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Short note

Micrometeorological assessment of sensitivity of canopy resistance to vapour pressure deficit in a Mediterranean oak forest *

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Summary — Canopy surface resistance to water vapour (r_c) of an extensive *Quercus ilex* L stand (Bosco Mesola, northeast Italy) has been evaluated by inverting the Penman–Monteith equation. The latent heat flux was estimated by applying the Bowen ratio-energy budget micrometeorological method. A linear relationship was found between r_c and the vapour pressure deficit. Canopy resistance increased regularly during the day and that yielded a recurring diurnal pattern of energy partitioning where most of the latent heat was dissipated in the early morning and the release of sensible heat increased after midday. This behaviour has been confirmed also by independent estimates of transpiration, based on measurements of sap flow velocity in small branches. Ecological consequences of this feature are briefly discussed applying the concept of coupling between canopy and atmosphere.

Quercus ilex **L / energy balance / evapotranspiration / canopy resistance / sap flow**

Résumé — Réponse d'un couvert de chênes méditerranéens au déficit de saturation de l'air : approche micrométéorologique. *La résistance du couvert à la vapeur d'eau* (r_c) *d'un peulement de* Quercus ilex *L (Bosco Mesola, nord-est de l'Italie) a été évaluée par inversion de l'équation de Penman-Monteith. Le flux de chaleur latente était estimé par la méthode du rapport de Bowen. Une relation linéaire entre* r_c *et le déficit de saturation de l'air a été trouvée. La résistance du couvert augmentait régulièrement durant la journée, ce qui conduisait à une évolution journalière de la partition de l'énergie : la plus grande part du flux de chaleur latente était dissipée le matin, le flux de chaleur sensible augmentant ensuite dans la journée. Ce fonctionnement a été confirmé par des mesures indépendantes de transpiration basées sur la mesure de flux de sève de petites branches. En utilisant le concept de couplage entre le couvert et l'atmosphère, les conséquences écologiques de ces observations ont été tirées.*

Quercus ilex ***L / bilan énergétique / évapotranspiration / résistance de la canopée / débit de sève***

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INTRODUCTION

Mediterranean climate often implies stressing conditions: heavy radiation load, high temperature, low hygrometry, irregular rainfall distribution are all commonly to be faced by plants (Tenhunen et al, 1987). Dissipation of a large amount of available energy by water evaporation is the fundamental process to prevent foliage temperature from reaching excessive values and to reduce respiratory losses, thus improving the whole-plant carbon balance. Excess of absorbed energy is released as sensible heat, but the efficiency of this transfer is related to the aerodynamics of vegetation–atmosphere interaction. The erratic availability of water has represented a major evolutionary pressure for terrestrial plants, yielding a conservative behaviour of the vegetation mainly based on the control capacity of stomata. This feature has been gradually interpreted as a complex regulatory system based on sensing of both environmental and physiological factors, aimed at preserving plant homeostasis. The feedback control pivoted on internal water status was also believed to prevent excessive water loss in very dry air (Hall et al, 1976). Later work, both theoretical and experimental, suggested that a reduction in transpiration during high evaporative demand conditions could not be obtained without considering also a feed-forward response of stomata to atmospheric water vapour deficit (Cowan, 1977; Cowan and Farquhar, 1977; Farquhar, 1978). Implications of sensitivity of foliage to vapour pressure deficit for water and energy budgets of the stand have been theoretically discussed by Choudhury and Monteith (1986).

Sensitivity of stomata to water vapour is thus a key feature to regulate the water budget of plants in a natural environment, and has been recognized in many species, mostly in cuvette experiments performed on single leaves or twigs (for a brief review, see Lösch and Tenhunen, 1981). Fewer works assessed this capacity at canopy scale, by obtaining estimates of bulk surface conductance of the stand from micrometeorological measurement of fluxes (Roberts, 1983; Lindroth, 1985; Stewart and de Bruin, 1985; Munro, 1987; Dolman and van den Burg, 1988; Munro, 1989; Grantz and Meinzer, 1990, 1991; Meinzer et al, 1993). Although this is actually the ultimate scale at which ecophysiological research most contributes in understanding the whole-plant performance, it must be stressed that the scaling of leaf properties is by no means a straightforward procedure. As a consequence, even if a link does exist between the leaf and the canopy diffusive resistance, the latter cannot be simply viewed as the resultant of a network of resistors representing leaf strata, but usually includes additional components related to the aerodynamics of the canopy interior (Thom, 1975; Lhomme, 1991).

Actually, the use of micrometeorological techniques to estimate integral properties of such a complex surface has been criticized since its very beginning (Tanner, 1963) and this approach typically does not discriminate transpiration from the bulk evapotranspiration flux. For all these reasons, studying responses of the bulk canopy resistance to the environmental factors is always affected by some uncertainty. Nevertheless, the analogy between leaf and canopy resistance may lead to useful consequences, allowing for sound models of leaf transpiration and energy balance to be applied to the entire stand. In particular, the Penman equation as extended by Monteith (1965) can be used to analyse several interesting features of the canopy functioning.

In this paper, bulk surface resistance has been estimated by a classical micrometeorological technique (the Bowen ratio-energy budget) to assess sensitivity of this parameter to air humidity in a Mediterranean oak forest. Measurements of transpiration were also obtained by monitoring sap flow rate in some branches, in order to get independent estimates of canopy resistance.

THEORETICAL BACKGROUND

For a vegetated surface, the energy balance holds:

$$R_n = C + \lambda E + J + G$$

where R_n is the net radiation flux density (W m^{-2}), C the sensible heat flux density (W m^{-2}), λE the latent heat flux density (W m^{-2}) , J the flux density of the energy stored in the canopy volume (biomass and air) (W m^{-2}), and G the soil heat flux density (W m^{-2}). As partitioning of the energy $H = \lambda E + C$ available at the canopy surface is affected by the surface resistance of the canopy itself, the latter may be inferred from the analysis of the fluxes.

The relationship between λE and the canopy resistance has been formalized by Monteith (1965), by extending the Penman equation:

$$\lambda E = \frac{\Delta H + \rho c_p VPD / r_a}{\Delta + \gamma \left(1 + \frac{r_c}{r_a}\right)}$$

where λ is the latent heat of vaporisation of water (≈ 2.45 MJ kg^{-1}), E the evapotranspiration flux density (kg m^{-2} s^{-1}), Δ the slope of the curve relating saturated vapour pressure to temperature (Pa K^{-1}) evaluated at the air temperature, ρ the air density (1.204 kg m^{-3}), c_p the specific heat capacity of the air at constant pressure (1 012 J kg^{-1} K^{-1}), VPD the vapour pressure deficit (Pa), γ the psychrometric constant (≈ 66 Pa K^{-1}), r_a the aerodynamic resistance (s m^{-1}), and r_c the canopy resistance for water vapour (s m^{-1}).

When all the components of the energy balance are known and r_a is estimated from the windspeed profile and the geometrical properties of the canopy, the Penman–Monteith (P–M) equation can be inverted to yield the surface resistance to evaporation:

$$r_c = \frac{\frac{\rho c_p}{\gamma} VPD}{\lambda E} + \left(\frac{\Delta}{\gamma} \; \frac{C}{\lambda E}\right) - 1 \quad r_a$$

If λE is estimated by the Bowen ratio-energy budget method, the previous equation reduces to:

$$r_c = \frac{\frac{\rho c_p}{\gamma} VPD}{\frac{H}{(1+\beta)}} + \left(\frac{\Delta}{\gamma} \beta - 1\right) r_a$$

where $\beta = C / \lambda E$ is the Bowen ratio, which, assuming the equality of turbulent transfer coefficient for heat and water vapour, can be computed from:

$$\beta = \gamma \frac{\partial \theta}{\partial e} \approx \gamma \frac{\theta_1 - \theta_2}{e_1 - e_2} = \gamma \frac{T_1 - T_2 + \Gamma (z_1 - z_2)}{e_1 - e_2}$$

where θ is the potential air temperature (K), related to the actual air temperature T (K) and to the adiabatic lapse rate γ (≈ 0.098 K m^{-1}), and e is the vapour pressure (Pa), each measured at two heights z (m) above the canopy.

MATERIALS AND METHODS

Site

Measurements were carried out from 25 July to 3 August 1990 in the natural reserve of Bosco

Mesola (Ferrara, Italy; 44°48'N, 12°22'E, few m asl). The forest extends over 1 060 ha on a flat tongue between two branches of the Po river delta and it is mostly covered with a dense and homogeneous *Quercus ilex* L canopy. It has been extensively studied as the largest residual patch of Mediterranean oak in northeastern Italy. Average annual air temperature is 13.3 °C and total rainfall is 614 mm (both derived from records of the period 1961–1980). Further climatological information can be found in Pitacco et al (1992). The area where measurements were taken has been regularly coppiced until 1979, leaving around 200 standards per hectare. Standing biomass volume in the experimental plot was around 233 m^3 ha^{-1}, with 1 620 stems.ha^{-1}. Average tree diameter was 14 cm. The leaf area index, indirectly estimated from diffuse radiation transmittance, was 3.9. Soil was 98% sand, with a thin organic layer at the surface. Average depth of the water table during the period was 1.5 m. Some rain occurred just before trial (35 mm on 24 July) and vegetation appeared to be healthy and not stressed.

Instrumentation

A mast was erected in a homogeneous site, where canopies formed a continuous layer with fairly uniform thickness and height. Average height of the canopy top was 10.1 m. The smallest fetch length was around 500 m. The air temperature used to compute the Bowen ratio was measured at two heights (10.5 and 12.0 m) above the canopy by fine-wire (0.08 mm) chromel-constantan thermocouples (model TCBR-3, Campbell Sci, UK). The junctions were neither aspirated nor shielded, but due to the small size, should not have experienced significant overheating even at low wind speed. At the same levels, vapour pressure was determined by a single dew point hygrometer (model DEW-10, General-Eastern, USA). A single instrument was used to prevent biases in vapour pressure measurements due to the possible mismatching of two separate sensors. The dew-point hygrometer was regularly switched between the two air sample lines every 2 min. Wind speed was also measured at the same heights by cup anemometers, having a lower threshold of 0.3 m s^{-1} (model A100M, Vector, UK). Net radiation was measured by a differential thermopile shielded with semi-rigid polyethylene domes (model DRN-301, Didcot, UK), placed 1.5 m above the top of the canopy.

Heat storage into the canopy biomass was evaluated assuming that its temperature could be related to the temperature of the air inside the canopy (Thom, 1975):

$$J_v = \int_0^h \rho_{veg}\, c_{veg} \frac{\partial T_{veg}}{\partial t}\, dz \approx 0.8\, m_{veg} \frac{\partial T_{air}}{\partial t}$$

where ρ_{veg} is the biomass density per unit canopy volume (kg m^{-3}), c_{veg} its specific heat (J kg^{-1} K^{-1}), m_{veg} is the biomass per unit ground area (kg m^{-2}), and T_{veg} and T_{air} (K) are wood and air temperature, respectively. Heat stored into the air was calculated as in Thom (1975).

Soil heat flux was determined by measuring deep storage with heat flux plates (model HFT-1, Radiation Energy Balance System, USA) buried at –0.1 m. Heat stored into the upper layer was calculated by measuring average soil temperature at two depths (–0.02 and –0.08 m) and using an empirical equation for the heat capacity of sandy soil.

Ancillary measurements of sap flow rate were obtained by heat balance method (Sakuratani, 1981; Baker and van Bavel, 1987) installing three gauges (model SGA10, Dynagage, USA). Total leaf area of the selected branches, directly measured at the end of the trial, ranged from 0.15 to 0.27 m^2, and the average stem diameter was 11 mm. Branches were distributed throughout the whole canopy layer, in order to obtain a representative value of transpiration for the average unitary leaf area. The flux density of transpiration expressed per ground area was subsequently obtained multiplying this value by the leaf area index.

All data were recorded by a CR21-X datalogger (Campbell Sci, UK), which also controlled the valve switching. Sampling rate for all sensors was 1 s, and averages were recorded every 20 min. Overall resolution of the measuring chain was better than 0.01 K m^{-1} and 0.01 kPa m^{-1} for temperature and vapour pressure differentials, respectively.

RESULTS

Micrometeorological measurements showed a recurrent pattern throughout the period.

The observations made on 3 August can be considered to be paradigmatic for the whole period. The energy balance of the canopy, analysed in its major components, is presented in figure 1a. Most of the available energy was dissipated as latent heat in the morning, while an increasing amount of heat was released after midday. Peak energy flux into the soil did not reach 70 W m^{-2}. Heat stored into the canopy (biomass and air; not shown in the graph) was almost not significant during daytime. However, it represented an important sink of available energy at dawn and, together with the heat released from the soil, contributed substantially to sustain some heat flux after sunset.

The partitioning of available energy in the two major fluxes of latent and sensible heat is best demonstrated by looking at the Bowen ratio (fig 1b). It steadily increased from the negative values of the early morning, up to around 2 in mid-afternoon. Then, the available energy released as sensible heat doubled the amount dissipated as latent heat.

The diurnal trend of canopy transpiration, as measured by sap flow gauges, roughly paralleled the diurnal course of micrometeorological estimate of latent heat flux (fig 1c). However, the daily integral of transpiration exceeded the latter (4.1 and 3.9 mm day^{-1}, respectively). That could be due to a possible overestimation of the leaf area index brought by the indirect technique that was used (which has not been corrected for the interception of radiation by wood), and to the poor representativeness of sampled branches.

Having determined the components of the energy balance, the inversion of the Penman–Monteith equation becomes possible, provided an estimate of the aerodynamical resistance is also given. The calculation of this parameter suffers from a range of difficulties, since the turbulent transfer of momentum, heat and water vapour is affected in a complex way by the geometry of the canopy, the spatial distribution of sources and sinks inside the foliage (which, as a rule, do not coincide, especially in tree crowns), and atmospheric stability. Usually, the Monin–Obukhov similarity theory is invoked. However, a brief analysis of the

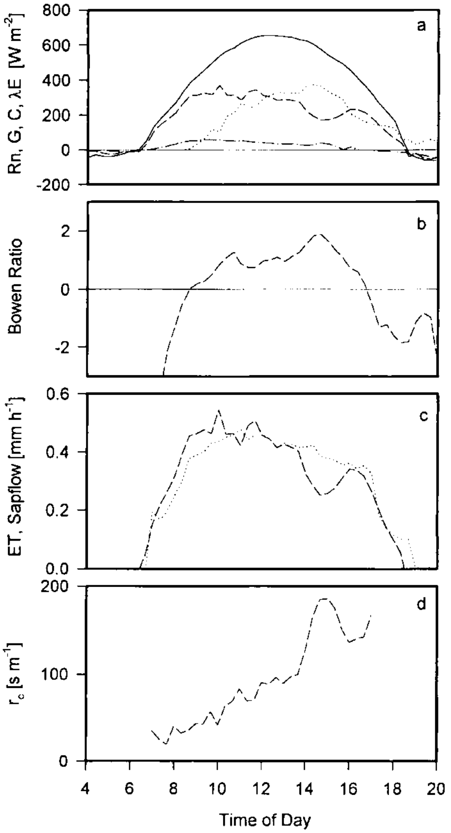

Fig 1. (**a**) Canopy energy balance of the *Quercus ilex* stand on 3 August 1990, at Bosco Mesola (Italy); net radiation (solid line), latent heat flux (dashed line), sensible heat flux (dotted line), soil heat flux (dashed-dotted line). (**b**) Diurnal trend of Bowen ratio. (**c**) Micrometeorologically measured evapotranspiration (dashed line) compared with transpiration measured by sap flow gauges (dotted line). (**d**) Calculated surface resistance of the stand. Only values with net radiation ≥ 75 W m^{-2} are shown.

P–M equation, along with the consideration that the aerodynamic resistance of forests is usually low, leads to the conclusion that the estimates of the canopy surface resistance are not very much affected by uncertainties in r_a, especially when $\beta \approx \gamma / \Delta$ (Thom, 1975; de Bruin and Holstag, 1982). Here, the aerodynamical resistance has thus been calculated using the standard equation of momentum transfer, disregarding any possible effect of atmosphere non-neutrality:

$$r_a = \frac{\ln\left(\frac{z-d}{z_0}\right)^2}{k^2 u}$$

in which z is the reference height (m), d the so-called zero-plane displacement (m), z_0 the roughness length for momentum (m), k the von Kármán parameter (≈0.41) and u the windspeed at the reference height (m s^{-1}). Both z_0 and d were referred to canopy height through empirical coefficients (0.1 and 0.7, respectively).

The diurnal course of the calculated canopy resistance linearly increased from the minimum value of around 25 s m^{-1} in the early morning, to almost 200 s m^{-1} in the late afternoon (fig 1d). This trend may suggest a conservative behaviour of the canopy, which tends to limit evapotranspiration losses. This pattern appears to be quite common in forest canopies, being observed by many authors in a range of environments. McNaughton and Black (1973), in trying to explain the afternoon increase in canopy surface resistance noted in a Douglas-fir forest, hypothesized water-stressing conditions, although these were quite unexpected as soil was still holding plentiful water. In addition, Jarvis et al (1975), discussing data gathered on *Pinus sylvestris* at Thetford (a moderately humid oceanic climate), suggested that the increase in canopy resistance they found could be due to leaf water stress. On the other hand, Roberts (1983) came to maintain that, while “a marked negative feedback response of surface resistance to climate restricts the range of transpiration losses, variations in soil water content, in most circumstances, have negligible effects on transpiration rates”. Afterwards, a number of papers reported similar results for experiments where the soil water content was not limiting at all, and focused their attention on the possible direct response of stomata to the vapour pressure deficit (Lindroth, 1985; Dolman and van den Burg, 1988; Munro, 1989).

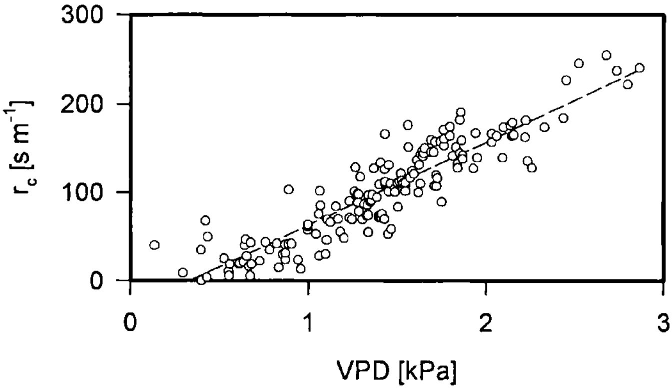

Fig 2. Relationship between canopy surface resistance of the *Quercus ilex* stand and water vapour pressure deficit during the period of 25 July to 3 August 1990, at Bosco Mesola (Italy). Only values with net radiation ≥ 75 W m^{-2} are reported.

Actually, the very same conditions occurred during this experiment in the Mesola Forest, since spot measurements of midday leaf water potential, performed on exposed twigs, never showed values below −1.9 MPa, a value that is far from being able to induce stomatal closure in a xerophilous oak.

A plot of canopy surface resistance against vapour pressure deficit indicates a direct relationship between the two (fig 2). Although *VPD* has been necessarily used to compute r_c, a linear regression has been fitted which yielded a statistically significant determination coefficient ($R^2 = 0.83$). In comparison with the relationships reviewed by Roberts (1983), the slope resulted around half (≈ 94 s m^{-1}/kPa). However, the range of *VPD* that has been encountered in the Mesola Forest was much wider than that found at Thetford. Linear correlation with R_n (using only data ≥ 50 W m^{-2}) was not significant ($R^2 = 0.06$).

CONCLUSION

The Mediterranean oak forest that has been investigated seems to dissipate most of the available energy as latent heat in the morning and gradually increase the release of sensible heat in the afternoon. This has been shown to be due to a regular increase of surface resistance throughout the day, linked to the increase in vapour pressure deficit. The coupling of sensitivity to water vapour deficit to sclerophylly and other xeromorphic traits has been proposed as an important adaptive feature of plant life forms in arid conditions (a brief review may be found in Lösch and Tenhunen, 1981). It may be considered as a most effective way to cope with a potentially stressing environment, without depleting too much gas exchange under favourable conditions. This feature, known for many years at leaf level, is actively checked at the present time also at canopy scale by direct micrometeorological techniques.

Actually, both structural and functional characteristics strongly interact in building up the new properties that a canopy shows with respect to a single leaf. The concept of canopy coupling coefficient Ω, as introduced by McNaughton and Jarvis (1983; see also Jarvis and McNaughton, 1986), is of greatest interest in interpreting such a complex interplay between plant and its environment. During this trial, as a consequence of the sensitivity of r_c to *VPD,* the forest appeared to show a recurrent diurnal pattern of coupling with the lower atmosphere, with Ω regularly decreasing from typical values of 0.9 in the early morning to an asymptotic minimum value around 0.1 in the afternoon. Consequences of this behaviour might be important for the water budget of the forest and its performance.

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