standard errors, and were less prone to systematic errors, when scaling was based on a solar equivalent leaf area rather than on basal area, stem volume, projected crown area, projected leaf area, or leaf dry mass. Weighing leaf area of individual trees by the time integrated relative irradiance accounted for the variability in $\boldsymbol{J}_S$ caused by exposure, which was only partially accounted for by the other, size-related variables.

A simpler approach is to assume that $\boldsymbol{E}_C$ is the product of two variables, $\boldsymbol{J}_S$ and A_S:A_G. The variance of $\boldsymbol{E}_C$, σ_E, can be calculated after the degree of correlation between the two variables is quantified [equation (6)]. The approach does not attempt to reduce the variability caused by a known factor – the degree of exposure of individual trees – as recommended by Cermák [13]. Thus, in stands in which distinct strata are formed in the canopy, it may be necessary to perform this scaling procedure in combination with the approach outlined by Granier et al. [26], thereby proportionally partitioning sample trees according to relative strata importance, and then accounting for the effect of competition within each stratum. Although this approach is not as elegant as that proposed by Cermák [13], it is statistically sound because it allows error to be propagated throughout all steps, and includes the correlation between variables for variance calculation. In this study, an inverse correlation between $\boldsymbol{J}_S$ and A_S:A_G *(figure 2)* resulted in a downward adjustment in σ_E [equation (6)]. Furthermore, the results shown in *figure 2* demonstrate that the reason that $\boldsymbol{J}_S$ was not distributed normally (inset in *figure 1*) is that it was affected by another variable, namely, competition. Removing the effect of competition resulted in a normally distributed J_S value.

There are several other sources of variability in J_S that may require an explicit treatment when σ_E is calculated. For example, it has long been recognized that in many species there is a radial pattern in J_S ([25]; see summary in Phillips et al. [51]). In the case of species displaying a radial pattern in J_S and a hydroactive xylem, which is greater in depth than the length of the sensor used, scaling to the stand should account for the variability in J_S in each depth interval and variability in A_S:A_G representing each depth interval. Eventually, a variance combining those of all intervals can be calculated for canopy transpiration [equation (4)]. Recently, investigators using Granier-Type sensors have begun to account for radial pattern in estimating long-term E_C by correcting the flux in the xylem beyond the reach of sensors by a factor based on a short-term, unreplicated study [7, 26, 41]. The correction was made to permit comparisons with two Cermák-Type sensors, to estimate canopy transpiration based on each sensor, and to calculate the number of sensors necessary to achieve a mean that falls within 10 % of the mean of all 24 sensors [7, 41]. Such a correction must be performed with the understanding that it does not take into account the dynamic nature of the conducting tissue. Under conditions of decreasing water availability, reduction in J_S in the inner xylem was greater than that in the outer xylem, and occasionally ceased entirely [5, 51]. Over 9 rainless days, the inner xylem J_S of *Pinus taeda* decreased, first gradually and then rapidly, from 44 to 36 % of the outer xylem [51]. Thus, to estimate E_C using sensors that do not transverse the hydroactive xylem, it is best to quantify the radial pattern by positioning sensors across the hydroactive xylem [26], and to assess the sensitivity of J_S at all hydroactive depths to soil water availability. Doing so, we demonstrated in *figure 3* that the commonly assumed uniformity in sap flux throughout the xylem can cause large errors in estimates of E_C, errors that increase with decreasing soil moisture.

A key issue in experimental design, with important implications for both data analyses and project costs, concerns the number of replicated experimental units. Granier et al. [26] summarized the results of several studies and showed that the coefficient of variation (CV) in J_S is ca 10–15 % in temperate forests, but is much larger in tropical forests (35–50 %). Diawara et al. [17] reported a 30–40 % CV ($N = 10$) in *P. pinaster* Ait. Furthermore, variability in J_S increases with drought, because large trees probably use water faster, and progress into drought stress (i.e. low J_S) earlier than smaller trees [26, 28, 44]. Variability in J_S also increases with manipulation of stand structure and resource availability [44, 58]. Using a total of 24 sensors, two variants of Cermák-Type and a Granier-Type, Köstner et al. [41] concluded that the mean of randomly selected subsets of sensors did not converge towards the overall mean when more than eight sensors were employed. Granier et al. [26] concluded that ten sensors should suffice for estimating canopy transpiration in temperate forests. We approached the question differently, asking how many sensors are necessary to obtain a reasonable CV? Choosing a CV of 15 %, we demonstrate in *table II* that the number of sensors necessary to quantify flux at the selected variability is highly variable among species, is higher for broadleaf than conifer species, and may be doubled by cultural treatments. For *P. taeda*, the number of sensors necessary to obtain the same CV in the inner xylem was similar to that in the outer xylem, showing a similar variability in J_S, as is demonstrated by the high correlation between J_{in} and J_{out}. However, variabil-

Table II. Sample sizes required to estimate mean daily sap flux, J_S, with a coefficient of variation of 15 % at $\alpha = 0.05$.

Species	Reference		Irrigated	Fertilized	Fert./Irrig.
	Outer	Inner			
Pinus taeda[1]	11	11	13	19	22
Picea abies[2]	7			12	14
Pinus contorta[3]	4				
Pinus flexilus[3]	11				
Abies lasiocarpa[3]	18				
Populus tremuloides[3]	29				
Liquidambar styraciflua[4]	23	17			
Quercus alba[4]	48	34			

Values are calculated from sap flow data collected using 20-mm Granier-Type sensors. Values calculated using half hourly heat flux, or mean daily flux were similar but not always identical. (Outer: outer 20 mm of xylem, inner: next 20 mm, data from: [1]Scotland County, NC, by Brent E. Ewers; [2]Flakaliden, Sweden, by Nathan Phillips; [3]Laramie Ridge, WY, by Diane E. Pataki, and [4]Duke Forest, NC, by Nathan Phillips.)

ity in J_{in} and J_{out} was not similar in broadleaf species, where the variability may increase or decrease with depth in the xylem. Additional sources of variation on sloping sites include a different diurnal pattern of J_S, depending on the aspect and the azimuth sampled [26]. It is clear that comparison among species, and within a species between stands on sites differing in quality, may require a different number of monitored individuals. Optimizing the use of resources, therefore, may not call for a balanced design with equal number of sensors in each forest type or stand.

Capitalizing on the simplifications arising from integration of flux measurements at the whole-individual level requires a detailed evaluation of potential sources of σ^2_{Js} [21]. Not accounting for radial and azimuthal variability may create errors in scaling flux density to the whole tree [23]; errors which will be carried to canopy-level estimates *(figure 3)*. Additional errors, and larger σ_E, will result if competition and exposure are not considered in the sample allocation design. It is likely that in open stands, competition for water may dominate tree-to-tree variability [17], but that as stands close, and perhaps become less coupled with the atmosphere, variation in irradiance, and thus exposure, becomes more important (Jarvis, per. comm.). The use of such information, should provide guidance for appropriate sampling design depending on the objectives of each study. If the objective of a study is to estimate a component flux by difference, then scaling to the same source area, and minimizing variance, are both requisite steps in the process.

4.2. Comparing E_C with LWB estimate of E_T

In this study, we used two methods to estimate E_T (LWB and micro-meteorology), and one to estimate E_C. The LWB is similar in principle to that used by Rambal [53] and Kelliher et al. [36]. After scaling each of the estimates, we tested whether

E_{SC} can be estimated from the difference between E_T and E_C. Our diurnal soil moisture extraction pattern, obtained with the LWB approach, was very similar to the diurnal of water uptake obtained from scaled J_S *(figure 4)*. Scaling J_S was based on J_{in} and J_{out}, and the inner and outer sapwood area index of the entire FACE plot [equation (4)]. Thus, only one source of variation was included in this scaling, which compared water uptake in the plot with soil moisture extraction in the same plot. The sensitivity of the TDR was sufficient to detect significant changes in θ only in the upper 0.1 m of the profile. Higher variability in measurement in lower soil layers, coupled with smaller changes in θ over the day *(figure 4a)*, prevented the obvious trend from being significant. Had the changes been significant, E_C would have accounted for 76 % of the daily soil moisture extraction, implying that ca 24 % of E_T may be E_{SC}, a similar estimate to that from the difference in eddy correlation measurements above and below the canopy (> 20 %). Using the LWB method, long-term data from both the FACE and Ref. 2 plots showed a significantly lower E_C relative to E_T [59]. The difference, reflecting evapotranspiration below the canopy, accounted for 36 % in the FACE and 25 % in Ref. 2, at a time when L in FACE was ca 15 % lower than in Ref. 2.

We propose that 1) two estimates of fluxes, from the same or different component, may be compared only if errors about the estimates account for the variability from the same source area; 2) before a difference between two components is attributed to a third, it is necessary to show first that it is significantly greater than zero, or, in other words, before accepting a budget as closed, the deviation from closure must be shown not to differ from zero. Employing these criteria in the comparison between E_C and LWB-estimated E_T *(figure 4)*, we concluded that the LWB approach is not suitable to estimate E_T for the total stand or, by difference with E_C, for the subcanopy, on time scales less than 1 day. The conclusion is based on lack of significant diurnal difference between the E_T and E_C estimates, although such differences were apparent in both long-term LWB based estimates of E_T, and in diurnal and daily eddy correlation estimates of E_T.

Bréda et al. [10] had performed a similar comparison between water source (rooting volume) and sink (uptake by trees). Over three study years, water uptake accounted for ca 0.95 of the soil water balance. The authors attributed the small difference to soil evaporation, perhaps because understory was absent under the high canopy L (= 6). However, precipitation input and drainage were not explicitly considered in that study. In a mixed stand of mature oaks, Bréda et al. [11], using a similar approach, identified that, in spring, the soil water balance showed greater water loss than was accounted for by scaled water uptake obtained with Granier-Type sensors. In spring, water uptake accounted for 0.73 of soil water loss, but the ratio increased to 0.85 by early summer, and 1.43 by late summer. The difference at the beginning of the season was attributed to evaporation from the soil. However, as in the previous study, there was no treatment of precipitation input or drainage. It is possible that drainage could account partially for the early season discrepancy, and uptake from layers below the measured depth for the late season discrepancy.

Rambal [53] studied the dynamics of water extraction by roots using, in principle, the same approach used in this study. His study demonstrated that water uptake from deep horizons increased with decreasing growing season precipitation; up to 23 % of soil moisture in his evergreen oak scrub was absorbed below 2 m of soil depth during the growing season.

While theoretically, LWB can be applied to great depths in the soil [32], the normal functioning of the forest will be disrupted if trenches must be dug to install soil moisture sensors in great depths and in numbers sufficient to quantify the change in θ.

We therefore recommend that the LWB method be used for time scales greater than a day, unless water uptake is high and concentrated in a thin soil layer, and drainage is relatively low in comparison to moisture extraction. In addition, the LWB requires that the variability in rainfall input to the soil is considered. In general, the method is difficult to use in rocky soils, or in vegetation supporting deep roots (> 2 m). The LWB is useful for estimating E_T in small plots, and over sloping ground, both situations unsuitable for the application of micro-meteorological techniques for estimating E_T.

4.3. Comparing E_C with micro-meteorological estimates of E_T

Briefly, micro-meteorological approaches to estimate component flux in forests include: 1) estimating E_T based on eddy correlation measurements above the canopy; and 2) estimating evapotranspiration from the soil, litter, and understory based on i) lysimeters, ii) eddy correlation measurements above the understory, or iii) process or empirical models for estimating the contribution to E_T from each subcanopy component. In many investigations, E_T is estimated above the canopy and E_{SC} above the understory. Although each estimate typically represents a different source area, and sometimes the areas differ in size by several orders of magnitude, it is common to subtract 2) from 1) and attribute the difference to E_C. Often, in addition to one or both of the other components, E_C is estimated directly, using scaled J_S, or indirectly, using models and input of environmental variables and parameterization with porometry data.

When either E_{SC} or E_T is measured or estimated with E_C, the unmeasured component is often calculated without considering source areas. If all three components are obtained, the closure in the budget is evaluated [2, 7, 8, 17, 24, 26, 36, 37, 39, 41, 64]. The closure is then judged based on assumed or estimated errors [6, 36, 37, 39] or on subjective criteria (e.g. difference from closure relative to E_T; [7]). If the closure is considered unacceptable, the budget is adjusted based on some post facto criteria [2]. When error estimates are used, they often 1) include component errors that are based on assumptions; 2) do not attempt to include the spatial variability from the same source area for all budget components; 3) use ensemble variance for one component and spatial variance for another; and 4) are not the product of a study design with an a priori objective to obtain reasonably small standard errors of estimates. The effect of not designing a study so as to minimize the standard error can be seen in *figure 4*. Replicates were sufficient to produce a very small standard error in soil moisture of the top layer, but were too few for producing small errors in deeper layers. Generally, without estimating standard errors, one relies on subjective criteria to judge the closure in the budget; with inappropriately estimated standard errors, one misjudges the closure; and with artificially large standard errors, one may always find closed budgets.

Comparing E_C obtained from J_S, with that using a combination of energy balance and understory lysimeters, Arneth et al. [2] found a difference of ca 30 % between the two estimates. Although standardizing whole-tree water flow by projected canopy area removed systematic variation in flux among crown classes, the authors excluded subcanopy individuals

< 110 mm in diameter from E_C calculations, which represented 60 % of trees and 15 % of the plot basal area. This reduced the difference between the two estimates of E_C to only 5–10 % which, in turn, was used to propose that trees of the small size class transpire less per unit of stem area. Furthermore, the authors suggested that, given the 10–20 % coefficient of variation for the two estimates, the differences between them are probably not statistically significant. However, an analysis of their results (*table III* in Arneth et al. [2]) showed that, in each of the six study days, estimates of E_C based on the two methods differed at $P < 0.03$ to 0.0001. Five measured variables were involved in the estimation of E_C based on the two methods: mass flow rate of xylem sap for a portion of tree circumference was combined with tree circumference into one variable, mass flow per tree (assuming no circumferential variance), and divided by crown area, to produce mass flow per unit of crown area. This facilitated a comparison with the following three variables: available energy, sensible heat flux density and subcanopy evaporation rate. The authors stated that some uncertainty may be associated with estimates based on scaling measurements and combining estimates. The implicit assumption in comparing the two E_C estimates is that the four estimated fluxes represent the same source area, or that the spatial average is represented by the source areas of each of the flux variables.

However, the failure to close the budget without excluding the smaller trees demonstrates that this fundamental assumption has not been met, as may often be the case [39]. Thus, an alternative choice may be to ignore the lysimeter-based estimate of subcanopy evaporation because, due to its very limited spatial sampling, it may not be representative of the mean, and retain the transpiration by subcanopy trees in the calculations. In doing so, the estimate of E_T is greater than the estimate of E_C by 0.3 mm on average [2]. The difference is significantly greater than zero ($P < 0.01$ or less for each day), and is thus attributable to the unmeasured budget component, E_{SC}. If this value better represents E_{SC}, then the flux estimated with lysemeter measurements may have over-estimated E_{SC} three-fold on average.

We have estimated daily E_C based on Granier-Type sensor measurements, expanded to the stand [equation (5)]. The values were compared to E_T obtained with eddy correlation from a similar source area (*figure 6*). Except for the day of the lowest measured flux, when apparent E_C exceeded E_T probably due to recharge of long-term depletion of stem water reserve [50], E_C was significantly lower than E_T. The slope of the relationship between E_C and E_T indicates that on average ca 31 % of E_T originates below the canopy, not very different from the long-term estimate using LWB (36 %; [59]). However, the daily ratio indicates that E_C / E_T can vary from 1.13 to 0.57, with an average of 0.73 (1 SE = 0.05). Subcanopy contribution varies appreciably among forests, and daily within forests, depending on stand structure, species composition, canopy L, soil moisture availability and atmospheric conditions [9, 47]. In certain forests, E_{SC} becomes a larger proportion of E_T as soil dries [37].

On a clear day, E_T, and J_S of stems and branches showed a similar pattern of increased flux in the morning, but the patterns diverged thereafter (*figure 7b*), reflecting the dynamics of hydraulic resistance in the stem and of water storage [26]. The time constant between transpiration and water uptake has been evaluated explicitly to permit estimation of E_C from measurements of water uptake [43, 51, 52]. The effect of the resulting time-lag will be addressed here only in the context of its effect on partitioning flux between contributing components within forests.

Comparing sapflow-based estimates of E_C with E_T diurnally, even when scaled to the same source area and including appropriate error calculation, may result in differences between the two components during certain hours, presumably attributable to E_{SC}, but potentially resulting from the time-lag between the two estimates. A time-lag not chosen carefully, may artificially reduce the difference at certain times and increase it at others. The time-lag not only shifts the course of uptake relative to E_C, but also changes its shape and buffers the high-frequency fluctuation in E_C.

We attempted to evaluate the use of branches, presumably containing little storage, for assessing the lag between E_T, E_C (i.e. J_S in branches) and uptake (J_S in stems). Unrelated to their position in the canopy, four of the six branches began to transpire without a time-lag and two branches lagged behind the stem *(figure 7c)*. All branches continued to recharge into the night after transpiration stopped, although they completed the recharge before the stem. Most importantly, however, was the clear asynchronous behavior of branch J_S during most of the day *(figure 7c)*, resulting in a smooth course of mean J_S *(figure 7b)*, and indicating that micro-climate variability is large in the canopy. Selecting branches to monitor in order to follow the diurnal course of E_C may not be possible.

Thus far, time-lag in stem J_S has been selected mostly by subjectively lagging uptake relative to E_T, radiation, or D, until there appears to be an acceptable match [26, 41]. Other approaches include: a cross-correlation analyses between uptake and these variables; resistance–capacitance formulations; and, recently, estimation of the stem storage dynamics and utilizing the information to translate uptake to E_C [43, 51, 52]. Regardless of the method used, errors in matching uptake to E_C affect not only calculations of canopy conductance [43, 50], but also confound the estimation of diurnal E_{SC}. Thus, due to the time-lag between transpiration and uptake, the shortest time interval for safely estimating E_C from J_S may be 1 d [15], and choices made in selecting the time over which measurements are integrated may also affect the results of comparison on a daily scale [17].

4.4. E_C in relation to estimated soil moisture depletion

We used our estimate of average $E_{SC} = 0.31E_T$ to make a similar analysis of E_C response to soil moisture depletion over a period for which θ was not measured. Over a 9-d drying cycle, we increased E_C to account for the E_{SC} of ca 31 % of E_T, and expressed E_C as a function of cumulative E_T *(figure 8)*. We consider cumulative E_T to only approximate soil moisture depletion, because, while drainage is quite negligible over such a short period during the growing season [36] – < 1 mm in total (*figure 4c*; [59]), daily transpiration of understory may be affected less by soil drought than overstory [9]. The variable contribution of subcanopy to E_T requires a different correction for E_C every day. We did not have such information, and therefore applied the average correction *(figure 6)* to all days.

The effect of soil moisture on stomatal conductance and transpiration is well documented [29, 55]. Reduction in soil moisture also affects the dynamics of water flux in stems, and increases the contribution of water stored in stems to E_C [43, 51]. Reduction in the total conductivity of the soil–tree system with soil moisture was explained by increased soil–root resistance at higher ($\theta = 0.33$; [4]) and lower ($\theta = 0.17$; [57]) levels, perhaps resulting from reduced root extension growth [56] and root–soil contact [46].

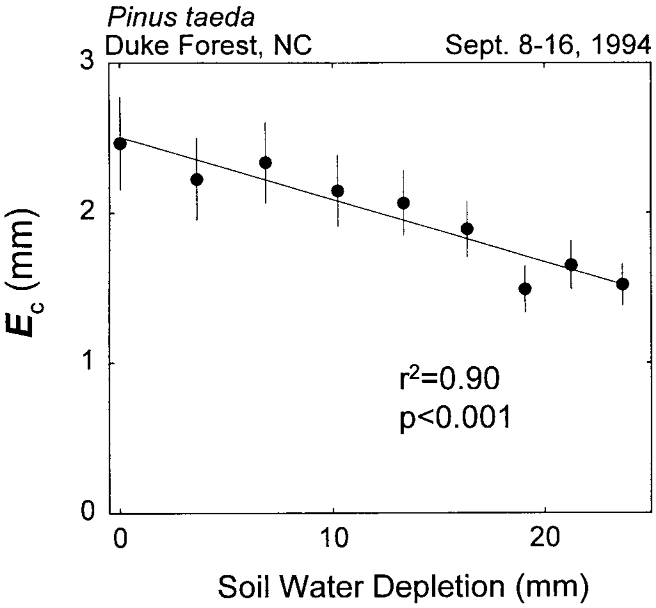

Figure 8. Canopy transpiration, E_C, estimated based on measurements with Granier-Type sensors, decreases linearly with soil moisture depletion over a 9-d drying period. Soil moisture depletion was calculated from cumulative E_C, corrected to account for depletion by total evapotranspiration, E_T

Daily transpiration is correlated to soil moisture during short drying periods and seasonally [11, 14, 20, 43, 46, 57, 58]. Granier and Loustau [23] showed that increasing soil moisture deficit during 8 d resulted in a decrease in E_C of maritime pine to a sixth of the initial value. In stands growing over deeper soils and transpiring at lower rates, the rate of decline in E_C with drought may be considerably lower [43].

In this study, approximately 90 % of the water used for transpiration is absorbed in the upper 0.35 m of the soil *(figure 4)*; when θ decreases below 0.18, canopy conductance decreases rapidly with θ [59]. Using the calculated cumulative E_T, θ in the main rooting layer decreased by ca 0.07, as E_C decreased to 60 % of its original value, a much lower sensitivity of E_C to change in θ than reported by Granier and Loustau [23]. Because daily E_C during this period was not related to D ($P > 0.3$), it is likely that θ was within the range in which it strongly influences canopy conductance, as demonstrated in Oren et al. [49].

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REFERENCES

[1] Amoozegar A., A compact constant-head permeameter for measuring saturated conductivity of the vadoze zone: comparison of the Glover solution with simultaneous-equations approach for measuring hydraulic conductivity, Soil Sci. Soc. Am. J. 53 (1989) 1356–1361.

[2] Arneth A., Kelliher F.M., Bauer G., Hollinger D.Y., Byers J.N., Hunt J.E., McSeveny T.M., Ziegler W., Vygodskaya N.N., Milukova I., Sogachov A., Varlagin A., Schulze E.-D., Environmental regulation of xylem sap flow and total conductance of Larix gmelinii trees in eastern Siberia, Tree Physiol. 16 (1996) 247–255.

[3] Baldocchi D.D., Luxmoore R.J., Harfield J.L., Discerning the forest from the trees: an essay on scaling canopy stomatal conductance, Agric. For. Meteorol. 54 (1991) 197–226.

[4] Barataud F., Moyne C., Bréda N., Granier A., Soil water dynamics in an oak stand. II. A model of the soil–root network compared with experimental data, Plant and Soil 172 (1995) 29–43.

[5] Becker P., Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods, Tree Physiol. 16 (1996) 295–299.

[6] Berbigier P., Bonnefond J.M., Loustau D., Ferreira M.I., David J.S., Pereira J.S., Transpiration of a 64-year-old maritime pine stand in Portugal. 2. Evapotranspiration and canopy stomatal conductance measured by an eddy covariance technique, Oecologia 107 (1996) 43–52.

[7] Bernhofer Ch., Gay L.W., Granier A., Joss U., Kessler A., Köstner B., Siegwolf R., Tenhunen J.D., Vogt R., The HartX-Synthesis: An experimental approach to water and carbon exchange of a Scots pine plantation, Theor. Appl. Climatol. 53 (1996) 173–183.

[8] Bernhofer Ch., Blanford J.H., Siegwolf R., Welder M., Applying single and two layer models to derive conductances of Scots pine plantation from micrometeorological measurements, Theor. Appl. Climatol. 53 (1996) 95–104.

[9] Black T.A., Kelliher F.M., Processes controlling understory evapotranspiration, Phil. Trans. Soc. Lond. B 324 (1989) 207–231.

[10] Bréda N., Cochard H., Dreyer E., Granier A., Water transfer in a mature oak stand (Quercus petraea):seasonal evolution and effects of severe drought, Can J. For. Res. 23 (1993) 1136–1143.

[11] Bréda N., Granier A., Barataud F., Moyne C., Soil water dynamics in an oak stand. I. Soil moisture, water potentials and water uptake by roots, Plant and Soil 172 (1995) 17–27.

[12] Cassel D.K., Kachanoski R.G., Topp G.C., Practical consideration for using a TDR cable tester, Soil Technol. 7 (1994) 113–126.

[13] Cermák J., Solar equivalent leaf area: an efficient biometrical parameter of individual leaves, trees and stands, Tree Physiol. 5 (1989) 269–289.

[14] Cermák J., Huzulák J., Penka M., Water potential and sap flow rate in adult trees with moist and dry soils as used for the assessment of root system depth, Biol. Plantarum (Praha) 22 (1980) 34–41.

[15] Cienciala E., Lindroth A., Cermák J., Hällgren J.-E., Kucera J., The effects of water availability on transpiration, water potential and growth of *Picea abies* during a growing season, J. Hydrol. 155 (1994) 57–71.

[16] Clapp R.B., Hornberger G.M., Empirical equations for some soil hydraulic properties, Water Resour. Res. 14 (1978) 601–604.

[17] Diawara A., Loustau D., Berbigier P., Comparison of two methods for estimating evaporation of a *Pinus pinaster* (Ait.) stand: Sap flow and energy balance with sensible heat measurements by an eddy correlation method, Agric. For. Meteorol. 54 (1991) 49–66.

[18] Eagleson P.S., Climate soil, and vegetation: 1. Introduction to water balance dynamics, Water Resour. Res. 14 (1978) 705–712.

[19] Ellsworth D.S., Oren R., Huang C., Phillips N., Hendrey G.R., Leaf and canopy responses to elevated CO_2 in a pine forest under free-air CO_2 enrichment, Oecologia 104 (1995) 139–146.

[20] Goulden M.L., Carbon assimilation and water-use efficiency by neighboring Mediterranean-climate oaks that differ in water access, Tree Physiol. 16 (1996) 417–424.

[21] Goulden M.L., Field C.B., Three methods for monitoring the gas exchange of individual tree canopies: ventilated-chamber, sap-flow and Penman-Monteith measurements on evergreen oaks, Funct. Ecol. 8 (1994) 125–135.

[22] Granier A., Une nouvelle méthode pour la mesure de flux de sève brute dans le tronc des arbes, Ann. Sci. For. 42 (1985) 193–200.

[23] Granier A., Loustau D., Measuring and modeling the transpiration of a maritime pine canopy from sap flow-data, Agric. For. Meteorol. 71 (1994) 61–81.

[24] Granier A., Bobay V., Gash J.H.C., Gelpe J., Saugier B., Shuttleworth W.J., Vapor flux density and transpiration rate comparisons in a stand of maritime pine (*Pinus pinaster* Ait.) in Les Andes Forest, Agric. For. Meteorol. 51 (1990) 309–319.

[25] Granier A., Anfodillo T., Sabatti M., Cochard H., Tomasi M., Valentini R., Bréda N., Axial

and radial water flow in the trunk of oak trees; a quantitative and qualitative analysis, Tree Physiol. 14 (1994) 1383–1396.

[26] Granier A., Biron P., Bréda N., Pontailler J.-Y., Saugier B., Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods, Global Change Biol. 2 (1996) 265–274.

[27] Granier A., Biron P., Köstner B., Gay L.W., Najjar G., Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine, Theor Appl. Climatol. 53 (1996) 115–122.

[28] Hatton T.J., Wu H.-I., Scaling theory to extrapolate individual tree water use to stand water use, Hydrol. Processes 9 (1995) 527–540.

[29] Hinckley T.M., Running S.W., Lassoie J.P., Temporal and spatial variations in the water status of forest trees, For. Sci. Monogr. 20 (1978) 1–72.

[30] Honeysett J.L., Beadle C.L., Turnbull C.R.A., Evapotranspiration and growth of two contrasting species of eucalyptus under non-limiting and limiting water availability, For. Ecol. Manag. 50 (1992) 203–216.

[31] Jarvis P.G., Scaling processes and problems, Plant Cell Environ. 18 (1995) 1079–1089.

[32] Jipp P.H., Nepstad D.C., Cassel D.K., Reis-de-Carvalho C., Deep soil moisture and transpiration in forests and pastures of seasonally-dry Amazonia, Climate Change (1998).

[33] Katul G.G., Wendroth O., Parlange M.B., Puente C.E., Nielsen D.R., Estimation of in situ hydraulic conductivity function from nonlinear filtering theory, Water Resour. Res. 29 (1993) 1066–1070.

[34] Katul G., Hsieh C.-I., Oren R., Ellsworth D., Phillips N., Latent and sensible heat flux predictions from a uniform pine forest using surface renewal and flux variance methods, Boundary-Layer Meteorol. 80 (1996) 249–282.

[35] Katul G., Todd Phillip, Pataki D., Kabala Z.J., Oren R., Soil water depletion by oak trees and the influence of root water uptake on the moisture content spatial statistics, Water Resour. Res. 33 (1997) 611–623.

[36] Kelliher F.M., Black T.A., Price D.T., Estimating the effects of understory removal from Douglas-fir forest using two-layer canopy evapotranspiration model, Water Resour. Res. 22 (1986) 1891–1899.

[37] Kelliher F.M., Whitehead D., McAneney K.J., Judd M.J., Partitioning evapotranspiration into tree and understory components in two *Pinus radiata* D. Don stands, Agric. For. Meteor. 50 (1990) 211–227.

[38] Kelliher F.M., Köstner B., Hollinger D.Y., Byers J.N., Hunt J.E., McSeveny T.M., Meserth R., Weir P.L., Schulze E.-D., Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad-leaved forest, Agric. For. Meteor. 62 (1992) 53–73.

[39] Kelliher F.M., Hollinger D.Y., Schulze E.-D., Vygodskaya N.N., Byers J.N., Hunt J.E., McSeveny T.M., Evaporation from eastern Siberian larch forest, Proc. Int. Symp. Forest Hydrol., Tokyo, Japan, 1994.

[40] Köstner B., Schulze E.-D., Kelliher F.M., Hollinger D.Y., Byers J.N., Hunt J.E., McSeveny T.M., Meserth R., Weir P.L., Transpiration and canopy conductance in a pristine broad-leaved forest of Nothofagus: an analysis of sap flow and eddy correlation measurements, Oecologia 91 (1992) 350–359.

[41] Köstner B., Biron P., Siegwolf R., Granier A., Estimating water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods, Theor. Appl. Climatol. 53 (1996) 105–113.

[42] Leverenz J., Deans J.D., Ford E.D., Jarvis P.G., Milne R., Whitehead D., Systematic spatial variation of stomatal conductance in Sitka spruce plantation, J. Appl. Ecol. 19 (1982) 835–851.

[43] Loustau D., Berbigier P., Roumagnac P., Arruda-Pacheco C., David J.S., Ferreira M.I., Pereira J.S., Tavares R., Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine, Oecologia 107 (1996) 33–42.

[44] Lu P., Biron P., Bréda N., Granier A., Water relations of adult Norway spruce (*Picea abies* (L) karst) under soil drought in the Vosges mountains: water potential, stomatal conductance and transpiration, Ann. Sci. For. 52 (1995) 117–129.

[45] Nikodem H.J., Effects of soil layering on the use of VHF radio waves for remote terrain analysis, Proc. 4th Symp. Remote Sensing Env., Univ. Mich. Ann. Arbor., 1966, pp. 691–703.

[46] Nnyamah J.U., Black T.A., Tan C.S., Resistance to water uptake in a Douglas-fir forest, Soil Sci. 126 (1978) 63–76.

[47] Oren R. Waring R.H., Stafford S.G., Barrett J.W., Twenty-four years of Ponderosa pine Growth in relation to canopy leaf area and understory competition, For. Sci. 33 (1987) 538–547.

[48] Oren R., Zimmermann R., Terborgh J., Transpiration in upper Amazonia floodplain and upland forests in response to drought breaking rains, Ecology 77 (1996) 968–973.

[49] Oren R., Ewers B.E., Phillips N., Todd P., Katul G., Soil moisture affects canopy con-

ductance at depths delineated with local water balance. Ecol. Appl. (1998).

[50] Phillips N., Oren R., A comparison of daily representations of canopy conductance based on two conditional time-averaging methods, Ann. Sci. For. (1998) 217–235.

[51] Phillips N., Oren R., Zimmermann R., Radial Patterns of xylem sap flow in non-, diffuse- and ring porous tree species, Plant Cell Environ. 19 (1996) 983–990.

[52] Phillips N., Nagchaudhuri A., Oren R., Katul G.G., Time constant for water uptake in loblolly pine trees estimated from time series of stem sapflow and evaporative demand, Trees 11 (1998) 412–419.

[53] Rambal S., Water balance and pattern of root water uptake by a Quercus coccifera L. evergreen scrub, Oecologia 62 (1984) 18–25.

[54] Sala A., Smith S.D., Devitt D.A., Water use by *Tamarix ramossisima* and associated phreatophytes in a Mojave Desert floodplain, Ecol. Appl. 6 (1996) 888–898.

[55] Schulze E.-D., Hall A.E., Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments, Encyclopedia Plant Physiology, New Series 12B, Springer-Verlag, Berlin, 1982, pp. 181–229.

[56] Squire R.O., Attiwill P.M., Neales T.F., Effects of changes of available water and nutrients on growth, root development and water use in *Pinus radiata* seedlings, Aust. For. Res. 17 (1987) 99–111 .

[57] Tan C.S., Black T.A., Factors affecting the canopy resistance of Douglas-fir forest, Boundary-Layer Meteorol. 10 (1976) 475–488.

[58] Teskey R.O., Sheriff D.W., Water use by *Pinus radiata* trees in a plantation, Tree Physiol. 16 (1996) 273–279.

[59] Todd P.H., Use of a local mass balance method to determine the effects of soil water conditions on canopy conductance and to estimate forest stand evapotranspiration in a natural forest and in growth chamber, MS Thesis, Duke University, Durham, NC, USA.

[60] Topp G.C., Davis J.L., Measurement of soil water content using time domain reflectometry (TDR): a field evaluation, Soil Sci. Soc. Am. J. 49 (1985) 19–24.

[61] Topp G.C., Davis J.L., Annon A.P., Electromagnetic determination of soil water content: measurements in coaxial transmission lines, Water Resour. Res. 16 (1980) 547–582.

[62] Vertessy R.A., Benyon R.G., O'Sullivan S.K., Gribben P.R., Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest, Tree Physiol. 15 (1995) 559–567.

[63] Vogt K.A., Grier C.C., Gower S.T., Sprugel T.G., Vogt D.J., Overestimation of net root production: A real or imaginary problem? Ecology 67 (1986) 577–579.

[64] Wedler M., Heindl B., Hahn S., Köstner B., Bernhofer Ch., Tenhunen J.D., Model-based estimates of water loss from "patches" of the understory mosaic of the Hartheim Scots pine plantation, Theor. Appl. Climatol. 53 (1996) 135–144.

[65] Werk K.S., Oren R., Schulze E.D., Zimmermann R., Meyer J., Performance of *Picea abies* (L.) Karst. Stands at different stages of decline. III. Canopy transpiration of green trees, Oecologia 76 (1988) 519–524.

[66] Wendroth O., Katul G.G., Parlange M.B., Puente C.E., Nielsen D.R., A nonlinear filtering approach for determining hydraulic conductivity functions in field soils, Soil Science 156 (1993) 293–301.