

WATER BALANCE DELINEATES THE SOIL LAYER IN WHICH MOISTURE AFFECTS CANOPY CONDUCTANCE

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Abstract. To link variation in canopy conductance to soil moisture in the rooting zone, measurements of throughfall (P_T), volumetric soil moisture (θ) to 0.7 m, transpiration from trees >10 mm in diameter (E_C), and vapor pressure deficit (D) were made in a forest dominated by *Pinus taeda*. Total evapotranspiration (E_T) was estimated from P_T , changes in volumetric soil water content within a defined soil volume (ΔS), and drainage out of that volume (Q), calculated from unsaturated soil hydraulic conductivity and θ . Our calculations suggest that over 145 growing-season days, Q was negligible, and most of P_T , averaging ~ 2 mm/d, was partitioned between soil moisture recharge (0.4 mm/d) and E_T (1.6 mm/d, not including ~ 0.4 mm/d of interception, I , by canopy trees), of which E_C was estimated from direct measurements at nearly 1.2 mm/d. Evapotranspiration by the subcanopy component accounted for slightly over 0.4 mm/d, about a third of E_T (a fourth if I is included). Most of the water used for E_T (>90%) was taken from the upper soil layer (top 0.35 m, or less). Canopy leaf conductance, calculated from E_C , D , and canopy leaf area, was strongly related to θ in the upper soil layer once θ decreased below 0.22.

Key words: canopy; evapotranspiration; *Pinus taeda*; soil water balance; subcanopy.

INTRODUCTION

Development of models to predict responses of forest ecosystems to climate change (Webb 1991, Prentice et al. 1992, Sellers et al. 1997) and, in turn, effects of forest ecosystems on biosphere–atmosphere exchanges of mass and energy (Ågren et al. 1991, Gärdenäs and Jansson 1995, Sellers et al. 1997) is an active research topic. Many such models require an estimate of stomatal, or canopy conductance (G_C), and its responses to changing environmental conditions (Shugart et al. 1986, Sellers et al. 1997), such as soil moisture availability.

Plant water status as indicated by predawn leaf water potential has been proposed, and frequently used, to determine soil water potential of the entire rooting zone (Kramer 1983). However, relationships between leaf water potential and leaf conductance remain elusive, with some studies finding good relationships (Pallardy and Kozłowski 1979, Schulze 1986, Reich and Hinckley 1989), and others failing to demonstrate a clear causal linkage or consistent relationship (Bates and Hall 1981, Gollan et al. 1986, Sands and Mulligan 1990). A possible reason for the range of responses observed in these and other studies is that predawn leaf water potential is related to conductance only when it is in equilibrium with soil moisture, and once water potential falls below a critical value (Reich and Hinckley 1989). Moreover, responses may vary because the zone in the soil from which water is taken up by the

plant, and thus the zone which affects plant water relationships (Crombie et al. 1988), is often ill-defined (Wallace 1995). This will introduce uncertainty into estimates of plant available water and, in turn, to predictions of G_C .

It is well recognized that spatial and temporal variation in soil moisture content (θ) within the rooting zone affects variation in canopy conductance of water vapor and CO_2 (Mansfield and Davies 1981, Schulze 1986, 1993, Pereira and Chaves 1993). In a few studies where detailed measurements were made throughout the rooting zone, linkages between soil moisture content and plant water relation variables were clear (Nnyamah et al. 1978, Aussenac et al. 1984, Granier and Loustau 1994, Bréda et al. 1995). In this study we demonstrate that it is possible to define the effect of θ on G_C by using a water balance method to identify the zone in the soil where most of the transpired water is absorbed.

We adapted a commonly used method to estimate evapotranspiration (E_T), the watershed mass balance (Baumgartner 1965, Helvey et al. 1965, Rutter 1965), in order to identify the zone in the soil from which water was taken up by plants. Briefly, the watershed mass balance method can be summarized as follows: after monitoring precipitation (P), throughfall precipitation (P_T), and outflow, canopy interception losses (I) are calculated as the difference between P and P_T , and E_T is calculated as the difference between P_T and outflow. Calculating E_T is based on the assumption that the change in water storage in the soil is negligible; this assumption may be correct if the calculations are made over time steps measured in years. To estimate

transpiration by plants in a watershed, it is also assumed that, except for I immediately following P events, evaporation from forest ecosystems with closed canopies is very small.

In light of these assumptions, the watershed mass balance method can only be used to estimate E_T over long periods of time, may incorporate large errors in estimating E_T , and cannot be used to identify the active root zone (Slatyer 1967, Hillel 1982, Kirsch 1993). However, by replacing the outflow component of the water budget with direct measurements of θ , it is possible to resolve the problems inherent to the watershed mass balance method, resulting in a reasonably precise estimate of E_T over short time-steps, and a delineation of the zone in the soil from which water is removed by plant roots (Rambal 1984). We refer to this approach, where all components of the mass balance are measured within a close proximity, as the local water balance (LWB) method.

The LWB method relies on measurements of moisture input (P_T), changes over time in volumetric soil water content in an operationally defined soil volume ($\Delta S = \Delta\theta \times \text{depth}$), and calculation of drainage (Q) to estimate forest E_T . When forest E_T is thus estimated with the LWB method, it is necessary to estimate Q precisely. In a root exclusion monolith, Q was calculated as the balance between P_T and ΔS , and the results were used to estimate the soil hydraulic properties, which in turn were used to estimate Q in vegetated plots. Then Q , and E_T resulting from water uptake at two soil depths, were estimated in two locations within the same 13-yr-old *Pinus taeda* L. stand. E_T was then compared to transpiration of canopy trees (E_C , diameter > 10 mm) obtained using sap flux measurement in stems (Granier 1987) so that E_T could be partitioned into E_C and evapotranspiration from the subcanopy (E_{SC}). Once we delineated the layer in the soil where most water was taken up by canopy trees, we investigated the effect of θ in that layer on a daily average G_C .

When E_T is estimated using a budget approach, the active rooting volume must be identified so that the relationships between θ in that volume and G_C can be studied. We briefly consider the theory and assumptions that are the basis for using LWB to estimate E_T in the following section.

THEORY

In order to estimate E_T in forest ecosystems with the LWB method, we used an operational hydrologic budget on a control volume defined by the root-soil-water system, simplified based on certain assumptions. As a first approximation, overland runoff and subsurface horizontal flow are negligible relative to E_T and P_T in the soil matrix. These assumptions appear justified given the uniformity of the stand and lack of slope (<2%). Another assumption, stated earlier, is that evaporation

from the soil surface is negligible relative to E_T in fully vegetated stands.

Assuming one-dimensional flux in the soil, ΔS is regulated by addition to and loss of water from a defined soil volume. Water is added as P_T to the soil system through an upper surface, and is removed as Q from an operationally defined bottom plane. When the soil contains active roots, additional loss of water from the soil volume occurs as plants take up water and transfer it to the atmosphere as E_T . By defining the system as the soil-root volume, ΔS during a time interval Δt can be expressed as

$$\begin{aligned} \Delta S &= P_T - Q - E_T = \int_{t_1}^{t_2} \left(\frac{dS}{dt} \right) \times dt \\ &= \int_{t_1}^{t_2} [p_T(t) - q(t) - e_T(t)] \times dt \end{aligned} \quad (1)$$

where p_T is the P_T rate, q is the Q rate, and e_T is the E_T rate.

It is evident from Eq. 1 that, in order to estimate E_T and P_T , ΔS must be measured, and Q must be estimated. We estimate Q out of the top 0.35-m layer of the soil and the following 0.35-m layer, by integrating q over time calculated based on Darcy's Law,

$$q = -K(\theta) \times \nabla H \quad (2)$$

where q is the flux rate of water out of the soil system, $K(\theta)$ is the unsaturated hydraulic conductivity of the soil (in millimeters per day), and ∇H is the total soil water potential gradient ($H = \psi(\theta) + z$), where z is the soil depth. Assuming that the ∇H is unity, the $K(\theta)$ equation developed by Clapp and Hornberger (1978) may be used to calculate Q . (We validated this assumption post facto by comparing drainage estimated from the model below with independent estimates generated from θ measurements during times of high input relative to output in the lower layer.) Thus, for a unit gradient,

$$Q = K(\theta) = K_s \left(\frac{\theta}{\theta_s} \right)^{2b+3} \quad (3)$$

where K_s is saturated hydraulic conductivity, θ_s is the saturated moisture content (in cubic meters per cubic meter), and the exponent b is empirical and related to soil type (Cosby et al. 1984). However, macropore flow tends to reduce b and increase K_s for any given soil texture in the presence of a root system (Katul et al. 1997).

MATERIALS AND METHODS

Study site

The site is located in the Blackwood Division of Duke Forest in Orange County, North Carolina, a transitional zone between the coastal plain and the piedmont plateau (35°52'00" N, 79°59'45" W). The surrounding terrain is rolling, with an elevation of ~130 m

TABLE 1. Stand characteristics (as of June 1994) for the Reference and the FACE plots in Duke Forest, North Carolina.

Characteristic	Reference	FACE
Plot area (m ²)	117	131
Age (years)	13	13
Density (trees/ha)	5240	3700
Basal area (m ² /ha)	24.8	17.1
Mean diameter (mm at 1.4 m height)	55	66
Mean height (m)	7.1	8.5
Projected leaf area index (m ² /m ²)	3.0	2.4

above sea level. The soil classification is an Enon Series, low-fertility, acidic Hapludalf, subject to minimal erosion due to <2% slope, and is described as a clayey loam in the upper 0.3 m and a clay from 0.3 to 0.7 m (Soil Survey of Orange County, North Carolina 1975), where the bedrock typically resides. Mean annual temperature is 15.5°C, and mean annual precipitation is 1140 mm. Rainfall is well distributed throughout the year and totaled 940 mm in 1994. July has the largest amount of precipitation, while November receives the least. Soil moisture is usually at a minimum during the spring and early summer.

In 1983, the site was clear-cut and burned, and seedlings were planted using a 2.4 × 2.4 m spacing. At the time of the study, the site was covered by a uniform, managed 13-yr-old stand of *P. taeda* L. The stand contains a small component of hardwood and coniferous trees, consisting primarily of *Liquidambar styraciflua* L., *Juniperus virginiana* L., *Quercus phellos* L., *Liriodendron tulipifera* L., and *P. taeda* recruits. Two plots (Ref. and FACE), which are part of another ongoing study (Ellsworth et al. 1995) and located ~50 m apart within a 4-ha stand, were sampled in this study (see Table 1 for plot characteristics). Differences between the plots stem from the greater competition in Ref. induced by a larger number of recruits in this plot relative to the FACE plot. The Ref. plot was untreated, while the FACE plot was encircled by the Free Air CO₂ Enrichment (FACE) Prototype which periodically enriched the canopy to approximately +20 Pa CO₂ above ambient, without any detectable effect on plant water relations (R. Oren, unpublished data).

Measurements

The experiment lasted 145 d during the growing season (8 July–29 November 1994). The instantaneous rate of change in θ ($d\theta/dt$), for use in the local mass balance, was estimated from θ calculated based on repeated measurements with a metallic Time Domain Reflectometer (TDR; Tektronix 1502-B, Redmond, Oregon), a nondestructive method for quantifying in situ θ (Topp et al. 1980, Topp 1985, Malicki and Skierucha 1989, Gardner et al. 1990, Roth et al. 1992).

In each of the two plots, pairs of steel rods were installed vertically to two depths in each of five locations. One pair was installed from the surface to a

depth of 0.35 m in the soil, and the other to 0.7 m. TDR measurements were made 20 times at variable sampling frequencies in intervals ranging from 3 to 27 d. In Ref., a 1-m² square subplot containing no vegetation was established from which water uptake by roots of surrounding trees was halted by installing a 1 m deep peripheral trench. Two pairs of TDR rods were installed in the center of the subplot to quantify ΔS at the same layer as in the plots, but with nearly no E_T . This subplot is referred to as "root enclosure" monolith and will be used to estimate the soil hydraulic properties, specifically b .

The TDR sends a voltage pulse and then determines its propagation velocity (PV), which is slower in materials with higher dielectric properties (e.g., wet soil), and is inversely proportional to the square root of the relative dielectric constant (relative permittivity), κ :

$$\kappa = \left(\frac{(l_t \times PV)}{l_r} \right)^2 \quad (4)$$

where l_t is the linear distance (in meters) that the trace travels along the transmission line, and the rod length (l_r) is in meters (Cassel et al. 1994). The sensitivity of κ is high to θ and low to soil type, which make it a useful general indicator of θ (Nikodem 1966).

An empirical relationship is typically derived to convert κ measurements to θ . Topp et al. (1980) derived a general relationship for different mineral soils which was found to be suitable for soils with low clay content, but is not suitable for soils with high montmorillonite clay content (Dasberg and Hopmans 1992), for organic soils (Herkelrath et al. 1991), or for fine-textured soils (Smith and Tice 1988, Dasberg and Hopmans 1992). We checked Topp's equation in the laboratory using homogenized soil samples from the field brought to predetermined levels of θ . The soils in this study ranged from clay to clay-loam, and did not depart from Topp's relationship. We therefore used the following relationship to calculate θ :

$$\theta = -0.053 + 0.029(\kappa) - 0.00055(\kappa)^2 + 0.0000043(\kappa)^3. \quad (5)$$

The K_S necessary for estimating Q (Eq. 3) was measured with a compact constant head permeameter (Amoozemeter, Ksat, Incorporated, Raleigh, North Carolina) which quantifies the steady-state flow of water through the soil horizons (Amoozegar 1990). At four of the five TDR measurement positions, measurements of K_S were made at 0.20–0.35 m and 0.55–0.70 m soil depths, and averaged in each plot.

Saturated soil moisture, θ_s , also necessary to estimate Q (Eq. 3), 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 depth. At each step, 0.1 m TDR rods were installed, and θ was measured after the soil was brought to sat-

uration by adding water after a large rain event. The high value of θ_s found in the lower layer (54%, in both sites $1 \text{ SE} \leq 1\%$) was verified with values obtained from gravimetric analysis of five intact soil cores of known volume brought to saturation and then dried to quantify water volume, and weighed to estimate bulk density.

P and P_T were measured after July 1993. Five rain gauges (Productive Alternatives, Incorporated, Fergus Falls, Minnesota) with circular openings (81.8 cm^2) were distributed under the canopy in Ref. to measure P_T . An additional rain gauge, and a tipping bucket (Texas Electronics, Incorporated, Model 525, Dallas, Texas) with a circular opening (475.8 cm^2), were used in an open field 50 m away to measure P . The tipping bucket resolution was 0.1 mm, and it was sampled every 30 s by a datalogger (DL2, Delta-T Devices, Burwell, Cambridge, UK). Water level in the rain gauges was recorded each time TDR measurements were made.

We found that the relationship between the precipitation values collected in the tipping buckets and the rain gauge in the open was not unity ($P_{\text{tipping bucket}} = 0.845 \times P_{\text{rain gauge}}$ (units are millimeters); $R^2 = 0.98$; $P < 0.001$; $N = 15$ events). The tipping bucket has a larger radius, which reduces errors induced by the gauge edge effects and provides more accurate measurements of P (Linsley et al. 1982). Therefore, the P_T values collected with the rain gauges under the canopy were corrected by a factor of 0.845. Because the two plots in this study did not display the same leaf area index (L) and basal area (see Table 1 for plot characteristics), consequent differences in I (Running and Coughlan 1988) were accounted for using an empirical canopy interception model that takes into account P and stand basal area (Stogsdill et al. 1989). The model was used to estimate I ratio of FACE/Ref. for each rain event. The ratio for each event (averaging 0.7 over all events) was then multiplied by the I measured at Ref. to estimate the corresponding values at FACE.

To estimate E_C directly, information is combined on water flux per unit of hydroactive xylem area (sap flux density, J_s , grams of H_2O per square meter of sapwood per second) in stems of individual trees (Granier 1987), and corrected for radial trends (Phillips et al. 1996) and the amount of hydroactive xylem or sapwood area of all trees per unit of ground ($A_S:A_G$, square meter of sapwood per square meter of ground). Ten *P. taeda* and one *L. styraciflua* individual were measured in each plot, and one *J. virginiana* was measured in FACE. In FACE, *P. taeda* sapwood accounted for $\sim 90\%$ of the total, and in Ref. $\sim 80\%$; the rest of the sapwood was mostly of *L. styraciflua*. *P. taeda* individuals selected for sap flux density measurements represented the range of sizes found in the plots (50–189 mm).

Sap flux density measurements within the xylem were made using a Granier-type flow meter composed of heated and unheated thermocouple pairs (see details in Granier 1987). Briefly, the apparatus consists of a

pair of fine-wire copper-constantan thermocouples joined at the constantan leads so that voltage measured across the copper leads represents the temperature difference (ΔT) between the thermocouples. The ΔT under nontranspiring conditions (e.g., at predawn or during long and heavy rain events) serves as a baseline from which any sap flow causes a decrease in ΔT . After subtracting the baseline ΔT , sap flux density is then calculated from the corrected ΔT . Potential errors in estimating the average J_s and in scaling it to E_C are discussed in detail in Oren et al. (1998), where the method for calculating the variance around E_C , $\sigma_{E_C}^2$, is also presented.

Tree canopy conductance, G_C , was calculated according to Monteith and Unsworth (1990: 250), but neglecting the total aerodynamic conductance. This approach is valid when the latter conductance is much greater than the former, a situation closely approximated in coniferous forests due to the large roughness length and the needle leaf shape (Gates 1968, McNaughton and Jarvis 1983), especially in relatively open stands supporting low L (Granier et al. 1994). The calculation uses atmospheric vapor pressure deficit (D) as a surrogate for leaf-to-air vapor pressure difference, thus assuming that leaf temperature is equal to air temperature. Furthermore, daily average conductance, G_C , was calculated as (1) a daily average conductance using mean daytime D , adjusting the temperature-dependent thermodynamic coefficients in the equation by mean daytime air temperature, as this approach avoids systematic underestimation inherent when using sap flux data to calculate diurnal G_C (Phillips and Oren 1998), and (2) as an average of half-hour G_C values from 1000 to 1500 EST (Eastern Standard Time).

D was calculated from air temperature and relative humidity according to Goff and Gratch (1946). A fast response temperature/relative humidity sensor (HMP35C, Vaisala, Incorporated, Woburn, Massachusetts) was installed in each plot at the canopy height representing the highest leaf area density (~ 8 m above-ground). Data were taken at the same frequency as J_s . When the total aerodynamic conductance is very high, G_C can be normalized by L to facilitate comparisons between stands, or between times within a stand, when L may differ appreciably. The L (projected) at the beginning of the experiment was 3.0 and 2.4 at Ref. and FACE, respectively, as measured with a Canopy Area Analyzer (LAI2000, Licor, Lincoln, Nebraska). The L in stands dominated by *P. taeda* displays a pronounced seasonal trend (Kinerson et al. 1974, Dougherty et al. 1995). To account for this trend in normalizing G_C to canopy leaf conductance G_{CL} , L values at the beginning of the experiment in each plot were used to initiate a model of seasonal L dynamics (Kinerson et al. 1974) to predict L for each time in which soil moisture was measured. Calculation of G_{CL} was restricted to FACE because we did not have a reliable estimate of seasonal

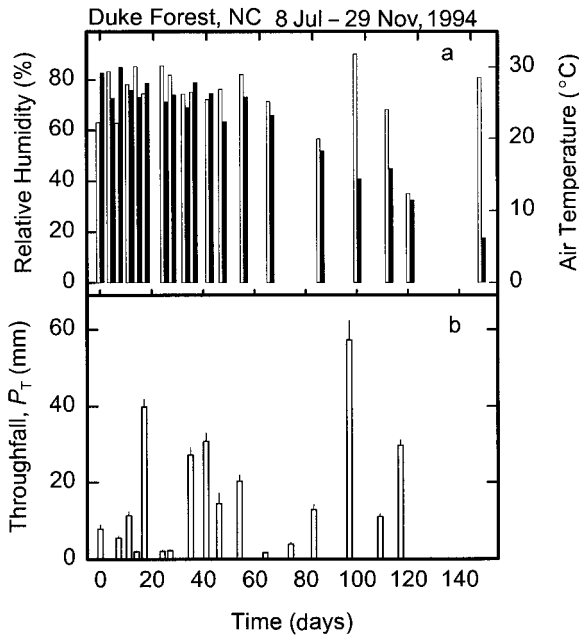


FIG. 1. (a) Seasonal pattern of daily air relative humidity (open bars), and air temperature (solid bars) are shown as average values for the two study plots; these variables were indistinguishable between the two plots ($P > 0.05$). Data are shown only for days in which soil water content was measured. (b) Mean and standard deviation of throughfall precipitation (P_T) as measured in the Reference plot ($n = 5$). Mean P_T was summed between consecutive dates of soil measurement.

L dynamic of *L. styraciflua*, which was a large component in Ref.

RESULTS

Air temperature and relative humidity were generally high until late October, when both declined appreciably (Fig. 1a). P_T was nonlinearly related to P ($P_T = 0.602P + 0.004P^2$, both variables in millimeters; Adjusted $R^2 = 0.97, P < 0.001, N = 15$). The coefficient of variation

in P_T was high, reaching up to 40% among gauges at Ref. (Fig. 1b). $P, I,$ and P_T , the latter two variables measured at Ref. and calculated for FACE, are shown in Table 2. Lower L in Face resulted in lower I and greater P_T .

Fig. 2 displays the time variation of θ at both plots. At FACE, one measurement point, which was positioned in a slight depression at the edge of the plot, consistently showed higher θ values from the other four. Over the study period, this point averaged $\theta = 0.39 \text{ m}^3/\text{m}^3$, compared to $0.25 \text{ m}^3/\text{m}^3$ in the other four (3.5 standard deviations) and was therefore excluded from the analysis of soil moisture fluctuations.

For the root enclosure, Q was calculated using a mass balance (Eq. 1) based only on P_T and ΔS , because E_T was eliminated and evaporation was assumed negligible. Over the study period, the mass balance estimate of Q in the root enclosure was 226 mm; the rest of P_T was accounted for by a 54-mm increase in ΔS (Fig. 2a and b). For each soil layer, Q in the root enclosure was then recalculated using Eq. 3 and θ , assuming that θ was constant between measurements (Fig. 2a and b). Using measured K_S, θ_S (Table 3) and θ, b in Eq. 3 was adjusted such that calculated Q from the bottom of each layer matched the mass balance estimated Q at the end of the study. The pattern of cumulative Q is shown in Fig. 2c for water draining from the bottom of the lower soil layer. The analysis was repeated for each of the two soil layers, and the estimated b values are presented in Table 3.

The seasonal variation in θ was similar at the two depths of both plots (Fig. 2a and b). By the end of the study, θ was higher than at the beginning in the top layer of both plots ($P < 0.05$), but the increase was very small in the deeper layer (Table 2). Drainage from each soil layer in the two plots was calculated using Eq. 3 and the estimated b values from the root enclosure (in Table 3). Q from the upper 0.35 m was similar (Student t test, $P > 0.05$) in both plots: 35 mm in Ref.

TABLE 2. Local water balance over 144 d (8 July–29 November 1994) in the root enclosure, and in Reference and FACE plots.

Measure	Root enclosure		Reference		FACE	
	(mm)	(%)	(mm)	(%)	(mm)	(%)
P	351	...	351	...	351	...
I	71	...	71	...	48	...
P_T	280 (24)	100	280 (24)	100	303 (26)	100
$\Delta S_{(0-0.35 \text{ m})}$	43 (2)	15	44 (1)	16	42 (2)	14
$\Delta S_{(0.35-0.7 \text{ m})}$	11 (2)	4	6 (2)	2	14 (2)	5
$Q_{(\text{below } 0.35 \text{ m})}$	237 (42)	85	35 (9)	13	23 (8)	8
$Q_{(\text{below } 0.7 \text{ m})}$	226 (38)	81	0	0	0	0
E_T	assumed 0	0	230 (26)	82	247 (30)	82
E_C	169 (21)	60	174 (20)	57
E_{UC}	110	39	152	50
E_{MC}	59	21	22	7
$E_{SC} (= E_T - E_C)$	61 (23)	22	73 (24)	25

Notes: Values in parentheses are 1 SE. Percentages are of P_T . Definitions: P , precipitation; I , interception; P_T , throughfall; ΔS , change in soil water content; Q , drainage; E_T , evapotranspiration (not including I); E_C , canopy transpiration; E_{UC} , upper canopy transpiration by *P. taeda*; E_{MC} , midcanopy transpiration by *L. styraciflua*; E_{SC} , subcanopy transpiration.

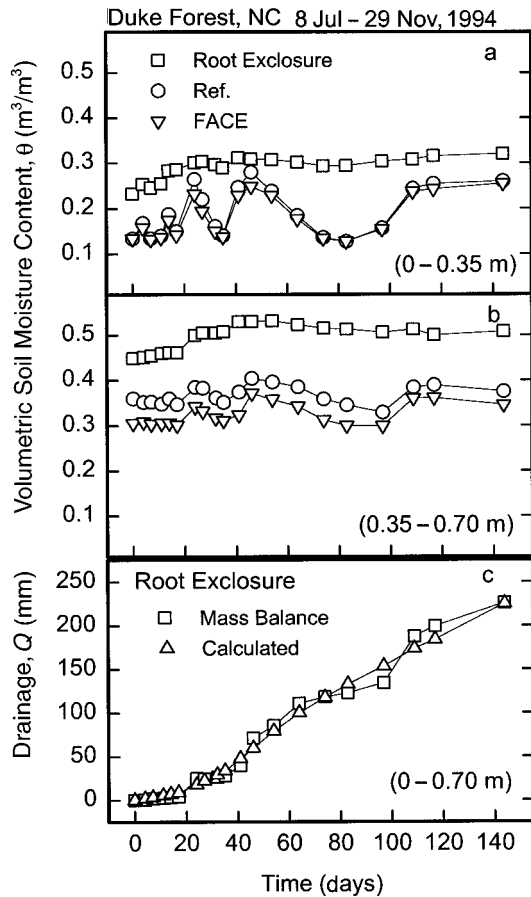


FIG. 2. The volumetric soil moisture content (θ) calculated from time domain reflectometer readings (see *Measurements*) in (a) the top 0.35 m soil layer, and (b) the layer between 0.35 and 0.70 m from the surface, obtained from the difference between (a) and readings to 0.70 m of the soil. (c) Drainage (Q) estimate based on local water balance at the root exclusion was used to parameterize a drainage model based on Clapp and Hornberger (1978).

and 23 mm in FACE (Table 2). A portion of this small amount of water draining from the top layer was retained in the next 0.35 m layer in the soil as ΔS (6 mm in Ref. and 14 mm in FACE; Table 2). Because Q from the deeper layer was calculated to be zero in both plots (Table 2; Fig. 3b and c), the difference between Q from the top layer, and ΔS in the deeper layer, represents the small amount of water taken up from the deeper layer in support of E_T . The deeper layer (0.35–0.70 m) contributed 29 mm in Ref. (13% of E_T) and 9 mm in FACE (4%); both values are not significantly different from zero ($P > 0.05$). Thus, moisture uptake in the top 0.35 m of the soil accounted for the majority of E_T .

Together with P_T and Q , ΔS values were used in Eq. 1 to estimate E_T from the entire 0.7 m layer based on the LWB method (Fig. 3b and c). E_T estimates were greater than E_C based on direct measurements with Granier-type sensors (Table 3). The LWB estimates of E_T were 230 mm in Ref. and 247 mm in FACE. The

TABLE 3. Parameters for Eq. 3 used in calculating drainage from the bottom of two soil layers in both Reference and FACE plots (see *Theory*).

Layer	Soil texture	θ_s (m ³ /m ³)	K_s (mm/d)	b
0–0.35 m	clay loam	0.54 (2)	200.0	2.49
0.35–0.7 m	clay	0.54 (2)	8.6	13.70

Note: θ_s is saturated volumetric soil moisture (± 1 SE); K_s is saturated hydraulic conductivity; b is an empirical coefficient for the drainage model after Clapp and Hornberger (1978).

E_C was 169 mm in Ref. and 174 mm in FACE. Thus, E_C accounted for 73 and 70% of E_T in Ref. and FACE, respectively. The differences between E_T and E_C were significant (one-sided Student t test, pooled standard error, $P = 0.06$ for Ref. and 0.03 for FACE), and thus attributable to evapotranspiration from the litter and subcanopy, E_{SC} (Table 2).

E_C was further partitioned into two components, one representing the upper canopy $P. taeda$, E_{UC} , and the

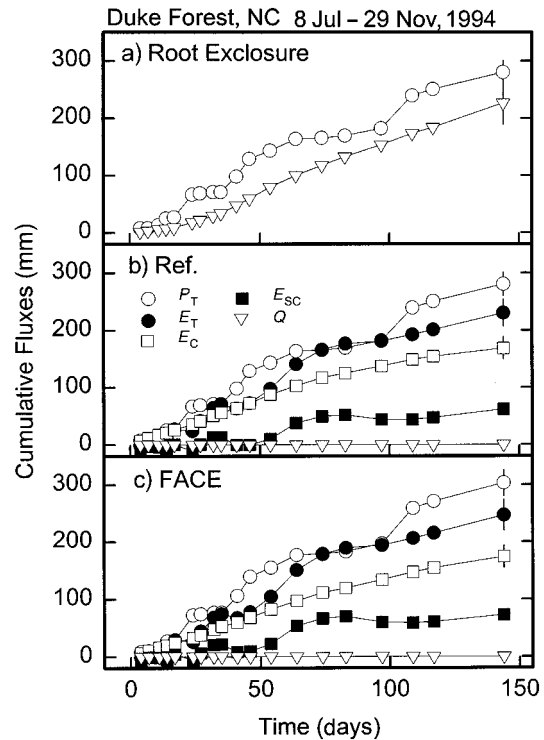


FIG. 3. Cumulative fluxes in the root exclusion (a) include throughfall precipitation (P_T) and drainage (Q) only. In the Reference (b) and FACE (c) plots, one line also represents the sum of Q and transpiration by trees with breast-height diameter > 50 mm (E_C), and another the sum of Q and total evapotranspiration (E_T) estimated in each plot based on local water balance (LWB) method. Decreases in cumulative E_T are due to measurement errors (see *Introduction*). The difference between E_T and E_C represent subcanopy evapotranspiration (E_{SC}). The difference between P_T and the next line below represents soil recharge (increasing distance) or discharge (decreasing distance).

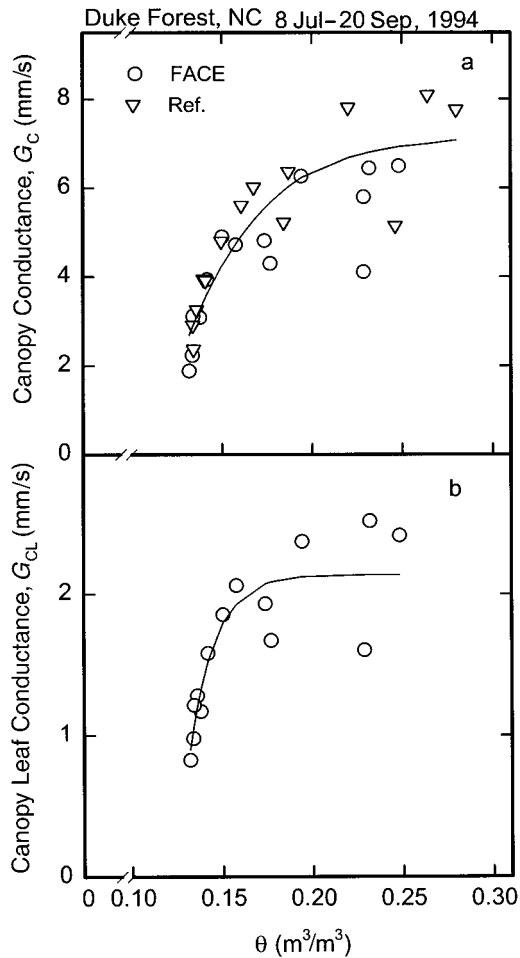


FIG. 4. Midday (1000–1500 EST) canopy conductance, G_C (a), and canopy leaf conductance, G_{CL} (b), in relation to the volumetric soil moisture in the upper layer at the Reference and FACE plots. There was no difference between Reference and FACE for either G_C or G_{CL} ($P < 0.05$). See Table 4 for curve-fit parameters and statistics.

other representing the remaining species forming the low-to-mid canopy (predominantly *L. styraciflua*), E_{MC} . While E_C was similar in both plots, E_{MC} was 2.7 times greater in Ref. than FACE, nearly making up the difference in E_{UC} between the plots (Table 2). The difference between plots in the partitioning of E_C to the two components reflects both higher density and basal area of *L. styraciflua* in Ref. as well as the generally higher J_S of this species. Due to the small sample size ($N = 2$ *L. styraciflua*, and 1 *J. virginiana*) of trees monitored for J_S in low-to-mid canopy, error terms were calculated only for E_C (Table 2).

In Fig. 3, we summarize the results of the LWB, excluding P and I , for both soil layers combined over the study period. The root enclosure yields two components, P_T and ΔS , with Q being the calculated difference. Drainage in the root enclosure is a major component of the balance, accounting for 81% of P_T . In contrast, Q is undetectable when transpiration is al-

TABLE 4. Nonlinear regression parameters for θ to G_C and G_{CL} relationships. Values of a , b , and c correspond to the parameters of $y = a[1 - \exp(-bx)] + c$ used in Fig. 4.

	a	b	c	R^2	P
G_C	81.33	30.46	-78.91	0.81	<0.001
G_{CL}	83.46	21.68	-75.99	0.89	<0.0001

lowed to proceed unimpaired, and E_T accounted for 82% of P_T in both plots. In both plots, total evapotranspiration (the sum of I and E_T) accounted for ~85% of P . The difference between P_T and the sum of Q and E_T is ΔS ; an increasing difference indicates a period of recharge in soil moisture, while decreasing differences represent soil moisture depletion. The LWB approach does not perform well on short time scales, as evidenced in that cumulative E_C was occasionally greater than cumulative E_T at the beginning of the period.

Daily mean G_C was unrelated to θ ($P > 0.05$). Mid-day (1000–1500 EST) G_C was highly related to θ in the top layer, and somewhat less to θ in the deeper layer ($P < 0.001$, $R^2 = 0.81$ for top layer analyses; $P < 0.06$, $R^2 = 0.53$ for deeper layer analyses), but the relationships were more significant ($P < 0.05$) in the upper layer. We consider the relationships found with θ in the deeper layer spurious because θ was always high, and changed only slightly. In contrast, the decline in G_C with θ in the upper layer is driven by a large range in θ which fell to very low levels (Fig. 4).

There was no difference between the plots in coefficients of the relationships between G_C and θ ($P < 0.05$), as reflected in Fig. 4. In order to remove the effect of large seasonal changes in L from the relationship between G_C and θ , G_C was normalized by L to G_{CL} in the FACE plot only because *P. taeda* represented a large proportion of the plot, and tree leaf area for other species was unknown. Despite large changes in L over the experiment period (1.8 to 2.6 in FACE), G_{CL} was highly correlated to θ (see Fig. 4, Table 4). The residuals in the relationships between both G_C and G_{CL} and θ were not related to D ($P > 0.05$). The variability in G_C was explained equally well ($P > 0.05$) whether we used θ or relative available water $[(\theta - \theta_{min})/(\theta_s - \theta_{min})]$ as in Bréda et al. (1993a).

DISCUSSION

Using the LWB method, the upper 0.35 m layer of the soil was delineated as the source of water for transpiration by all vegetation in the forest (Fig. 2). Given the low rate of Q from the upper layer in this study (Fig. 3b and c), and the pattern in soil moisture in the lower layer (Fig. 2b), it was ascertained that the deeper layer did not play an important role in the hydrology of the forest during the study period. This is supported by a 1997 investigation in this forest that found a complete absence of fine roots below 0.3 m from the surface (R. Matamala and W. H. Schlesinger, unpublished data). Thus, soil moisture variation in the top layer

controlled G_C (Fig. 4). The remaining variation in G_C was only slightly related to the seasonal dynamics in L . However, G_C was unrelated to D , as was previously shown during a 10-d soil drying cycle in which soil moisture depletion, but not D , controlled both E_C and G_C (Oren et al. 1998, Phillips and Oren 1998). Consequently, G_{CL} was similarly related to θ , but not to D .

Total, canopy, and subcanopy evapotranspiration

Estimates of E_T for pine stands of various species range from 0.9 to 3.8 mm/d (Roberts et al. 1980, Granier et al. 1990, Peck and Mayer 1996, also see Whitehead and Jarvis 1981, Cermák et al. 1995). Annually, mean daily E_T in pine stands of similar L in the coastal plains of southeastern United States was estimated at a similar 1.4–1.6 mm (McCarthy and Skaggs 1992), but the mean includes the low E_T values of midwinter, so the mean for a period parallel to our study would have been somewhat higher. The mean daily E_T of 1.6 mm in this study was lower than that in other *P. taeda* stands of similar basal area, which ranged from ~2.5 to 4.2 mm in a dry and wet years, respectively (Stogsdill et al. 1992). It was similar to total evapotranspiration in *Pinus pinaster* Ait. stands (2.2 mm, Granier et al. 1990) if I (0.3–0.5 mm/d; Table 2) is added to E_T , producing a value representing total evapotranspiration. When water uptake by roots was eliminated in this study, Q was 226 mm, or 81% of P_T (Table 2). However, when water uptake was not curtailed, Q was undetectable, indicating that pools of water used in E_T and ΔS during the study period nearly equaled P_T , as previously found in another study with *P. taeda* (Stogsdill et al. 1992).

E_C calculated using scaled sapflux yielded very good agreement with eddy covariance estimates of E_T in several studies (Köstner et al. 1992, Bernhofer et al. 1996, David et al. 1997, Oren et al. 1998). In this study, E_C accounted for a similarly large proportion of E_T in both plots (averaging ~0.72), a nearly identical proportion to that found in another study in this stand (0.69) when E_C was compared to E_T estimated using eddy covariance method under dry canopy conditions (Oren et al. 1998). Mean daily E_C , 1.1–1.2 mm, was lower than in other *P. taeda* stands (Stogsdill et al. 1992), perhaps due to differences in L or G_{CL} but within the range found for pine stands (0.5–2.1 mm; Peck and Mayer 1996). While E_C was similar in both plots (Table 2), E_{MC} was greater in Ref. than in FACE, reflecting a larger low-to-mid canopy component in Ref., mostly *L. styraciflua*, which supports high J_S . The difference between E_T and E_C , which was significantly greater than zero (Table 2, Fig. 3), was used to estimate E_{SC} . Mean daily E_{SC} was 0.4 and 0.5 mm at Ref. and FACE, respectively, lower than values reported for a *Pinus sylvestris* L. stand, ranging between 1 and 2 mm (Roberts et al. 1980). Here, E_{SC} was estimated at ~28% of E_T (or ~20% if I is included in E_T). Subcanopy evapotranspiration in pine stands of similar L ranged from

20 to 30% of total transpiration (Roberts et al. 1980, Granier et al. 1990), but has a much wider range, 19–70% of E_T , when other coniferous forests are considered (Tan et al. 1978, Roberts et al. 1980). E_{SC} proportion of E_T increases in response to increasing net radiation, air saturation deficit, and when soil dries (Whitehead and Jarvis 1981, Black and Kelliher 1989). With increasing canopy L , both subcanopy L and light decrease, and in turn, E_{SC} decreases as a proportion of E_T (Oren et al. 1987, Whitehead et al. 1994, Oren and Sheriff 1995). Subcanopy L in a stand of similar basal area to ours was <1 m²/m² (Cregg et al. 1990). If subcanopy L in our plots was similar, this would indicate that the understory transpired in direct proportion to its leaf area. We note that E_{SC} was estimated by difference, and thus contains the accumulated errors in the other components of the budget, as discussed later.

Roberts (1983) suggested that transpiration is a conservative process in forests whereby lower E_C is compensated by a higher E_{SC} . It is possible that his supposition is more general. Based on this study, despite large differences between the plots in canopy structure and the proportions of the two prevalent species, E_C was similar because lower E_{UC} of *P. taeda* in Ref. was compensated by a higher E_{MC} of *L. styraciflua*.

Soil moisture and canopy conductance

Pinus taeda is particularly sensitive to drought (Stransky and Wilson 1964). Thus, in the southeastern United States, soil moisture commonly limits the growth of *P. taeda*, one of the most widely naturally distributed and planted tree species (Coile 1936, Bassett 1964, Moehring and Ralston 1967, Manogaran 1973, Kramer 1983). However, based on the results from this study, water stress may develop in *P. taeda* even where soil moisture is high not far from the surface (Fig. 2b) due to limitations imposed on rooting depth.

Based on the LWB method, 90% or more of the water needed for E_T was absorbed from the upper 0.35 m of the soil. This is in contrast to findings in areas with a pronounced dry season, or in experimental manipulations, where water uptake occurred from progressively deeper horizons as the length of drought (natural or imposed) increased (Cermák et al. 1980, Rambal 1984, Granier 1987, Bréda et al. 1995). In a *P. taeda* plantation in Oklahoma, over the same seasonal period, water uptake occurred to a depth of at least 1.2 m during both a drier and a wetter year than the year of this study (Stogsdill et al. 1992). Experimental reduction in *P. taeda* stand density resulted in increased soil water potential to 1.2 m depth by reducing both canopy interception losses and transpiration, but predawn leaf water potential was unaffected, indicating that roots were drawing water from deeper horizons (Cregg et al. 1988). The most likely reason for the lower E_T in this study is a limit imposed on rooting depth (R. Matamala and W. H. Schlesinger, unpublished data) by a hard

clay pan, the legacy of a prolonged intensive agriculture in the recent past, indicated by $<1/20 K_s$ in the lower than the upper layer. This is further supported by the finding that G_C decreased rapidly with θ in the upper layer below a threshold of $\sim 0.22 \text{ m}^3/\text{m}^3$ (Fig. 4), while θ was much higher below 0.35 m depth (Fig. 2).

Deep-rooting species, or trees growing where deep rooting is possible, show a gradual decline in stomatal conductance, as they progressively draw water from deeper layers (Bréda et al. 1993b, 1995). In contrast, limited rooting depth results in a strong negative diurnal stomatal conductance response to D , even under moist soil conditions (Köstner et al. 1992, Bréda et al. 1993a, Granier and Loustau 1994, Pataki et al. 1998). Frequent reduction of soil moisture to levels that lower total conductivity of the soil–tree system have been both measured and modeled (Nnyamah et al. 1978, Barataud et al. 1995, Bréda et al. 1995). Given the relationship between available soil moisture and predawn plant water potential (e.g., Sucoff 1972, Bréda et al. 1995), and between predawn water potential and stomatal conductance (e.g., Bréda et al. 1993b), the relationship between soil moisture availability and conductance should exhibit a similar pattern to that shown in Fig. 4a and b. Seedlings of three conifer species showed a similar response to decreasing soil moisture in a limited soil volume (Havranek and Benecke 1978). When θ is low, so is $K(\theta)$, and the supply of water to roots is controlled by the soil. Combined, a high sensitivity of G_C to θ in the upper layer (Fig. 4), and a high frequency of θ below the threshold in this layer (Fig. 2a), resulted in curtailed transpiration rates.

We found that θ describes the variability in G_{CL} equally as well as the relative extractable water described by Bréda et al. (1995). The relationship between G_C and θ in FACE did not change when the effect of seasonal dynamics in L were accounted for by estimating the average stomatal conductance of the canopy, G_{CL} . The greatest change in L for *P. taeda* stands occurs in the last half of the growing season, corresponding in this study to a period in which soil moisture was high (Fig. 2), and conductance might have been affected more by light than by soil moisture. Variation in conductance caused by low temperature was removed from the data by excluding from analysis all late-season days when temperature remained $<15^\circ\text{C}$ ($N = 5$), a temperature associated with large reductions in transpiration and conductance in *P. taeda* (Kramer 1942). The combined outcome of the high variation in L coinciding with a period of high soil moisture, and the exclusion of data collected in a period of low temperatures, was that the decline in G_{CL} with θ below $\sim 0.22 \text{ m}^3/\text{m}^3$ was similar to the decline in G_C . We conclude that in shallow-rooted *P. taeda* stands growing on sites with similar soils, G_C and E_C is controlled during much of the growing season by θ in the upper layer when θ falls below $\sim 0.22 \text{ m}^3/\text{m}^3$.

Sources of errors in the local water balance

The LWB method, similar to that used by Rambal (1984), allows estimation of E_T in forest ecosystems at temporal scales of a day or longer, depending on K_s , θ , and E_T , but not at shorter temporal scales (Oren et al. 1998). The LWB can also be used to provide estimates of E_T at many sampling points in a stand at a rather modest cost. Combined with direct measurements of tree transpiration (Bréda et al. 1995), G_{CL} may be calculated for canopy and subcanopy, the latter if it is reasonable to assume that subcanopy evaporation is negligible relative to transpiration. Furthermore, the method facilitates quantifying G_{CL} responses to variation in θ at different soil depths.

Field studies present certain challenges in estimating E_T using any method. In using the LWB method, these challenges include estimation of P_T and Q . Interception, and in turn P_T , are related to L (Running and Coughlan 1988, McCarthy and Skaggs 1992), and vary widely within a stand (Fig. 1; Lawson 1967, Swank et al. 1972, Anderson et al. 1976). The pattern of mean P_T in relation to P found in this study is typical (Running and Coughlan 1988). However, LWB requires that P_T be estimated at, or for practical reasons, near, the point where θ is measured. In this study, I was 20% of P in Ref. (Table 2), close to the 17% measured in a stand of *P. taeda* of similar basal area (Stogsdill et al. 1989). However, we did not measure P_T in FACE, so I was estimated by adjusting the values measured in Ref. according to the basal area in FACE, after Stogsdill et al. (1989). This resulted in I accounting for 14% of P in FACE, in comparison to 10% in another *P. taeda* stand in which basal area was experimentally reduced to a similar level found in FACE (Stogsdill et al. 1989). Although lower I in FACE relative to Ref. seems reasonable, spatial variation in I is large, and could introduce a large error in the estimation of P_T in that plot.

In this study, two other sources of error may affect the estimation of water input to the soil: litter interception may reduce water flux into the soil, and stemflow may increase it. Litter interception may range from 2 to 13% of P (Helvey and Patric 1965, Bouten et al. 1992). On the other hand, stemflow input was 9% of P in a stand 0.4 times the stem density of Ref. and 0.6 times the density of FACE (Swank et al. 1972). Comparing between two plots, it is likely that litter interception would be higher in the more open FACE, and that stemflow would be higher in Ref. This would tend to reduce somewhat the difference in P_T calculated for the two plots (Table 2), reducing the disparity between E_T and E_C in FACE, and increasing it in Ref.

Errors in estimating Q will also affect estimates of E_T . An underestimation of Q can be caused by sampling procedure, resulting in an overestimation of E_T . A sampling procedure that does not require site visits immediately after each substantial rain event may miss

high values of θ , an occurrence particularly likely in soils of high K_S , or when sampling intervals are long. Because Q is exponentially related to θ , infrequent sampling in areas with frequent rain events, or sampling that coincides with rain events in generally dry areas, may cause large inaccuracies in estimation of Q . Moreover, the empirical coefficient in the semiempirical model proposed by Clapp and Hornberger (1978) for calculating Q must be obtained with great care.

Using literature values to parameterize the drainage model is convenient, but may introduce large errors. The value of b in the upper layer was lower than that of the same soil class reported for a very large sample size by Cosby et al. (1984), but the values of K_S and θ_S were similar; in the lower layer, values of b and θ_S were similar to those reported, but K_S was much lower. This is not surprising given that hydraulic parameters are highly variable (fivefold for some) even within a given soil class (Tietje and Hennings 1996). Our low value of b in the upper layer lends support to the thought that the presence of roots increases macropore flow (Katul et al. 1997), highlighting the need to parameterize the model in situ using root closures that still contain root mass.

In this study, we parameterized the model in a root closure monolith with no understory, but with an intact litter layer. This may result in a slight overestimation of precipitation input into the soil. As a consequence, b may be overestimated, leading to an overestimated drainage. We also did not account for soil evaporation. Soil evaporation in fully stocked forest stands with intact understory and a litter layer should be quite low because of poor coupling with the atmosphere, low wind speed and direct radiation, and high resistance to water vapor lost from the soil once the upper few millimeters dry (Hillel 1982). Kelliher et al. (1986) and Black and Kelliher (1989) showed that, under such conditions, $\sim 3.5\%$ of total E_T is evaporated from the soil surface. In our study, this will also be hidden in b , constituting a second source of error that also contributes to an overestimation of Q . Removing the litter layer, or measuring throughfall below the litter, and covering the surface of the monolith between rain events would have eliminated these sources of error. Nevertheless, a sensitivity analysis showed that the drainage model is sensitive to the exact value of the coefficient only when the soil is near saturation. This hardly ever happens during the growing season, despite relatively frequent rain events. Furthermore, despite the potential overestimation of drainage, averaged for both plots, Q below 35 cm was only 10% of water reaching the litter (compared to 85% in the root closure). This, coupled with the minimal changes in soil moisture in the layer between 35 and 70 cm, indicates that the bottom layer was not important during the study period for water uptake.

While hydraulic lift at night of water from deeper soil layers of high water potential to shallower, drier

layers has been shown to contribute significant amounts of water for consumption during the day (Dawson 1993, Emerman and Dawson 1996), the absence of deep roots in this study site, as recently reported, excludes this mechanism from consideration. A counter gradient in soil water potential could pull water from the lower to the upper layer to replenish some of the moisture drawn from the upper layer. However, this mechanism permits only slow rates of water redistribution in the soil when the soil is not very moist. Based on our calculations, the contribution of the lower layer to E_T approximately equals the drainage into it, or $\sim 12\%$ of E_T . If drainage was indeed slightly overestimated due to the parameterization procedure, this estimate ($0.12E_T$) represents an upper limit to the contribution of this layer.

Application

Simplifying process-based models for calculating forest productivity is an essential step in transforming models from serving primarily as research tools to having value for practical forest managers (Landsberg and Waring 1997). Simplification is also necessary if process-based models are to be used for estimating landscape-level carbon fixation and water, CO_2 , and energy flux (White and Running 1994). Simplified models aimed at providing information useful for practitioners often rely on a set of functions describing the relations between a response variable and environmental controls. For example, gross primary production may be estimated from absorbed photosynthetically active radiation, reduced by modifiers that reflect reductions from a maximum canopy stomatal conductance due to high vapor pressure deficit, subfreezing temperatures, and low water availability in the rooting zone (Landsberg and Waring 1997). Here we describe and test a method for assessing the effect of soil moisture depletion on canopy stomatal conductance. Thus, information available on maximum stomata conductance in various terrestrial ecosystems (Schulze et al. 1994) can be coupled with information on rooting depth and distribution at the global scale (Canadell et al. 1996, Jackson et al. 1996), and the response of G_{CL} to changing θ (e.g., Fig. 4), to facilitate flux estimates from forests. In forests where the soil layer from which water uptake occurs changes over time, a combination of LWB and stable isotopes may help identify the soil layer where moisture affects canopy conductance. In systems without a dense clay pan and with a relatively rainless growing season, fine root production deeper in the soil will necessitate continuous update in models of the relevant soil depth. The method proposed here can provide such information easily and inexpensively. It can thus be used to identify times in which the relationship between G_{CL} and θ appears to change, and focus at these times the efforts invested in collecting and analyzing root cores for assessing root distribution, and samples for stable isotope analysis for identifying the source of

water. In combination with root coring and stable isotope analysis, LWB can provide greater detail in the analysis of water flux, and the effect of soil moisture distribution on G_{CL} for use in forest growth and biosphere-atmosphere exchange models.

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