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Heat balance, porometer, and deuterium estimates of transpiration from potted trees

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ABSTRACT

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The objective of this study was to quantify the accuracy of transpiration estimated using heat balance gauges, porometry, and deuterium tracers methods. Measurements were made on one Eucalyptus tree and three Prunus trees during three measurement periods (MPs) in the summer of 1991 at the Institute of Hydrology, Wallingford, UK. Gravimetric measurements of transpiration (T_g) of the potted trees were used as the standard for comparison. Continuous estimates of transpiration were made using constant-power heat balance gauges (T_h). A stomatal conductance-based transpiration (T_s) was calculated using the Penman–Monteith equation. Deuterium oxide was used as a tracer for calculating transpiration (T_d) for 5-day periods. There were no systematic differences between daily T_g and T_h for the one Prunus tree for which daily T_g could be accurately measured, or, for all trees, between T_g and T_h for the entire MP. The root mean square difference (RMSD) between daily T_g and T_h was 0.26 kg per tree day^{-1} for the one Prunus tree. There was a consistent underestimation of daily T_g by T_s, while T_h on these days was closer and not consistently different. The RMSD between daily T_g and T_d was 1.0 kg per tree day^{-1}, more than twice the error for T_h. For daily and 5-day periods, the T_h RMSD was lower than the RMSD from T_s and T_d, respectively. Positive and negative aspects of each method are discussed.

INTRODUCTION

Evapotranspiration measurements from forested areas, or transpiration measurements from individual trees, are needed for many reasons. Forest evapotranspiration can be measured using micrometeorological methods (Bernhofer and Gay, 1989; Vogt and Jaeger, 1990) or water balance methods (Sharma et al., 1982). However, either method may be inappropriate because, for example, of inadequate fetch or uncertainty of water balance component terms. When trees do not form a complete canopy, but are still a significant

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component of the water balance (e.g. savannahs or orchards) or when individual plant physiological processes are the object of study, there may be no alternative but to directly measure individual tree transpiration.

Several methods have been used to determine transpiration from individual trees, including tracer measurements for calculation of sap flow or sap velocity and porometer measurements of leaf transpiration or stomatal conductance. Chemical tracers have been used for sap flow calculations in trees (Calder et al., 1986, 1992; Calder, 1991). Recently, much work has been done using a continuous supply of heat as a tracer (Sakuratani, 1987; Baker and Van Bavel, 1987; Dugas, 1990; Dugas et al., 1992). With this method, mass sap flow, considered equal to transpiration if the averaging period is sufficiently long such that plant water capacitance can be ignored, is calculated from a heat balance.

Porometers have been used to measure leaf stomatal conductance (g_s) or transpiration itself. Leaf transpiration can be calculated from g_s if leaf temperature and air temperature and humidity are measured. Direct measurements of transpiration using porometers are not likely to be representative of the whole tree (McDermitt, 1990) because the attachment of the porometer chamber modifies the leaf micro-environmental conditions of wind speed (Fichtner and Schulze, 1990) and humidity. However, if the chamber is only applied to the leaf for a short time during which the stomatal aperture does not change, an accurate and representative g_s can be measured. Measurements of g_s on a sample of leaves can then be scaled up using total leaf area and other climatic variables to calculate whole-tree transpiration. The accuracy of this whole-tree transpiration calculation depends upon leaf size, canopy aerodynamic conductance, and within-tree gradients of leaf area and vapor pressure (Pearcy et al., 1989). Inaccessibility of leaves and variation between leaves (Leverenz et al., 1982) and trees (Hatton and Vertessy, 1989) may also affect the accuracy of g_s-based transpiration estimates. Nevertheless as there is often no alternative, this method has been widely used for trees (e.g. Schulze et al., 1985; Munro, 1989).

Several examples exist comparing two of these methods (Heine and Farr, 1973; Green et al., 1989; Hatton and Vertessy, 1990; Steinberg et al., 1990; Dugas and Mayeux, 1991). A comparison of transpiration from heat balance gauges, porometry, and deuterium tracers to a standard (i.e. gravimetric transpiration measurements) has not been made for trees. The objective of this study was to determine the accuracy of transpiration measured using these methods for Eucalyptus and Prunus trees.

METHODS

Measurements were made in 1991 at the Institute of Hydrology (51°36′N, 1°07′W, elevation 48 m), Wallingford, UK, during three measurement periods: 6–21 June, 3–16 July, and 13–27 August, termed MP I, MP II, and MP III, respectively.

One *Eucalyptus gunnii* (Hook F.) tree (termed EU) and three *Prunus serrulata* (Lindl., cv. Longipes) trees (termed individually PR1, PR2, and PR3 and collectively PR) were used during MP I and MP II. Only EU and PR1 were used during MP III. The EU was about 5 years old, 2.5 m tall, and in a round, 377 l, 2 m diameter pot. It had a spherical canopy shape with an mean canopy diameter of 2 m and a stem diameter of 50 mm at a height 0.5 m above the soil surface. The PR were 3 years old, 2 m tall, and in round, 92 l, 0.45 m diameter pots. They had a mean canopy diameter of 1.2 m and a stem diameter of 20 mm at a height 0.3 m above the soil surface. Each of the PR had about five 1- to 2-m long branches coming off of the central stem. Pots were filled with a peat-based planting compost, covered with black plastic to suppress soil evaporation and to direct all precipitation striking the plastic toward the stem and into the soil, and sealed on the bottom to prevent drainage.

Leaf area of PR2 and PR3 was measured at the end of MP II and of EU and PR1 at the end of MP III by passing all leaves from each tree through a leaf area meter (Li-Cor Model 3100, Li-Cor Corp., Lincoln, NE). For MPs before leaf area was destructively measured, tree leaf area was calculated from leaf numbers counted at the end of each MP and mean area per leaf determined from destructive leaf area measurements. The leaf area (one sided) of the EU and each PR was about 5 m^2 and 1 m^2, respectively.

Hourly net radiation (R_n), wind speed at 2.0 m, wet and dry bulb temperature at 1.0 m, and precipitation were measured using an automatic weather station (Strangeways, 1985) over grass about 10 m from the trees.

Gravimetric

Gravimetrically-measured transpiration (T_g), calculated from sequential mass measurements and corrected for precipitation using the pot surface area, was considered the standard against which transpiration estimates were compared. Tree masses were measured continuously or instantaneously.

Ten-min means of EU mass were measured continuously during all MPs using the mean output of three 454-kg capacity load cells (Model 41/571-06, RDP Electronics, Wolverhampton, UK). Load cell non-linearity and hysteresis specifications each translated to a measurement uncertainty of ± 454 g. Load cell drift, determined by placing a constant mass on the cells in the field, was large (approximately 1 kg for a day) and, thus, for EU T_g for 5-day periods or longer could be used to compare with other transpiration estimates (Table 1). This drift was likely caused by temperature effects on the load cell.

Instantaneous mass measurements were made of PR1 in MP I and of PR2 and PR3 in MP I and MP II using a 100-kg capacity top-loading balance

TABLE 1

Period length for which transpiration calculated by three methods used in this study were compared against gravimetric transpiration for each tree

Method	Tree	
	Eucalyptus, Prunus No. 2, and Prunus No. 3	Prunus No. 1
Heat balance	Entire measurement period	Entire measurement period (I) or daily (II and III)[a]
Porometer	Not applicable	Daily
Deuterium	5 days	5 days

[a] I, II and III correspond to measurement periods I, II, and III, respectively.

(Model D20L-MO, Ohaus Scale Corp., Florham Park, NJ). Measurements were made between one and three times per day. Balance display resolution, the most limiting instrument specification, was 0.2 kg. This resolution meant that T_g for 5-day periods or longer could be used for comparison (Table 1).

Ten-min means of PR1 mass were measured continuously in MP II and MP III using a 50-kg capacity load cell (Model U4000, Maywood Instruments, Basingstoke, UK). Load cell non-linearity and hysteresis specifications each translated to a measurement uncertainty of ± 10 g. Load cell drift, determined by placing a constant mass on the cell in the field, was about 30 g for a day. Field tests of cell repeatability showed an uncertainty of mass measurement of 20 g. Given these load cell performance specifications, accurate daily T_g measurements were possible and these were compared with other transpiration calculations for PR1 in MPs II and III (Table 1).

Constant power heat balance

Continuous sap flow measurements were made in all MPs using the constant-power heat balance method. One model SGB50 (EU) and three model SGB19 (PR) sap flow gauges (Dynamax, Houston, TX) were used. The transpiration from the heat balance gauges (T_h) was calculated as a residual of the heat balance of the stem to which a known, constant heat input was applied:

$$T_h = \frac{P - K_{st}A\dfrac{\Delta T_a + \Delta T_b}{\Delta x} - K_{sh}E}{C\Delta T_{ba}} \qquad (1)$$

where P is input power (W), K_{st} is stem thermal conductivity (W m^{-1} K^{-1}), A is stem area (m^2), ΔT_a and ΔT_b are vertical temperature gradients (K) above and below the heater, respectively, Δx is distance (m) between two thermocouple junctions both above and below the heater, K_{sh} is a gauge factor (W V^{-1}) representing the radial power loss, per V, through the gauge when T_h = 0, E is the voltage (V) of a thermopile mounted outside of the heater, C is specific heat capacity (J g^{-1} K^{-1}) of xylem sap, and ΔT_{ba} is temperature difference (K) across the heater. The second and third terms in the numerator of eqn. (1) are losses associated with vertical heat conduction along the stem and radial heat conduction outward through the gauge, respectively.

Dielectric silicon was applied to the stem before gauge attachment to improve stem/gauge contact. Gauges were attached about 0.3 m above the soil. After attachment, gauges were covered with clear plastic cling film for water protection and with aluminum foil to reflect radiation. A reflective weather shield and foam insulation were placed above and below the gauge on EU to minimize externally-induced temperature gradients.

The P was about 1 and 0.3 W for EU and PR, respectively. The K_{st} (0.76 W m^{-1} K^{-1}) was taken from Swanson and Whitfield (1981) and Kollmann (1987). Sap flow calculations are relatively insensitive to K_{st} (Ishida et al., 1991). The K_{sh} was visually estimated for each tree in each MP from a time series graph of the apparent K_{sh}, calculated daily by solving eqn. (1) for T_h = 0 from 00:00 to 05:00 h British Summer Time (BST). In all MPs, the apparent K_{sh} was approximately 3.5 W mV^{-1} for EU and approximately 1.1 W mV^{-1} for PR. The K_{sh} for a tree and a MP varied little (standard deviation of K_{sh} in each MP approximately 0.2 W mV^{-1} for the EU and approximately 0.05 W mV^{-1} for each PR). The K_{sh} determined in this manner was approximately equal (± 0.1 W mV^{-1}) to the K_{sh} calculated when all leaves had been removed for leaf area measurement and when all leaves had been covered with black plastic bags to terminate transpiration. Thus, our assumption that $T_h = 0$ at night was probably valid in this case.

Gauge signals (ΔT_a, ΔT_b, E, and ΔT_{ba}) and P were averaged over hourly periods. A software filter was used to eliminate spurious flow calculations during low flow conditions (Van Bavel and Van Bavel, 1990).

Porometer

The g_s of leaves on all trees (both surfaces) was measured using a Model LCA-3 portable photosynthesis system (Analytical Development Co. (ADC), Hoddesdon, UK) and an ADC Model PLC3(B) leaf chamber (Parkinson, 1985). Conductances, calculated from measurements of equilibrium chamber relative humidity (with dry air entering the chamber), temperature, and flow rate and a constant leaf boundary layer conductance, were measured every 90 min from about 06:00 to 21:00 h BST on 20 June (MP I), 4, 10, and 12 July (MP II), and 21 and 25 August (MP III). Relative humidity sensors in the PLC3(B) were calibrated in the laboratory before measurements on 20 June and after measurements on 12 July. No drift in calibration was observed.

During each set of measurements, g_s was measured on 12 (EU) and six (PR) leaves. Measurements were made on several branches and on sunlit and shaded leaves. Different leaves were selected throughout the day. The leaf chamber was attached to each leaf for about 20–30 s per measurement and the equilibrium relative humidity at the end of this period varied from about 10% in the early-morning and early-evening to about 40% at midday, while ambient relative humidity varied from near 100% in the early morning to about 60% in the late-afternoon.

The g_s-estimate of T_s for PR1 was calculated using the Penman–Monteith equation (Monteith, 1965)

$$T_s = LA\frac{sR_n + \rho c_p D g_b}{\lambda\left[s + \gamma\left(1 + \frac{g_b}{g_s}\right)\right]} \tag{2}$$

where LA is tree leaf area (m^2); s is slope of saturation vapor pressure vs. temperature (kPa °C^{-1}); ρ is air density (kg m^{-3}); c_p is specific heat of air (J kg^{-1} K^{-1}); D is vapor pressure deficit (kPa) calculated from wet and dry bulb temperatures; g_b is leaf boundary layer conductance (m s^{-1}) calculated (Grace, 1983) from resistances associated with forced and free convection (combined in parallel) determined using wind speed, leaf and air temperatures (the former calculated within the LCA-3 from the leaf energy balance), and leaf width; λ is latent heat of vaporization (J kg^{-1}); and γ is psychometric constant (kPa °C^{-1}). For wind speeds < 3 m s^{-1}, the g_b of Eucalyptus leaves calculated in this manner has been shown to be similar to that measured with wetted filter paper leaf replicas (Roberts et al., 1992).

Equation (2) was evaluated for each g_s measured using the appropriate hourly Rn, D, and, for calculation of g_b, wind speed and air temperature. These T_s values were then averaged. For PR1, each daily T_s, calculated by summing the 90 min averages, was compared with the T_g. The daily period was defined by the times of the first and last porometer measurements.

Equation (2) has been used in this manner (i.e. calculating T_s per unit leaf area and scaling up to a tree using total tree leaf area) for trees (Green et al., 1989). Implicit assumptions are that: (1) the Rn measured by a horizontal net radiometer over grass is representative of that incident upon tree leaves; (2) there is no horizontal divergence of energy from or to a leaf. While the former may not be strictly correct, the introduction of more complicated canopy models, involving leaf elevation and azimuth angle distributions and canopy geometry, to estimate Rn for individual leaves was considered unnecessarily complex in this case. The latter assumption was likely reasonable in this study given the moderate climate at this site, small tree heights, and surrounding green, well-watered grass.

Deuterium tracer

Deuterium oxide (D_2O), with a minimum isotopic purity of 99.9% D (MSD Isotopes, Merck Frosst, Montreal, Que.), was used as a tracer for estimating T_d using the 'total counts' method (Calder, 1991). A known mass of deuterium is injected into the stem of a tree and the deuterium concentration of the condensate (collected from bagged leaves) is measured from samples taken subsequent to injection. The time course of concentrations is used to calculate the mean flow rate through the tree.

According to Calder (1991), by assuming uniform tracer distribution within the tree and that all the tracer passes through the tree before the last deuterium concentration measurement, this method does not required any calibration. The finite difference form of the relevant equation is

$$T_d = \frac{M}{\sum_{i=1}^{i=\mathrm{Time}} C_i t_i} \qquad (3)$$

where M is tracer mass injected (g), C_i is volume ratio of D_2O:H_2O (assumed equal to the ratio of D:H) in the ith time increment, t_i is duration of the ith time increment (day), and Time is last time increment in which tracer is present. In this study, Time was defined as the time when 90% of the tracer had passed through the plant (approximately 5 days). For all trees and MPs, there was a < 10% difference between T_d calculated if Time was defined in this manner and T_d calculated if Time was defined as the last time when tracer was present (approximately 10 days).

The T_d was compared with T_g for this 5-day period. Calder (1991) has pointed out the T_d calculated using eqn. (3) is a weighted mean of instantaneous flow rates, where the weighting factor is C_i. Strictly, this T_d can only be compared with T_g if daily T_g does not vary with time. To account for varying T_g, an additional comparison between T_d and T_g was made for PR1 in MP II and III by calculating the weighted mean gravimetric flow rate, T_gw, from the following

$$T_{gw} = \frac{\sum_{i=1}^{i=\mathrm{Time}} T_{g,i} C_i t_i}{\sum_{i=1}^{i=\mathrm{Time}} C_i t_i} \qquad (4)$$

where $T_{g,i}$ is the measured gravimetric flow in the ith time increment.

At the beginning of each MP, 4 g of D_2O were injected using a hypodermic needle into holes drilled into the stem of EU and 1 g was injected into each PR. For EU, six 3-mm diameter, 20 mm-deep holes were drilled into the stem

TABLE 2

Average daily transpiration (kg per tree day^{-1}) measured gravimetrically for a Eucalyptus tree and three Prunus trees during three measurement periods

Measurement period	Eucalyptus	Prunus No. 1	Prunus No. 2	Prunus No. 3
I	1.9	0.57	0.59	0.67
II	2.9	0.72	0.77	1.00
III	0.96	0.50		

at regular intervals around the stem circumference at about a 45° angle (pointed downward) about 0.2 m above the soil surface and below the heat balance gauge. For PR, three 3-mm diameter, 10 mm-deep holes were drilled below the gauge. Deuterium was injected over a 10–20 min period. After injection, holes were sealed with silicon. The injection level was moved upward about 20 mm with each MP. On all trees, the first branch was >1 m above the injection point.

Clear plastic bags, each containing more than six leaves, were placed on the ends of six branches of EU and on two branches of each PR. Condensate in each bag was extracted about every day and new bags were applied. Branches upon which bags were placed were changed occasionally during each MP.

The C_i (eqn. (3)), expressed as the difference between the measured D_2O:H_2O ratio and a standard ratio, was measured on a mass spectrometer at the Institute of Hydrology using the standard zinc reduction technique for stable hydrogen isotope analysis (Coleman et al., 1982; Kendall and Coplen, 1985). For MP I and MP III, all condensate samples for a tree on a day were pooled. For MP III, results are presented only for PR1 because samples for EU were lost. For MP II, all condensate samples were analyzed separately.

RESULTS AND DISCUSSION

During MP I, maximum temperatures were about 12°C, global radiation was low, and precipitation occurred on 13 days. Skies were clearer and temperatures were higher (daily maximums approximately 25°C) during MPs II and III. Precipitation occurred on 4 days and 2 days in MP II and MP III, respectively.

Heat balance

For each tree, the average daily T_g was greatest during MP II (Table 2). Because of the greater leaf area, transpiration was greatest for EU. The low T_g for EU in MP III (Table 2) was associated with a decreased g_s (see below) caused by a soil water deficit stress.

For PR1 in MP II daily T_g was very close to T_h, but, for unknown reasons,

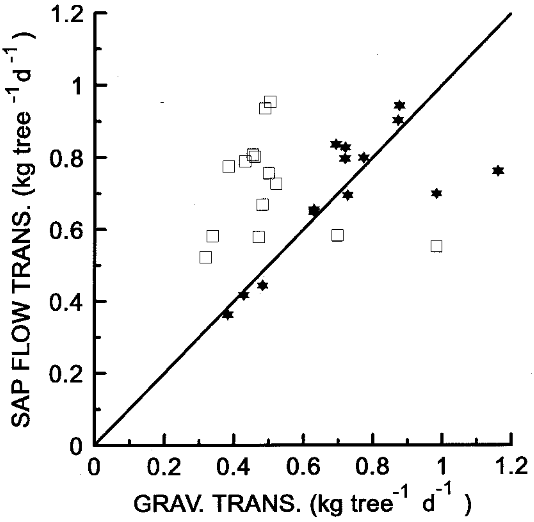

Fig. 1. Total daily transpiration determined from sap flow measurements using heat balance gauges vs. transpiration measured gravimetrically for a Prunus tree (PR1) during measurement periods II (★) and III (□). The 1:1 line is shown. The slope (and standard error) of sap flow transpiration vs. gravimetric transpiration, forced through the origin, was 1.06(0.07).

differences were greater in MP III (Fig. 1). The two outliers during MP II correspond to days with precipitation. The root mean square difference (RMSD; RMSD $= [\Sigma(T_h - T_g)^2/(n-1)]^{0.5}$ between daily T_g and T_h for MPs II and III was 0.26 kg per tree day^{-1} for PR1, as compared with the mean T_g of 0.61 kg per tree day^{-1} (Table 2). The RMSD has similar statistical properties to a standard deviation, e.g. with a large sample size (*n* is approximately 30), 68% of the predicted values will be within ±1 RMSD of T_g. It provides a quantitative measure of the accuracy with which transpiration can be estimated by heat balance gauges.

For the entire MP, the T_h was also close to T_g for all trees and the slope was = 1.0 (Fig. 2). There was, however, a consistent underestimate of T_g for PR2. This may have been due to the effect of xylem damage caused by drilling holes in the stem below the gauge. This damage was evidenced by a darkened stem color seen when the stem was cut at the end of the experiment at a point about 50 mm below the gauge position. About 10% of the stem area of PR2 was discolored. No damage was evident on PR1 or PR3. The damage on PR2 may have affected the flow geometry within the stem and, thus, the accuracy of gauge measurements. Deuterium injection above the gauge would have eliminated this problem.

Porometer

The diurnal pattern of g_s was similar for all trees on 10 July (Fig. 3). The

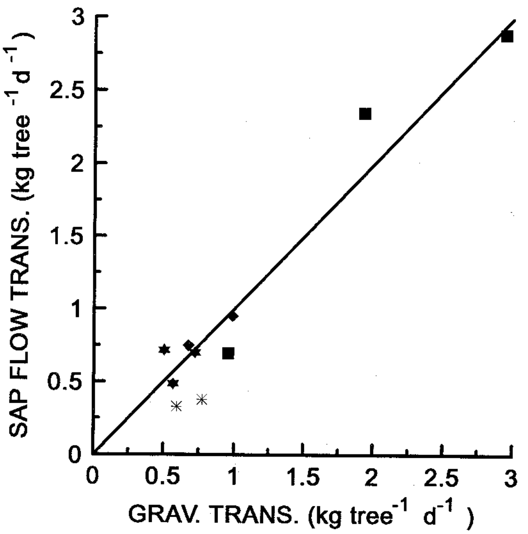

Fig. 2. Average daily transpiration determined from sap flow measurements using heat balance gauges vs. transpiration measured gravimetrically for Eucalyptus (■) and three Prunus trees (PR1(★), PR2(∗), and PR3(◆)). Averages were calculated for all days in each measurements period. The 1:1 line is shown. The slope (and standard error) of sap flow transpiration vs. gravimetric transpiration, forced through the origin, was 1.00(0.06).

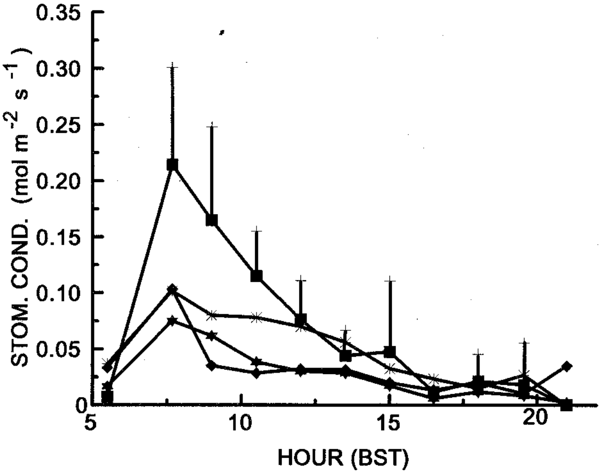

Fig. 3. Stomatal conductance measured on Eucalyptus (■) and three Prunus trees [PR1(★), PR2(∗), and PR3(◆)] on 10 July 1991. The sample standard deviation (n = 12) of conductance measurements on the Eucalyptus tree is shown as a vertical line. BST, British Summer Time.

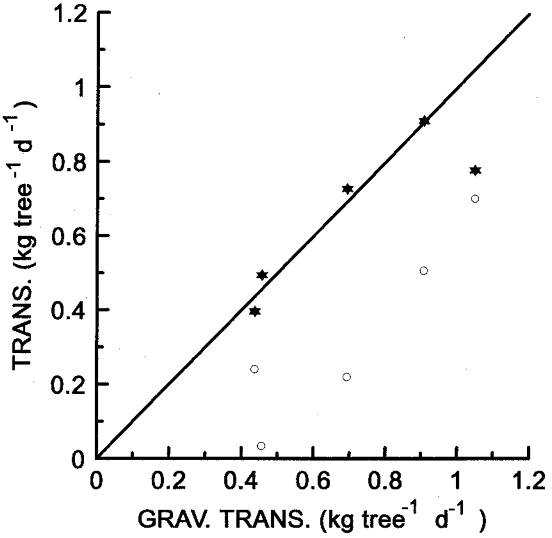

Fig. 4. Daily transpiration calculated from porometer measurements (o) and determined from sap flow measurements (★) using heat balance gauges vs. transpiration measured gravimetrically for a Prunus tree (PR1) in measurement periods II and III. The 1:1 line is shown. The slope (and standard error) of sap flow transpiration vs. gravimetric transpiration, forced through the origin, was 0.90(0.06). For porometer transpiration, the slope was 0.56 (0.09).

average g_s for EU, PR1, PR2, and PR3 on 10 July was 0.066 mol m^{-2} s^{-1}, 0.027 mol m^{-2} s^{-1}, 0.047 mol m^{-2} s^{-1}, and 0.032 mol m^{-2} s^{-1}, respectively. These values are similar to the average g_s measured for these trees on 20 June and 4 and 12 July. However, the average daily g_s decreased to 0.020 mol m^{-2} s^{-1} and 0.010 mol m^{-2} s^{-1} for EU and PR1, respectively, during the two August measurements. The g_b was more consistent diurnally and averaged about 4 mol m^{-2} s^{-1}. The g_b:g_s ratio (eqn. (2)) was at a minimum in the mid-morning and a maximum in the late afternoon.

There was a consistent underestimation of daily T_g by T_s, while T_h was closer to and not consistently different from T_g (Fig. 4). Differences were reflected in the slopes (Fig. 4) and RMSDs (Table 3). The average T_g for the data in Fig. 4 was 0.7 kg per tree day^{-1}. The systematic underestimate of T_g by T_s may have been due to dry air being passed over the leaf in the porometer chamber which could have reduced g_s (Turner, 1991) or an invalid assumption that the Rn of each leaf was equal to that measured over grass. The underestimate by T_s would result, for example, if the average leaf irradiance as a result of non-horizontal display was greater than that on a horizontal plane.

Deuterium

Condensate deuterium concentrations increased rapidly to a maximum a

TABLE 3

Root mean square difference between heat balance-, porometer-, and deuterium-estimated transpiration and measured gravimetric transpiration for daily and 5-day averaging periods

Averaging period	Heat balance (kg per tree day^{-1})	Porometer (kg per tree day^{-1})	Deuterium (kg per tree day^{-1})	*n*
Daily	0.14	0.42	Not applicable	5[a]
Ca. 5-d	0.40	Not applicable	1.0	9[b]

[a] Prunus tree No. 1 (PR1) on days in measurement Periods II and III when porometer measurements were made (see Fig. 4).

[b] All trees and measurement periods (see Fig. 6). Period length varied (see text), but was typically 5 days. *n*, sample size. Valid comparisons are only possible within a row, i.e. across methods for a period.

few days after injection and gradually decreased to the standard mean ocean water concentration after about 10 days (Fig. 5). The latter supports the assumption that all deuterium passed through the tree. Shapes of concentration curves were similar for other MPs and trees (results not shown).

The variability of deuterium measurements on EU was assessed using the measurements from MP II, where the six replicate samples were not pooled. The coefficient of variation (CV) of the area under the six concentration curves was 24%. This statistic allows one to evaluate the number of deuterium sampling locations required to obtain a representative value of transpiration

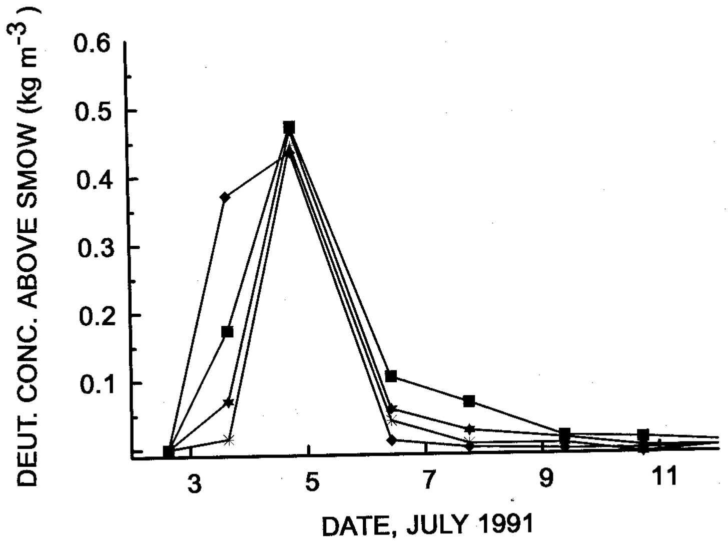

Fig. 5. Deuterium concentration (above standard mean ocean water, SMOW) for Eucalyptus (■) and three Prunus trees [PR1(★), PR2(*), and PR3(◆)] during the second measurement period. The $n = 6$ for EU and $n = 2$ for each Prunus tree.

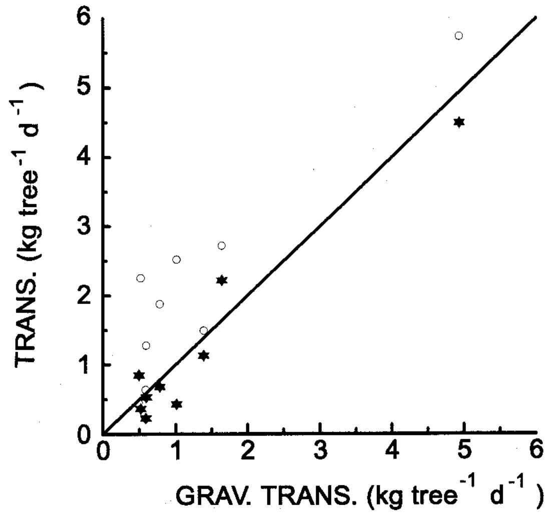

Fig. 6. Average daily transpiration determined from deuterium concentrations (o) and from sap flow measurements (★) using heat balance gauges vs. transpiration measured gravimetrically. Results are shown for all measurements periods and averages are for 5-day periods. The 1:1 line is shown. The slope (and standard error) of sap flow transpiration vs. gravimetric transpiration, forced through the origin, was 0.93(0.06). For deuterium transpiration, the slope was 1.30 (0.15).

for an individual tree. This variability is somewhat higher than the 10–15% CV observed by Calder et al. (1986). As also shown by Calder et al. (1986), deuterium concentrations in this study were greater in the lower canopy portion before the peak concentration and were greater in the upper canopy after the peak (results not shown).

The T_d calculated from eqn. (3) was generally greater than T_g (Fig. 6). For PR1 in MPs II and III, it was possible to compare T_d with T_{gw} (eqn. (4)) because daily T_g could be accurately measured (Table 1). However, the average T_g and T_{gw} of PR1 for the first 5 days of each MP were equal (both 0.8 kg per tree day^{-1} for MP II and 0.5 kg per tree day^{-1} for MP III). This equality of T_g and T_{gw} was a result of the low variability of T_g for PR1 (CV of 20% and 7% for the first 5 days in MP II and III, respectively). However, Calder et al. (1992) showed small differences in T_g and T_{gw} even with T_g CVs of 10–49%.

The T_d RMSD was 1.0 kg per tree day^{-1}, more than twice the error for T_h (Table 3). The magnitude of these errors for T_d are similar to those presented by Calder et al. (1992) who showed validation results from two experiments on Eucalyptus in India. Their results, however, did not show a consistent overestimate of T_g. In their study, the T_g and T_d were 6.7 kg per tree day^{-1} and 5.8 kg per tree day^{-1} for the first experiment and 3.3 kg per tree day^{-1}

and 3.4 kg per tree day^{-1}, respectively, for the second, or a mean absolute error of 0.5 kg per tree day^{-1}.

A portion of the systematic overestimate in this study may be explained by deuterium spillage during injection. Stem holes were filled with deuterium until a positive meniscus was formed. In some instances, too much deuterium was injected and some deuterium ran down the stem. This loss would have resulted in overestimates of T_g by T_d.

CONCLUSIONS

Transpiration calculated using constant power heat balance gauges, porometer measurements of stomatal conductance, and deuterium tracers was compared against gravimetric measurements of transpiration. Errors (with respect to gravimetric measurements) were calculated. Differences between gravimetric and heat balance transpiration were less than differences between either porometer or deuterium transpiration and gravimetric transpiration (Table 3).

Each method has positive and negative aspects. Heat balance gauges provide continuous, non-destructive, and direct measurements of transpiration and are a valuable tool for transpiration measurements for small plants and trees. Field use requires careful experimental procedures and data analyses procedures may be complicated. Precautions associated with the use of porometers (McDermitt, 1990; Turner, 1991) include calibration of humidity sensors and ensuring an adequate sample of leaves. Porometers do provide an excellent complement to other measurements because conductance differences owing to the environment can be evaluated over time or between species. Measurements using this instrument are, however, non-automated and non-continuous. The large temporal and spatial variability may require a large number of measurements. Deuterium tracing has substantial potential for applications where the long temporal resolution of the measurement and possible high analytical costs are not limiting. The usefulness of the deuterium method, however, is limited by the fact that it gives a weighted mean flow rate, where the weighting factors (measured flow between the times of condensate sampling) would not normally be known in the field. This might preclude its use in environments where daily flow rates are variable.

The choice of the most appropriate method clearly depends on the requirements of each particular investigation. This study has quantified the errors associated with each method.

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