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Boundary layer conductance for contrasting leaf shapes in a deciduous broadleaved forest canopy

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Abstract

A new method of constructing light, flexible and more realistic replica leaves for continuous determination of leaf boundary layer conductance to heat transfer (g_b^h) was developed and tested in a mature oak ($Quercus \, robur \, L$.) and sycamore ($Acer \, pseudoplatanus \, L$.) tree canopy. The replicas were used to determine the difference between oak and sycamore leaf g_b^h in exposed sites in the upper canopy, the relationship of g_b^h with wind speed, the seasonal changes in g_b^h in the canopy as leaf cover developed, and values for Ω , the decoupling coefficient. The replicas showed similar gradients in temperature at their margins to those in real leaves. When exposed, the g_b^h of the larger sycamore leaves was 66% of that of oak leaves under the same conditions. Linear relationships were found with g_b^h and wind speed across the measured range of 0.3–3.5 m s⁻¹, and flow in the replica boundary layers was laminar in all conditions. The leafless canopy produced a substantial sheltering effect, reducing g_b^h by 12–28% in light winds. Sycamore replicas in the leafed canopy showed a 19–29% lower g_b^h at a given external wind speed than when outside, but there was little difference between 'sun' and 'shade' position shoots, because of the density of the shoots, and the close branching pattern. In contrast, in oak g_b^h at a given wind speed was 15–21% lower for 'sun' leaves than that for replicas outside the canopy, with a larger reduction (approximately 28%) in denser 'shade' sites. Although wind speed in the canopy was often low, leaves of both species were usually well coupled to the canopy airstream ($\Omega < 0.3$). Sun leaves were substantially less well coupled than shade leaves, despite the lower shelter effect, because of their higher stomatal conductance values. In the lightest winds (<0.5 m s⁻¹) and with high stomatal conductance, coupling may on many occasions be poor for sun leaves, particularly for the larger sycamore leaves.

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Keywords: Boundary layer conductance; Oak; Sycamore; Leaf shape; Leaf temperature; Transpiration

1. Introduction

The extent of radiative and diffusive coupling between a leaf and the microclimate determines the energy balance of a leaf (Monteith, 1981), and thus leaf temperature, which affects many physiological and ecological processes. Diffusive and convective cou-

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pling depends on both the stomatal and boundary layer conductances (g_s and g_b), and their ratio determines the contribution of a leaf to overall canopy conductance to water vapour (Jarvis and McNaughton, 1986; Schuepp, 1993; Brenner and Jarvis, 1995). Leaf shape, edge characteristics and surface smoothness affect the air flow over the leaf and the thickness, regularity and stability of the boundary layer (Grace, 1983; Schuepp, 1993) and therefore are major determinants of g_b . Values of g_b measured for leaves agree in general with theory developed from flat plates, although leaves often

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Nomenclature

- projected (single-sided) leaf area (m²) Aheat capacity of air (1010 J kg⁻¹ °C⁻¹) c_p
- $d_{\rm w}, d_{\rm l}$ characteristic dimension of leaf, across width or along length (cm)
- stomatal conductance for water vapour $g_{\rm s}$ $(cm s^{-1})$
- $g_{\rm b}^{\rm h}, g_{\rm b}^{\rm w}$ boundary layer conductance for heat h or water vapour w (cm s⁻¹)
- I_{\circ} short wave (solar) irradiance (W m⁻²)
- long wave radiation from heated and $L_{\rm h}, L_{\rm u}$ unheated replicas (W m⁻²)
- $P_{\rm e}$ electrical power to heater (W)
- resistance of shunt resistor (Ω) $R_{\rm s}$
- **RTD** resistive temperature device
- slope of the saturated vapour pressure versus temperature relationship $(kPa K^{-1})$
- $T_{\rm a}$ air temperature (°C)
- $T_{\rm u}$, $T_{\rm h}$, $T_{\rm o}$ temperature of unheated or heated leaf replicas, or offset between replicas when neither heated (°C)
- wind speed (m s⁻¹)
- $V_{\rm s}, V_{\rm h}, V_{\rm m}, V_{\rm ref}$ voltage supply, and voltages measured across heater, RTD or RTD at known reference temperature (V)

Greek letters

- enhancement factor, increase in heat β transfer over that predicted for flat plate
- γ
- psychrometric constant (J g⁻¹) density of air (1.225 kg m⁻³ at 15 °C) ρ
- decoupling coefficient (0-1, dimension-Ω less)

have higher g_b compared to flat plates because of their small size, and surface and edge features (Monteith, 1973; Schuepp, 1993). Lobed leaves have smaller effective dimensions, reduced boundary layer thickness and thus higher gb than simple shaped leaves (Baker and Myhre, 1969; Gottschlich and Smith, 1982; Schuepp, 1993). For example, Vogel (1970) determined that the heat dissipation of a Quercus alba sun leaf replica made from copper sheet was approximately 10% higher at low wind speeds than for a less deeply lobed shade leaf replica. Computer simulation of small model leaves has also shown shape to have a considerable effect on the surface temperature pattern even in zero and low (1 cm s⁻¹) wind speeds (Roth-Nebelsick, 2001).

Much of the older research on leaf boundary layers was carried out in wind tunnels using laminar airflow, whereas incident flow in a tree canopy is almost always turbulent, due to the high surface roughness of tree crowns, the presence of branches and leaf movement (Grace, 1978; Schuepp, 1993). As there has been relatively little study of leaf boundary layers in the field, it is not clear whether leaves in canopies have turbulent or laminar boundary layers (Schuepp, 1993), nor how well they are coupled to the adjacent mixed air stream (Daudet et al., 1999). Canopy branching patterns differ between species, with small-leaved species generally having more orders of branching than larger leafed species (Buck-Sorlin and Bell, 2000), which must affect airflow and thus the effectiveness of leaf coupling.

Early studies on leaf g_b (reviewed by Brenner and Jarvis, 1995) used wet paper, plaster of Paris or fabric models to estimate boundary layer conductance to water vapour (g_h^w) and heated metal replicas to determine boundary layer conductance to heat (g_b^h) . Heated metal replicas have a more uniform surface temperature than leaves which may be a problem, particularly where there are pronounced effects of edges on heat transfer (Schuepp, 1993; Roth-Nebelsick, 2001). In addition, most rigid replicas do not move or flap, but the effect of this will depend on the characteristics of the turbulence and the leaf movement. For example, Parlange et al. (1971) found leaf flutter had no significant effect on g_h^h when flow was turbulent, while Schuepp (1972) found fluttering increased conductance by 40%. More recently heated pairs of leaf replicas have been used in the field, with temperatures determined with thermocouples, either sandwiched between layers of thin metal sheet, or stuck to the surface. Leuning and Foster (1990) and Brenner and Jarvis (1995) used heated replica pairs to measure g_b continuously in Eucalyptus and millet canopies, respectively. Leuning and Foster (1990) used replica pairs made from aluminium and plastic sheets, with only one of the pair heated. Brenner and Jarvis (1995) used pairs of brass replicas, which were heated alternately with an electric current. An "offset" period when both replicas were unheated was used to record the difference in temperature between the two replicas in order to correct for any difference in incident radiation. Both in the wind tunnel and in the field, they found that the critical wind speeds when the boundary layer over millet leaves became turbulent was quite low (above 2.7 m s⁻¹) and turbulent incident flows produced higher g_b^h than laminar incident flows. Smith et al. (1997) used brass replica pairs in Azadirachta indica tree crowns to estimate g_b^h . As in the millet study (Brenner and Jarvis, 1995) g_b^h values were found to be proportional to u^n , where u is wind speed and n varied between 0.5 and 0.8; the values expected for laminar and turbulent boundary layers, respectively. For cotton leaves, Grantz and Vaughn (1999) used pairs of brass replicas deformed to reflect the characteristic threedimensional shape of actual leaves. The replicas were used at different heights in the cotton crop canopy to determine profiles of g_b^h and thus 'leaf-effective' wind speed. Daudet et al. (1998, 1999) used concentric heated and unheated areas on the same leaf replica constructed from metal sheet for studies of g_b^h in vineyards and tree crowns. This approach gave the advantage of only one replica being needed, rather than pairs, although individual calibration was needed. Importantly, Daudet et al. (1999) were able to combine the resulting g_h^h estimates with stomatal conductance distributions in order to investigate leaf-to-atmosphere coupling within walnut tree crowns. They found that although leaves within tree crowns experienced low wind speeds, they were relatively well coupled to the air stream, compared to sun-lit leaves on the crown edge with high stomatal conductance.

Therefore our objective was to measure the boundary layer conductance of leaves of two contrasting deciduous tree species in the canopy, in order to compare the extent of leaf coupling to the air stream. We contrasted the small lobed leaves of the highly branched pedunculate oak (*Quercus robur* L.), with the larger, less dissected leaves of the less-branched sycamore (*Acer pseudoplatanus* L.). To ensure valid comparisons in such contrasting situations, new methods of producing realistic leaf replicas were developed, field tested and evaluated. The replicas were then used to characterise seasonal changes in g_b^h and the influence of exposure and shelter on leaf coupling in the upper canopy of a mature forest.

2. Methods and materials

2.1. Development of replica leaves

Heated replica leaves were made from flexible, 0.1 mm thick Mylar[®] sheet, with a 1 mm wide copper heating track etched all over one side in a series of connected, folded track 10 mm × 10 mm blocks. The Mylar[®] was cut to the shapes of mature oak and sycamore leaves with projected leaf areas of 17 cm² (oak) and 96 cm² (sycamore). The maximum length and width dimensions were: 7.7 and 4.4 cm (oak) and 12.0 and 12.4 cm (sycamore), respectively. On the reverse side 8 m of enamelled 0.05 mm diameter copper wire was glued (Loctite[®] 330 and activator

7387, Loctite UK Ltd., Welwyn Garden City, Herts, UK) in a continuous, often overlapping track across all areas of the leaf (to within 1–5 mm of the margin) to make a resistive temperature device (RTD). The replica leaves were painted with white acrylic car spray paint (Polar white, Halfords Ltd., Redditch, Worcester, UK) to give an assumed emissivity of 0.91 (Woodward and Sheehy, 1983). A flat plastic stick was glued to the underside of the leaf to act as a "midrib" and provide some strength. The sycamore and oak replicas were installed in the canopy in pairs for alternate heating (Fig. 1).

2.2. Power supply and heating cycle

A datalogger and multiplexer (CR10X and AM32, Campbell Scientific Ltd., Shepshed, Leicestershire, UK) were used to run four pairs of alternately heated leaves. Power was supplied to the etched copper track of the replicas by individual purpose-designed, adjustable oscillator circuits (Powerpot, Bartington Associates Ltd., Frating, Essex, UK). The datalogger program executed every 20 s, with a 15 min complete





Fig. 1. Sycamore (upper) and oak (lower) replica pairs installed in the "sun-shoot" positions, photographed on 21 May 2001. This figure also shows the patchy radiation environment within the canopy and hence the need for the temperature measurement offset period.

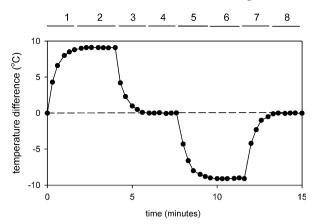


Fig. 2. Diagram of the 15 min heating and cooling cycle showing temperature difference between replicas during the different phases: (1) leaf A warming; (2) leaf A measurement; (3) leaf A cooling; (4) offset 1; (5) leaf B warming; (6) leaf B measurement; (7) leaf B cooling; (8) offset 2.

measurement cycle (Fig. 2) in which a constant power was supplied first to replica leaf A of each pair and then to replica leaf B. Leaf A of each replica pair was heated for 1 min and 40 s, allowing them to warm up, before measurements were taken every 20 s for 2 min and 20 s. Leaves then cooled passively for 1 min and 40 s before the first offset period, during which measurements were taken for 2 min. The cycle was then repeated with leaf B of each pair. The offset measurement periods between the two heating periods were included to remove any effect of different solar radiation receipt on the two replicas, as in Brenner and Jarvis (1995).

2.3. Calculations

The average current through the heating track during a heating period was calculated from the voltage $V_{\rm h}$ measured across a shunt resistor, $R_{\rm s}$ (0.1 Ω). The electrical power, $P_{\rm e}$ (W m $^{-2}$), to each replica during its heating period was therefore calculated as:

$$P_{\rm e} = \frac{[(V_{\rm h}/R_{\rm s})0.93V_{\rm s}]}{2A} \tag{1}$$

where $V_{\rm s}$ is voltage supply (regulated 12 V), 0.93 is the Powerpot heating efficiency and A is projected leaf replica area in m² so the factor 2 accounts for heat transfer from both sides. The voltage across the RTD wires was measured using a bridge configuration, with a constant current. For each replica $V_{\rm h}$ and the RTD voltage measured after stabilisation ($V_{\rm m}$) during each of the measurement and offset periods were averaged by the datalogger and output every 15 min. The temperature difference between the heated and unheated replica

in each pair $(T_{\rm h}-T_{\rm u},\,^{\circ}{\rm C})$ was calculated from the $V_{\rm m}$ and the reference voltage for each replica, $V_{\rm ref}$, recorded at a known common temperature, using the usual RTD equation. The offset temperature $(T_{\rm o})$ between replicas in a pair during unheated offset periods was calculated similarly. Laboratory tests with low incident radiation showed RTD derived temperature differences closely matched those from point thermocouples attached to the middle areas of the replicas.

Thus g_b^h (both sides of the leaf) was calculated for each of the pair of replicas using equations modified from those given by Leuning and Foster (1990):

$$g_{b}^{h} = \frac{[P_{e} - (L_{h} - L_{u})]}{[\rho c_{p} (T_{h} - T_{u} - T_{o})]}$$
(2)

where ρ and c_p are the density and heat capacity of air and L_h and L_u are the outgoing long wave radiation from the heated and unheated replicas, respectively, calculated from the measured temperatures. Note that Eq. (2) explicitly considers the long wave radiation from the two replicas separately, unlike the equations used by Leuning and Foster (1990) and others since, which made approximations based on the air temperature. This is because compared to metal replicas, the replicas used here had high emissivity, and with the large $T_{\rm h} - T_{\rm u}$ differences that occurred, particularly at low wind speeds, the difference in the long wave radiation loss from the heated and unheated replicas could become significant. However, because their individual temperatures were measured through the RTDs, the fuller Eq. (2) could be readily implemented. For comparison with the standard engineering formulas for heat transfer from a single sided plate g_b^h needs to be divided by two (e.g. Grace, 1983; Schuepp, 1993). Boundary layer conductance to water vapour, g_h^w , was calculated from g_b^h using the usual 2/3 power ratio of the diffusion coefficients for heat and water vapour in the laminar boundary layer (=0.93, Grace, 1983):

$$g_{\rm b}^{\rm W} = \frac{g_{\rm b}^{\rm h}}{2 \times 0.93} \tag{3}$$

and dividing by the factor 2 because transpiration was only from the lower surface, as the leaves of these oak and sycamore species are completely hypostomatous. The characteristic lengths d of the replicas were calculated using Eq. (12) in Schuepp (1993) assuming laminar flow either across ($d_{\rm w}$) or along the leaf ($d_{\rm l}$) and were: 9.0 and 3.0 cm for sycamore and oak $d_{\rm w}$, respectively, and 8.3 and 5.2 cm for $d_{\rm l}$.

2.4. Installation in the canopy

The site was in Wytham Woods, Oxfordshire, UK (51°46′N1°20′W, Grid reference SP4608, altitude 160 m) classified as W8e, *Geranium robertianum* subcommunity of *Fraxinus – Acer campestre – Mercurialis* (W8) woodland in the British National Vegetation Classification (Rodwell, 1991). The dominant canopy species is pedunculate oak (*Quercus robur* L.) with sycamore (*Acer pseudoplatanus* L.), ash (*Fraxinus excelsior* L.), beech (*Fagus sylvatica* L.) and birch (*Betula pendula* Roth.) also reaching the upper canopy. The maximum canopy height was 17.5 m, and canopy depth was approximately 10 m. Access to the upper parts of the canopy was provided by a scaffolding walkway. A full description is given in Morecroft and Roberts (1999).

Matching pairs of replicas were installed in the canopy of oak or sycamore trees on 3 April 2001, prior to leaf emergence. A thin thermocouple (0.5 mm diameter junction) was installed adjacent to each pair for continuous measurement of local air temperature. The replicas were mounted by attaching the cable "petiole" to aluminium welding rods attached to branches. The wires were closely attached to the supporting branch and twigs so that they would not interfere with airflow patterns. One replica pair of each species was mounted on a well exposed "sun" branch in the upper 3 m of the canopy and the other pair was mounted at the same height on a "shade" branch within the canopy. "Shade" branches were still within the upper crown but were generally shaded by other branches from most angles, although sunflecks would have been common. The two replicas in a pair were mounted horizontally in the canopy, within 25 cm of each other (Fig. 1A and B). Typical power supplied to the leaves was 9-10 W for the sycamore replicas and 1.6–2.0 W for the oak replicas, resulting in power inputs of 400-540 W m⁻². Heated oak replicas were usually between 9 and 18 °C higher than air temperature, and sycamore replicas between 13 and 26 °C warmer than the air. Temperatures of the two leaves of each replica pair were within 4 °C of each other when heated, and the temperature differences caused by sunflecks were corrected with the offset measurement.

Meteorological sensors were positioned on the railing edge of the walkway, which had created a gap between the tree crowns. They were within 8 m of the replicas and at approximately the same height. The instruments consisted of a three cup reed switch anemometer with 0.2 m s⁻¹ threshold speed and 2.3 m distance constant (A100R, Vector Instruments, Rhyl, Clwyd, UK), potentiometric windvane with

0.6 m s⁻¹ threshold speed (W200P, Vector Instruments), light energy sensor (filtered for 400–700 nm wavelengths, model SKE, Skye Instruments, Llandrindod Wells, Powys, UK), screened humidity sensor (SKH 2012, Skye Instruments), net radiometer (DRN301, Didcot Instruments, Didcot, UK), leaf wetness sensor (model 237, Campbell Scientific Ltd.) and screened air temperature thermocouples (0.5 mm diameter junction). Instruments were well exposed to wind from a SW–W direction. Measurements were taken at 20 s intervals, and average values were recorded every 15 min from all sensors.

In mid-summer all replica pairs were removed from the branch locations and exposed together adjacent to the meteorological sensors for two weeks for a direct comparison of oak and sycamore g_h^h .

2.5. Measurements of stomatal conductance

Stomatal conductance (g_s) was measured on oak and sycamore sun and shade leaves under ambient light conditions throughout the season from May to November in 1999 (15 occasions) and 2000 (13 occasions). Measurements were made using a portable gas exchange system (CIRAS 1, PP Systems, Hitchin, Herts, UK) fitted with a 2.5 cm^2 broadleaf chamber (PLC (B), PP Systems). The chamber CO₂ concentration and humidity were set to ambient levels. Measurements were taken rapidly between 09:00 and 14:00 h GMT in dry weather conditions, using five leaves for each species and canopy position at similar locations to the replicas (Stokes, 2002).

2.6. Statistical treatment

For comparison of linear regressions, multiple regression analysis was used (SPSS v. 11.5), using species (oak or sycamore), position (sun or shade) or period (early before leafing, late full leafing), and their interactions, as categorical factors as appropriate (McClave and Sincich, 2000). The significance of including different factors in the regression model was tested using nested model procedures. Where the species difference was very clear, the fitted lines shown are those derived from fits to each species separately, with the factors of position and period, and their interaction.

2.7. Thermal images

In order to compare the temperature distributions of replicas and real leaves, a thermal camera (TH7102MV

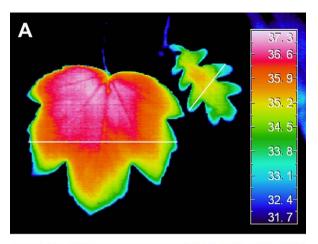
Thermo Tracer, NEC San-ei Instruments Ltd., Tokyo) with a temperature resolution of 0.08 °C was used. At the camera-object distance used, the spatial resolution produced pixel sizes of approximately 0.8 mm × 0.8 mm. Sycamore and oak leaves were collected from the University of Essex campus, Colchester, UK in June 2005, and the underside completely coated with silicone grease to prevent transpiration. Leaves or replicas were held above a uniform temperature water surface, under strong solar radiation in a temperature controlled glasshouse. Ventilation was provided by an axial propeller fan, and wind speed measured with a hot wire anemometer close to the leaf.

3. Results

3.1. Functioning of the replica leaves

The thin Mylar sheet used for the replicas resulted in some flexing of the replica margins, and attaching them to the branches allowed considerable movement in the wind. The replicas proved robust enough to withstand most strong winds although after several months some of the sycamore RTD wires did break. Whenever the leaf wetness sensor recorded moisture due to rainfall or dew, data were characterised by large offset values, and low values of $T_h - T_u$. These "wet" data were discarded (50% of the complete data set) resulting in rejection of a lot of night time data. For the remaining 'dry' data, offset values (T_0) were less than $\pm 15\%$ of $T_h - T_u$ for fully exposed replicas. When replicas were placed in the canopy, offset values for sycamore were nearly always less than $\pm 10\%$ and for oak they were typically within $\pm 15\%$ because of the smaller $T_{\rm h}-T_{\rm u}$. There was no significant change in offset values before and after budbreak and leaf expansion indicating that both replicas of the pairs were equally affected by the canopy leafing, and indicating that the method used here of frequent alternating of heating of replicas largely removed the problem of uneven radiation. Using the temperature of both heated and unheated replicas to calculate long wave loss rather than the usual approximation based on air temperature (see Section 2, Eq. (2)) resulted in lower g_b^h values, particularly at lower wind speeds. For sycamore the typical overestimate if the approximation had been made would have been 7%, but rising to 16% at lowest wind speeds. For oak, the comparable overestimate values would have been 4% up to 12%, respectively.

Subsequent to the field experiments a thermal camera was used to compare the temperature distributions across the replicas and across real, but non-



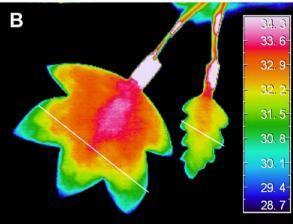


Fig. 3. Thermal images of (A) non-transpiring leaves and (B) replicas of sycamore and oak. Conditions during measurements: mean wind speed = 0.6 m s $^{-1}$, air temperature = 30.2 °C, background temperature = 26.5 °C, photon flux density = 910 μ mol m $^{-2}$ s $^{-1}$ (a) and 1210 μ mol m $^{-2}$ s $^{-1}$ (b). Temperature range is same in both figures, but the scale in (b) is 3 °C lower. White lines indicate positions of transects shown in Fig. 4.

transpiring, leaves (Fig. 3) in light wind conditions under strong solar heating. While the absolute replica and leaf temperatures cannot be compared directly because of different insolation and reflectivity, the temperature spatial distributions were very similar in leaves and replicas (Fig. 3), indicating similar heat transfer and thermal properties. Both leaves and replicas are cooler at the margins, which in these conditions are about 3-5 and 8-10 mm wide, for oak and sycamore, respectively, leading to strong gradients in temperature of about 0.4–0.6 °C mm⁻¹ (Fig. 4). The warmest area around the base of the sycamore leaf is more extensive than in the replicas, perhaps because of the slightly concave leaf shape, which may shelter this region, compared to the flatter (but also slightly concave) replicas.

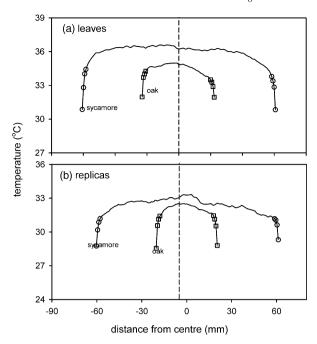


Fig. 4. Transects of temperature across leaves and replicas of sycamore and oak, taken from the thermal images in Fig. 3. For clarity, only the data from the first and last 4 pixel on the transects are shown with symbols.

3.2. Replica comparison test in exposed conditions

When replicas were exposed on the open walkway at upper canopy height from mid to late July, the calculated g_b^h of each leaf type tracked wind speed (u) measured by an adjacent anemometer closely (Fig. 5, showing two of the days), as expected. However, in this whole two week period wind speeds in the upper canopy air space never exceeded 1.2 m s⁻¹.

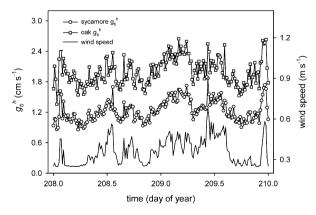


Fig. 5. Time course over two days in July of boundary layer conductance $(g_h^b, \text{ cm s}^{-1})$, for sycamore and oak leaf replicas and wind speed (m s⁻¹) when replicas were exposed side-by-side in the open at canopy level. Data are 15 min averages, averaged across two replica pairs. Day of year 208 is 27 July.

The sycamore replica pairs gave almost identical values of g_b^h across a range from 0.5 to 1.5 cm s⁻¹, with a mean difference of only 3.4%. The oak replica g_b^h values were between 1.0 and 3.0 cm s⁻¹, approximately double the values of the sycamore replicas, and the mean difference between pairs was only 6.9%.

While there were clear relationships between replica g_b^h and u for these exposed leaves and no overlap between oak and sycamore datasets, there was considerable scatter when all 'dry' data for the 14-day period was used (data not shown). Filtering the data to include only those occasions when the wind was in the prevailing SW to W direction, when both anemometer and replicas were well exposed (44% of the data rejected), reduced the scatter considerably. Over this limited wind speed range, g_b^h was linearly related to u, with significantly higher slopes and intercepts for the oak replicas (Fig. 6). Fitted linear regression were for oak $g_b^h = 1.471u + 1.551$, $R^2 = 0.590$ and for sycamore $g_b^h = 1.234u + 0.851$, $R^2 = 0.590$ 0.754. To avoid the possibility of additional solar heating effects, data were further filtered to use only data from night time periods ($I_s < 10 \text{ W m}^{-2}$), but while this slightly reduced the slopes by about 5%, it did not change the intercepts of the regressions. The observed results are close to that predicted from standard flat plate theory (e.g. Grantz and Vaughn, 1999, $g_b^h = 2 \times 0.60 \kappa [u/(dv)]^n$, where κ and ν are the diffusivity and kinematic viscosity of air, respectively, and d the characteristic dimension) and assuming laminar boundary layer conditions, n = 0.5

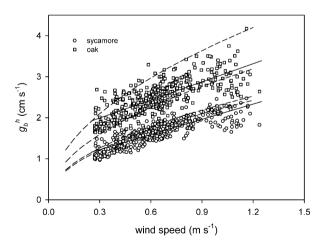


Fig. 6. Relationship between boundary layer conductance $(g_h^b, \text{cm s}^{-1})$ and wind speed $(u, \text{m s}^{-1})$ for sycamore and oak leaf replicas when exposed side-by-side in the open. Data are 15 min averages, averaged across two replica pairs, over a 14-day period, showing only dry data, when wind speed $>0.27 \text{ m s}^{-1}$, and wind direction between 220 and 280°. Solid lines are linear regressions, $R^2 = 0.590$ and 0.754 for oak and sycamore, respectively. Dotted lines are theoretical relationships for flat plates with characteristic stream wise dimensions across width (d_w) or along length (d_1) .

(Fig. 6). For the sycamore replicas the width and lengthwise characteristic dimensions (d_w and d_1 calculated as in Schuepp, 1993, Eq. (12)) were almost the same (9.0 and 8.3 cm), and the observed values are close to, but usually a little lower than the theoretical curves. For the oak replicas $d_{\rm w}$ and $d_{\rm l}$ differ (3.0 and 5.2 cm, respectively), but although the data are more scattered, the theoretical relationships envelope much of the data (Fig. 6). Analysing the relationship between $ln(g_h^h)$ and ln(u) gave slopes (i.e. n values) of 0.38 and 0.49 (95% CL of 0.35-0.40 and 0.46-0.51) for oak and sycamore, respectively, suggesting that replica boundary layers at these low wind speeds were laminar. Measured g_h^h at low wind speeds for the oak replicas in particular were higher than the theory suggests (Fig. 6), probably indicating that at low wind speeds the consequent high replica temperatures caused enhanced free convection. However, for the higher wind speeds, g_h^h values did not show the normal enhancement over flat plate theory often reported.

There was a close linear relationship between the mean g_b^h values for sycamore and oak replicas for the 14-day period (Fig. 7). The slope of the linear regression equation of all 'dry' data for sycamore against oak g_b^h values, 0.658 (95% CL 0.653–0.663, P < 0.001, $R^2 = 0.829$, n = 428) was between the values for the ratio of the characteristic widthways and lengthways dimensions, d_w and d_l , assuming an n coefficient value appropriate for laminar flow $([d_w^{oak}/d_w^{syc}]^{0.5} = 0.57, [d_1^{oak}/d_1^{syc}]^{0.5} = 0.79$). When night time values only were analysed, the slope was hardly changed, but

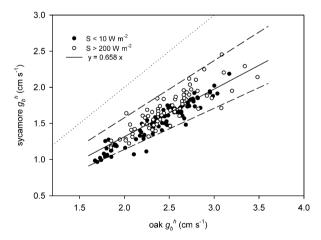


Fig. 7. Comparison of mean sycamore and oak replica boundary layer conductance $(g_b^h, \text{ cm s}^{-1})$ when exposed side-by-side in open conditions. Open symbols are data where solar radiation $> 200 \text{ W m}^{-2}$, solid symbols for $< 10 \text{ W m}^{-2}$. Solid line is fitted linear regression through all data, including that in intermediate solar radiation (data points not shown). Data filtered as in Fig. 6. Dashed lines show calculated relationship between plates with ratios of $d_w = 0.75$ (upper) and $d_1 = 0.57$ (lower). Dotted line is y = x.

there was some evidence that the difference between sycamore and oak at small g_b^h values was slightly larger during high insolation conditions ($I_s > 200 \text{ W m}^{-2}$) than at night, suggesting that when strongly illuminated in light wind conditions the larger sycamore leaves may have had more free convection enhancement than the oaks.

3.3. Seasonal changes in daily mean g_h^h

Replicas were placed in both 'shade-shoot' and more exposed 'sun-shoot' positions in the canopy from early spring, before bud break, and measurements of g_b^h made through to mid-summer, when leaf area had reached maximum values (peak leaf area index values for this site are between 3.5 and 5.5, Stokes, 2002). Fig. 8c

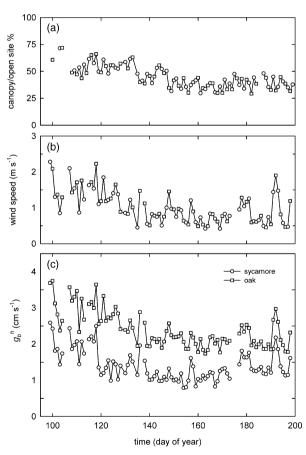


Fig. 8. Seasonal time course from 10 March to 19 July 2001 of (a) wind speed as percent of that at an open grassland site nearby; (b) mean wind speed (m s⁻¹); (c) mean daily boundary layer conductance $(g_b^h, \text{cm s}^{-1})$, for sycamore and oak leaf replicas exposed in the canopy (average of two replica pairs for each species). In (b) and (c) mean daily values were calculated from 15 min average data, when the canopy was dry, in (a) calculated from all conditions. Gaps indicate missing or incomplete data (<3 h per day).

shows the seasonal time course of mean daily g_h^h averaged across both pairs of replicas in the two canopy positions for oak and sycamore, but including only data when replicas were dry. Daily mean wind speed values in the canopy dropped from above 2 m s⁻¹ to below 0.5 m s^{-1} over the season (Fig. 8b), and therefore g_h^h values for oak fell from nearly 4 cm s⁻¹ to nearly 2 cm s^{-1} (Fig. 8c). Values for sycamore g_h^h were 66– 56% of those of oak, the ratio dropping over the season. Buds started breaking around 19 April (day of year (DOY) 109), and 50% budbreak at about 13 days after that (DOY 122). This coincided with the date that both u and g_h^h started to decline. In the climate of the British Isles, mean wind speed drops during the summer due to a change in weather conditions, but clearly in the canopy u is also reduced due to the momentum absorption by the leaves. This shelter effect can be gauged from the change in canopy wind speed relative to that at an open grassland site nearby (500 m away at same altitude). Prior to budbreak, the mean daily wind speed measured in the canopy was approximately 60% of that measured above grass (at 2 m height, Fig. 8a). This fell to approximately 35% after leaf expansion. However, the intensity of turbulence in the canopy

remained approximately constant with a mean value of 35% (S.D. 10%, turbulence intensity calculated as the standard deviation of wind speed, divided by mean speed each 15 min period).

3.4. The effect of canopy position on g_h^h

Replicas placed within the canopy nearly always showed a lower g_h^h value for any given u than during the comparison period in the open, even early on in the season before 50% budbreak (i.e. the leafless period, prior to DOY 120, 30 April). In Fig. 9, most data points are below the dotted lines, which are the $ln(g_b^h)$ versus ln(u) relationships for exposed replicas calculated from Fig. 6. The reduction in g_b^h was larger during the later season, when the canopy was fully leafed (DOY > 185, 4 July). The largest range of wind speed was in the early spring period (highest daily means, Fig. 8b) and 15 min average speeds were up to 3.5 m s⁻¹. Nevertheless, the logarithmic relationship between g_b^h and u was uniform for oak and sycamore replicas in both 'sun-shoot' and 'shade-shoot' positions (Fig. 9). At the lowest speeds $(<0.6 \text{ m s}^{-1})$ g_b^h values were higher than expected, particularly when the canopy was leafed, probably

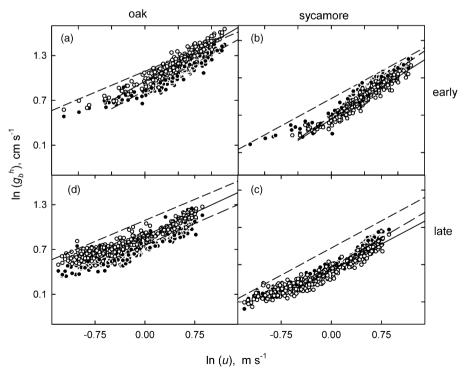


Fig. 9. Relationship between $\ln(g_b^h)$, cm s⁻¹, and $\ln(u)$, m s⁻¹, for oak (a and c) and sycamore (b and d) leaf replicas when exposed in the canopy, either during the early season (a and b), when the canopy was leafless, or later during July when fully leafed (c and d). Data are 15 min averages, either in 'sun-shoot' (open symbols) or 'shade-shoot' (closed symbols) positions. Data filtered as in Fig. 6. Regression lines for the two periods are shown, fitted to values $u > 0.6 \text{ m s}^{-1}$ (parameters in Table 1), and the dotted line is the relationship found when leaves exposed in the open.

Table 1 Fitted parameters for linear regressions of $\ln(g_b^h)$ against $\ln(u)$ for oak and sycamore leaf replicas when exposed in the canopy, either during the early season when the canopy was leafless, or later during July when fully leafed (see Fig. 9)

	Early season, leafless canopy		Mid-summer, leafed canopy	
	Slope	Intercept	Slope	Intercept
Oak				
Sun	0.513	0.957	0.414	0.883
Shade	0.486	0.832	0.387	0.758
Sycamore				
Sun	0.567	0.448	0.475	0.420
Shade	0.620	0.491	0.528	0.463

In all the fitted equations the differences in parameter values between periods or positions are significant at P < 0.05.

indicating free convection, as in Fig. 6. As the wind speed was recorded in the open area of the walkway, the actual wind speeds over the replicas in the canopy were obviously lower than those shown in Fig. 9, particularly when leafed. However, a change in slope would still be expected if the boundary layer regime changed from laminar to turbulent. There was no evidence of such a change at higher speeds and the slopes for both oak and sycamore replicas in the $\ln(g_b^h)$ versus $\ln(u)$ relationships of between 0.4 and 0.6 either before or after leafing indicate that the boundary layers were laminar (see Table 1).

The g_h^h values measured in the canopy at a particular wind speed as shown in Fig. 9 compared to those for exposed replicas indicate the degree of shelter produced by the canopy structure alone, prior to leafing, and when leafed. Thus using the regression equations the shelter of the branches in the oak canopy only caused a 12% reduction in g_h^h in 'sun-shoot' positions at $u = 1 \text{ m s}^{-1}$ (Table 2), but 23% reduction for oak leaves placed deeper within the upper tree crowns ('shade-shoot' positions). The shelter effect was higher for the sycamore sun-shoots (24% at 1 m s⁻¹), than the oaks, but there was little difference between sun- and shadeshoot positions in the leafless period, bearing in mind the uncertainties in the regression equations (Table 2). As expected, at higher wind speeds the shelter effect was reduced, so that for the 'sun-shoot' oak, the shelter effect was negligible at wind speeds > 2 m s⁻¹. The data for these comparisons were selected to include only those with a SW-W wind direction, as including other directions resulted in substantial scatter. Presumably this was due to shelter effects for other wind directions differently affecting the anemometer in the open walkway area and the replicas within the canopy. In

Table 2
Estimated shelter effect (%) at different wind speeds for oak and sycamore leaf replicas in either 'sun-shoot' or 'shade-shoot' positions in the upper canopy of an oak-sycamore wood

Wind speed (m s ⁻¹)	Sun-sh	oots	Shade-shoots	
	Oak	Sycamore	Oak	Sycamore
Early season, leafless	canopy			
0.5	20.4	28.2	28.4	27.8
1	12.4	24.1	22.7	20.7
1.5	7.4	21.6	19.2	16.3
2.5	0.6	18.2	14.5	10.4
3	-1.9	17.0	12.7	8.2
Mid-summer, leafed c	anopy			
0.5	20.8	25.6	28.8	25.1
1	18.7	26.2	28.2	22.9
1.5	17.4	26.5	27.9	21.6
2.5	15.7	26.9	27.4	19.9
3	15.1	27.1	27.3	19.3

Shelter effect estimated as percent reduction of leaf boundary layer conductance, g_b^h , from that for exposed replicas. g_b^h calculated from fitted linear regressions of $\ln(g_b^h)$ against $\ln(\text{wind speed})$.

mid-summer when the canopy was fully leafed, the shelter effect was almost the same at low speed $(0.5~{\rm m~s^{-1}})$ as when leafless (Table 2). The shelter at $1~{\rm m~s^{-1}}$ increased to 19% and 28% in oak sun and shade-shoots but showed only a slight increase in sycamore. However, in both oak and sycamore the shelter was much more pronounced at higher speeds in the leafed canopy, so that there was little or no change as wind speed increased. As earlier, there was little difference in shelter for sycamore leaves in the two shoot positions, whereas the sun-shoot oak replicas were substantially less sheltered than the shade-shoots.

Clearly, these differing amounts of shelter in the canopy meant that the relationship between sycamore and oak g_b^h at any wind speed differed with canopy position (Fig. 10). In 'sun-shoot' positions, the ratio between sycamore and oak g_b^h was only slightly lower (0.624) than when replicas were in the open (0.658, Fig. 7), whether the canopy was leafless or in leaf. However, in the 'shade-shoot' position, because the oak leaves experienced relatively more shelter (Table 2), the difference between oak and sycamore declined (sycamore $g_b^h = 0.759$ oak g_b^h , Fig. 10).

3.5. Leaf-to-air coupling

Stomatal conductance (g_s) values for oak and sycamore sun and shade leaves were determined *in situ* at ambient light levels on many occasions throughout the season in 1999 and 2000 (Stokes, 2002). Although there was considerable variation, in

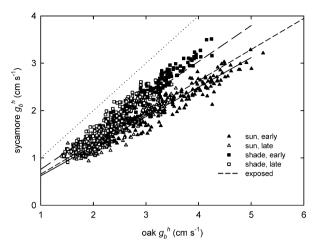


Fig. 10. Comparison of mean sycamore and oak replica boundary layer conductance $(g_b^h, \operatorname{cm s}^{-1})$ when exposed in the canopy in either 'sun-shoot' or 'shade-shoot' positions. Data are 15 min averages; either for the leafless period (open symbols) or during July when the canopy was fully leafed (filled symbols). Data filtered as in Fig. 6. Lines shown are fitted regressions for sun (solid line) or shade-shoot positions (dashed line). The dotted line is the fitted line when leaves were well exposed, redrawn from Fig. 7.

general mean g_s values for oak sun leaves were higher than for sycamore, but there was little difference for shade leaves (sun: $190 \text{ cf. } 131 \text{ mmol m}^{-2} \text{ s}^{-1}$; shade: 98cf. 86 mmol m⁻² s⁻¹, values in cm s⁻¹ are: 0.48, 0.33, 0.25 and 0.22, respectively). The mean g_s values and the relationships determined in Figs. 6 and 9 between g_h^h and wind speed in different positions in the canopy were used to examine differences between species and position in the degree of leaf coupling to the air stream (Fig. 11). The decoupling factor, Ω , was calculated using the formulation for hypostomatous leaves: $\Omega = (s/\gamma + 2)/(s/\gamma + 2 + 2g_h^w/g_s)$, where s is the slope of the saturation vapour pressure versus temperature relationship, and γ the psychrometric constant, as usual (Jarvis and McNaughton, 1986). At wind speeds above 1 m s⁻¹ leaves of both species were well coupled (Ω < 0.3), although sun leaves with higher g_s values were substantially more decoupled than shade leaves, despite the lower sheltering effect, because of higher g_s values. However, it is worth noting that low wind speeds are the norm in the canopy (see Fig. 8b for daily mean values). Mean wind speed measured on the walkway was $<1 \text{ m s}^{-1}$ for 74% of all day time 15 min periods from leafing to the end of July in 2001, and $<0.5 \text{ m s}^{-1}$ for 27% of the time. Values for the whole of the 2000 leafed season up to the end of September were comparable (72% and 16%). The differences in g_b^h and g_s between oak and sycamore sun leaves largely compensate for each other, so that for (hypothetical)

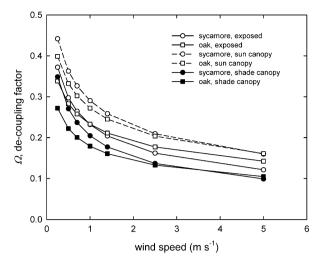


Fig. 11. Change of the decoupling coefficient, Ω , with wind speed for oak and sycamore leaves. Calculated from the fitted relationships between $\ln(g_h^b)$ and $\ln(u)$ for replicas, and assuming sun and shade leaves have stomatal conductance values of: 190 and 131 mmol m⁻² s⁻¹ for oak, and 98 and 86 mmol m⁻² s⁻¹ for sycamore. Lines are for sun leaves in completely exposed positions (solid), in sun-shoot positions (dashed) and in shade leaves in shade-shoot positions (filled symbols). Dotted line is y = x.

leaves fully exposed there is almost no difference in coupling (Fig. 11). However, for leaves in real positions in the canopy, oak leaves do show better coupling (lower Ω values), although the differences are small at $u > 2.5 \text{ m s}^{-1}$ (Fig. 11).

4. Discussion

4.1. Functioning of the replica leaves

The thin, flexible Mylar sheet used here made more realistic leaf models than the metal replicas used in several other studies in some important aspects. Firstly, there was some flexing of the replica margins and attaching them to branches flexibly allowed the whole replica to move in the wind, although they did not flutter like real leaves, nor move sufficiently to streamline. Secondly, there was no airflow interference from any support frames as used in some other studies. For example, Brenner and Jarvis (1995) speculated that the low wind speed at which the boundary layer changed from laminar to turbulent in their experiment might be because of 'tripping' effects from the frame or replica suspension wires. Thirdly, a major advantage of the plastic replicas was that there were similar gradients in temperature across the replicas as in leaves, as shown in Fig. 3, obviously more realistic than highly conductive and more isothermal metal replicas. The disadvantage is that it therefore required a method of measuring the average temperature of the leaf, so we used a long resistance wire placed across all areas of the leaf. However, this provides another advantage over single point thermocouples used in much previous work; for example, in the sycamore leaf and replica shown in Fig. 3, the temperature in the middle was about 0.7 °C warmer than the average temperature determined from the images, and from the RTD. Another advantage was that because of their low thermal mass, the replicas heated and cooled rapidly, compared to metal replicas, allowing more frequent alternation of heating. For example, the time constant of the large sycamore replicas was approximately 53 s even in very still conditions, while Leuning and Foster (1990) quoted a time constant for their 2 mm thick aluminium and plastic replicas of approximately 2 min, although they did not specify the wind speed. The short time constant of our replicas had two benefits: reducing some of the problems with spatially and temporally patchy solar radiation affecting the replicas differently (e.g. Grantz and Vaughn, 1999), and better sampling of rapidly fluctuating wind speeds. For example, in our system the mid-point of the measurement of offsets was a little less than 4 min after the mid-point of the $(T_h - T_u)$ measurement and this also meant g_b^h of both leaves in the pair could be determined within a 15 min cycle. In comparison, in the work with millet (Brenner and Jarvis, 1995), windbreak crowns (Smith et al., 1997) and cotton (Grantz and Vaughn, 1999) the delays between the mid-point of the $(T_{\rm h}-T_{\rm u})$ measurements and the mid-point of the offsets were 15 min and a complete cycle for a pair took 1 h. Lastly, our replicas also had a similar emissivity to leaves (0.91 cf. 0.97), so that the long wave radiative environment would have been more similar to that of leaves than are high emissivity metal replicas.

Overall these replicas successfully enabled the estimation of daily and seasonal time courses of g_b^h in the canopy (Figs. 5 and 8), and demonstrated that values for oak were always 30–40% higher than those for sycamore.

4.2. Boundary layer conductance values

The values of g_b^h determined here matched the standard 'flat plate' values well (Fig. 6), which agrees with several other determinations using various replicas in the field (see Schuepp, 1993 for review of earlier work). The sycamore g_b^h values agreed with recent field measurements with replicas of grape vine leaves (Daudet et al., 1998) and cotton leaves (Grantz and Vaughn, 1999) which have similar lobed or partly

dissected shapes and characteristic dimensions (d) as the sycamore replicas. Furthermore, the 66% lower value of g_h^h for sycamore than oak also agreed with calculations from their relative characteristic dimensions, d (Fig. 7). Many (but not all) previous results have found enhanced heat transfer from leaves compared to the theory derived for extensive, flat, smooth plates, particularly in turbulent flow regimes, and enhancement factors (β) ranging from 1.0 to 2.5 have been reported (Schuepp, 1993), with values >1 usually being attributed to edge and surface roughness effects. For example, Grantz and Vaughn (1999) estimated $\beta = 1.15$ for cotton replicas, although Daudet et al. (1998) did not report any enhancement for grape vine replicas. In the present study there was no evidence of enhanced heat transfer when replicas were well exposed; although the limited range of low wind speeds here does not permit a conclusive analysis. The lack of enhancement may be because of the strong temperature gradients that occurred across the plastic replicas (e.g. Figs. 3 and 4), compared to metal replicas.

Brenner and Jarvis (1995) pointed out that air-leaf and air-replica temperature differences may not be the same, resulting in different amounts of free convection. In their system, they found that the resulting error in g_b^h was not large in day time (approximately 4%) because of strong forced convection, whilst in stiller night time conditions the error was as much as 24%. In the present study, there was some evidence of higher heat transfer at low speeds because of enhanced convection from the leaves (Figs. 6 and 9). Daudet et al. (1999) found a similar effect for ellipsoidal replicas of walnut leaflets which were similar in area to the sycamore replicas, but with a cross leaf dimension closer to that of the oaks. As sycamore replicas were substantially larger than the oak replicas and also warmer, it might be expected that more free convection may occur at night than for oak replicas. Calculated Grashof numbers for the oak and sycamore characteristic dimensions and the largest measured $T_h - T_a$ temperature differences were approximately 1.9×10^6 and 2.5×10^7 , respectively. However, investigation of the relationship between day and night time g_b^h and wind speed showed no difference between day and night time values in either oak or sycamore replicas (data not shown) and the relationship between the two replica shapes was not significantly different between night time and day time conditions (Fig. 7). Enhanced convection in the replicas could be minimised by reducing the electrical heating, but this would require a control and measurement system akin to that in constant temperature hot-wire anemometers to allow g_b^h to be measured across a range of wind speeds. This would add considerable complexity.

4.3. Canopy shelter and leaf-to-air coupling

It is important to note that the wind speed we measured 'outside' the canopy was outside the individual trees crowns, but within the upper parts of the overall tree canopy, and at approximately the same height as the leaf replicas. It is therefore not the above canopy wind speed, and is not comparable with any standard climatological measurements. comparison with wind speed over open grassland nearby showed that the mean wind flow was reduced by 40% in the leafless upper canopy (Fig. 8a), and the reduction increased with leafing to 65%. We used the difference in the relationship between the outside canopy wind speed and the measured g_b^h to determine the degree of shelter for replicas in the different parts of the upper canopy. It is noteworthy that even the bare branches reduced g_b^h appreciably (by 20–28% at 0.5 m s⁻¹, Table 2), and leafing did not increase significantly this effect in light winds in either species. However, leafing produced substantially more shelter at higher wind speeds (16-27% reduction in g_b^h at 2.5 m s⁻¹), compared to only 0–18% shelter when there were no leaves (Table 2). Our approach to estimating the extent of shelter in the canopy is similar to that of Landsberg and Powell (1973) who calculated a "shelter factor" as the ratio of water vapour exchange coefficients with and without aerodynamic interference from other leaves in small replica apple trees. It is difficult to compare their data directly, as they used wet filter paper replicas and did not use exposed isolated replicas as their reference and we did not measure the

foliage density in the canopy. Nevertheless, their data produce shelter effects of 33-41% for a range of leaf densities at 1.5 m s⁻¹, rather higher than found here for the denser shoots (17–28%, Table 2). However, in their wind tunnel experiment the shelter effect increased with increasing wind speeds (e.g. from 22% at 0.5 m s⁻¹ to 36% at 4.5 m s^{-1}), whereas in our field experiment it either did not change or decreased with increasing speed, which is more intuitively reasonable. It is noteworthy that when shelter effects for momentum transfer on real apple trees were derived in the wind tunnel, they showed almost constant shelter effects across the wind speed range from 0.5 to 3 m s^{-1} (approximately 24%) declining slightly at higher speeds (16% at 7 m s⁻¹, Landsberg and Powell, 1973). This is quite comparable with the data in Table 2.

As there was no replication of the different canopy positions for the two species, the leaf replica position data should be interpreted with caution. Clearly it will depend on canopy structure, leaf area density and the resulting wind speed distribution. Thus the exact relationships are unique to this experiment. However, it does appear that the degree of shelter in 'sun-shoot' and 'shade-shoot' positions for sycamore was very similar, while oak replicas in 'sun-shoot' positions had substantially (approximately 10%) higher g_b^h at any outside wind speed than those in 'shade-shoot' positions (Table 2). This is consistent with the different branching patterns and consequently more clustered leaf arrangements in sycamore canopies than in oak (Buck-Sorlin and Bell, 2000).

Despite the low wind speeds measured in the canopy space and the reduction in wind speed within the individual tree crowns, the estimates of the mean decoupling factor (Ω) derived here confirm the usual view that leaves in tree canopies are well coupled to the air stream (see Jarvis and McNaughton, 1986). The decoupling factor, Ω , was <0.3 for all wind speeds $>1 \text{ m s}^{-1}$, even for sun leaves which typically have higher mean stomatal conductances. Oak leaves were only slightly better coupled than sycamore leaves, and any differences between species are probably only significant in very still conditions. However, mean g_s values on any particular occasion were up to twice the seasonal mean values used for the calculations in Fig. 11 and wind speed is often $<0.5 \text{ m s}^{-1}$. In these conditions, poor coupling ($\Omega \cong 0.6$) may limit heat and gas exchange for either oak or sycamore, and reduce the effectiveness of stomatal control of transpiration. Certainly, subsequent casual observations with a thermal camera show that temperatures of exposed 'sun-shoot' leaves in tree canopies are frequently 10-15 °C higher than air temperature in light wind and bright sun conditions.

5. Conclusions

The new method of producing realistic leaf replicas to determine g_b^h in the canopy proved successful. Mounting these light replicas on branches allowed some movement, and the resistive temperature device recorded average temperature across the whole replica surface, accounting for edge effects. Temperature patterns on the replicas were very similar to those on real leaves, with strong temperature gradients at the margins. This approach would be suitable for long-term monitoring of boundary layer conductance and 'leaf-effective' wind speeds in the canopy.

The values of g_b^h for both oak and sycamore were broadly in agreement with standard flat plate heat transfer theory, and gh of the larger sycamore leaf replicas was approximately 66% of that of the smaller oak replicas. With the relatively low wind speeds observed in the upper canopy, flow was laminar in the boundary layers of both replica types even in the turbulent airflow within the canopy. Replicas within the leafless canopy showed that the branches alone reduced g_b^h by 12–28% in light winds ($\leq 1 \text{ m s}^{-1}$), with more effect in the sycamore canopy than in the oak. Mean daily g_b^h declined substantially (by 50%) as the leaf cover in the canopy developed, due in part to a decline in wind speed within the canopy air space, and due to increased shelter for leaves within the individual branches. However, the shelter effect was not large, reducing g_h^h by 19–29% in light winds. Comparison of g_b^h in different positions inside the canopies showed that for oak leaves 'shade-shoot' positions were more sheltered than exposed 'sun-shoot' leaves, but for sycamore there was little difference, illustrating the importance of branching pattern to leaf microclimate. Both sun- and shade-shoot leaves were well coupled to the air stream, except in very light winds and under conditions of high stomatal conductance when sunshoot leaves would be poorly coupled.

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