PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Leaf Energy Balances: Developments and Applications [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1989 **324**, 191-206
doi: 10.1098/rstb.1989.0044

Phil. Trans. R. Soc. Lond. B **324**, 191–206 (1989)
Printed in Great Britain

Leaf energy balances: developments and applications

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Theory of leaf energy balances is outlined in the context of four applications: (1) prediction of leaf temperatures during clear nights; (2) estimation of transpiration rates and stomatal conductances of individual leaves by using pairs of coated and normal leaves; (3) measurement of leaf boundary-layer conductances using pairs of artificial, electrically heated leaves; and (4) use of method (2) to assess validity of whole-tree transpiration rates measured with large ventilated chambers.

Good agreement was found between predicted and measured leaf temperatures on clear nights. Leaf temperatures were controlled mainly by loss of thermal radiation to cold skies and by gain of sensible and latent heat from surrounding air. Leaves with condensation on them were 1–2 °C warmer than dry leaves under otherwise similar ambient conditions. Free convection was unimportant relative to forced convection as a mechanism for heat transfer to leaves during calm, clear nights.

Satisfactory estimates of single-leaf transpiration were obtained using pairs of coated and uncoated leaves provided both were equally exposed to incoming radiation. Electrically heated facsimile leaves gave satisfactory estimates of leaf boundary-layer conductances in the field.

Large ventilated chambers had a small influence on measured transpiration rates according to estimates made with the Penman–Monteith equation for both chamber positions.

1. Introduction

Energy balances of plant leaves have been investigated by many workers. Problems addressed include: (1) establishment of quantitative relations between wind speed and leaf boundary-layer conductance (see, for example, Raschke 1956; Parkhurst *et al.* 1968; Pearman *et al.* 1972; (2) determining influences of air turbulence and leaf flapping on these conductances (see, for example, Parlange *et al.* 1971; Parlange & Waggoner 1972; Parkhurst & Pearman 1974); and (3) establishing whether boundary layers on leaves are laminar or turbulent (Grace & Wilson 1976). Transfer processes at leaf surfaces have also been incorporated into models for heat, mass and momentum transport within plant canopies (Cowan 1968; Thom 1972; Finnigan & Raupach 1987).

Concepts of leaf energy balances were applied by Leuning (1988) to prediction of leaf temperatures during clear nights. The study aimed at helping ecologists distinguish between biological responses of plant organs to temperature and the effects on leaf temperature of variations in plant microhabitat (e.g. leaf height or ground cover (Leuning & Cremer 1988)). Two models to predict equilibrium temperatures of isolated leaves subject to radiation frost were developed (Leuning 1988). Effects on leaf temperature of soil thermal conductivity, leaf size, orientation and height above ground were incorporated in nonlinear theory. The model also included influence of surface-shading, whereby leaf proximity causes the temperature of the ground surface immediately below the leaf to be higher than ground exposed to clear skies. This largely explained observed convergence of leaf and air temperatures at ground level (Leuning

& Cremer 1988). A simplified quasi-linear model, applicable when leaf height above ground is greater than its width, showed that leaves with condensation (frost or dew) were several degrees Celsius warmer than those without condensation at similar ambient temperatures. Real leaves were instrumented and results for leaf–air temperature differences were compared with predictions of linear theory.

Leaf energy-balance techniques were also used to examine possible bias in whole-tree transpiration rates measured with large ventilated chambers (Foster & Leuning 1987). These enclosures have been used in Western Australia to measure transpiration rates of trees in an effort to select species most suitable for maximizing evapotranspiration rates and to minimize or stop the rise of saline water tables (Greenwood & Beresford 1979). However, the enclosure may introduce errors into transpiration estimates because radiation, temperature, humidity, and turbulence may all be altered when it is used. Foster & Leuning (1987) used two techniques that could be applied both with and without the chamber in place to assess validity of transpiration rates estimated with the chamber. A leaf energy-balance method (Impens 1966; Linacre 1972) utilized paired leaves, one of which was prevented from transpiring, whereas the other behaved normally. Temperature differences between the two leaves were used to estimate transpiration rates of the undisturbed leaf through solution of energy-balance equations for the leaf pair. Leaf boundary-layer conductances required for the leaf energy-balance technique were measured *in situ* by using pairs of facsimile leaves, one heated electrically and the other unheated (Parkhurst *et al.* 1968). A second set of transpiration estimates was obtained by application of the Penman–Monteith combination equation to single leaves, by measurements of net radiation, humidity, air temperature and leaf boundary-layer and stomatal conductances for both chamber positions.

The paired leaf energy-balance method was applied at another site to measure transpiration rates and stomatal conductances of individual leaves. This work was part of a larger micrometeorological experiment investigating transfer processes at leaf surfaces and within forest canopies.

2. THEORY

2.1. *Leaf temperatures*

Leaves exchange radiation with the sky and ground and also exchange sensible and latent heat with the surrounding air. Changes in energy storage in the leaf may also occur. These processes satisfy the energy-balance equation

$$R_{\mathrm{lu}}+R_{\mathrm{ll}}+H_{\mathrm{l}}+\lambda E_{\mathrm{l}}+\frac{1}{A}\int_{V} c_{\mathrm{l}}\rho_{\mathrm{l}}(\partial T_{\mathrm{l}}/\partial t)\,\mathrm{d}V=0, \tag{1}$$

where R_{lu} and R_{ll} are net radiant flux densities at the upper and lower leaf surfaces, respectively; H_{l} and λE_{l} sensible and latent heat flux densities for both surfaces combined and λ is latent heat of phase change. The last term in equation (1) represents change in energy storage in a leaf with volume V and surface area A; c_{l} and ρ_{l} are the specific heat and density of the leaf, respectively. The storage term will be neglected because only steady-state temperatures and energy fluxes are considered below.

The sum of sensible and latent heat flux densities from air to the leaf with closed stomata at night may be written as

$$H_{\mathrm{l}}+\lambda E_{\mathrm{l}} = C_1 g_{\mathrm{h}}[(T_{\mathrm{a}}-T_{\mathrm{l}})+C_2(e_{\mathrm{a}}-e_{\mathrm{l}}^{*})], \tag{2}$$

provided $e_a > e_l^*$. Parameters C_1 and C_2 are defined as

$$C_1 = 2\rho_a c_p, \tag{3a}$$

$$C_2 = \begin{cases} g_w/(p\gamma g_h) & \text{while condensation is forming on leaf;} \\ 0 & \text{with no condensation on leaf.} \end{cases} \tag{3b}$$

Air density and specific heat at constant pressure are given by ρ_a and c_p, respectively; p is total atmospheric pressure, g_h and g_w are boundary layer conductances for sensible heat and water vapour; γ is the psychrometric constant $(c_p M_a/\lambda M_w)$ evaluated by using the appropriate value of λ (for condensation or sublimation); T and e^* are the temperature and saturation water vapour pressure, with subscript 'l' designating leaf, and subscript 'a' air.

Frost deposition is assumed to be uniform and variation of temperature across the leaf lamina is neglected in writing equation (2). The factor 2 in equation (3a) arises because g_h and g_w are defined for one side of the leaf and heat and mass transfer are assumed to occur equally on both sides. Thus equation (2) represents spatially averaged fluxes in terms of spatially averaged transfer coefficients, temperatures and humidities.

The sum of net radiation absorbed by upper and lower leaf surfaces at night is given by

$$R_{lu} + R_{ll} = \epsilon_l \sigma (T_{sk}^4 - T_l^4) + \epsilon_l \sigma (T_{gs}^4 - T_l^4), \tag{4}$$

where ϵ_l is leaf emissivity and where the ground and sky are treated as black body radiators $(\epsilon = 1)$; σ is the Stefan–Boltzmann constant and subscripts 'sk' and 'gs' refer to sky and ground surface, respectively. Note temperatures in equation (4) are in kelvins.

The radiative temperature of a clear sky at night (T_{sk}) can be estimated accurately from standard meteorological screen temperature (T_s) by using the data of Unsworth & Monteith (1975), namely

$$T_{sk}^4 = T_s^4 - 100/\sigma, \tag{5}$$

in which 100 is an empirical constant. This correlation is successful because downward flux of radiation from the sky is primarily dependent on air temperature and absolute humidity in the lowest tens of metres above the surface (Deacon 1970). Also, air temperature and absolute humidity are well correlated near the ground at night (Monteith 1964; Deacon 1970) allowing successful use of a single variable, T_s, in equation (5).

Combining equations (2) and (4), the energy balance for the leaf becomes

$$\epsilon_l \sigma (T_{sk}^4 + T_{gs}^4 - 2T_l^4) + C_1 g_h[(T_a - T_l) + C_2(e_a - e_l^*)] = 0. \tag{6}$$

This equation shows that energy loss from the leaf by radiation is balanced by radiation gain from the sky and ground and by transfer of sensible and latent heat from the air.

Radiative sky temperatures on clear nights are estimated from screen temperatures by using equation (5). Equation (6) can then be linearized by writing T_l, T_s and T_{gs} as small departures from T_a, the temperature of air surrounding the leaf, e.g. $T_l = T_a - \Delta T_l$. The term T_l^4 is approximated by

$$T_l^4 \approx T_a^4(1 - 4\Delta T_l/T_a), \tag{7}$$

because $\Delta T_l \ll T_a$. Similar expressions apply for T_s^4 and T_{sg}^4. Further simplifications to equation (6) are possible by assuming that $\epsilon_l = 1$ and that air outside the leaf boundary layer is saturated with water vapour. The term $e_a - e_l^*$ may then be written as

$$e_a - e_l^* = s(T_a - T_l), \tag{8}$$

where S is the slope of the curve relating air temperature to saturation water-vapour pressure over ice or water.

With the above assumptions and approximations, equation (6) may be solved for $T_l - T_a$ to give

$$T_l - T_a = b_T[T_{gs} + T_s - 2T_a - 100/(4\sigma T_a^3)], \tag{9}$$

where

$$b_T^{-1} = [g_h C_1/(4\sigma T_a^3)](1 + C_2 s) + 2. \tag{10}$$

If no latent heat is transferred to the leaf, $C_2 s = 0$.

Departure of leaf temperature from that of the surrounding air is seen to be a linear function of ground and screen temperatures but a nonlinear function of air temperature. The last term in brackets in equation (9) dominates the others numerically for typical values of T_a, T_{gs} and T_s.

2.2. *Transpiration by single leaves*

One method of measuring transpiration of single leaves utilizes leaf pairs, where one leaf is prevented from transpiring by application of an impermeable film, whereas the other remains undisturbed (Impens 1966; Linacre 1972). Latent heat flux density is calculated as a residual between energy balances for the two leaves.

Steady-state energy balances for coated and normal, hypostomatous leaves can be written as

$$R_{n1} = H_1 = C_1 g_h (T_1 - T_a) \tag{11a}$$

and

$$R_{n2} = H_2 + \lambda E_2 = C_1 g_h (T_2 - T_a) + \lambda E_2, \tag{11b}$$

in which R_{n1}, R_{n2} are the net radiation, H_1, H_2 the sensible heat flux density, T_1, T_2, the average leaf temperature, T_a the air temperature and λE_2 the latent heat flux density. Subscripts '1' and '2' refer to non-transpiring and transpiring leaves, respectively. Temperatures and energy fluxes are taken as spatial averages across leaf surfaces which are assumed to be symmetrical so that H and R_n are each sums of fluxes from both sides of the leaf. Equation (11*b*) is written for a hypostomatous leaf, assuming sensible heat transfer occurs equally on both sides of the leaf but transpiration from one side only.

Subtracting equation (11*b*) from (11*a*) eliminates T_a to yield

$$R_{n1} - R_{n2} = C_1 g_h (T_1 - T_2) - \lambda E_2. \tag{12}$$

Foster & Leuning (1987) showed that $R_{n1} - R_{n2}$ could be written as

$$R_{n1} - R_{n2} = -2\epsilon\sigma(T_1^4 - T_2^4), \tag{13}$$

provided leaf absorptances and incoming radiation fields are identical for both leaves. Differences in net radiation between the two leaves are then solely the result of differences in their radiative temperatures. (The factor 2 arises because both surfaces of each leaf exchange radiation.) Equation (13) may be linearized following procedures similar to those used to obtain equation (7), thus

$$R_{n1} - R_{n2} = -8\epsilon\sigma T_2^3 (T_1 - T_2). \tag{14}$$

Combining equations (12) and (14) and solving for λE_2 yields

$$\lambda E_2 = (C_1 g_h + 8\epsilon\sigma T_2^3)(T_1 - T_2). \tag{15}$$

Flux densities for each side of symmetrical amphistomatous leaves are half of that given in equation (15).

Three quantities are necessary to estimate λE_2 using the paired leaf energy-balance method (equation (15)): g_h, $T_1 - T_2$, and T_2. The latter can be approximated by T_a with small error (*ca.* 0.2% change in λE_2 for a 1 °C error in T_2). The temperature difference $(T_1 - T_2)$, is measured directly by using fine-wire thermocouples and a method for estimating g_h is presented below.

2.3. *Leaf boundary-layer conductances*

Similarity theory for flat plates (Schlichting 1968) may be used to estimate g_h, provided windspeeds near the leaf are known. Alternatively, electrically heated facsimile leaves (Parkhurst *et al.* 1968; Pearman *et al.* 1972; Dixon & Grace 1983) may be used to estimate boundary layer conductances *in situ*.

Steady-state energy balances for dry, unheated (R_u) and heated (R_h) facsimile leaves exposed equally to radiation and wind may be written as:

$$R_u = C_1 g_h (T_u - T_a) \quad \text{and} \quad R_h + 2P_e = C_1 g_h (T_h - T_a), \tag{16a, b}$$

where T_u and T_h are the temperatures of unheated and heated leaves, respectively. Electrical power dissipated in the heated leaf is $P_e = VI/2A$, where A is area of a single side and V and I refer to the voltage across and current through the heater ribbon in the facsimile, respectively.

An expression for g_h may be derived from equation (16*a*, *b*) in a manner similar to that used above to obtain λE_2 for real leaves, with the result:

$$g_h = (2/C_1)\,[P_e/(T_h - T_u) - 4\epsilon\sigma T_u^3]. \tag{17}$$

2.4. *Penman–Monteith equation for hypostomatous leaves*

Transpiration rates measured by using a large ventilated chamber were divided by total single-sided leaf area of the study tree to enable comparison with single-leaf rates obtained by using equation (15). The Penman–Monteith (PM) equation for hypostomatous leaves (Jarvis & McNaughton 1986) provided a third estimate of transpiration rates at the leaf scale. The equation is written as

$$\lambda E_p = [\tfrac{1}{2}R_l + (\rho_a c_p/s)\, g_h D]/[\tfrac{1}{2} + (\gamma/s)\,(1 + g_h/g_s)], \tag{18}$$

where D is the water vapour pressure deficit of air $(e_a^* - e_a)$, R_l is the net radiation absorbed by the leaf and g_s is the stomatal conductance.

2.5. *Stomatal conductance*

Stomatal conductances were estimated from λE_2 as follows. Transpiration rates for individual leaves may be expressed as

$$\lambda E_2 = \frac{\rho_a c_p}{\gamma} \frac{(e_1^* - e_a)}{(1/g_s + 1/g_h)}, \tag{19}$$

in which e_1^* is saturation water-vapour pressure at leaf temperature. Temperature differences between coated and normal leaves were measured directly for use with equation (15).

However, absolute leaf temperature was not measured, so D was used to estimate $e_1^* - e_a$. With this approximation, equation (19) may be solved for $1/g_s$ to yield

$$\frac{1}{g_s} = \frac{\rho_a c_p}{\gamma} \frac{D}{\lambda E_2} - \frac{1}{g_h}. \tag{20}$$

Good estimates of g_s are obtained from equation (20) provided leaf and air temperatures are similar and $g_s \ll g_h$.

3. Methods

Leaf temperatures during frost experiments were measured by using 75 μm copper constantan thermocouples inserted into leaf laminae and referenced to a Pt-100 thermometer in water. Similar, unshielded wires were used to measure air temperatures. Further details of frost experiments are given by Leuning & Cremer (1988).

A thermocouple junction (25 μm, chromel constantan) was attached to the surface of each facsimile leaf to measure $T_h - T_u$, which is required in equation (17) to estimate g_h. A similar arrangement was used on pairs of real leaves to measure $T_1 - T_2$, needed to estimate λE_2 from equation (15). Temperatures T_u and T_2 were approximated by T_a in these equations, introducing only small errors into estimates of g_h and λE_2.

Measurements of meteorological variables, description of ventilated chamber operation and details of constructing facsimile leaves are discussed by Foster & Leuning (1987). Heating current was supplied to only one facsimile in their work but this was modified in later experiments so that current flowed through each in turn for periods of 7.5 min. A null period of 1 min between half-cycles allowed one facsimile to heat and the other to cool before the data logger resumed sampling thermocouple voltages. Polarity of thermocouple signals was inverted during every second 7.5 min period and results were averaged for 15 min. This switching and rectification procedure eliminated systematic errors in thermocouple thermometry.

4. Results

4.1. *Leaf temperatures*

Typical temperature profiles for air and two sizes of leaves displayed horizontally above a grass surface on a clear night are shown in figure 1. At a given height, larger leaves (mean width 48 mm) were cooler than small ones (mean width 10 mm) and both were colder than air. Leaf and air temperatures were lowest near the ground and all temperatures increased with height. Temperature gradients were steepest near the ground although leaf and air temperatures were similar there.

A nonlinear theory presented by Leuning (1988) to describe radiation and heat exchange between horizontal leaves and their surroundings was largely successful in explaining convergence of air and leaf temperatures near the ground (figure 1). Shading of the ground by the leaf caused surface temperatures immediately below the leaf to be higher than surrounding ground exposed to clear skies. This in turn raised leaf temperatures through enhanced radiation receipt from the warmer ground surface. Profiles of measured $T_l - T_a$ for two leaf sizes are compared in figure 2 to three predictions of nonlinear theory corresponding to different choices of formulae to estimate boundary-layer conductance, g_h: (1) free convection (Kreith 1966); (2) 'mixed' convection from results of Dixon & Grace (1983); and (3) forced convection (Schlichting 1968) at an assumed constant wind speed of 0.2 m s^{-1}. Both mixed and

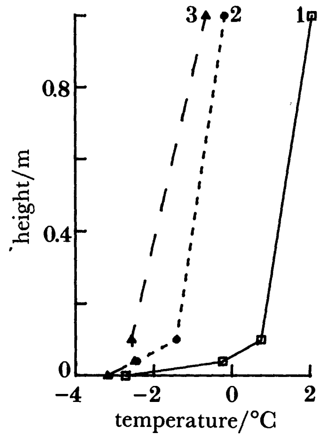

FIGURE 1. Typical night-time temperature profiles for (1) air, (2) small leaves of *Eucalyptus viminalis* Lab. II (mean width 10 mm) and (3) larger leaves of *Eucalyptus pauciflora* Sieb ex Spreng (mean width 48 mm). All leaves held horizontally. (After Leuning & Cremer 1988.)

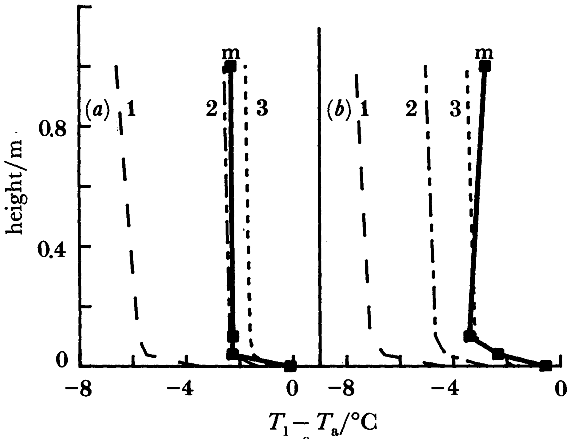

FIGURE 2. Measured night-time profiles (m) of leaf-to-air temperature differences $T_l - T_a$, for (*a*) *E. viminalis* and (*b*) *E. pauciflora* leaves held horizontally. Predicted profiles were calculated from nonlinear theory of Leuning (1988) for three choices of formulae to estimate boundary layer conductance g_h; (1) free convection, (2) 'mixed' convection and (3) forced convection at an assumed constant wind speed of 0.2 m s^{-1}.

forced convection formulae for g_h provided acceptable agreement between measured and predicted values of $T_l - T_a$ for small leaves (figure 2*a*) but good agreement for the large leaf was only achieved when the forced convection formula was used to determine the value of g_h (figure 2*b*). Free-convection formulae for g_h resulted in large overpredictions in $|T_l - T_a|$ for both leaf sizes (figure 2) and Leuning (1988) concluded that free convection was not important for heat transfer to leaves under still conditions found during nocturnal inversions.

When leaf temperature reaches the dew/frost point of the air, condensation forms and latent heat is released. For a given set of ambient conditions represented by T_{gs}, T_s and T_a, leaves with condensation on them are thus closer to air temperature than leaves without condensation. An example of quantitative predictions of $T_a - T_l$ from equation (9) is shown in figure 3 for leaves with and without frost, assuming a leaf width of 50 mm, $T_s = 0$ °C, $T_a = -4$ °C, two wind speeds (0.20 and 0.05 m s^{-1}) and variable ground surface temperature T_{gs}. Reduction in wind speed caused $|T_l - T_a|$ to increase for both frost covered and frost free leaves. Absence

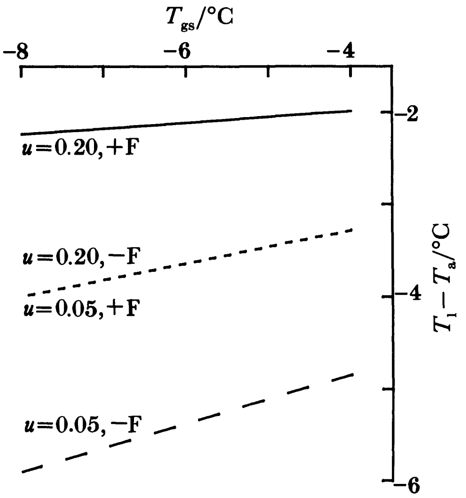

FIGURE 3. Predictions of leaf-to-air temperature differences $T_l - T_a$, from linear theory of Leuning (1988). $T_l - T_a$ was calculated as a function of ground surface temperature T_{gs}, at two wind speeds ($u = 0.20\ \mathrm{m\ s^{-1}}$ and $u = 0.05\ \mathrm{m\ s^{-1}}$), assuming meteorological screen temperature $T_s = 0$ °C, air temperature $T_a = -4$ °C for a horizontal leaf 50 mm wide. Leaves with frost (+F) are *ca.* 1.5 °C warmer than those without frost (−F).

of frost lowers leaf temperatures by *ca.* 1.5 °C at $u = 0.2\ \mathrm{m\ s^{-1}}$ and by *ca.* 1.7 °C at $u = 0.05\ \mathrm{m\ s^{-1}}$ compared with frost-covered leaves. Variation in T_{gs} from −4 to −8 °C caused predicted $T_a - T_l$ to decrease by only 0.4 °C for a frost-coated leaf at $u = 0.20\ \mathrm{m\ s^{-1}}$ but a decrease of 1.1 °C for a leaf without frost at a wind speed of $0.05\ \mathrm{m\ s^{-1}}$. Frost-free leaves at $u = 0.20\ \mathrm{m\ s^{-1}}$ are predicted to have identical temperatures to frosted leaves at the lower windspeed of $0.05\ \mathrm{m\ s^{-1}}$.

Predictions of $T_a - T_l$ were computed using equations (9) and (10) for two sizes of horizontal leaves (10 to 50 mm) assuming $T_{gs} + T_s = 2T_a$. Wind speeds, u, measured at 0.4 m with a sonic anemometer, were used to calculate g_h from classical flat-plate theory for forced convection (Schlichting 1968), i.e. $g_h = 0.60\,K(u/\nu d)^{\frac{1}{2}}$, where K is the thermal diffusivity, ν is the kinematic viscosity and d the leaf width. Two values of $T_a - T_l$ were calculated, corresponding to fully wet or fully dry leaves, and results closest to the measured values for each 15 min run were chosen. Figure 4 shows that linear theory accurately predicts temperatures for both sizes of isolated

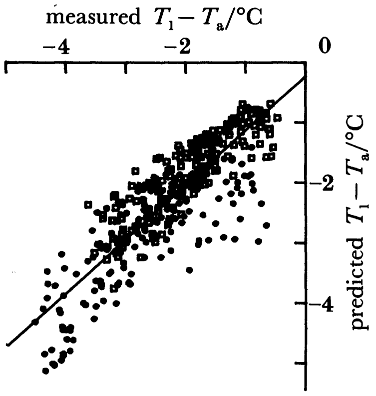

FIGURE 4. Values of $T_l - T_a$ predicted from equations (9) and (10) by using measured wind speeds and air temperatures, plotted against $T_l - T_a$ measured directly with fine thermocouples. Linear regression line: $y = -0.24 + 0.90x$, $r^2 = 0.76$, $n = 343$.

leaves, provided it is known whether leaves do or do not have condensation on them. This may be facilitated by measuring the dewpoint of air, although leaves often are not uniformly wet as assumed in the analysis, thereby complicating problems of prediction.

4.2. *Ventilated chamber*

Transpiration measurements obtained with the leaf energy-balance technique on *Eucalyptus resinifera* leaves are compared with mean, single-leaf rates from the ventilated chamber in figure 5. Error bars depicting one standard deviation for half-hourly means are also shown for representative points. Satisfactory agreement was observed between the two methods, with the leaf energy-balance technique tending to overestimate relative to the ventilated chamber by *ca.* 10–15% of maximum rates.

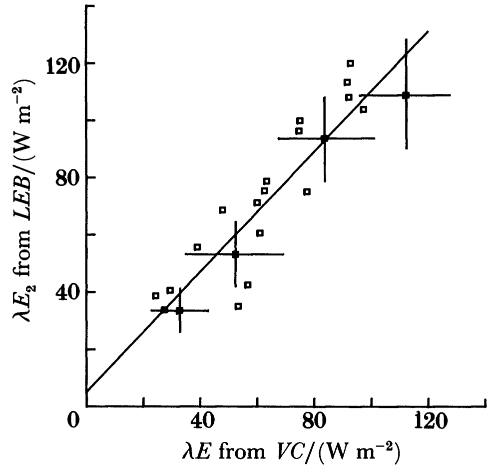

FIGURE 5. Mean transpiration rates (in energy units) estimated by using a leaf energy budget method (*LEB*, equation (15)) compared with rates measured by a large ventilated chamber (*VC*). Error bars on typical points are one standard deviation of the mean. Linear regression line: $y = 11.7 + 1.11x$, $r^2 = 0.84$, $n = 23$. (After Foster & Leuning (1987).)

Average latent-heat flux densities at the leaf scale were obtained by using the Penman–Monteith (*PM*) equation (equation 18)), with measured values of D, g_h, g_s and R_l. A thermistor and Vaisala humicap were used to determine D, and boundary-layer conductances were measured *in situ* with facsimile leaves. Portable leaf porometers (Li-Cor 1600, Li-Cor Inc., U.S.A.) were used to estimate mean conductances of 50 leaves per run. Net radiation absorbed by the 'mean leaf' was calculated as $R_l = (R_{nf} - R_{nm})/A_L$, where R_{nf} is net radiation measured above the crown (but within the *VC*), R_{nm} is the mean of four linear net radiometers placed within the canopy and A_L is leaf area index of the tree ($A_L = 3.1$). Net radiation within the canopy was less than 100 W m^{-2}, *ca.* 10–15% of midday values observed above the canopy. Excellent agreement was observed between the *PM* estimates of λE and direct measurements from the *VC* (figure 6).

Smooth diurnal curves were drawn through half-hourly averages of all measurements taken when the ventilated chamber was raised and similar curves were drawn for data collected when it was down. Values for air temperature, humidity, net radiation, stomatal and leaf boundary-layer conductances were interpolated from these curves at half-hourly intervals. This provided

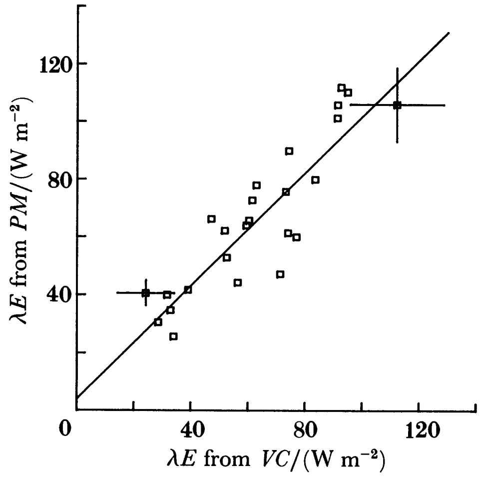

FIGURE 6. Transpiration rates estimated with the Penman–Monteith equation (PM, equation (18)) as a function of rates measured by a ventilated chamber (VC). Linear regression line: $y = 7.8+0.97x$, $r^2 = 0.82$, $n = 23$. Line does not differ significantly from 1:1 line. (After Foster & Leuning (1987).)

two synthetic data sets, one characteristic of conditions within the ventilated chamber during operation and the other representative of undisturbed conditions. The two data sets were then used with the PM equation to compute transpiration rates for single leaves for the two chamber states. Results of this comparison are shown in figure 7. Rates of transpiration within the ventilated chamber were similar until λE reached *ca.* 90 W m^{-2}, but were considerably reduced relative to natural conditions at high values of λE. The PM equation predicted reduced transpiration rates within the chamber from *ca.* 09h00 to 15h00 each day, and enhanced rates at other times (data not shown).

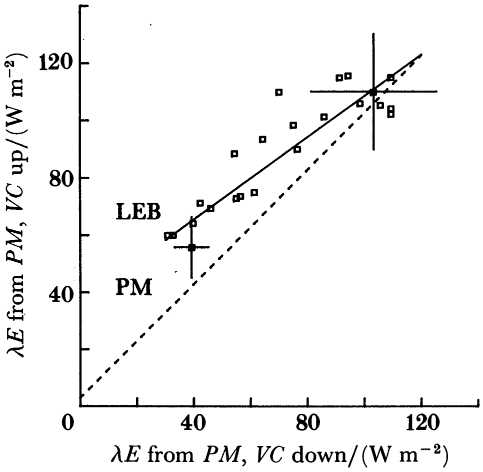

FIGURE 7. Comparison of half-hourly transpiration rates estimated with the PM equation with interpolated data for R_1, D, g_s and g_h for the two chamber positions. The VC causes little change in λE up to values of *ca.* 90 W m^{-2}, but significantly underestimates λE at higher external values.

Separate smooth curves could not be drawn through LEB estimates of λE for the two chamber positions because of insufficient data. However, LEB results for adjacent runs with the chamber up and down did not support PM predictions that transpiration rates were significantly altered by the VC.

Both methods of estimating λE are subject to experimental errors, *PM* predictions of lower λE within the chamber resulted from large apparent changes in R_l; D and g_s changed little between the two chamber states and variations in g_h had only a small influence on calculated λE (Foster & Leuning 1987). The *LEB* technique requires that both leaves have equal irradiance. This is particularly difficult when the *VC* is down; one leaf may be in full sun, the other in shade, thus causing spuriously high estimates of $(T_1 - T_2)$ and hence λE from equation (15). Examination of leaf pairs for unequal illumination during each run and editing of raw data eliminated obviously invalid measurements. These errors were insignificant when the *VC* was up because radiation within it was almost totally diffuse.

Comparison of *LEB* and *PM* results suggest that the arrangement of radiometers employed by Foster & Leuning (1987) may have overestimated the change in R_l with chamber position, and that changes in λE were somewhat less than indicated by figure 7.

4.3. *Transpiration by single leaves*

The leaf energy-balance technique was also used to estimate transpiration rates and stomatal conductances of leaves in an open woodland community at 'Moga' (35° 35″ S, 149° 53″ E). This work was part of a larger micrometeorological experiment designed to study transfer processes within forest canopies and at leaf surfaces.

Diurnal variations in available energy R–G and in mean transpiration rates λE_2, for 16 leaves are presented in figure 8*a*, *b*, where R is the net radiation measured above the canopy and G is the soil heat flux. Variation in λE_2 was largely independent of R–G, particularly on 5 February. Transpiration rates were also similar for the two days shown, although magnitudes and diurnal variation in water vapour pressure deficit, D, were quite different (figure 8*c*, *d*).

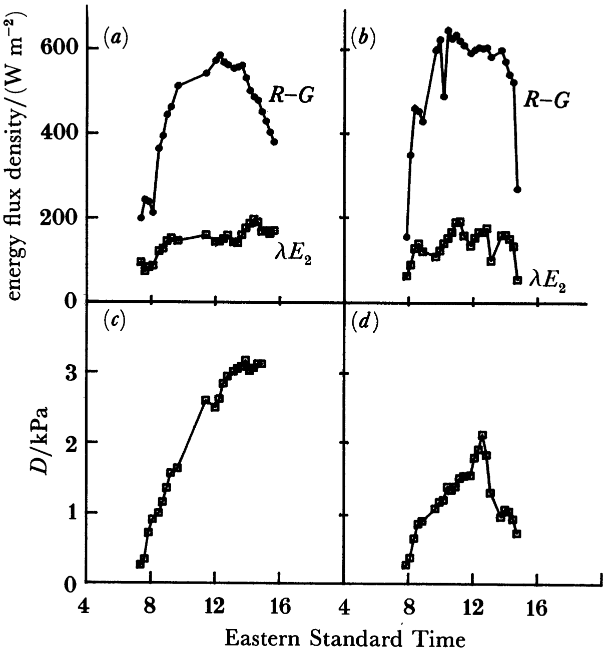

FIGURE 8. Diurnal variation of available energy $(R-G)$ for whole canopy and single-leaf transpiration rates (λE_2) for (*a*) 5 February and (*b*) 6 February 1986 at 'Moga'. Water vapour pressure deficit (D) is shown for these days in (*c*) and (*d*).

Stomatal conductances shown in figure 9 were estimated from λE_2 and D by using equation (20). Leaf boundary-layer conductances were an order of magnitude greater than estimated stomatal conductances for most of the day, thus satisfying approximations used to derive this equation. As a direct consequence of approximately equal transpiration rates but differing values for D for the two days (figure 8), stomatal conductances on 5 February were about half of those of the following day (figure 9). This suggests that stomata in leaves of *Eucalyptus rossii* R. T. Bak et H. G. Sm. are sensitive to humidity, as found for many other species (see review by Schulze & Hall (1982)).

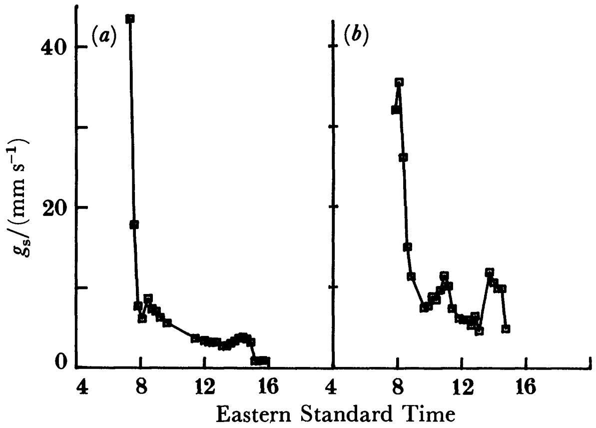

FIGURE 9. Stomatal conductances, g_s, computed from data in figure 8 by using equation (20). Transpiration fluxes were similar on both days but D differed (figure 8). This caused calculated stomatal conductances to be lower for 5 (*a*) than for 6 February (*b*).

5. DISCUSSION

Principles of energy conservation at leaf surfaces were applied to problems of predicting equilibrium leaf temperatures on clear nights, to measuring transpiration rates of individual leaves and to estimating leaf boundary-layer conductances.

Theory successfully predicted temperatures of isolated leaves exposed to clear skies from measurements of air temperature and wind speeds (figures 2 and 4). However, dewpoint temperatures were also required to determine whether or not leaves had condensation on them because dry leaves could be 1–2 °C colder than wet ones under similar ambient conditions (figure 3). Non-uniformity of water or frost covering on leaves complicates prediction of leaf temperatures. A major function of the models presented was to incorporate an understanding of the physics into mathematical relations between major variables controlling leaf temperatures. Appreciation of these factors may assist ecologists to interpret temperature responses of plant organs in the field.

Transpiration rates of individual leaves can be measured by solving energy-balance equations for coated and normal leaves (figure 5). Satisfactory estimates of stomatal conductances were also obtained with the leaf energy-balance method during the Moga experiment (figure 9). Radiation absorbed by the two leaves must be identical to ensure that measured differences in temperature are directly related to transpiration from the normal leaf and to differences in emitted longwave radiation. These conditions may be difficult to meet in practice because coated leaves may not have the same spectral characteristics as normal ones (Paw U & Daughtry 1984). Ensuring equal irradiance on both leaves as they move about is also difficult. Best results were obtained with the leaf energy-balance technique during measurements within the ventilated chamber (figure 5) because diffuse radiation then ensured equal irradiance on both leaves.

Finnigan & Raupach (1987) showed that quantitative descriptions of heat and mass transfer at leaf surfaces are important for linking processes at leaf scales to those of the canopy and surrounding atmosphere. They emphasized that the physiological state of a plant community influences the microclimate within the canopy and vice versa. However, the degree to which a plant community influences its local microclimate depends on rates of air exchange between canopy and surrounding atmosphere (Jarvis & McNaughton 1986), i.e. on levels of atmospheric turbulence and canopy density.

Within the well-stirred environment of the ventilated chamber, water-vapour pressure deficit, D, rather than net radiation, R_1, made the dominant contribution to λE_p (equation (18)). Net radiation contributed an average 13% to total transpiration rates when the chamber was in position and this increased to 28% for undisturbed conditions. However, net radiation accounted for up to 60% of λE_p during sunny periods on humid days. Figures 8 and 9 confirm that transpiration rates are largely governed by water-vapour pressure deficits and stomatal conductances in open woodland trees growing in dry climates.

6. Conclusions

Equilibrium leaf temperatures at night were determined by net loss of thermal radiation to the sky and by sensible and latent heat transfer from surrounding air. Leaves with condensation on them were 1–2 °C warmer than dry leaves under otherwise similar ambient conditions. Free convection was not important relative to forced convection as a mechanism for heat transfer to leaves during nocturnal inversions.

Pairs of coated and uncoated leaves gave satisfactory estimates of transpiration rates from individual leaves provided both absorbed equal amounts of incoming radiation. Facsimile leaves provided accurate estimates of leaf boundary layer conductances *in situ*.

Transpiration rates from leaves of trees in open canopies appeared to be largely controlled by stomatal conductances and water-vapour pressure deficits and to a lesser extent by net radiation.

Large ventilated chambers significantly reduced transpiration rates during midday hours, according to estimates made with the Penman–Monteith equation. This resulted from reduction in radiant energy available for transpiration within the chamber, relative to normal conditions.

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Discussion

J. Grace (*Department of Forestry and Natural Resources, University of Edinburgh, U.K.*). There is great uncertainty in modelling convection at low wind speeds. When is convection forced, when is it hybrid and when free? The literature gives us only 'rules of thumb' about this. Is it reasonable to model the overall convective process as two resistors in parallel, one for forced and one for free convection? This avoids the arbitrariness of the choice and seems to give the right answers.

Were Dr Leuning's convection régimes really forced, considering his mention of 'clear still nights'?

R. Leuning. I agree there is uncertainty in estimating leaf boundary layer conductances at low wind speeds and that is why I chose three convection régimes for modelling equilibrium leaf temperatures. Free convection provided results inconsistent with observations and so I concluded that forced convection was the main mechanism for heat transfer in our experiments.

According to the literature, free and forced convection were expected to dominate heat transfer when $Gr/Re^2 > ca.\ 10$ and $Gr/Re^2 < ca.\ 0.1$, respectively; where Gr is the Grashof number and *Re* the Reynolds number. This leaves a wide range of Gr/Re^2 values where convection occurs by the two processes acting with similar effectiveness. It is therefore reasonable to assume that total heat transfer is the sum of two processes acting in parallel.

I attempted to test this hypothesis by measuring boundary-layer conductances on calm, clear nights by using pairs of facsimile leaves similar to those described in the paper. Wind speeds were measured at a height of 0.4 m with a sonic anemometer. The experimental results proved to be unsatisfactory because I did not know at which times facsimile leaves were wet or dry. This information is vital because two values of g_h can be calculated assuming either fully wet or dry leaves. Numerically, g_h differs by a factor of *ca.* 2 for these two cases. I plotted both possible values as dimensionless transfer coefficients (Nusselt number, *Nu*) as a function of Reynolds number *Re* and observed no systematic deviation from the theoretical line ($Nu = 0.6\ Re^{0.5}$) at low *Re*.

Wind speeds as low as 0.02 m s^{-1} were measured, with leaf–air temperature differences of 2–3 °C. Under these conditions, forced convection is expected to be an order of magnitude more important than free convection as a mechanism of heat transfer for both 10 mm and 50 mm wide leaves.

J. L. Monteith, F.R.S. (*International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India*). Is it possible that the lack of evidence for free convection is a consequence of the nature of the wind régime? During long calm periods, free convection might be dominant but might be responsible for much less transfer of heat than forced convection during short periods of gustiness, which are characteristic of clear nights.

R. Leuning. Wind speeds are highly intermittent near the ground during stable conditions. Although our observations were averaged for 15 min periods, we observed marked variations in mean wind speed and estimated boundary-layer conductances from one run to the next.

The sequence of events suggested by Professor Monteith may account for apparent underestimates of g_h observed on some occasions. Temperature differences $T_\mathrm{h} - T_\mathrm{u}$ (equation (17)) during periods of free convection will be greater than during forced convection for a constant electrical power dissipation *Pe*. If periods of free convection occur for the greater part of the averaging period then $T_\mathrm{h} - T_\mathrm{u}$ will be greater than expected from forced convection at the mean wind speed, leading to an underestimate of g_h.

J. R. Milford (*Department of Meteorology, University of Reading, U.K.*). Recent experiments in a high-turbulence wind tunnel in Reading measured the boundary-layer conductance from artificial leaves while varying wind speed, angle of attack, turbulence intensity, scale length of the turbulence and irregularities at the leading edge of the leaf. For both sensible heat and water vapour conductance, increases over the Pohlhausen theory reached 80% near resonance points, and were rarely less than 20%. Only turbulence on scales similar to the leaf size was effective but in a canopy where wake turbulence or leaf irregularities are significant an average enhancement of 40% is feasible. Are there circumstances where this might significantly affect the modelled water loss from trees?

R. Leuning. Changes in leaf boundary-layer conductances may increase, decrease or have no influence on transpiration rates of leaves, depending on the particular combination of the variables in the Penman–Monteith equation; namely, net radiation, water vapour-pressure deficit and stomatal conductance. Changes of ±20% in g_h resulted in estimated transpiration variation of only ±6% in our study.

M. H. Unsworth (*Department of Physiology and Environmental Science, University of Nottingham, U.K.*). The techniques described for the chamber study required that leaves were constrained so that they could not flutter. Is this constraint likely to influence rates of heat transfer?

R. Leuning. Our technique prevents leaf flutter but does not prevent movement of the branch to which leaves are attached. This may influence the magnitude of leaf boundary-layer conductances to some extent but the influence on transpiration rates is expected to be small (see comment by Milford on previous page).

D. Fowler (*NERC Institute of Terrestrial Ecology, Penicuik, U.K.*). Are the large single-tree chambers Dr Leuning described intended to provide estimates of fluxes of water vapour for trees within a canopy, and what are the major uncertainties with the technique?

R. Leuning. Ventilated chambers have been used in Western Australia to measure transpiration rates of single trees in an attempt to select species most suitable for maximizing evapotranspiration rates and to minimize or stop the rise of some water tables.

Uncertainties in the technique arise because all variables controlling transpiration (net radiation, water-vapour pressure deficit canopy conductance and aerodynamic conductance) may be altered by the enclosure. Our task was to estimate biases in transpiration rates measured by the chamber. I conclude from Penman–Monteith calculations that the chamber introduced negligible bias, although this was not confirmed by using the paired-leaf technique.