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Three methods for monitoring the gas exchange of individual tree canopies: ventilated-chamber, sap-flow and Penman–Monteith measurements on evergreen oaks

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Summary

1. Physiological methods applicable to scales between individual leaves and whole forests have the potential to improve substantially our understanding of ecosystem gas exchange.
2. We compared three approaches for determining the canopy gas exchange of individuals representing a pair of mediterranean-climate oak species.
3. We estimated transpiration from the Penman–Monteith equation, measured sap flow with heat-balance sensors, and also measured net CO₂ assimilation, transpiration and conductance with a whole-canopy gas-exchange system.
4. Simultaneously measured sap flow and chamber transpiration were qualitatively similar, provided that the sensors were designed to compensate for thermal gradients along the tree trunk. Both *in situ* and bench-top measurements indicated that the quantitative relationship between transpiration and the signal from the sap-flow sensor varied among stems. The sap flow of individual trees measured on consecutive days with the tree in the chamber 1 day, and out the next, was similar, indicating that enclosure had only a small impact on transpiration. Total daily sap flow, which was similar during atmospherically moist period to the Penman–Monteith transpiration calculated assuming a fixed stomatal conductance, became almost insensitive to further increases in evaporative demand during hot and dry intervals.
5. While the application of each approach is limited by experimental considerations, these shortcomings may be overcome by using the techniques in combination.

Key-words: Conductance, evaporation, *Quercus agrifolia*, *Quercus durata*, transpiration

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Introduction

Researchers need a better understanding of the role plants play in controlling the flux of water vapour and carbon dioxide between forests and the atmosphere (Jarvis & McNaughton 1986; Committee on Global Change 1990). Achieving this understanding will require an interdisciplinary effort to link leaf-level physiology with canopy measurements based on micrometeorological techniques. One possible strategy is to scale gas exchange directly from the leaf to the canopy, bypassing explicit consideration of

processes that occur at the whole-plant level (Baldocchi, Luxmoore & Hatfield 1991; Baldocchi 1993). While this approach holds promise, it precludes the possibility of drawing upon a body of theory, derived from community (Tilman 1988) and evolutionary (Bloom, Chapin & Mooney 1985) studies, that is based on the response of the individual to the environment. In contrast, approaches that explicitly consider whole-plant processes have the potential to explore the consequences of plant-to-plant variation in physiological characteristics and access to resources, as well as capitalize on possible simplifications resulting from physiological integration at the level of the individual. Unfortunately, past progress in this direction has been limited by the unavailability

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of reliable and non-labour-intensive gas-exchange techniques that are directly applicable to whole-tree canopies.

At least three approaches for monitoring gas exchange, chamber methods, sap-flow methods, and energy balance methods may be applied to individual plant canopies (Denmead 1984). Ventilated chambers, operated as open gas-exchange systems (Field, Ball & Berry 1989), allow continuous measurement of whole-tree transpiration and photosynthesis (Wong & Dunin 1987; Garcia, Norman & McDermitt 1990; Leuning & Foster 1990). While chamber measurements have the advantage of directly measuring the exchange of a range of gases, they can be criticized because the microenvironment of the plant is substantially changed. Enclosure alters the canopy boundary layer (Denmead 1984), vapour pressure deficit (Lee 1966), radiation budget (Denmead 1984; Leuning & Foster 1990) and light penetration (Wong & Dunin 1987; Legg 1988).

Heat-balance sap-flow sensors provide a second technology for directly measuring whole-tree transpiration (Dugas 1990). Although the potential accuracy of sap-flow sensors is well established (Schulze *et al.* 1985; Dugas 1990), other aspects of their interpretation and analysis remain unclear. Outstanding issues include the significance of longitudinal temperature gradients that may confound the signal of some designs (Cermak & Kucera 1981), the possibility that circumferential or radial heterogeneity in flow may create errors in scaling flux density to the whole tree (Edwards & Booker 1984), and the magnitude of the time lag between sap flow and transpiration (Schulze *et al.* 1985).

A third approach is to analyse the plant's energy budget in order to predict transpiration from measured environmental and physiological parameters. The Penman-Monteith equation requires net radiation, saturation vapour deficit, air temperature and bulk stomatal and boundary layer conductances as inputs for a prediction of individual tree transpiration. The plant may be treated as a single 'big leaf' described by average parameters or broken into several horizontal layers which are considered separately. The usefulness of the Penman-Monteith equation is limited by the difficulty of obtaining the required parameters with satisfactory accuracy (Denmead 1984).

In this study we used each of these approaches to determine the canopy gas exchange of evergreen oaks with projected areas from 3 to 14 m². The purpose of this paper is threefold. First we cross-validate the methods and discuss consequences of using them in combination. Limitations of each approach can be overcome by simultaneously applying multiple approaches. Second, we modified each approach and describe these modifications. Third, we discuss ground-area-based transpiration, conductance, photosynthesis and boundary layer conductance as

well as evidence of the relationship between evaporative demand and transpiration for the study plants.

Materials and methods

STUDY SITE

This project was conducted at Stanford University's Jasper Ridge Biological Preserve, in the eastern foothills of the Santa Cruz mountains, 37°24'N 122°13'W, San Mateo county, California, USA. The study site was level and located on soil derived from serpentine rock. The vegetation was a heterogeneous mix of chaparral shrubs, evergreen sclerophyllous trees, and patches of grassland. A similar site 0.7 km to the north-west was characterized by Davis & Mooney (1986). The work described here was part of a larger study investigating the causes and consequences of rooting depth in a comparison of two evergreen oaks (Goulden 1991). *Quercus durata* Jeps. is a serpentine endemic shrub, while *Q. agrifolia* Nee is a common tree throughout coastal California. At the study site *Q. agrifolia* is much less deeply rooted than *Q. durata* and comes under severe water stress early in the summer drought. *Quercus durata* is limited to 3 m in height, has low leaf area indices (LAI, 1.5–3 m² m⁻²) and small leaves (1–2 × 2–4 cm) while *Q. agrifolia* may grow to 20 m, has a variable LAI (1–10 m² m⁻²) and moderate-sized leaves (2–4 × 3–6 cm).

LONG-TERM MEASUREMENTS

The local microclimate of a meadow 100 m from the study was monitored and the rate of sap flow through five *Q. agrifolia* and four *Q. durata* was measured from October 1989 to January 1991. Data loggers (21X, Campbell Scientific, Logan, Utah, USA) recorded hourly means of wind speed (μ) measured with a cup anemometer, air temperature at 1.5 m (T_{air}) measured with a thermistor, incoming short-wave radiation (R_s) measured with a silicon pyranometer, relative humidity measured with a capacitance sensor and sap flow.

SAP-FLOW PROBE DESIGN AND INSTALLATION

Granier (1985, 1987b) described a simple sap-flow sensor applicable to trees. A pair of probes separated vertically by 10–15 cm is implanted in the sap-wood (Fig. 1). The top probe is heated with constant power and the temperature difference between the probes monitored with thermocouples (ΔT_{raw}). As sap flow increases, progressively more heat is swept away from the top probe, decreasing ΔT_{raw} . Granier (1985) provided a one-dimensional analytical solution along with excised stem calibrations indicating

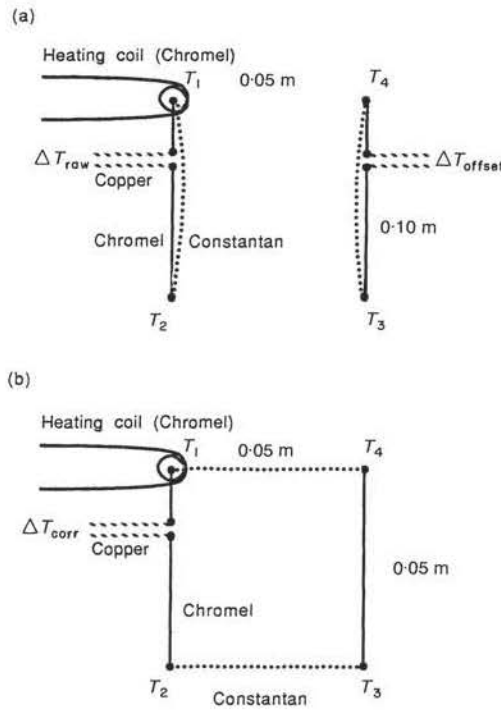


Fig. 1. (a) Thermocouple array for determining the impact of temperature gradients on sap-flow measurements. Black lines are chromel wire, dotted are constantan and dashed are copper communication cable. The raw sap-flow signal ($\Delta T_{\text{raw}} = T_1 - T_2$), and the thermal offset ($\Delta T_{\text{offset}} = T_4 - T_3$). (b) Thermocouple array for temperature gradient-corrected measurements under normal operating conditions. The corrected signal ($\Delta T_{\text{corr}} = (T_1 - T_2) - (T_4 - T_3)$).

that sap flow is almost linearly related to the dimensionless sap-flow coefficient (K). K is calculated as:

$$K = (\Delta T_m - \Delta T_{\text{raw}}) / \Delta T_{\text{raw}} \quad \text{eqn 1}$$

where ΔT_m is the signal in the absence of flow (recorded at 04.00–05.00h).

Sensors were constructed according to the design of Granier (1985) with the following modifications. Aluminium cylinders (1 cm long) were used for both the heated and reference probes and surfaces were insulated with a thin coat of nitrocellulose wood sealer to reduce errors associated with stray voltages. The probes were installed in freshly bored holes in the outermost 1 cm of sap-wood which were packed with silicone heat sink compound. The main probe was heated at approximately 50mW using a 75mA constant power source. The sensors were shielded from rain with polyethylene sheet and the stem was thermally insulated with 0.160m thick fibreglass extending approximately 0.3m above and below the sensor. The sensors were connected to the data logger through a multiplexer (AM32, Campbell Scientific), using low capacitance data communication cable. The data logger scanned the probe signals every 5s and recorded hourly means, converting the probe voltage to $^{\circ}\text{C}$ using a Seebeck coefficient of $62 \mu\text{V}^{\circ}\text{C}^{-1}$.

TEMPERATURE GRADIENT COMPENSATION

Granier's method (1985) assumes the tree stem is isothermal in the absence of applied heating while Cermak & Kucera (1981) observed substantial longitudinal temperature gradients over the course of 1 day. Because naturally occurring longitudinal temperature offsets (ΔT_{offset}) are included in the probe signal (ΔT_{raw}) fluctuating temperature gradients will appear in the sensor signal and may be incorrectly attributed to changes in sap flow. In order to investigate the importance of temperature gradients, two sets of probes were installed, separated 5cm circumferentially in the stem of a *Q. agrifolia* (Fig. 1a). The left set was positioned according to the original design of Granier (1985). The upper probe (T_1) was continuously heated with 50mW and its temperature referenced to the probe 10cm below (T_2) (ΔT_{raw}). Neither probe of the right set was heated and the signal was thus proportional to the vertical temperature gradient in the absence of applied heat (ΔT_{offset}).

These investigations established that substantial temperature gradients were common in the stems of our study trees. Consequently, the design of Granier (1985) was modified to include a thermocouple network for automatically compensating natural thermal gradients (Fig. 1b; Cermak & Kucera 1981). The modified probes produce the corrected temperature signal, ΔT_{corr} , defined as:

$$\Delta T_{\text{corr}} = (T_1 - T_2) - (T_4 - T_3) \quad \text{eqn 2}$$

where T_1 is the signal from the upper left probe (heated), T_2 from the lower left probe, T_3 from the lower right probe and T_4 from the upper right probe. This configuration effectively eliminates longitudinal and circumferential temperature gradients from the measurement of ΔT_{corr} . Because heating at T_1 has minimal influence on the reference probes (T_2 , T_3 and T_4) the resulting signal should conform to the analysis of Granier (1985). In practice, several implantations were sometimes necessary to ensure that, in the absence of applied heat, ΔT_{corr} remained below 0.1°C over the course of 1 day.

SAP-FLOW SENSOR CALIBRATION

We determined the relationship between the sap-flow coefficient K and water flow per sap-wood area in the laboratory by clamping excised stem segments (0.1 m diameter, 0.3 m long) of *Q. agrifolia* between a pair of O-rings and 0.95 cm thick plexiglass plates. A sap-flow sensor was installed in each segment and 10mm citric acid was drawn through the stem, using pressure differentials up to 6kPa (Sperry, Donnelly & Tyree 1988). Thirty minutes was allowed for equilibration following all flow changes and the sensor signal was determined at no flow (ΔT_m) every 3–4 calibration points. Sap-wood area was measured

by perfusing the stem with safranin-o dye, cutting the stem at the sensor and weighing an acetate tracing of the stained sap-wood. The stem cross-section was examined for qualitative variation in staining intensity.

VENTILATED CHAMBER

We followed the daily course of transpiration and its relationship to sap flow for four trees with canopies up to 14 m² using a large, open gas-exchange system. Measurements were made on sunny, cool days under well-watered conditions during November 1990 and March and April 1991. The chambers were simple envelopes, constructed by sealing a pair of clear 0.15-mm thick polyethylene sheets, each up to 7.7 × 8.4 m, on two edges by heat impulse and on the other edges with adhesive-backed 1.9 cm wide Velcro strips. The Velcro provided an opening for admitting the tree and, in combination with tape around the base of the trunk, sealed the chamber. Air was forced into the chamber using a 0.23 m³ s⁻¹ (free air) blower and mixed within the chamber using a 4.4 m³ s⁻¹ fan hung in the canopy. Air left the bag through a 0.104-m diameter duct placed opposite the inlet and through numerous small leaks along the seams. The high inlet flow created a positive pressure that lifted the polyethylene off the foliage. We varied air flow into the chamber using restrictions over the blower inlet to maintain sufficient water vapour and CO₂ concentration changes across the bag. Flow into the bag was monitored through a 0.158-m diameter, 0.8-m long PVC duct using a 0–10 m s⁻¹ solid-state anemometer (Sierra Instruments, Carmel, California, USA). We calibrated the anemometer to total flow by measuring the time required to inflate a 10-m long × 0.47-m diameter (1.73 m³ total volume) collapsible polyethylene duct. Flow past the anemometer was constant until the polyethylene duct was almost fully inflated.

Leaf temperature was measured within the chamber using 15 0.15-mm chromel–constantan thermocouples affixed to leaves with porous medical tape (T_{leaf}). Air water content and temperature were monitored in the two ducts using capacitance humidity sensors and either platinum resistance temperature detectors or chromel–constantan thermocouples. CO₂ exchange was monitored by passing air directly from the inlet and outlet ducts through a differential IRGA (LI-6251, Li-Cor, Lincoln, Nebraska, USA). The IRGA zero was automatically checked every 2 h. The instrument was calibrated at the start of the campaign in absolute mode and the raw differential signal was converted to $\mu\text{l l}^{-1}$ by assuming an ambient CO₂ concentration of 365 $\mu\text{l l}^{-1}$ (Li-Cor 1988). We measured photosynthetically active photon flux density with a horizontal quantum sensor in a clearing near the chamber (LI-190sb, Li-Cor). All sensors were monitored at 5-s

intervals and recorded as 15-min means. A 550-W gasoline generator 20 m from the tree supplied power. Calculations followed Field *et al.* (1989) for an open system except that water vapour dilution effects were ignored in the photosynthesis and intercellular CO₂ (c_i) calculations. Intercellular CO₂ was calculated ignoring the contribution of wood respiration to net CO₂ exchange and assuming a concentration of 365 $\mu\text{l l}^{-1}$ entering the bag (typical ambient conditions during March and April 1991). Canopy transpiration (E), net assimilation (A_n) and stomatal conductance (g_s') are expressed per unit of ground area. Sap flow was simultaneously logged at 15-min intervals using sensors installed during October 1989.

PLANT BOUNDARY LAYER CONDUCTANCE

The boundary layer conductance (g_a) of an individual 3-m tall moderately exposed *Q. durata* was determined from the plant's energy balance (Thorpe & Butler 1977). We measured incoming short-wave radiation with a silicon pyranometer (LI-200sb, Li-Cor) placed parallel to the plant surface and plant surface temperature with a tripod mounted IR thermometer (Everest Interscience, California, USA) positioned to view approximately 0.25 m². Incoming long-wave radiation was estimated from the Swinbank equation and outgoing long-wave radiation from the Stefan–Boltzmann law assuming an emissivity of 1.0 (Monteith 1973). Daily average short-wave reflectance and transmittance were determined with a thermopile pyranometer (Eppley Laboratory, Rhode Island, USA). Latent heat was calculated from sap flow assuming no water storage time lag. Air temperature and wind speed were determined 1 m directly above the canopy using a low-threshold cup anemometer and a fine-wire thermocouple. Heat storage in the canopy, reflected short-wave intercepted by the canopy and below-canopy long-wave transfer were neglected. All sensors were monitored at 5-s intervals recorded as 15-min means over the course of several days. The plant boundary layer conductance was calculated from the air-to-plant temperature difference and the sensible heat exchange estimated as the residual energy not measured as radiation or latent heat (Monteith 1973; Campbell 1977; Thorpe & Butler 1977). Only data points with greater than 200 W m⁻² net radiation and 0.7° air-to-leaf temperature differentials were used.

PENMAN–MONTEITH TRANSPIRATION

Total daily transpiration in the absence of stomatal closure or seasonal changes in LAI was calculated from the Penman–Monteith equation (Campbell 1977; Jarvis & McNaughton 1986). Canopy conductance (g_c) for each plant was set at the maximum observed for that individual over the course of a

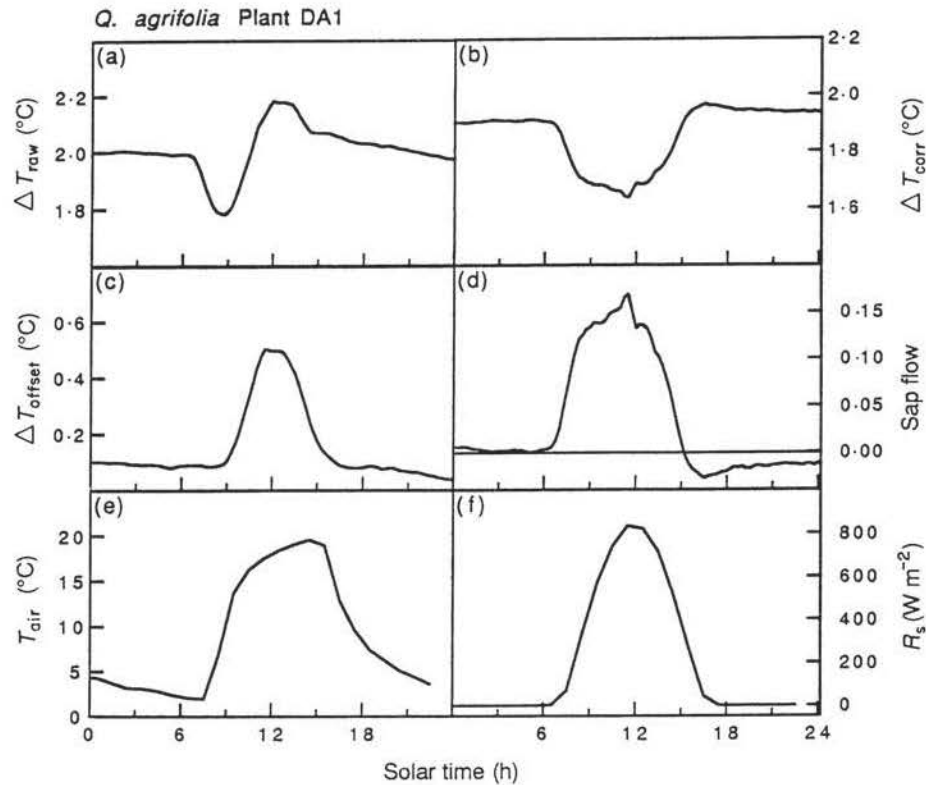


Fig. 2. Diurnal course of (a) raw sap-flow signal (ΔT_{raw}), (b) corrected sap-flow signal (ΔT_{corr}), (c) longitudinal temperature gradient over 0.1 m of stem (ΔT_{offset}), (d) dimensionless sap-flow coefficient (K), (e) air temperature at 1.5 m (T_{air}), and (f) solar radiation (R_s). (a–d) Data are for an individual of *Quercus agrifolia* plotted as lines connecting 15-min means; (e and f) the lines connect 60-min means. Naturally occurring temperature gradients were removed in the calculation of the corrected sap-flow signal and K by subtracting ΔT_{offset} from ΔT_{raw} .

spring day using the ventilated chamber. Peak stomatal conductance typically occurred early in the day, prior to the onset of elevated chamber air temperature and associated stomatal closure. Boundary layer conductance (g_a) for all plants was calculated as:

$$g_a = m(\mu)^{0.5} + c \quad \text{eqn 3}$$

where μ is wind velocity and the coefficients m and c were determined using a single linear regression derived from the energy budget of a *Q. durata*. Incoming and outgoing long-wave radiation were calculated as above. Intercepted radiation was calculated using the reflectance and transmittance values measured above. Hourly measurements of sap flow, air temperature, relative humidity, wind speed and solar radiation were taken from the long-term data set. Sap flow (K) was converted to E ($\text{mmol m}^{-2} \text{s}^{-1}$) using the ventilated-chamber relationship for each plant. On occasion the anemometer malfunctioned and we substituted a typical wind speed of 1 m s^{-1} . This had little impact on the calculated transpiration rate since stomatal conductance was always substantially lower than boundary layer conductance (i.e. a low Ω ; Jarvis & McNaughton 1986; Valentini *et al.* 1991). In August 1990 the main weather station failed and we used meteorological data from a secondary

station located approximately 3 km to the north-west. Differences between the meteorological conditions at the two stations were minor (data not shown).

Results

IMPACT OF TEMPERATURE GRADIENTS ON SAP-FLOW SENSORS

The raw sap-flow signal bears little resemblance to the signal expected from a typical daily course of transpiration (Fig. 2a). ΔT_{raw} increased after mid-morning, leading to the unlikely conclusion that sap flow was maximal at 08.00h and minimal at 12.00h. ΔT_{offset} peaked at 0.5°C (Fig. 2). Temperature offsets of this magnitude, presumably the result of large diurnal oscillations in air temperature (Fig. 2e), are sufficiently large to obscure the cooling effect of sap flow on the heated sensor. In order to correct for the longitudinal temperature gradients, ΔT_{corr} was calculated as the difference between ΔT_{raw} and ΔT_{offset} . The corrected sensor signal (Fig. 2b) and the corrected K (Fig. 2d) broadly parallel the temporal pattern of incoming solar radiation (R_s ; Fig. 2f). In the absence of applied heat (data not shown) the two sets of probes (ΔT_{raw} and ΔT_{offset}) did not deviate from each other by more than 0.1° over the course of a day.

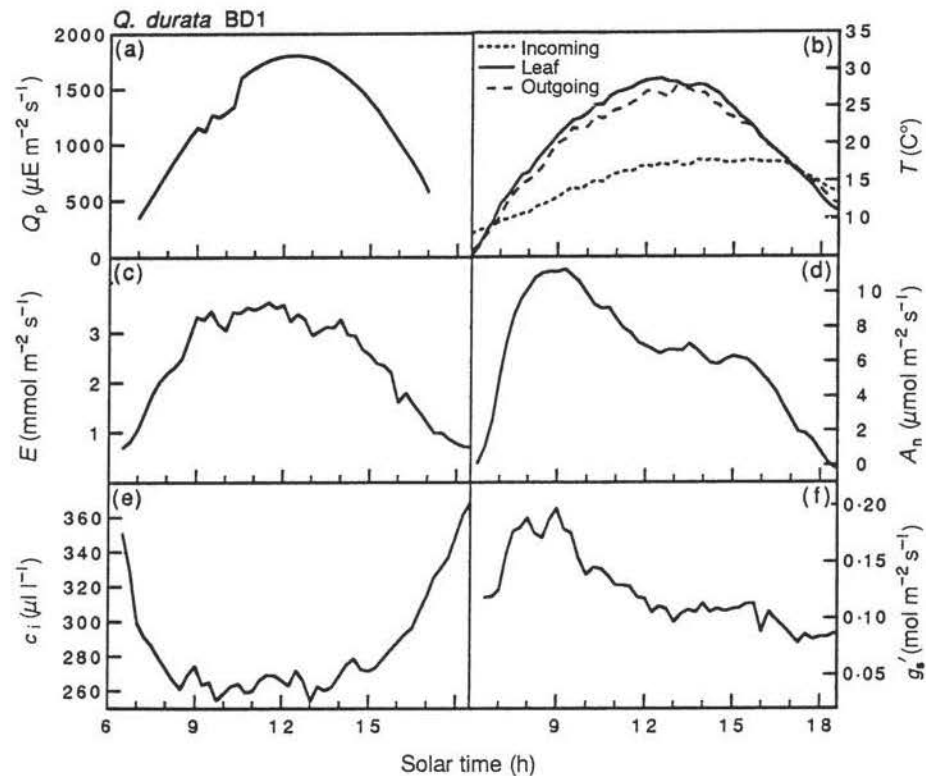


Fig. 3. Diurnal course of (a) photon flux density (Q_p), (b) leaf, chamber air temperature (outgoing), and ambient air temperature (incoming), (T), (c) ground-area-based transpiration (E), (d) ground-area-based net photosynthesis (A_n), (e) leaf intercellular CO_2 concentration (c_i) and (f) ground-area-based stomatal conductance (g_s'), measured on a 3-m² *Q. durata* (plant BD1, 11 April 1991) using the ventilated chamber. All data plotted as line segments connecting 15-min means.

VENTILATED-CHAMBER MEASUREMENTS

Figure 3 reports the daily course of gas exchange for a 3-m² (ground area) *Q. durata*. The day was cool and sunny except for a few mid-morning clouds (Fig. 3a,b). Air temperature within the chamber was substantially elevated over ambient temperature, while leaf and chamber temperatures within the bag were similar (Fig. 3b). Transpiration (E) peaked (09.00h) and began declining (12.00–14.00h) ahead of horizontal PFD (Q_p) (Fig. 3a,c). This was probably a result of exposure, as the plant was unobstructed to the south-east and received the sun's first light, while to the south-west it was shaded by neighbours. Photosynthesis (A_n) and conductance (g_s') were highest in the mid-morning, decreasing to approximately 60% of maximum in the mid-afternoon (Fig. 3d,f). The intercellular CO_2 concentration (c_i) remained constant over the middle of the day (Fig. 3e). Among plants, peak photosynthesis was variable (6–38 $\mu\text{mol m}^{-2} \text{s}^{-1}$), but tended to parallel plant-to-plant variation in LAI (Goulden 1991).

The daily courses of transpiration measured with the ventilated chamber (E) and sap flow (K) measured with an implanted sensor were qualitatively similar, with sap flow lagging transpiration by approximately 30 min (Fig. 4). Additional measurements (not shown) yielded lag times from 0 to 60 min that were not related to plant size. The response of

sap flow to abrupt changes in transpiration was reduced (cf. Fig. 4b at 08.00h).

Figure 5 reports the daily course of sap flow (K) over consecutive days, with and without the chamber in place. The chamber was placed over the plant on

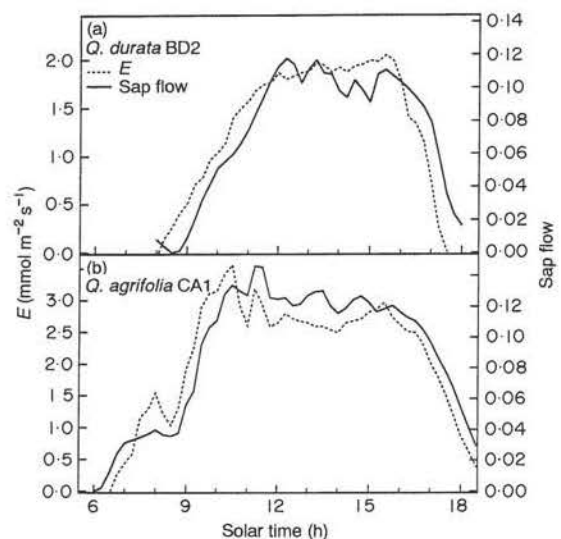


Fig. 4. Simultaneous diurnal course of ventilated-chamber transpiration (E , lines connecting 15-min means) and sap flow (K , 15-min means) for (a) *Quercus durata* (plant BD2, 8 March 1991) and (b) *Q. agrifolia* (plant CA1, 16 April 1991).

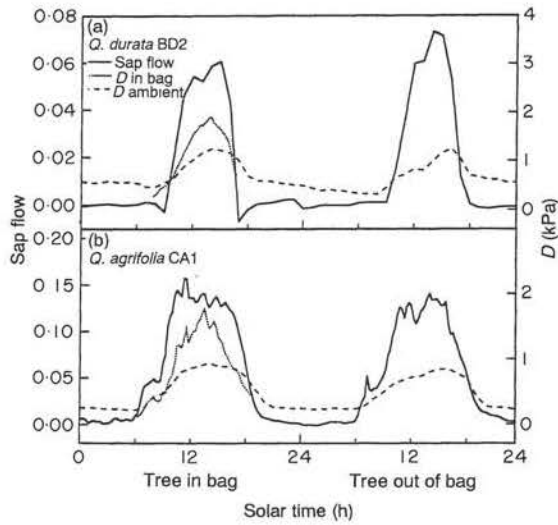


Fig. 5. Sap flow on consecutive days with the plant in (day 1) and out (day 2) of the ventilated chamber for (a) *Quercus durata* (plant BD2, 30 November 1990–1 December 1990) and (b) *Q. agrifolia* (plant CA1, 16 April 1991–17 April 1991). Sap-flow plots are lines connecting (a) 60-min means or (b) 15-min means, vapour saturation deficit (D , 15-min means) inside the chamber was measured at the exhaust duct and ambient D (60-min means) was measured in a nearby clearing.

the afternoon before the data set began and removed from the plant at dusk on the first day. Air temperature and vapour saturation deficit (D) were substantially elevated over ambient within the chamber, while ambient vapour saturation deficit was similar between the 2 days of each run (Fig. 5a,b). In spite of the increase in vapour saturation deficit and almost certain changes in boundary layer conductance, sap flow was similar between the 2 days of each run. The difference in vapour saturation deficit coupled with the similarity in sap flow between the 2 days indicates that conductance and presumably photosynthesis were reduced within the chamber.

SAP-FLOW SENSOR CALIBRATION

A comparison of the quantitative relationship between the sap-flow signal (K) and ground-area based transpiration (E) for four trees in the field is shown in Fig. 6. In order to reduce the role of hysteresis caused by water storage, transpiration was lagged relative to sap flow to maximize the fit ($r^2 = 0.80\text{--}0.95$). The slope of the relationship for three of the plants was similar ($17.7\text{--}23.9\text{ mmol s}^{-1}\text{ m}^{-2}$) while a fourth differed markedly ($2.9\text{ mmol s}^{-1}\text{ m}^{-2}$).

The relationship between water flow and sensor signal (K) was also linear for four excised stems of *Q. agrifolia* (Fig. 7; $r^2 = 0.92\text{--}0.99$). Three of the sensors had similar responses ($51.7\text{--}59.8\text{ mol s}^{-1}\text{ m}^{-2}$), while a fourth was more sensitive to flow ($20.3\text{ mol s}^{-1}\text{ m}^{-2}$). All of the calibration slopes were higher than those reported by Granier (1985) as the sensors are less sensitive at the lower power inputs used in this study. Qualitative examinations of staining across the sap-wood indicated that four to five growth rings were hydroactive. Staining intensity across the sap-wood of the stem with the unusual calibration curve was circumferentially uneven. The stem apparently had been wounded in the past, creating an area of low flow in a region longitudinally close but circumferentially displaced from the sensor.

PLANT BOUNDARY LAYER CONDUCTANCE AND PENMAN-MONTEITH TRANSPIRATION

Plant boundary layer conductance (g_a) on a ground-area basis was linearly related to the square root of wind speed (μ) by the function:

$$g_a = 0.34 + 5.66(\mu)^{0.5} \quad \text{eqn 4}$$

($r^2 = 0.49$, $n = 73$) (Fig. 8). This relationship was combined with the peak canopy stomatal conductance measured using the ventilated chamber on two

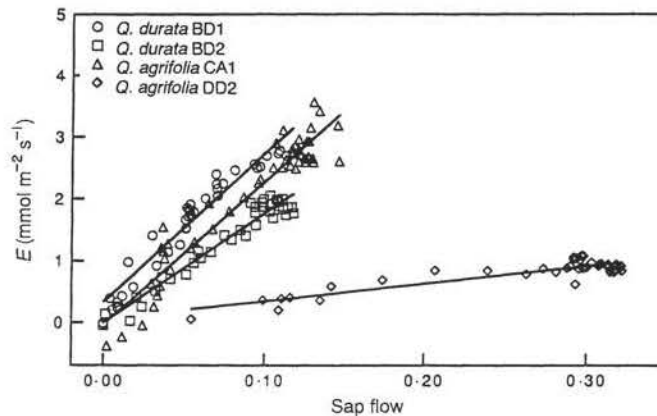


Fig. 6. Sap flow (K) vs ground-area transpiration (E) for four study plants. E was lagged separately for each plant (0–60 min) to maximize fit ($r^2 = 0.80\text{--}0.95$). The slope of the relationship varied between 17.7 and $23.9\text{ mmol s}^{-1}\text{ m}^{-2}$ for BD1, BD2 and CA1, and was $2.9\text{ mmol s}^{-1}\text{ m}^{-2}$ for DD2.

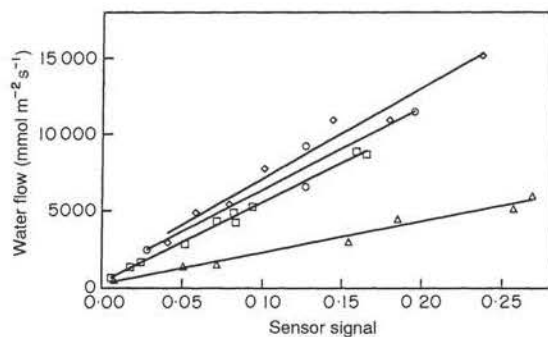


Fig. 7. Excised stem calibration for four stems of *Quercus agrifolia*. Water flow is on a sap-wood area basis and sap flow (K) is dimensionless. Slopes were 51.7 – $59.8 \text{ mol s}^{-1} \text{ m}^{-2}$ for the circle, square and diamond plots and $20.3 \text{ mol s}^{-1} \text{ m}^{-2}$ for the triangle plot.

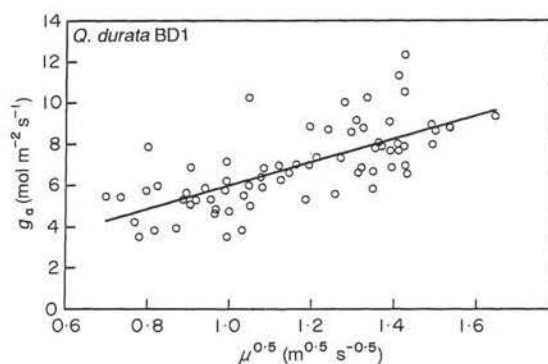


Fig. 8. Aerodynamic boundary layer conductance (g_a , 15-min means over several days) for *Quercus durata* (plant BD1, 14 February 1991–18 February 1991) as a function of the square root of wind speed, $g_a \text{ (mol m}^{-2} \text{ s}^{-1}) = 0.34 + 5.66 \mu^{0.5} \text{ (m}^{0.5} \text{ s}^{-0.5})$ ($r^2 = 0.49$, $n = 73$).

trees (*Q. agrifolia* plant CA1, 16 April 1991, $g_c = 0.22 \text{ mol m}^{-2} \text{ s}^{-1}$; *Q. durata* plant BD2, 8 March 1991, $g_c = 0.08 \text{ mol m}^{-2} \text{ s}^{-1}$) to calculate the Penman–Monteith transpiration over the study period. Sap-flow and Penman–Monteith transpiration in *Q. durata* were approximately equal under conditions of moderate evaporative demand while water use was independent of atmospheric conditions during hot-dry periods (Fig. 9a). The relationship was similar for the individual of the shallowly rooted species *Q. agrifolia* during periods of favourable soil moisture (Fig. 9b, circles; January 1990–June 1990; Goulden 1991), while during periods of drought (October 1989–December 1989 and June 1990–October 1990, diamonds), sap flow was consistently low. The quantitative agreement between sap-flow and Penman–Monteith transpiration establishes the internal consistency of the methods. However, the intercomparison does not ensure the absolute accuracy of the two measures as both are derived from a single set of ventilated-chamber observations.

Discussion

SAP-FLOW SENSOR FUNCTION

Longitudinal temperature offsets similar to those reported by Cermak & Kucera (1981) were not eliminated with thermal insulation, but their impact was reduced by measuring the offset with a second pair of adjacent probes (Figs. 1b and 2). This approach is similar to that described by Cermak & Kucera (1981). Granier (1985, 1987b) did not report errors associated with thermal gradients, probably because the original sensor design used more power to heat the main probe. Increased probe power causes a larger temperature decrease for a given K and also raises the sensitivity of K to sap flow (Granier 1985) both of which tend to minimize the impact of thermal gradients. Strong heating, however, may increase the risk of thermal damage to

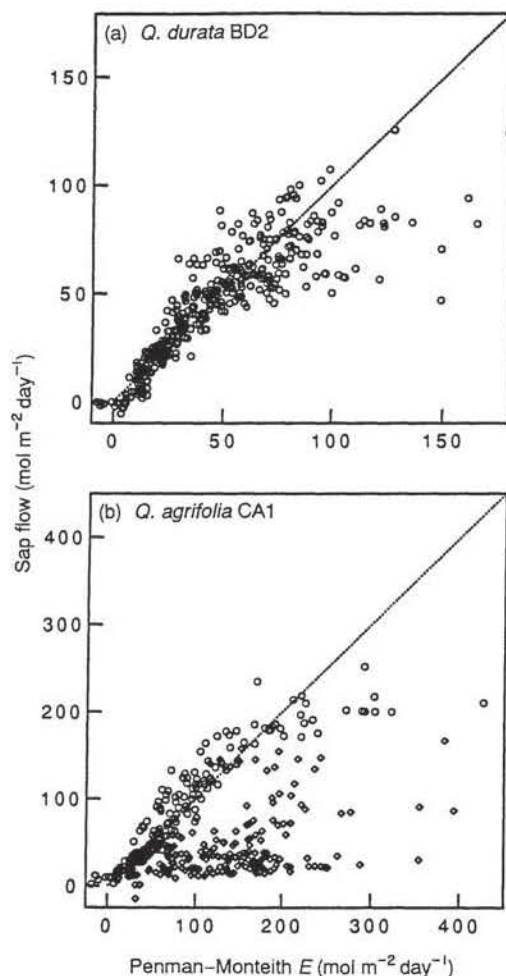


Fig. 9. Daily integrated sap flow (calibrated with the ventilated chamber) as a function of Penman–Monteith E . For the calculation of Penman–Monteith E , hourly means of wind speed, air temperature, relative humidity and solar radiation were measured in a nearby clearing, g_c was set at the maximum measured over the course of a spring day in the ventilated chamber (BD2, 8 March 1991, $g_c = 0.08 \text{ mol m}^{-2} \text{ s}^{-1}$; CA1, 16 April 1991, $g_c = 0.22 \text{ mol m}^{-2} \text{ s}^{-1}$), and g_a was calculated from the relationship in Fig. 7.

the sap-wood and the lower power in the design reported here brings the temperature elevation closer to that used in other sensor designs (Schulze *et al.* 1985). The lower power also allows the probes to be placed closer together, reducing the temperature offset. Researchers following the original Granier protocol can check for the magnitude of temperature offsets by monitoring the daily course of sensor signal in the absence of heating.

The daily course of sap flow and transpiration were qualitatively similar and differed in a manner consistent with a modest water storage in the stem (Fig. 4). The damping of sap flow relative to transpiration is similar to that reported by Decker & Skau (1964) and indicates that the sensors should not be used for short-term measurements of E under rapidly changing conditions. The morning lag times between sap flow and transpiration were shorter than those observed by Schulze *et al.* (1985). This is probably a result of differences in plant size, even though size and lag time did not appear to be related in this study.

The relationship between flow and the sensor signal (K) may vary between plants (Figs. 6 and 7). The variation among the excised stem calibrations (Fig. 7) probably resulted from heterogeneous flow across the sap-wood. The stem responsible for the unusual curve had apparently been wounded in the past. Remaining effects of the injury forced proportionally more flow past the sensor, creating an increase in sensor signal for given flow per unit of total sap-wood area. This is consistent with the observation of Sperry, Donnelly & Tyree (1988) that hydraulic conductance may be circumferentially heterogeneous as a result of embolism in sugar maple, but contrasts with the reports of Granier (1987a) and Schulze *et al.* (1985) that sap flow does not vary substantially around the circumference of tree stems in the field. Edwards & Booker (1984) noted radial variation in sap velocity, and this may also have implications for quantitative determinations of sap flow.

The factors responsible for the calibration curve with extremely high sensitivity of K to E in the ventilated chamber are unknown (Fig. 6). The temperature compensation for that tree was comparatively ineffective, and the resulting temperature gradient opposite to the one in Fig. 1c may have increased the apparent rate of sap flow. Alternatively, the anomalous calibration may have resulted from the relationship between plant ground area and sap-wood, or from heterogeneous flow across the xylem. An additional concern is the impact of sap-wood thermal conductance on calibration. In some plants, pre-dawn probe temperature (ΔT_m) varied markedly over the season, presumably as a result of changing stem water content (Goulden 1991). As sensor power impacts calibration (presumably as a result of changing heat field size) the observation of changing ΔT_m (which were

undoubtedly associated with varying fields) suggests that the calibration may change over the course of the year in drought-stressed systems.

VENTILATED-CHAMBER MEASUREMENTS

The ventilated chamber proved to be an effective tool for measuring the gas exchange of whole-tree canopies in the field, but it significantly altered environmental conditions. The leaf-to-air temperature differentials within the chamber were similar to those under ambient conditions, but the air temperature in the chamber was elevated 5–10°C above ambient (Fig. 3b). Coupled with previous reports that chambers of similar design do not dramatically change canopy net radiation (Lee 1966), this indicates that the boundary layer conductance within the bag was reasonable and that mixing was sufficient to ensure representative exhaust sampling. Air temperature, water vapour content of the air and vapour saturation deficit were all substantially elevated within the chamber over ambient levels (Figs. 3b and 5). Increasing the air flow through the chamber would have decreased these changes but would have impacted the accuracy of the transpiration measurements by magnifying any humidity sensor offset errors. Ventilating chambers that rely on infrared absorption to monitor water vapour can be operated with much smaller humidity differentials, allowing nearly ambient temperatures and humidities (Wong & Dunin 1987).

In spite of the altered conditions within the bag, enclosure did not dramatically change transpiration (Fig. 5). These results are similar to those of Dunin & Greenwood (1986) but contrast with reports by Leuning & Foster (1990) and Lee (1966). The differences may result from chamber design, plant physiology or environmental conditions. At high temperatures, sap flow becomes insensitive to evaporative demand (Fig. 9). If sap flow is already at the physiological maximum, the chamber will not impact transpiration, even if vapour pressure deficit is increased.

The maximum rates of photosynthesis and conductance on a ground-area basis (Fig. 3) were approximately 70% greater than light-saturated leaf measurements made on the same plant during the spring of 1990 using a portable gas-exchange system (Goulden 1991). This is consistent with the LAI of the plant (2.6 m² m⁻² by harvest) and the observation that in *Eucalyptus* spp., canopy gas exchange exceeds that of mature leaves by 30% (Wong & Dunin 1987). The internal CO₂ concentrations (Fig. 3) were approximately 40 μl l⁻¹ higher than those measured for sunlit leaves during the spring of 1990. This may result from temporal variation in c_a or c_i and methodological differences, but probably also reflects the contribution of shaded leaves and branch respiration to the canopy measurement. The

ventilated-chamber photosynthetic rates were similar to, and the conductances lower than, the eddy correlation measurements made in Italian macchia by Valentini *et al.* (1991). The higher conductances observed by Valentini *et al.* may be due to surface evaporation (R. Valentini, personal communication). Alternatively, the differences may be due to plant-to-plant heterogeneity. Peak gas exchange was quite variable among plants (Goulden 1991) and analysing the relationship between chamber gas exchange and eddy flux measurements is not possible without a larger number of samples.

PLANT BOUNDARY LAYER

The plant boundary layer conductances determined in the field were similar to published values. The measured conductances were 20% higher than those predicted by Campbell (1977) for laminar flow over a two-sided flat leaf with an effective width of 1 cm and 35% lower than those predicted by Nobel (1983) for a similar leaf in turbulent flow. This correspondence may be fortuitous as the canopy aerodynamic conductance reported here is not strictly equivalent to leaf boundary layer conductance and the LAI of the study plant was greater than $1 \text{ m}^2 \text{ m}^{-2}$. The observed conductances are approximately 40% higher than those measured above a macchia stand by Valentini *et al.* (1991) using micrometeorological techniques. This difference may result from the reference heights used in the two studies. Valentini *et al.* placed their sensor array 3 m above the canopy, while the reference point used in this study was at 1 m.

PLANT REGULATION OF TRANSPIRATION

On atmospherically moist days (*Q. durata* Penman–Monteith $E < 60 \text{ mol m}^{-2} \text{ day}^{-1}$) sap-flow and Penman–Monteith transpiration were similar, indicating that stomatal conductance remains at the maximum for each plant (Fig. 9a). Back calculations of plant conductance from sap flow using the Penman–Monteith equation confirm this; only on relatively infrequent hot days does stomatal closure provide a significant limitation to E (Goulden 1991). Midday stomatal closure, as occurred in the ventilated chamber under elevated temperatures (Fig. 3f), is relatively rare. On most days evaporative demand (primarily D) controls transpiration. On hot days (*Q. durata* Penman–Monteith $E > 75 \text{ mol m}^{-2} \text{ day}^{-1}$) stomatal closure acts to maintain a maximum E under all environmental conditions. This pattern is consistent with a number of leaf level studies. The incorporation of a conductance model derived from leaf work into the Penman–Monteith calculations consequently represents a logical extension of the work described and also an opportunity for comparing stomatal parameterizations (Jarvis *et al.* 1981; Collatz *et al.* 1991). Apparently the stomata respond

to the environment (or perhaps directly to E ; Mott & Parkhurst 1991) in a way that prevents E and consequently leaf Ψ from exceeding a critical value. This value may correspond to the point where the plant becomes subject to some type of permanent damage (Tyree & Sperry 1988).

In contrast to *Q. durata*, sap flow in the shallowly rooted *Q. agrifolia* was a function of both evaporative demand and the availability of moisture in the surface soil (Fig. 9b; Goulden 1991). This difference is indicative of the need to consider individual plant processes explicitly in analyses of ecosystem gas exchange. Because the response of the two species to water deficit is most likely non-linear, and the two species differ in access to soil moisture, predictions of transpiration based on ecosystem average water stress and evaporative demand will result in errors. A similar situation will occur anytime plants respond in non-linear ways to heterogeneously distributed resources and conditions. In such cases it is likely that models which explicitly consider plant-to-plant variation will improve our ability to simulate whole-forest gas exchange.

Conclusions

The three approaches explored provide valuable information but are all subject to strong constraints. Ventilated chambers accurately measure canopy gas exchange but disturb the plant microenvironment and require considerable set-up and maintenance time. Sap-flow sensors are inexpensive to construct and continuously monitor undisturbed transpiration with little effort, but their quantitative application is limited by the varying relationship between the sensor signal and transpiration. The Penman–Monteith equation is theoretically sound and can be used to understand the forces controlling transpiration, but difficulties in determining whole-plant boundary layer and stomatal conductance limit its usefulness.

By using the three methods in combination these problems may be overcome. The ventilated chamber can be used to calibrate the sap-flow sensors and to measure canopy stomatal conductance for the Penman–Monteith equation. Sap-flow sensors can be used to develop long-term data sets of undisturbed transpiration and in conjunction with radiation measurements used to measure boundary layer conductance. The Penman–Monteith equation can be used for quantitative predictions of transpiration under new conditions and to dissect the determinants of transpiration. By collecting long-term data sets using the approaches outlined in this paper it should be possible to evaluate the distribution of canopy gas exchange across plant communities as a function of resource distribution and as a result of genetic differences within and between species. Studies of this type have the potential to improve our understanding of ecosystem gas exchange substantially by

allowing explicit consideration of processes occurring at the individual level.

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