Modelling the surface conductance of a broad-leaf canopy: effects of partial decoupling from the atmosphere

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ABSTRACT

The transpiration of a mature beech (*Fagus sylvatica* L.) forest was measured over a whole season by the heat pulse velocity technique and the results analysed in terms of a new analytical canopy conductance model, which takes into account the effects of partial decoupling from the atmosphere on the local humidity environment experienced by the canopy. Stand daily transpiration ranged from 0·62 to 2·97 mm d^{-1}, with a seasonal mean value of 1·97 mm d^{-1}. Maximum canopy conductance was 18·5 mm s^{-1}, with a mean estimated value of 5·0 mm s^{-1}; computed values were little affected by the assumption of neutral atmospheric conditions. The decoupling coefficient Ω varied greatly on a daily and seasonal basis, with an average value of 0·28. As a result of partial decoupling, the estimated vapour pressure deficit at the notional canopy surface exceeded the values measured above the canopy by 380 Pa on average. When correctly expressed in terms of humidity at the canopy surface, the model explained 80% of the variance in half-hourly transpiration measurements. Upon cross-validation it still explained 72% of the variance, as compared to only 40% when correction for partial decoupling was not introduced. A baseline canopy conductance of 0·7 mm s^{-1}, not modulated by the environment, was estimated. The implications of the model are discussed for the representation of canopy conductance and transpiration of broad-leaf forests.

Key-words: *Fagus sylvatica* L.; beech; Bowen ratio; canopy conductance model; decoupling coefficient; heat pulse velocity; humidity gradients; transpiration.

INTRODUCTION

A proper understanding of the interaction between transpiration and the environment is necessary to represent not only local hydrological processes but also, at a regional and global scale, the exchange of latent and sensible heat at the base of the planetary boundary layer in soil-vegetation-atmosphere transfer (SVAT) schemes (Wood 1991; Garratt

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1993; Randall *et al*. 1996). Simple but realistic models have to be developed and a correct parametrization for the principal vegetation types in the world is obviously needed (Dolman 1993; Schulze *et al*. 1994). As a result the representation of transpiration from extensive vegetation canopies has attracted much attention over the last decade.

Canopy transpiration results from the integration of processes at the leaf level, and two complementary perspectives are evident in the literature (Raupach & Finnigan 1988; Lhomme 1991; Baldocchi 1993). In the 'bottom-up' modelling approach the spatial variability in both environmental and physiological conditions within the crown is conveniently described, and a general picture for the canopy as a whole results from the upscaling of processes at this finer level of organization (Dye & Olbrich 1993; Roberts & Rosier 1994; Baldocchi & Harley 1995). In the 'top-down' approach, in contrast, the canopy is treated as a single entity, characterized by a bulk canopy conductance to the transfer of water and by the aerodynamic conductance to the transfer of momentum and scalars between a notional canopy surface and the atmosphere; the canopy is thus considered as a single 'big-leaf'. Such a simple approach has been successfully applied to derive the bulk canopy conductance of coniferous canopies (Lindroth 1985; Granier & Loustau 1994) and of both temperate (Herbst 1995; Ogink-Hendricks 1995) and tropical broadleaf forests (Lloyd *et al*. 1995).

Several empirical models have been proposed to capture salient features of the response of stomatal conductance to the leaf environment (Jarvis 1976; Lohammar *et al*. 1980; Collatz *et al*. 1991; Leuning 1995). The same models have also been directly applied to represent, in a 'big-leaf' approach, the relationship between canopy conductance and average environmental variables for the forest as a whole, as measured at a reference point above the canopy.

This raises the question of what should be considered as effective surface conditions, directly experienced by the bulk canopy (Jarvis & McNaughton 1986). As long as coniferous forests are considered, conditions at the notional canopy surface can be well approximated by measurements taken just a few metres above, as these canopies are aerodynamically well coupled to the atmosphere (McNaughton & Jarvis 1991). This assumption, however, is no longer valid when dealing with short vegetation or, to

a lesser extent, with tropical and temperate broad-leaf forests. Because of the dimensions of their leaves and higher stomatal conductances, broad-leaf canopies are partly decoupled from the atmosphere (Kostner *et al*. 1992; Lindroth 1993; Hinckley *et al*. 1994; Herbst 1995; Meinzer *et al*. 1997) and considerable vertical gradients of temperature and humidity can develop over just a few metres (Aussenac & Ducrey 1977; Shuttleworth *et al*. 1985; Jarvis & McNaughton 1986; van Eimern & Riedinger 1986).

The need to consider the effects of a partial decoupling has long been recognized in stomatal conductance studies (Bunce 1985; Monteith 1990; Aphalo & Jarvis 1993). In an early analysis of the response of stomata to the environment, Grace, Malcolm & Bradbury (1975) suggested that the apparent effect of wind speed on stomatal resistance was just the result of humidity gradients developing around the transpiring leaves under calm conditions.

Although the effects of partial decoupling are even more important at the canopy scale (Jarvis & McNaughton 1986), they have never been taken into account in the analysis of the response of canopy conductance and transpiration to the environment. A new 'top-down' analytical model had therefore to be developed to represent and predict transpiration from partially decoupled vegetation, based on standard micrometeorological measurements above the canopy yet correctly expressing the response of canopy conductance to the bulk conditions at the notional canopy surface.

The model was then compared to sap flow data from a mature beech (*Fagus sylvatica* L.) forest, in order to assess the suitability of a 'big-leaf' approach, once corrected for partial decoupling, for prediction of canopy conductance and stand transpiration of this important broad-leaf species.

MATERIALS AND METHODS

The seasonal course of transpiration was measured in an even-aged 35-year-old beech stand of the Abetone forest (Northern Apennines, Italy, 10°40′ E, 44°07′ N, 1230 m a.s.l.), with a projected leaf area index of 3·8, a stand basal area of 25 m^2 ha^{-1} and a top height of 19 m. No understorey was present under the main tree canopy, a condition typical of the *Fagetum sylvaticae* association (Teissier du Cros 1981).

Measurement of canopy transpiration

Sap flow was measured from June to September 1992 on a cohort of one dominant and two intermediate beech trees, with partially overlapping crowns, by the thermoelectric heat pulse technique, using a heat pulse velocity (HPV) meter (Custom, Soil Conservation Centre, Palmerston North, New Zealand). On each tree, four heating probes were inserted to different depths in the sapwood, at right angles to the surface and 1·30 m above the ground.

Heat pulse velocity was measured every 30 min; sap flow was derived by the compensation technique (Huber &

Schmidt 1937; Marshall 1958). Swanson & Whitfield's (1974) analysis was applied to correct for inhomogeneities caused by probe implantation wounds, which could seriously affect the accuracy of the results (Olbrich 1991); wound size was assumed to exceed by 5% the diameter of the drill (Dye & Olbrich 1993).

Measured probe depth was also corrected for stem radial increments over the season. The volumetric volume fraction of water in the xylem, a parameter required in computations, was monitored regularly throughout the growing season on wood cores extracted from the stem of five other beech trees growing at the study site; it was assumed to be constant over the sapwood, as it varied by no more than 7% in the outermost 10 cm of cores extracted at the end of the experiment, ranging from 0·41 in the external growth rings to 0·38 closer to the centre.

Plant transpiration was assumed to be equal to sap flow measured at the base of the stem, as concurrent measurements of sap flow and twig water potential showed that tissue capacitance in the plants studied was minimal (Magnani & Borghetti 1995). Canopy transpiration per unit ground area (E) was computed by summing up the sap flow rate of single trees to obtain the cohort's transpiration and dividing this value by the cohort's crown projection area (Hatton, Moore & Reece 1995). Very similar results were obtained when scaling-up on a basal area basis.

The HPV technique is prone to overestimate low sap flow rates (Barrett *et al*. 1995), resulting in apparent transpiration rates at night (Heimann & Stickan 1993); data were therefore discarded whenever $R_n < 0$ or air relative humidity was more than 90%. This should have also excluded from computations any periods of wet canopy.

Micrometeorological measurements

Global radiation (R_g) and net radiation (R_n) were measured 3 m above the canopy from a tower adjacent to the tree cohort by a pyranometer (Kipp & Zonen, Delft, The Netherlands) and a Funk-type net pyrradiometer (Middleton Instr., Port Melbourne, Australia), respectively. Air temperature (T_r) and air vapour pressure deficit (D_r) were also measured at the same reference point by a linearized thermistor and a capacitive humidity sensor (ACME, Sesto Fiorentino, Italy); horizontal wind speed (u_r) was sensed using a cup anemometer (Vector Instr., Clwyd, UK). All parameters were measured every 10 s and the readings averaged every 30 min and recorded on a datalogger (ACME, Sesto Fiorentino, Italy). Sap flow rates and meteorological measurements were considered as concurrent variables when they lagged by no more than 15 min.

Canopy decoupling

The aerodynamic conductance of the canopy to the exchange of scalars such as heat and water vapour (g_a) results from the sum in series of two components (Thom 1975; Choudhury & Monteith 1988): a boundary-layer resistance (r_b) related to the quasi-laminar transport of heat and vapour across the

boundary layer adjacent to the leaf surface and a turbulent resistance (r_t), due to the movement of air eddies between the canopy and the atmosphere (Appendix B):

$$\frac{1}{g_a} = r_b + r_t \, . \tag{1}$$

Whilst the turbulent resistance is a function of wind speed and canopy aerodynamic roughness alone, as determined by canopy height and leaf area index (Monteith & Unsworth 1990), the quasi-laminar component strongly increases with leaf dimensions; its contribution is therefore negligible in conifers but cannot be neglected when dealing with broad-leaf species (Thom 1972).

Bulk canopy conductance (g_c) was obtained by inverting the Penman-Monteith equation (Monteith & Unsworth 1990), under the assumptions of negligible heat storage and soil heat flux (see Appendix A for parameters and units):

$$\lambda E = \frac{s R_n + \rho_a c_p D_r g_a}{s + \gamma \left(1 + \dfrac{g_a}{g_c} \right)} \, . \tag{2}$$

The degree of coupling of the canopy to the atmosphere can be captured as a decoupling coefficient Ω (McNaughton & Jarvis 1983), defined as

$$\Omega = \frac{(s/\gamma + 1)}{(s/\gamma + 1 + g_a/g_c)} \, . \tag{3}$$

The decoupling coefficient effectively represents the sensitivity of transpiration to a change in canopy conductance.

Modelling canopy conductance under partial decoupling

The response of bulk canopy conductance to the environmental conditions at the surface of the 'big-leaf' was represented by a multiplicative model of the form

$$g_c = g_0 + g_m f(T_s) f(R_g) f(D_s), \tag{4}$$

where g_0 is a baseline value not modulated by environmental conditions, $(g_0 + g_m)$ is maximum conductance under optimal conditions, T_s and D_s are, respectively, temperature and vapour pressure deficit at the notional canopy surface, and the scaling functions $f(T_s)$, $f(R_g)$ and $f(D_s)$, ranging from 0 to 1, account for the response of canopy conductance to the local environment. Any effects of soil water content on canopy conductance were not taken into account, as pre-dawn water potential never fell below -0.2 MPa at the study site (Magnani & Borghetti 1995).

The response to incoming global radiation was represented by the Michaelis-Menten quadratic hyperbolic function (Thornley & Johnson 1990)

$$f(R_g) = R_g/(R_g + R_{1/2}), \tag{5}$$

where $R_{1/2}$ is a fitted parameter, representing the value of global radiation which reduces canopy conductance to one half of its maximum value.

The effects of surface temperature were represented by the bell-shaped function (Massman & Kaufmann 1991; Jarvis 1976)

$$f(T_s) = \frac{(T_s - T_{min})}{(T_{opt} - T_{min})} \frac{(T_{max} - T_s)^a}{(T_{max} - T_{opt})^a}, \tag{6}$$

where T_{opt} is optimum temperature, T_{min} and T_{max} are minimum and maximum temperatures for stomatal opening and a is a parameter which accounts for the asymmetry of the response around T_{opt}; arbitrary values of -5 °C and 0.5 were assumed throughout for T_{min} and a, respectively.

Canopy temperature was assumed to equal air temperature as measured above the forest, since temperature gradients are usually small in forest canopies (Aussenac & Ducrey 1977; van Eimern & Riedinger 1986). In order to assess the error introduced, the temperature difference between the canopy and the atmosphere can be roughly estimated, under the assumptions of negligible heat storage and soil heat flux, as (Jones 1992)

$$(T_s - T_r) = \frac{R_n - \lambda E}{\rho_a c_p g_a} \tag{7}$$

The response of canopy conductance to the vapour pressure deficit at the notional canopy surface is represented by the so-called Lohammar's model (Lohammar *et al.* 1980), which has been found to best represent the humidity response at the leaf scale (Morison & Gifford 1983; Massman & Kaufmann 1991; Leuning 1995) and has been suggested to have a mechanistic justification (Dewar 1995)

$$f(D_s) = \frac{1}{1 + D_s/D_{1/2}}, \tag{8}$$

where $D_{1/2}$ is the value of vapour pressure deficit at which canopy conductance is halved.

The vapour pressure deficit at the canopy surface has been observed to differ considerably from the values measured above broad-leaf forests (Aussenac & Ducrey 1977; Shuttleworth *et al.* 1985; Jarvis & McNaughton 1986; Meinzer *et al.* 1997); moreover, stomatal conductance is generally much more sensitive to humidity than it is, for example, to temperature (Schulze 1970; Massman & Kaufmann 1991). It is therefore important to represent correctly the response to the local humidity conditions at the notional canopy surface and to take into account the partial decoupling of the canopy from the atmosphere (Monteith 1990; McNaughton & Jarvis 1991).

The vapour pressure deficit at the canopy surface is a rather complex function of the humidity in the atmosphere, net radiation, aerodynamic conductance and canopy conductance itself (Monteith 1990):

$$D_s = \frac{s R_n/(\rho_a c_p) + g_a D_r}{g_a + g_c (\varepsilon + 1)} \, . \tag{9}$$

By substituting this expression for D_s into Eqn 8, a model is obtained which correctly represents the response of

canopy conductance to local humidity, as a function of environmental parameters measured above the canopy:

$$g_c = \frac{-a_2 + \sqrt{a_2{}^2 - 4a_1 a_3}}{2a_1}, \tag{10}$$

$$a_1 = (\varepsilon + 1),$$

$$a_2 = g_a - (g_1 + g_0)(\varepsilon + 1) + \frac{D_r}{D_{1/2}}(g_a + \varepsilon g_i),$$

$$a_3 = -g_a(g_1 + g_0) - g_0 \frac{D_r}{D_{1/2}}(g_a + \varepsilon g_i),$$

where g_1 is maximum canopy conductance modulated by light and temperature only:

$$g_1 = g_{max} f(R_g) f(T_s)$$

and g_i is a 'climatological conductance' (Jarvis 1981), defined as

$$g_i = \frac{g R_n}{\rho_a c_p D_r}.$$

Model evaluation and comparison

The response of canopy transpiration to the external environment can be eventually represented by combining Eqn 10 with the Penman-Monteith model of Eqn 2. The resulting ('partial coupling') model was fitted on untransformed transpiration data using the SAS statistical package (SAS Institute Inc. 1988) and the results compared with those obtained when the effects of decoupling are neglected ('perfect coupling' model) by assuming in Eqn 8 that stomata respond directly to air humidity measured above the canopy.

The data-set was split into two parts and both models were alternatively calibrated on either half and cross-validated on the other (Wallach & Goffinet 1989). Model goodness-of-fit could then be conveniently evaluated in terms of mean squared errors of predictions (MSE) and of its systematic and non-systematic components (Wallach & Goffinet 1987; Willmott 1981). By comparing MSE differences with MSE variance (Wallach & Goffinet 1989), the statistical significance of the superiority of the 'partial coupling' model could also be assessed.

Error analysis

In the present study, canopy aerodynamic conductance was not directly measured, but estimated on the basis of K-theory and several parameters had to be assumed from the literature (Appendix B). It is apparent from Eqns 2 and 3 that any errors in the determination of g_a would result in biased estimates of g_c and of canopy decoupling.

In the absence of an independent measurement of sensible heat flux, as in the present case, the effects of thermal instability on aerodynamic conductance (Appendix B) are often neglected (Kostner *et al.* 1992; Lindroth 1993;

Herbst 1995), leading to an overestimation of Ω (Grace *et al.* 1995). The flux of sensible heat, however, can be evaluated in first approximation from canopy energy balance, as the difference between net radiation and latent heat flux. Aerodynamic and canopy conductance under non-neutral conditions could then be evaluated by an iterative procedure and the error induced by the assumption of neutrality quantified in terms of mean average percentage deviation (MAD%) (Mayer & Butler 1993).

Another potential source of error in the determination of g_c and Ω rests in the evaluation of aerodynamic and boundary-layer parameters in Appendix B, which in the present study had to be desumed from the literature. The sensitivity of canopy conductance and decoupling to a ± 10% parameter change was therefore also preliminarily assessed (Miller 1974).

RESULTS AND DISCUSSION

Measured heat pulse velocity was similar to values reported in the literature for beech trees (Visser *et al.* 1989; Heimann & Stickan 1993). Maximum sap velocity varied between 20 and 80 mm h^{-1}, values of the same order of magnitude of those measured in other diffuse porous hardwood species (Dunn & Connor 1993). When expressed on a per plant basis, transpiration was significantly greater for the dominant than for the intermediate trees; similarly, Kostner *et al.* (1992) found strong differences in transpiration rates between emergent and codominant *Nothofagus* trees.

Estimated stand daily transpiration ranged from 0·62 to 2·97 mm d^{-1}, with a seasonal mean value of 1·97 mm d^{-1}. Very similar values have been reported for other *F. sylvatica* forests over Europe (Aussenac & Granier 1979; Aussenac & Boulangeat 1980; Roberts & Rosier 1994), lending some support to the suggestion that transpiration is rather conservative at a regional scale as a result of a complex structure of stabilizing feed-back loops (Roberts 1983; Jarvis & McNaughton 1986).

The average value of gc, computed under assumptions of thermal neutrality, was 5·0 mm s^{-1}, 66% of the values being in the range 3·3–6·4 mm s^{-1}; the maximum value was 18·5 mm s^{-1}. These values are in good agreement with figures reported elsewhere for temperate deciduous broadleaves (Schulze *et al.* 1994; Kelliher *et al.* 1995), and compare well with maximum stomatal conductances reported in the literature for *F. sylvatica* (Schulze 1970; Roberts & Rosier 1994; Herbst 1995). Much higher values of canopy conductance, in contrast, have been computed for a beech forest (Herbst 1995), based on measurements of transpiration by the Bowen ratio method.

Canopy conductance was typically large early in the morning (Fig. 1), under conditions of sufficient irradiance and still low vapour pressure deficit, and decreased steadily during the day, mirroring the time course of air humidity. A second maximum of canopy conductance was sometimes observed late in the afternoon, a pattern expected under conditions of relatively low aerodynamic conductance (Collatz *et al.* 1991).
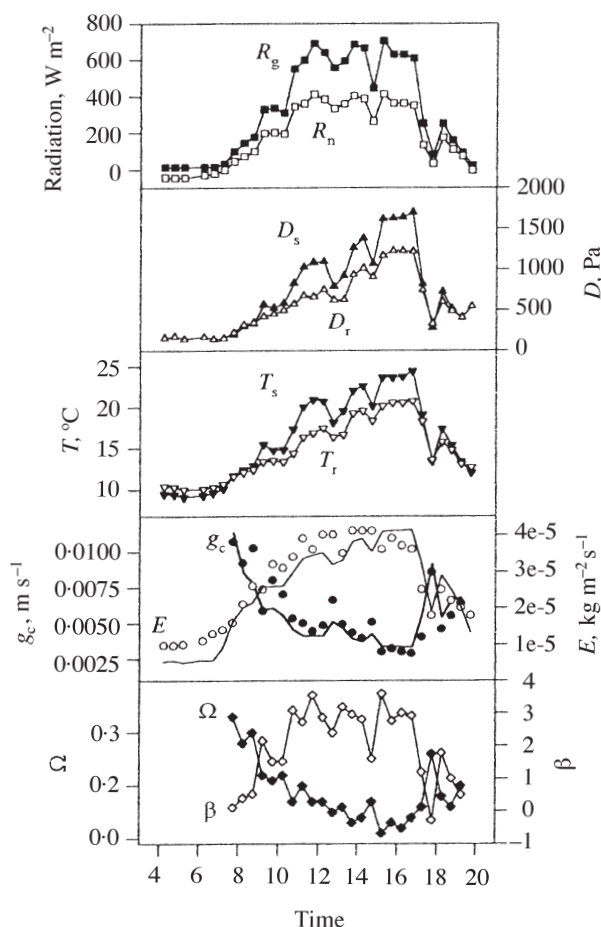
The reason for these differences can be essentially traced to the two terms of aerodynamic conductance (Eqn 1). In agricultural crops, stature, canopy closure and leaf dimensions result in high values of decoupling coefficient. In contrast, the good coupling of coniferous forests arises from the combination of low turbulence (because of roughness and stand structure) and leaf boundary-layer resistances (because of small leaf dimensions). The poorer coupling of broad-leaves mainly arises from larger leaf dimensions (about 5 cm in beech) and higher quasi-laminar resistances. In beech, turbulent resistance averaged 15·9 s m^{-1} over the season, in comparison with a mean value of 11·7 s m^{-1} for r_b; this corresponds to an average value of 2·93 for the interfacial sublayer parameter B^{-1} (Garratt 1992). This figure will, if anything, underestimate the real value in a hypostomatous species, as resistance for water vapour was assumed to be equal to the value for heat. In a Scots pine canopy, Stewart & Thom (1973) estimated that excess resistance is about 50% of turbulent resistance, but Verma *et al.* (1986) measured a value of up to 2/3 of turbulent resistance in a deciduous forest. Neglecting the boundary-layer contribution in Eqn 1 would have considerably overestimated g_c and underestimated canopy decoupling (MAD% = 17·3 and 30·3, respectively), as already pointed out by Verma *et al.* (1986) and discussed by Monteith & Unsworth (1990). Neglect of the buoyancy effects of thermal instability resulted in a smaller error in the computation both of g_c (MAD% = 8·37) and of Ω (MAD% = 16·5). Because of the uncertainty in the evaluation of sensible heat flux, thermal neutrality was therefore assumed in the rest of the analysis.
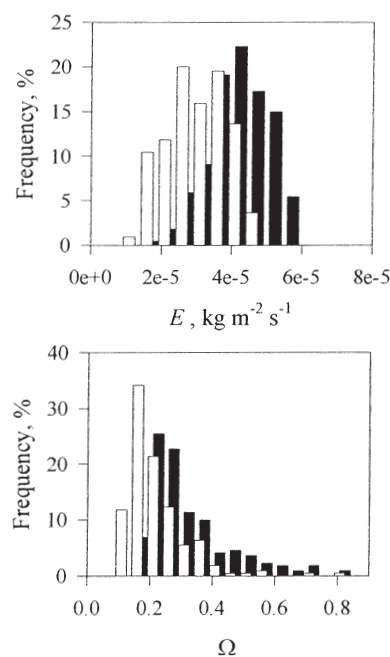

Figure 1. Diurnal course of measured ($\bigcirc$) and modelled (thin line) transpiration (E), computed ($\bullet$) and modelled (thick line) canopy conductance (g_c), the decoupling coefficient Ω and the Bowen ratio β. Also shown are net radiation (R_n), global radiation (R_g) and temperature and vapour pressure deficit measured at the reference height above the canopy (T_r and D_r) or estimated for the canopy surface (T_s and D_s).

The canopy was often poorly coupled to the atmosphere early in the morning (Fig. 1), as a result of large canopy conductances and low wind velocities; a similar decrease in the Ω factor over the course of the day has also been reported for a *Populus* stand (Hinckley *et al.* 1994) and a *Nothofagus* forest (Kostner *et al.* 1992). The canopy decoupling coefficent was generally lower in the first half of the season (Fig. 2), under reduced transpiration rates. The average value over the whole season was 0·28, in good agreement with the value previously reported for a similar *Nothofagus* forest (Kostner *et al.* 1992) but somewhat larger than those previously reported for mature beech canopies (Meinzer 1993; Herbst 1995). Mature temperate broad-leaf canopies therefore appear to be not as well coupled to the atmosphere as coniferous forests of similar structure (Jarvis & McNaughton 1986), but better coupled than tropical forests (Meinzer 1993; Meinzer *et al.* 1997), short-rotation forests (Lindroth 1993; Hinckley *et al.* 1994) or crop canopies (Grantz & Meinzer 1990).

Figure 2. Frequency distribution of half-hourly transpiration rates (E) and decoupling coefficient (Ω) over the first (open bars) and the second (filled bars) halves of the measurement period, as used for model cross-validation.

More confidence in the estimated results came also from the sensitivity analysis, as the effect of a ±10% change in any aerodynamic parameter resulted in a deviation of results of no more than 3·9% for g_c and 5·3% in the case of Ω (Table 1).

Canopy temperature (as estimated from Eqn 8) followed quite closely the air temperature above the forest (Fig. 1), in good agreement with other reports in the literature of temperature gradients of no more than 5 °C (Aussenac & Ducrey 1977; van Eimern & Riedinger 1986). However, under conditions of poor coupling this temperature difference induced strong humidity gradients over the canopy, the vapour pressure deficit at the notional surface being slightly smaller than that in the atmosphere early in the morning (Fig. 1), but on average about 400 Pa higher (Fig. 3), and was little affected by thermal stability assumptions. The analysis of micrometeorological profiles above and within a beech canopy (Aussenac & Ducrey 1977) shows that, despite the continuous input of water vapour transpired by the plants, which *per se* results in higher absolute humidity within the crown, the vapour pressure deficit is higher during the day at the top of the canopy than it is in the atmosphere because of temperature gradients. The sign of the difference depends on the balance between imposed and equilibrium transpiration (Appendix C), as suggested by McNaughton & Jarvis (1991), and is opposite in the case of beech to the values reported for crop canopies (Aussenac & Ducrey 1977; Shuttleworth *et al.* 1985; Jarvis & McNaughton 1986; Grantz & Meinzer 1990) or tropical forests (Meinzer *et al.* 1997).

The need to take into account these discrepancies and correctly model canopy conductance in terms of the local humidity environment is apparent when the former is plotted either against the vapour pressure deficit at the canopy surface, as derived from Eqn 9, or against the values measured above the canopy (Fig. 4): the large scatter in Fig. 4b appears to be largely a result of decoupling, but a clear
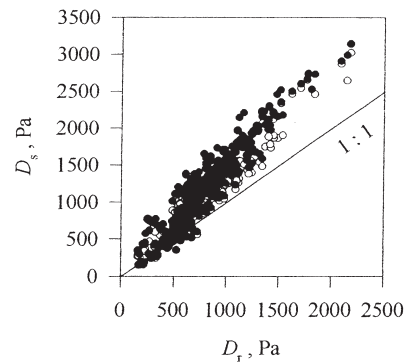

Figure 3. Vapour pressure deficit gradients above the beech canopy, as computed from Eqn 9 assuming neutral (●) or non-neutral (○) stability conditions.

response results when these effects are corrected for (Meinzer *et al.* 1997). This hyperbolic response, as captured by Lohammar's model of Eqn 8, is almost equivalent to the linear relationship between local humidity and stomatal resistance often reported at the leaf level for several species (Leuning 1995) including beech (Schulze 1970; Kerstiens 1995), or to the linear decline in leaf conductance with increasing transpiration highlighted by Monteith (1995a). Indeed, the only difference between Monteith's (1995a,b) model and the 'partial coupling' model lies in the inclusion in Eqn 10 of g_o, a baseline conductance that is not modulated by the environment (Collatz *et al.* 1991; Massman & Kaufmann 1991; Leuning 1995) and could be explained in terms of a cuticular component of total leaf conductance. Cuticular conductance (on a projected leaf area basis) has been found to amount to about 0·15–0·20 mm s^{-1} in beech (Vangardingen & Grace 1992; Kerstiens 1995) and to be only marginally affected by leaf hydration and air humidity (Vangardingen & Grace 1992). When these figures are scaled up to the canopy level, this cuticular component could well account for g_o, as estimated by fitting the 'partial coupling' model on the entire data-set (Table 2). The implications of a baseline conductance for the response of transpiration to the forest environment are worth considering: with increasing vapour pressure deficit canopy conductance will not fall to zero but will settle to a constant positive value (Fig. 4), so that transpiration will not level off but will continue to increase, albeit at a reduced rate (Fig. 5). The analytical model proposed by Monteith (1995b), despite its great simplicity and elegance, fails therefore to consider one potentially important component of canopy conductance.

The need to take explicitly into account the effects of partial decoupling is apparent from the comparison of the 'partial coupling' and 'complete coupling' models (Fig. 6). The two models performed in a similar way when fitted to the entire data-set, explaining, respectively, 80 and 74% of total variance (Table 3). However, because of the differences in transpiration rates and canopy decoupling between the two data-sets (Fig. 2), after cross-validation the 'partial coupling' model still
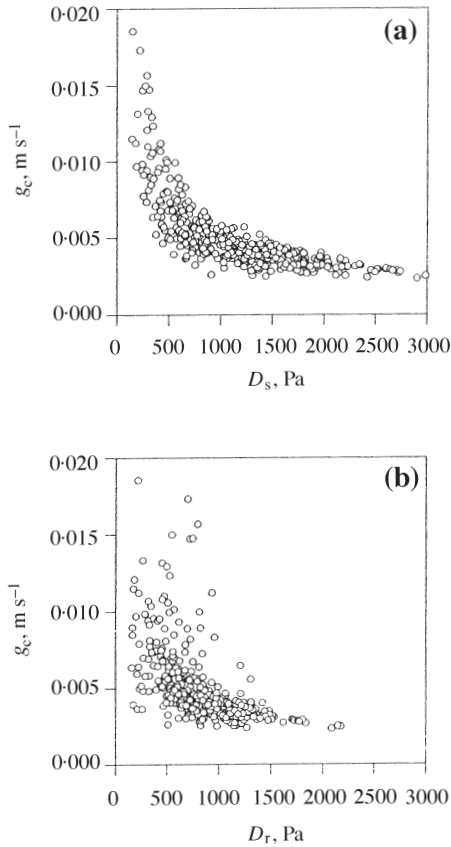
Table 1. Analysis of the sensitivity of computed canopy conductance (g_c) and decoupling coefficient (Ω) to changes in aerodynamic parameters: mean absolute percentage deviation from the standard run (MAD%) corresponding to a ±10% change in the height of the zero plane (d), the canopy roughness length for momentum (z_{0M}), the extinction factor of wind speed in the canopy (α) or the scaling coefficient for leaf boundary-layer conductance (b)

Parameter		MAD%	
		g_c	Ω
d	+10%	2·32	3·25
	−10%	3·87	5·30
z_{0M}	+10%	2·22	3·30
	−10%	2·70	3·81
a	+10%	0·88	1·37
	−10%	0·86	1·36
b	+10%	1·40	2·22
	−10%	1·68	2·61

Figure 4. Plot of computed canopy conductance (g_c) against vapour pressure deficit (a) at the canopy surface (D_s) or (b) measured above the canopy (D_r).

Table 2. Parameters and asymptotic standard errors for the 'partial coupling' transpiration model, as fitted by least-squares regression on the entire data-set ($n = 423$, $R^2 = 0.80$)

	Estimate	Asymptotic SE
g_0, mm s^{-1}	0.7	0.2
g_{max}, mm s^{-1}	92.1	18.0
$D_{1/2}$, Pa	60.3	16.8
$R_{1/2}$, W m^{-2}	26.6	4.2
T_{opt}, °C	29.2	2.1

explained 73% of total variance, compared with only 43% when the effects of decoupling are not taken into account. The difference resulted from a parallel increase in both systematic and non-systematic errors (Table 3). The 'complete coupling' model tended to underpredict transpiration: when calibrated on the first half of the data-set, in particular, it was unable to predict accurately the higher transpiration rates that were observed later in the season. The exercise demonstrates the value of cross-validation both as a test of model structure and as a guarantee of predicting ability (Bossel 1994). Although apparent, though, the superiority of the 'partial coupling'

model was not statistically significant, as the difference in MSE was only slightly larger than MSE variance (Wallach & Goffinet 1989).

Conclusions

The use of simple single-layer models to represent transpiration from broad-leaf forests has often been questioned, because of the vertical gradients observed both
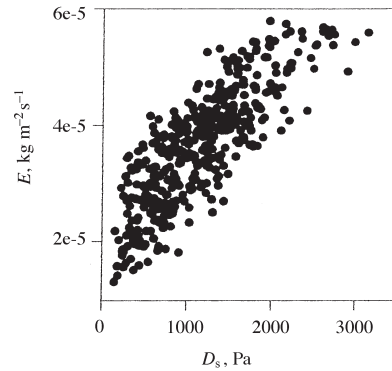

Figure 5. Changes in transpiration rates (E) as a function of vapour pressure deficit at the canopy surface (D_s), as estimated from Eqn 9.
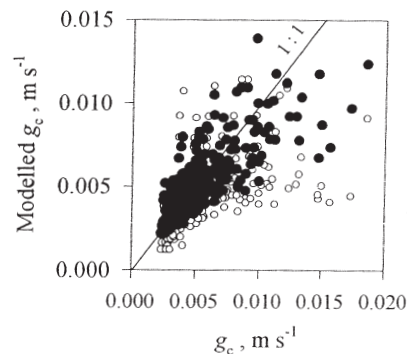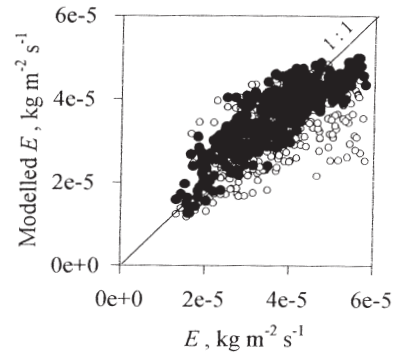

Figure 6. Predicted versus observed values of transpiration (E) and canopy conductance (g_c) when either the 'partial coupling' model (●) or the 'complete coupling' model (○) were cross-validated on independent data-sets.

	R^2	MSE $\times 10^{-11}$	MSE_s $\times 10^{-11}$	MSE_n $\times 10^{-11}$	$\sqrt{var(MSE)}$ $\times 10^{-11}$
Partial coupling model	0·72 (0·80)	2·87	1·22	1·65	3·56
Complete coupling model	0·43 (0·74)	7·32	3·04	4·26	
Difference		4·45			

Table 3. Comparison of 'partial coupling' and 'complete coupling' transpiration models. Models were fitted on, alternately, each half of transpiration measurements and tested on the remaining data-set. The Pearson coefficient (R^2) and mean squared error (MSE) of predicted versus observed g_c are reported. The R^2 of the model fitted on the entire data-set is also reported in brackets for comparison. The MSE is further partitioned in a systematic (MSE_s) and a non-systematic component (MSE_n). The comparison of MSE difference with the square root of MSE variance yields an estimate of its statistical significance

above and within the canopy (Jarvis & McNaughton 1986; Lhomme 1991). It appears, in contrast, that when the partial decoupling of the canopy from the overlying atmosphere is correctly accounted for, a 'big-leaf' approach can be used to explain and predict canopy conductance and transpiration, although the relationship between estimated stand-scale parameters and leaf physiological responses is not straightforward (Lhomme 1988; Lhomme 1991).

The effects of vertical gradients above the canopy appear to be significant for a temperate forest canopy, and would be arguably even more relevant in the case of grassland or tropical forests; in all these cases the model proposed could represent a convenient compromise between realism and simplicity (Raupach & Finnigan 1988).

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APPENDIX A: LIST OF VARIABLES AND PARAMETERS, UNITS AND VALUES USED IN THE ANALYSIS

Symbol	Variable or parameter	Value	Units
a	exponent in the response to temperature	0·5	
b	scaling coefficient for leaf boundary-layer resistance	0·0067	$m\,s^{-1/2}$
C	sensible heat flux		$W\,m^{-2}$
c_p	specific heat capacity of air	1012	$J\,kg^{-1}\,K^{-1}$
d	height of zero plane	0·75 H	m
$D_{1/2}$	coefficient for response to vapour pressure deficit		Pa
D_r	vapour pressure deficit at reference height		Pa
D_s	vapour pressure deficit at canopy surface		Pa
E	canopy transpiration per unit ground area		$kg\,m^{-2}\,s^{-1}$
E_{eq}	equilibrium transpiration		$kg\,m^{-2}\,s^{-1}$
E_{imp}	imposed transpiration		$kg\,m^{-2}\,s^{-1}$
g	acceleration by gravity	9·8	$m\,s^{-2}$
g_o	baseline canopy conductance		$m\,s^{-1}$
g_c	canopy conductance		$m\,s^{-1}$
g_i	climatological conductance		$m\,s^{-1}$
g_m	maximum modulated conductance		$m\,s^{-1}$
H	canopy height	19	m
k	Von Kármán's constant	0·41	
L	Monin-Obukhov length		m
LAI	projected leaf area index	3·8	
$R_{1/2}$	coefficient for response to global radiation		$W\,m^{-2}$
g_a	canopy aerodynamic conductance to scalars		$m\,s^{-1}$
r_b	canopy boundary-layer resistance		$s\,m^{-1}$
r_b^{un}	leaf boundary-layer resistance		$s\,m^{-1}$
R_g	incoming global radiation		$W\,m^{-2}$
R_n	net radiation above the canopy		$W\,m^{-2}$
r_t	canopy turbulent resistance to scalars		$s\,m^{-1}$
s	slope of saturation vapour pressure-temperature curve		$Pa\,K^{-1}$
T_{max}	maximum temperature for stomatal opening		°C
T_{min}	minimum temperature for stomatal opening	– 5	°C
T_{opt}	optimum temperature for stomatal opening		°C
T_r	air temperature at reference height		°C
T_s	canopy temperature		°C
u_*	friction velocity		$m\,s^{-1}$
$u(z)$	wind speed at height z (suffix: r, at reference height)		$m\,s^{-1}$
w	leaf width	0·05	m
z_{0M}	roughness length for momentum	0·1 H	m
z_r	reference height	22	m
α	attenuation coefficient for wind speed inside the canopy	3	
γ	psychrometer constant	≈ 66·1	$Pa\,K^{-1}$
ζ	stability parameter		
λ	latent heat of vaporization of water	≈ 2·45 × 10^6	$J\,kg^{-1}$
ρ_a	density of dry air	≈ 1·204	$kg\,m^{-3}$
Φ_H	stability function for heat and vapour		
Φ_M	stability function for momentum		
Ψ_H	deviation function for heat and vapour		
Ψ_M	deviation function for momentum		
Ω	decoupling coefficient		

APPENDIX B: COMPUTATION OF CANOPY AERODYNAMIC CONDUCTANCE

The aerodynamic conductance of the canopy to the exchange of scalars (g_a) results from the sum in series of a boundary-layer resistance (r_b) and a turbulent resistance (r_t):

$$\frac{1}{g_a} = r_b + r_t. \tag{B1}$$

The turbulent resistance to the exchange of scalars between the air within the canopy and the reference height z_r can be represented as (Garratt 1992)

$$r_t = \frac{1}{k\,u_*} \ln\left(\frac{z_r - d}{z_{0M}}\right) + \frac{1}{k\,u_*}\,\Psi_H, \tag{B2}$$

where d is displacement height, z_{0M} is the canopy roughness length for momentum, k is Von Kármán's constant and Ψ_H is a deviation function for temperature and water vapour. Values for parameters d and z_{0M} were derived from the literature (Rauner 1976; Dolman 1986; Garratt 1992) and were assumed to be independent of wind speed and constant over the season, since all measurements followed complete leaf expansion (Lindroth 1993). Whilst the first term in Eqn B2 is equal to the turbulent resistance to the exchange of momentum under neutral conditions, the second term accounts for the thermal instability induced by the flux of sensible heat (Monteith & Unsworth 1990) and resulting in lapse or inversion conditions.

Friction velocity can be either directly measured or derived from wind speed measurements at reference height u_r as (Garratt 1992):

$$u_* = \frac{k\,u_r}{\ln\left(\dfrac{z_r - d}{z_{0M}}\right) - \Psi_M}, \tag{B3}$$

where Ψ_M is a deviation function for momentum, analogous to Ψ_H

Since form drag, rather than skin friction, is the dominant mechanism for the absorption of momentum, the boundary-layer resistance is often regarded as an excess resistance involved in the transfer of scalars alone (Monteith & Unsworth 1990). In the case of the individual leaf, the boundary-layer resistance $r_b{}^{un}$ is a function both of local wind speed $u(z)$ and of leaf width w. Following Nobel (1991) it can be represented as:

$$r_b{}^{un} = b\,\sqrt{\frac{w}{u(z)}}, \tag{B4}$$

where b is a proportionality coefficient. In the case of the entire canopy, the boundary-layer resistance is a complex function of leaf area and wind speed distribution. However, under the simplifying assumptions of exponential wind profile (Garratt 1992) and uniform leaf area distribution, Choudhury & Monteith (1988) have

demonstrated that it can be derived from Eqn B2 and expressed as:

$$r_b = \frac{1}{LAI}\ b\ \sqrt{\frac{w}{u(H)}\ \frac{\alpha}{[1 - \exp(-\alpha/2)]}}, \tag{B5}$$

where LAI is the canopy projected leaf area index and α is an attenuation coefficient for wind speed inside the canopy. The wind speed at the top of the canopy $u(H)$ can be estimated from friction velocity $u*$ as:

$$u(H) = \frac{u_*}{k}\left[\ln\left(\frac{H - d}{z_{0M}}\right) - \Psi_M\right]. \tag{B6}$$

Computation of deviation functions under non-neutral conditions in Eqns B2, B3 and B6 is based on Monin-Obukhov similarity theory (Monteith & Unsworth 1990; Garratt 1992). Stability conditions are characterized by the value of the stability parameter ζ:

$$\zeta = \frac{z_r - d}{L}. \tag{B7}$$

The Monin-Obukhov length is given by:

$$L = -\frac{\rho\,c_p\,u_*^3\,T_r}{k\,g\,C}, \tag{B8}$$

where T_r is the absolute air temperature at the reference height, g is acceleration by gravity and C is sensible heat flux.

Under unstable (lapse) conditions (for $\zeta < 0$):

$$\Psi_M = 2\ln\left(\frac{1 + \dfrac{1}{\Phi_M}}{2}\right) + \ln\left(\frac{1 + \dfrac{1}{\Phi_M{}^2}}{2}\right) - 2\ \tan^{-1}\frac{1}{\Phi_M} + \frac{v}{2}, \tag{B9}$$

$$\Psi_H = 2\ln\left(\frac{1 + \dfrac{1}{\Phi_H}}{2}\right) \tag{B10}$$

where the stability functions for heat and for momentum are given by:

$$\Phi_H = \Phi_M{}^2 = (1 - 16\zeta)^{-1/2}. \tag{B11}$$

Under stable (inversion) conditions (for $\zeta > 0$) or neutral conditions (for $\zeta = 0$):

$$\Psi_M = \Psi_H = -5\zeta. \tag{B12}$$

APPENDIX C: VAPOUR PRESSURE DEFICIT GRADIENTS UNDER CONDITIONS OF PARTIAL COUPLING

The vapour pressure deficit at the canopy surface (D_s) exceeds the value above the canopy (D_r) if equilibrium

transpiration E_{eq} exceeds imposed transpiration E_{imp}, defined as (Jarvis & McNaughton 1986):

$$E_{eq} = \frac{s\, R_n}{\lambda\,(s+g)}, \tag{C1}$$

$$E_{imp} = \frac{\rho_a\, c_p}{\lambda\,\gamma}\, g_c\, D_r, \tag{C2}$$

$$E = \Omega\, E_{eq} + (1-\Omega)\, E_{imp}. \tag{C3}$$

It can be seen that:

$$\Omega\,(E_{eq} - E_{imp}) = E - E_{imp} = \frac{\rho_a\, c_p}{\lambda\,\gamma}\, g_c\,(D_s - D_r). \tag{C4}$$

From Eqn C4 it follows that:

$$(D_s - D_r) = (E_{eq} - E_{imp})\,\Omega\,\frac{\lambda\,\gamma}{\rho_a\, c_p\, g_c}, \tag{C5}$$

and, since both g_c and the decoupling coefficient Ω are always positive, the sign of the humidity gradient is determined by the balance between equilibrium and imposed transpiration. It follows from Eqn C5 that the different behaviour of temperate and tropical broad-leaf forests and crop canopies reported in the literature (Aussenac & Ducrey 1977; Shuttleworth *et al.* 1985; Jarvis & McNaughton 1986; Grantz & Meinzer 1990; Meinzer *et al.* 1997) derives not only from their different degrees of coupling, but also from site microclimate and stomatal characteristics.