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Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo

E. Cienciala[a,*], J. Kučera[b,1], A. Malmer[c,2]

[a]*Department of Soil Sciences, Swedish University of Agricultural Sciences, Box 7014, 750 07 Uppsala, Sweden*
[b]*Environmental Measuring Systems, Turistická 5, 621 00 Brno, Czech Republic*
[c]*Department of Forest Ecology, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden*

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Abstract

Water use of *Acacia mangium* trees grown in plantations was measured by a heat balance method in two stands that largely differed in tree density. Tree sap flow was closely coupled to climatic drivers and responded with minimal time delay. Using no time shift, sap flow rate could be tightly fitted to a simple equation that combined a parabolic response to radiation and an inverse linear response to air humidity. On the contrary, the analysis of canopy conductance showed no meaningful response to either individual or combined microclimatic variables. No indication of water deficit was observed, though the measurement period was during the dry period of the year. The measurements indicate a minimal diurnal use of water stored in plant tissues. The difference in tree water use from the two studied stands was effectively scaled by tree sapwood area. Canopy transpiration of the densest stand reached in average 3.9 mm d^{-1} compared with 2.7 mm d^{-1} for the stand representing the average conditions in the catchment. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Canopy conductance; Plant resistance; Sapwood area; Scaling; Tropics

1. Introduction

In Borneo, virgin tropical forests are being logged and successively reforested by mostly imported fast growing species with a short rotation period. The species commonly used for planting are several imported species of *Acacia* and *Eucalyptus*. The expectations are high with respect to sustainability and production performance of these plantations of the fast-growing species. Naturally, it is particularly vital to assess the environmental aspects of the newly created ecosystems (Bruijnzeel, 1996). In the Malaysian state of Sabah, Borneo, *Acacia mangium* represents one of the most important species planted on the clear-felled areas (Nykvist et al., 1996). *A. mangium* belongs to diffuse porous species with a medium-quality wood of light density (Peh and Khoo, 1984). A stand average tree diameter can reach more than 20 cm and a height of 25 m in less than 10 years. Hereby, it can be expected that water use is crucially important to support the intensive growth rate of these plantations. We assume that soil water must be available in sufficient amounts, and secondly, tree water uptake and transport along conductive pathways must be effective to maintain leaf turgor and intensive

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* Corresponding author. Tel.: +46-18-671168; fax: +46-18-672795.

E-mail addresses: emil.cienciala@mv.slu.se (E. Cienciala), jkucera-ems@iol.cz (J. Kučera), anders.malmer@sek.slu.se (A. Malmer).

[1] Fax: +420-5-41225344.

[2] Fax: +46-90-7867750.

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assimilation of carbon. However, detailed hydrological and physiological process studies focussed on water use in these forests are still rare (Bruijnzeel, 1997).

This paper examines water use of *A. mangium* trees in two 9.5 years old stands. One represented the average growth conditions and with an average tree density. The other stand was one of the densest stands representing the best production sites in the area that was reforested manually. Our aim was to: (a) quantify differences in tree water use in two stands of contrasting tree density; (b) detect possible water deficit conditions in a local dry period; (c) study instantaneous responses of tree water flux to the local evaporative demand and microclimatic factors. The presented measurements should also provide the basis for more detail analyses of water physiology and growth of *Acacia* trees for a later application of climate-driven process model.

2. Material and methods

2.1. Research area

The study site is located on the foothills of Mount Lumaku, Crocker range, 35 km inland from Sipitang at 115°E, 5°N on the west coast of Sabah (Northern Borneo), Malaysia. The area is used to study the environmental impacts of converting rain forest to forest plantations (Nykvist et al., 1994; Malmer and Grip, 1994; Malmer, 1996a). It is situated at 650–750 m on the foothills of Gunung Lumako (1967 m alt.), Crocker Range. The bedrock of the research area consists mainly of sandstone and siltstone (Grip et al., 1994). Soil in the area consists of two main types and several intermediate forms. The two main types are Haplic Acrisol with clayey topsoil and Gleyic Podsol with sandy topsoil. Both soil types formed on frequently inter-layered dark shales, siltstones and sandstones. The uppermost 20 cm of both soils has a low bulk density and high infiltrability (Malmer and Grip, 1990). Soil reaches depths of 1–3 m, with subsoils of high clay content and low hydraulic conductivity (Malmer and Grip, 1990; Malmer, 1996b). Except for a few periods of rainless days, soils are generally wet at 20 and 50 cm depth (less than 10 kPa soil suction) both in clear-felled areas and under forest cover (Malmer, 1996b). The area was originally mainly covered by dipterocarp forest, but during recent decades those have been intensively converted into forest plantations.

For the period 1986–1997, the mean annual number of days with rain at the Mendolong tree nursery (see below) was 215 (192–243). Monthly mean daily sunshine reached 4.59 (2.23–7.31) hours. The annual precipitation at the Mendolong tree nursery was 3280 mm (Anonymous, 1998). It was 5.4% higher in the experimental catchments at higher elevation, but this difference was lower than the methodological dissimilarity between the Brannan rain gauge used at Mendolong and the gauges with plastic funnels used in the experimental catchments (Malmer, 1992). Most rainfall occurs as convective precipitation and prevalent winds seldom exceed 3 m s^{-1} (Anonymous, 1998). There is a seasonal variation in rainfall amounts, with the most rainfall occurring from September through November and during April and May, in connection with the passages of the inter-tropical convergence zone.

2.2. Meteorology

Climatic data were measured in an open field at the Mendolong tree nursery, 3 km distant from the studied stands, at an altitude of 500 m. Short-wave radiation, air temperature, air humidity and wind-speed were measured every minute and stored in a datalogger as mean values of 15-min periods. Apart from the above measurements established by us, the local nursery station has a long-term measuring program. This consisted of manual or semi-manual recordings of daily minimum and maximum air temperature, air temperature and relative humidity read at 07.00 and 14.00 h local time, and daily precipitation and sunshine duration.

Using the intensive measurements of the weather variables, we established the correction and conversion factors for the basic variables from the nursery station on daily basis ($n = 20$ complete days). The established relationship for daily mean air temperature (T_a; °C) was

$$T_a = 5.12 + 0.80 * [(T_{a07} + T_{a14})/2] \qquad (r^2 = 0.81) \tag{1}$$

where T_{a07} and T_{a14}, respectively, are the temperature

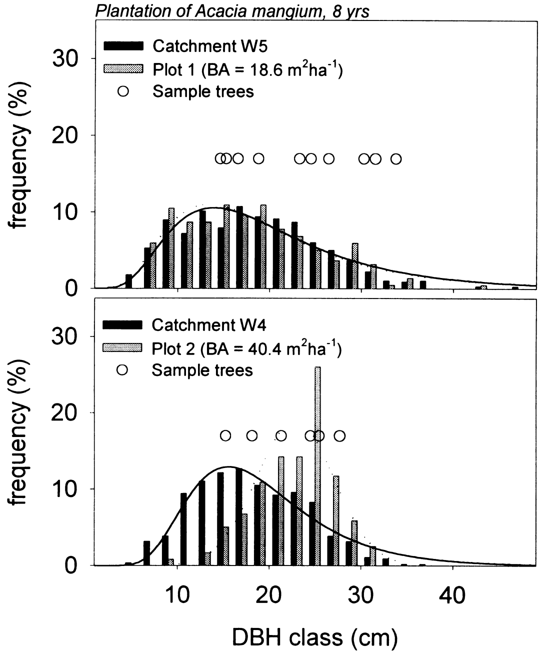

Fig. 1. Frequency distribution of tree diameters at breast height (DBH): the studied plots 1 (above) and 2 (below) and the corresponding frequencies for the whole catchments W5 and W4, respectively. DBH of the sample trees selected for the respective plots are noted by a symbol. Inserted in both plots are distribution functions for trees in the catchment (solid line) and in the studied stand (dotted line) of these catchments.

readings at 07.00 and 14.00 h local time at the nursery station. Daily global radiation (R_g; MJ d^{-1}) was calculated as

$$R_g = 8.04 * (1 + S_D)^{0.408} \qquad (r^2 = 0.87) \tag{2}$$

where S_D is sunshine duration (h d^{-1}). The correction for the daily mean relative air humidity (RH) was obtained as for air temperature (Eq. (1)), but the intercept was set to zero. This was required because the range of the daily mean values in the data set available for the parameterization ($n = 20$) was too small. Using the zero intercept, the slope parameter indicated only a 2% difference between the daily mean RH from the high-resolution automatic measurements and from the two readings at the nursery station.

2.3. Measured stands

The studied stands were the first generation plantations of *A. mangium*, 9.5 years old. They were established by manual planting using seedlings on burned and unburned area after clear-cutting of the former virgin forest. We studied two plots in the neighboring catchments W5 (Plot 1) and W4 (Plot 2) at the altitude of 700 m, both sites having Acrisol soil.

Plot 1 represented the average growth conditions for the catchment W5, with tree density of about 1020 trees ha^{-1} and a similar frequency distribution of tree diameters as in the catchment W5 (Fig. 1). *A. mangium* represented 69% of the total stand basal area, which reached 18.6 m^2 ha^{-1}. A mosaic of local dipterocarp and Eucalyptus species represented the remaining minor part, which obviously penetrated later after planting. These individuals had typically smaller size as compared to the major species *A. mangium*, which had a mean diameter at the breast height (DBH) of 17.9 cm. Plot 2, situated in the catchment W4, was the best stand in the catchment area, representing the likely upper production potential at this site. The mean tree DBH was 22.8 cm and the basal area reached 40.4 m^2 ha^{-1}, consisting almost exclusively of *A. mangium* (99%). Plot 2 had the frequency distribution of tree diameters shifted towards higher dimensions as compared with that of the catchment W4 (Fig. 1). Stand height was about 26 m for both plots. The rooting depth of *Acacia* trees was not directly measured, but it was observed to be deeper than 1 m in the neighboring areas. There was a developed understory vegetation layer with occasional shrubs and wild banana plants in the less dense Plot 1. The understory in Plot 2 was sparse and consisted mainly of fern species. This paper describes woody tree and canopy transpiration of these stands at the final growth stage before felling.

It should be noted that the catchments W5 and W4 differed in their management history, which, herewith, affected growth and water use in the two studied plots as above. On W5, logs were extracted by tractors and the remaining slash was burnt (i.e. normal practice), whereas on W4 the log extraction and clearing the slash was performed manually and without burning (Malmer and Grip, 1990; Nykvist et al., 1996). The management with tractors reduced the porosity on 24% of the area of the catchment W5. It affected the structure of the catchments and hence their water budget and wood production (Sim and Nykvist, 1990;

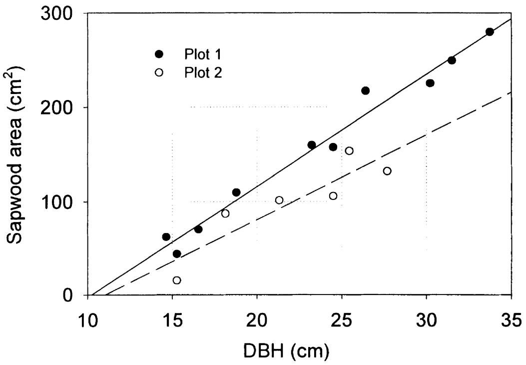

Fig. 2. Sapwood area against tree diameter at the breast height (DBH) for the measured sample trees in Plot 1 (solid line, $r^2 = 0.98$, $n = 10$) and Plot 2 (dashed line, $r^2 = 0.80$, $n = 6$).

Malmer, 1992; Nykvist, et al., 1996). In mid 1997, mean tree height was 26 m and mean DBH was similar in both catchments (18.6 and 19.0 cm in W4 and W5, respectively), but the number of surviving stems per hectare was about double in W4 compared to W5 (A. Malmer, unpublished).

2.4. Measurements of sap flow and transpiration

Tree sap flow was measured by the tissue heat balance method (THB) using the standard sap flow meter P 4.1 from Environmental Measuring Systems (EMS, Brno, Czech Republic). This method is based on the work of Čermák et al. (1973) and Kučera et al. (1977) and it yields sap flux in absolute volume and time units. Heat is applied to a well-defined space in the conductive xylem using the alternating current passing between the set of thin stainless steel plates. These electrodes are inserted in the tree trunk, penetrating sapwood band. Sap flux is calculated from the quantified heat loss due to passing water flux (Kučera et al., 1977). Two measuring points were usually applied on each sample tree to minimize the likely flux variation around the stem circumference (Čermák et al., 1992). An extensive review on sap flow measurements was published by Swanson (1994).

Altogether 10 *A. mangium* trees were measured in Plot 1 within the period 7–17 August 1997 and six trees on Plot 2 during 18–22 August 1997. The diameter at breast height (DBH) of the measured trees ranged from 14 to 33 cm (Fig. 1). To facilitate scaling tree sap fluxes to a stand level, sapwood area was measured for all sample trees. The yellowish sapwood area of *A. mangium* was easy to distinguish from the dark-colored heartwood. A typical width of the sapwood band was about 2 cm. Sapwood area was linearly related to tree diameter at breast height (Fig. 2). These dependencies were used to estimate the sapwood area for all trees in the studied stands.

Tree sap flow (Q_{wt}) was scaled to stand transpiration (E_{Q}) using tree sapwood area. Scaling was applied separately for each stand. We used a simple linear relationship between the mean daily Q_{wt} and corresponding tree sapwood area for the measured trees (Fig. 6). These scaling lines were applied to all Acacia trees according to their respective frequency distribution of tree diameters (and corresponding sapwood areas) in the individual stands. Since Acacia in the two plots represented 69% (Plot 1, W5) and 99% (Plot 2, W4) of the total stand basal area, the remaining tree species (mostly *Eucalyptus*) were assumed to behave similarly. Stand transpiration was scaled accordingly so as to correspond to the total stand basal area. Hence, the stand fluxes shown below relate to the total stand basal area for the respective plots.

2.5. Canopy conductance

The qualitative response of canopy conductance (g_{c}) to climatic driving variables was evaluated with the help of the actual data of stand transpiration (E_{Q}) for Plot 1. The actual g_{c} was calculated from the inverted Penman–Monteith equation as

$$g_{\mathrm{c}} = 1/\{\Delta * R_{\mathrm{n}} r_{\mathrm{a}}/(\lambda E * \gamma) + \rho * C_{\mathrm{p}} \delta e/(\lambda E * \gamma) - \Delta * r_{\mathrm{a}}/\gamma - r_{\mathrm{a}}\} \quad (3)$$

where the actual stand flux (E_{Q}; g m^{-2} s^{-1}); is used to substitute the evaporation member (E; g m^{-2} s^{-1}), λ is the in latent heat of vaporization of water (2465 J g^{-1}), δe equals ($e_{\mathrm{s}}(T_{\mathrm{a}}) - e_{\mathrm{a}}$), which is vapour pressure deficit, $e_{\mathrm{s}}(T_{\mathrm{a}}$; Pa) is saturation vapour pressure at air temperature T_{a} (Pa), e_{a} is vapour pressure (Pa), Δ is the slope of saturation water pressure curve (Pa K^{-1}), γ is psychrometric "constant" (65.5 Pa K^{-1}), ρ is density of dry air (1225 g m^{-3}), c_{p} is specific heat of air at constant pressure (1.01 J g^{-1} K^{-1}), R_{n} is equal to net radiation (see below), r_{a} (s m^{-1}) is the aerodynamic resistance calculated from the logarithmic wind profile for

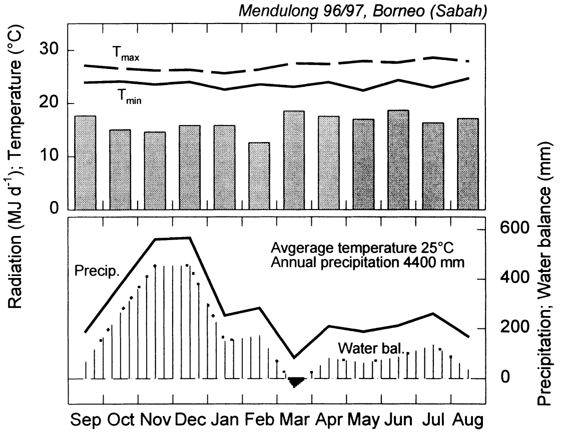

Fig. 3. Climate diagram for the Mendolong nursery from September 1996 to August 1997. Above: monthly average daily short-wave radiation, minimum and maximum air temperature. Below: precipitation and water balance, calculated as the difference between precipitation and evaporation using Thornthwaite (1948) equation.

neutral conditions as

$$r_a = \ln[(z_h - z_d)/z_0]^2/u * k^2 \tag{4}$$

where z_h (m) is the reference height above the canopy, z_d (m) is the displacement height set as 2/3 of the stand height, z_0 (m) is the roughness length set as 1/10 of the stand height, k is von Karman's constant and u (m s^{-1}) is wind speed above the canopy. No correction was made for stability. Since no tower was available in the research area, wind-speed from the meteorological station as described above was used to represent wind-speed above the canopy in Eq. (4). This procedure might tend to increase the importance of r_a in our calculations, because the wind-speed was likely larger above the canopy at the research plot compared with that at the meteorological station. Net radiation (R_n; W m^{-2}), not measured, was derived from the measured short-wave radiation (R_s; W m^{-2}) based on the findings of Bastable et al. (1993) who reported

$$R_n = R_s * 0.80 - 0.37 \tag{5}$$

for the Amazonian tropical forest representing the end of the local dry period. It should be noted that the derived R_n was used only for specific and limited purpose of deriving canopy conductance (see below), completely excluding the night-time values when an error of using a constant representing the long-wave component is relatively largest.

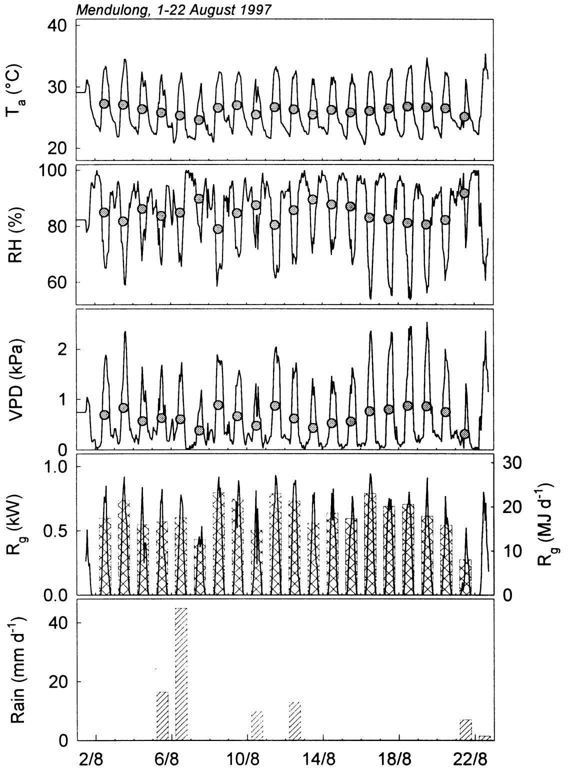

Fig. 4. Climatic data for the measurement period (August 1–22), reading from top: air temperature (T_a), relative humidity (RH) and vapor pressure deficit (VPD), respectively, in 15-min (line) and daily mean (symbol) resolution; short-wave radiation (R_g) in 15-min mean values (line, left scale) and daily sums (right scale); daily precipitation (Rain, bars).

The analysis of g_c was performed for the Plot 1 (W5) and the period of five days (12–16 August), when most of the measured data needed were available. Rainy, night-time and early morning values were eliminated so that only the values when relative humidity was less than 90% and net radiation was more than 0.05 kW m^{-2} were actually used to assess a functional dependence of g_c to microclimatic variables.

3. Results

3.1. Climatic conditions

The monthly climatic diagram (Fig. 3) corresponding approximately for the local hydrological year shows that August was the last month of the drier

Table 1
Sample trees at the respective plots (catchments): diameter at the breast height (DBH), tree height, coefficient of determination (r^2) for the fitted Eq. (6) to n 15-min measured values. Mean daily sap flow (transpiration) for the period 2–21 August (missing data extrapolated by the fitted Eq. (6))

Plot (Catchment)	DBH (cm)	Height (m)	Fit Eq. (6) (r^2; (n))	Mean Q_w (kg d^{-1})
P1 (W5)	33.7	28.0	0.92 (451)	183
P1 (W5)	31.5	23.4	0.94 (451)	78.6
P1 (W5)	30.2	24.4	0.96 (417)	94.1
P1 (W5)	26.4	24.0	0.96 (417)	106
P1 (W5)	24.5	26.1	0.95 (868)	73.1
P1 (W5)	23.2	21.8	0.96 (868)	86.6
P1 (W5)	18.8	25.1	0.94 (417)	57.8
P1 (W5)	16.6	16.1	0.91 (451)	4.62
P1 (W5)	15.3	14.3	0.95 (417)	9.33
P1 (W5)	14.6	16.0	0.92 (451)	16.2
P2 (W4)	27.7	25.9	0.98 (192)	68.5
P2 (W4)	25.5	28.2	0.98 (192)	61.6
P2 (W4)	24.5	25.2	0.97 (192)	27.7
P2 (W4)	21.3	25.9	0.95 (139)	56.3
P2 (W4)	18.1	23.5	0.98 (192)	29.4
P2 (W4)	15.3	22.6	0.92 (192)	2.98

period that started in March. The simple water balance derived as the difference between precipitation and potential evaporation by Thornthwaite (1948) remains positive for most of the annual period. However, water balance may occasionally become negative for the period March–August, which is usually a drier period of a year at the site. Overall, the year preceding and including the measurement campaign was fairly typical as for the annual precipitation ($\Sigma = 3340$ mm) and the number of rainy days ($n = 194$) relative to the long-term averages (see Section 2).

August is usually a drier month relative to the annual monthly mean and there were only 6 days with precipitation during the 22 day long measurement period (1–22 August; Fig. 4). Solar radiation topped at 0.96 kW m^{-2}, but the maximum daily radiation sum was only about 22–23 MJ m^{-2}. The diurnal oscillations of temperature were mostly between 22 and 32°C and daily average around 26°C. Air humidity fluctuated from 100 to less than 60% and daily mean was mostly above 80%. Vapor pressure deficit exceeded 2 kPa on some days, though the daily mean remained relatively low (Fig. 4).

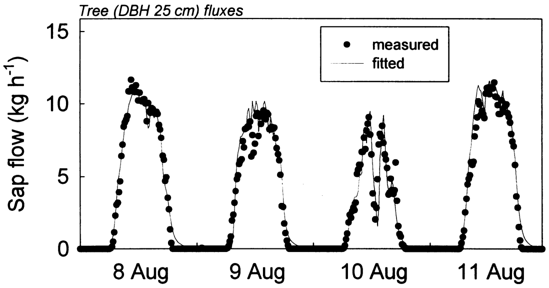

Fig. 5. Example of the measured and fitted (Eq. (6)) sap flow in 15-min resolution. Note that no time delay was applied when fitting the function (Eq. (6)).

3.2. Sap flow coupling to climate

The dynamic response of the measured sap flow (Q_{wt}) to atmospheric forcing was practically immediate. Q_{wt} was so tightly coupled to the climatic variables that no time shift was needed to fit a simple static microclimatic model to mimic Q_{wt}. The most successful equation combined the non-linear response to short-wave radiation and the linear response to air humidity in the form

$$Q_{wt} = a * R_s/(c + R_s) * (100 - b * \mathrm{RH}) \tag{6}$$

where a, b, c are fitted parameters. The data used for fitting included from about 200 to over 800 cases, each representing 15-min time step values of two to eight days excluding the rainy ones. The

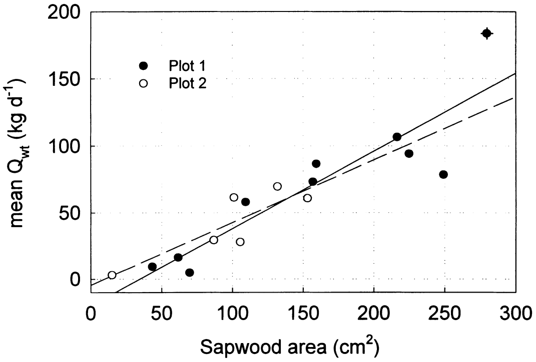

Fig. 6. Mean daily tree sap flow (Q_{wt}) against the sapwood area. Mean daily Q_{wt} was calculated for $n = 20$ complete days (2–21 August) for all sample trees in the two plots. Corresponding regression lines are show (Plot 1, solid line, $r^2 = 0.82$; Plot 2, dashed line, $r^2 = 0.74$).

explained variability in the measured tree sap flow varied between 91 and 98% for the trees in both stands (Table 1; Fig. 5). Incorporating air temperature, either directly or integrated within vapor pressure deficit, resulted in slightly weaker fits.

The function (Eq. (6)), parameterized for the individual trees, was used to extrapolate the measured tree fluxes for the whole experimental period and consequently calculate canopy transpiration (E_{Q}). This enabled comparison of water use for the two studied stands (Plot 1 and 2, respectively), which were not measured simultaneously (see below). For the high degree of the explained variation in the actual fluxes at a tree level, the parameterized and measured tree fluxes were herewith considered equal for the experimental period.

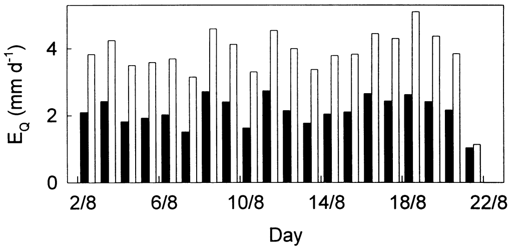

Fig. 7. Stand transpiration (E_{Q}) for the studied plots W5 (filled bars) and W4 (empty bars), respectively.

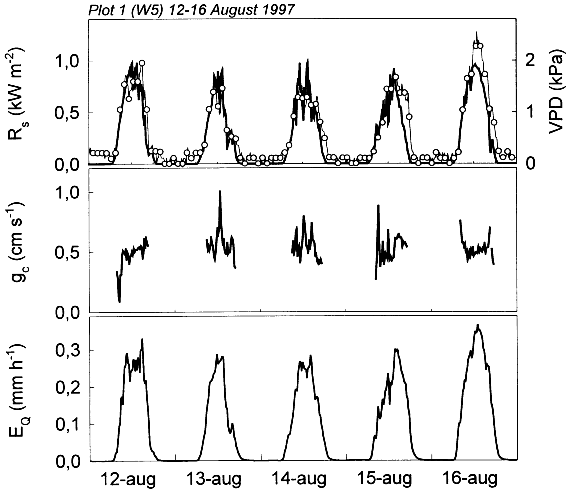

Fig. 8. Top: diurnal courses of short-wave radiation (R_{s}; thick line) and vapour pressure deficit (VPD; thin line with symbols) for the period 12–16 August. Middle: canopy conductance (g_{c}; thick line) for the Plot 1. Bottom: the actual canopy transpiration (E_{Q}) in Plot 1.

3.3. Tree and stand level fluxes

The mean daily tree transpiration (tree sap flow and tree transpiration can be considered equal on daily basis under non-limiting soil water conditions) ranged from several kilograms per day for the smallest sample trees up to above 180 kg for the largest measured tree (Fig. 6). The highest measured daily sap flow reached 207 kg for this tree sample (DBH = 33 cm). The most typical daily rates reached 80–90 kg at Plot 1 and about 60 kg at Plot 2. The fluxes increased mostly linearly with the increasing tree sapwood area (Fig. 6): that relationship was strong for Plot 1 ($r^2 = 0.82$, $n = 10$, $P < 0.001$) and, likely due to a smaller sample size, somewhat weaker for Plot 2 ($r^2 = 0.74$, $n = 6$, $P = 0.028$).

To compare stand transpiration for the two stands during the period of the entire measuring campaign (1–22 August), missing data for each measured tree were filled using the fitted Q_{wt} (Eq. (6); Table 1) prior to scaling to stand fluxes. Stand transpiration reached maximum of about 3 mm d^{-1} for the less dense Plot 1 and about 5 mm for the dense Plot 2 (Fig. 7). For the period of the actual measurements in Plot 1 (8–16 August), the stand transpiration reached in average about 2.3 mm d^{-1} in Plot 1 (basal area 18.6 m^2), with a maximum value of 2.7 mm d^{-1}. The stand

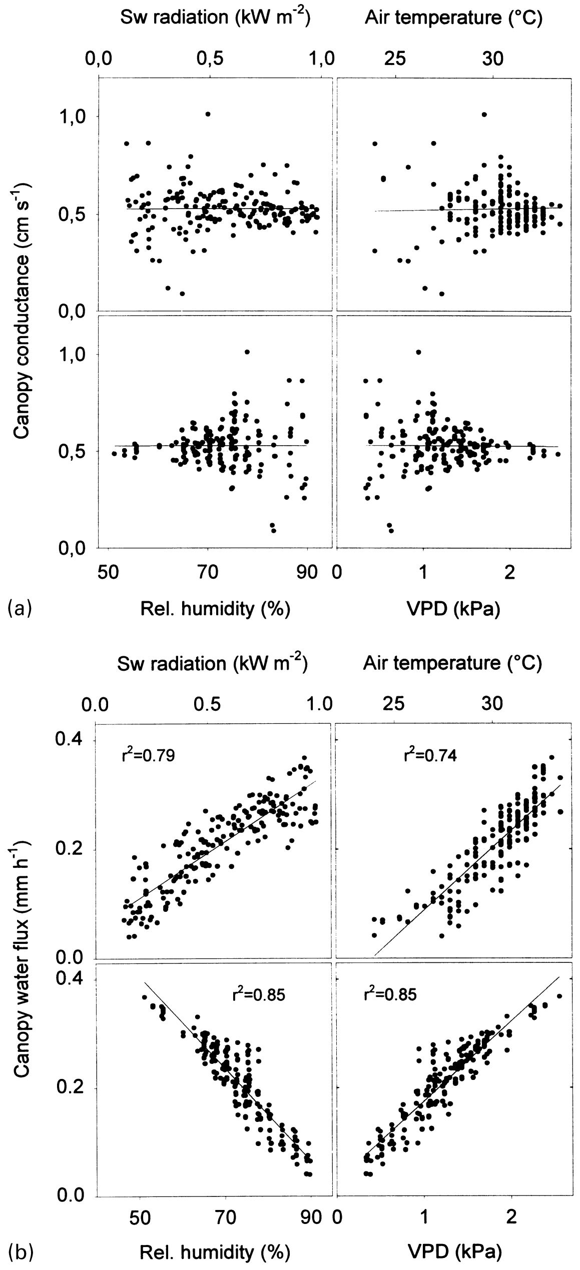

Fig. 9. (a) Scatter diagram of canopy conductance (mean values of 15 min) as shown in Fig. 8 against short-wave radiation (R_s), air temperature, (T_a), relative humidity (RH) and vapour pressure deficit (VPD); (b) similarly shown dependence of E_Q on the above climatic drivers.

transpiration for Plot 2 (basal area 40.4 $m^2\,ha^{-1}$) calculated for this period reached an average of about 3.9 mm (maximum of 4.6 mm d^{-1}). It gives the proportion of about 3:5 for stand transpiration in Plot 1 and Plot 2. This also represents the difference in stand fluxes for an average stand in the area and for the stand with the best production performance.

3.4. Controls of transpiration

For the period of 12–16 August, canopy conductance (g_c) on Plot 1 (catchment W5) reached the mean of 0.53 cm s^{-1} with rather low variation (SD = 0.16 $cm\,s^{-1}$; $n = 557$; Fig. 8). We did not observe any meaningful correlation of g_c to any of the tested climatic variables — radiation, air temperature, relative humidity or vapor pressure deficit (Fig. 9a). On the other hand, the actual transpiration (E_Q) was always strongly correlated with these variables and the simple linear regression to a single climatic variable explained 74–85% of the variation in E_Q using the identical data set (Fig. 9b).

A multivariate analysis also confirmed a very weak dependence of g_c on a combined response to microclimatic variables. For example, the commonly used Lohammar et al. (1980) form of a tree-parameter (p_1, p_2, p_3) equation combining a parabolic response of g_c to radiation (R_s) and a hyperbolic decline of g_c to rising vapour pressure deficit (VPD) as

$$g_c = p_1 * R_s/(R_s + p_2)/(1 - p_3 * \mathrm{VPD}) \qquad (7)$$

did not bring any meaningful fit to the data. On the other hand, a multi-linear regression of E_Q to radiation and VPD showed still stronger fit ($r^2 = 0.91$) than the simple regression to either variable as above.

4. Discussion

The observed tight coupling of sap flow rate to climatic drivers suggests that the resistance along the conductive pathway was not limiting water transport. This also means that the tree water storage was small and its expression was limited to a time scale of at most some minutes. Finally, the strong coupling of sap flow to climatic drivers indicates that during the measurement period, soil water was available to the trees in sufficient amounts.

Plant resistance may limit water uptake under high evaporative conditions regardless of soil water conditions (e.g. Hogg et al., 1997; Margolis and Ryan, 1997). If this occurs, instantaneous water uptake becomes uncoupled from the course of evaporative demand (represented mostly by vapour pressure deficit (VPD)) and the canopy resistance increases. We did not observe this for *A. mangium* trees: on the contrary, the relation of water flux to VPD remained strongly linear even for the values around 2 kPa (Fig. 9b). The identification of the plant resistance that limits transpiration is uneasy because it is coupled to soil water potential, soil/root resistance and to stomatal resistance. Plant resistance can also be altered by embolism of conductive tissues (Tyree and Ewers, 1991; Machado and Tyree, 1994), especially during drought. During our measurement period, we did not observe any reduction of transpiration that would suggest a change in tree resistance or embolism of the conductive system.

Tree water storage and its importance have been frequently discussed in the physiological literature (e.g. Waring and Running, 1978; Milne, 1989; Phillips et al., 1997). The water stored in stem and canopy that can be removed during a day represents most often just a fraction of daily water use (e.g. Schulze et al., 1985; Loustau et al., 1996). Hence, water stored in the stem has mostly negligible importance under longer periods of drought, but is very important on a diurnal time scale. It acts as a buffer for the instantaneous transpiration loss during a day. Water storage is therefore included as a capacitance term in SVAT models that consider both water uptake and transpiration at the hourly and minute time scale (Granier and Loustau, 1994; Cienciala et al., 1994). The above-cited findings were derived from investigations on coniferous trees with low speed of water transport. Tropical woody species may behave similarly: Goldstein et al. (1998) estimated the water storage capacity extractable on a diurnal basis to represent 9–15% of the daily tree water use. The tight and direct coupling of sap flow to climatic drivers observed here for *A. mangium* (Fig. 5; Table 1) indicates even smaller buffering expression of stem water storage in diurnal water use.

We tested several weather variables for approximation of sap flow. Surprisingly, the function combining radiation with relative humidity (RH; Eq. (6)) always yielded a slightly better fit compared with alternative functions that would use air temperature (T_a). This was also true when T_a was used indirectly by combining radiation with vapor pressure deficit. The evaporation theory (Penman, 1953) also suggests that the effect of temperature on evaporation becomes relatively weaker for higher temperature values. Additional explanation may be the fact that T_a fluctuations were small, whereas the diurnal range of RH was large. Unfortunately, the measurement period was too short to explore the relationship of sap flow to these climatic drivers in detail.

The small importance of stomata in regulating water use was indicated by the poor correlation of the climatic variables with stomatal conductance (Fig. 9a). However, these results should be interpreted carefully. First, we had only limited data on atmospheric turbulence available. It would certainly be helpful to assess air mixing in and above the canopy, or at least have wind-speed measurements available directly above the studied stands. Our data only indicate that the importance of the available energy in driving transpiration was large, whereas the importance of stomatal control was relatively small. In the situations when stomatal control is small and not enhanced, e.g. by drought conditions, the simple analysis performed here gives too little information for any generalization. It would particularly be useful to know more about the energy partitioning in these ecosystems to thoroughly assess the controls of transpiration. Several authors recently stressed the urgent need of reassessment of the commonly accepted view on determinism of canopy surface resistance (e.g. Monteith, 1995) and provided new solid arguments for a further exploration of this problem (Alves and Pereira, 2000).

A common formula to express the relative sensitivity of canopy transpiration to a marginal change in stomatal conductance was introduced by McNaughton and Jarvis (1983) and Jarvis and McNaughton (1986). They brought in a dimensionless decoupling coefficient Ω that approaches unity as stomatal control decreases. The low values, typical for conifers, suggest a strong stomatal control and strong coupling to climate. We have not estimated Ω due to rather inadequate weather data (mainly wind-speed that was not measured above the forest stand). However, the very weak correlation of g_c and the strong correlation of E_Q to climatic drivers (Figs. 9a and b) suggest that *A. mangium* should belong to species with higher Ω, similar to several other tropical woody species (Meinzer et al., 1997; Wullschleger et al., 1998).

The maximum water flux found for the largest tree would belong to the highest values reported for various tree species by Wullschleger et al. (1998). Stand density strongly affected tree-level fluxes. The trees from the less dense stand (Plot 1) reached generally higher values compared with those from the dense stand of Plot 2 (Table 1), which corresponded to the observed differences in sapwood area for trees in the two stands (Fig. 2). Tree sapwood area was a particularly strong scaling parameter, which was obvious when comparing tree fluxes from the two studied plots: the slope of the regression lines for the relationship of tree sap flow and tree sapwood area was similar for both groups of trees, and the scatter remained small (Fig. 6). In contrast to this, using tree basal area for scaling lines would obviously be less appropriate here. It would increase the differences in slope parameters (0.18 kg cm^{-2} d^{-1} for Plot 1 vs. 0.13 kg cm^{-2} d^{-1} for Plot 2), and the coefficient of determination would decrease (from $r^2 = 0.81$–0.77 for Plot 1 and from 0.74 to 0.60 for Plot 2). Hence, sapwood area effectively scales fluxes of *Acacia* trees grown at stands of different densities, provided soil and climatic conditions remain equal.

The differences between canopy transpiration for the two plots remained large at the stand level (3:5 for Plot 1 to Plot 2), despite the reversed flux quantities at tree level discussed above. The total stand evaporation may, however, be more balanced if the contribution of understory evaporation were included. Unlike in Plot 2, the less dense Plot 1 had considerable ground vegetation with shrubs and wild banana plants, the contribution of which was not estimated in this study. The transpiration quantity, however, is partly uncertain due to the limited amount of sample trees measured. Despite the relatively strong relationship between the tree sapwood area and the actually measured tree water flux (Fig. 6), the uncertainty of scaling tree water flux to stand transpiration remains high. It is roughly indicated by the unexplained part of the scaling lines (Fig. 6), i.e. 18 and 26% for Plot 1 and Plot 2, respectively. On the other hand, this uncertainty does not affect the relative responses of sap flow and canopy conductance to the microclimate as discussed above.

Considering annual quantities of stand transpiration, it must be stressed that a simple extrapolation of the measured values from short periods would be very uncertain. Some researchers have already pointed out that evaporation in wet tropical regions may be limited by rain events, because of the high frequency of rainfall and high interception evaporation (Bruijnzeel, 1996; Dykes, 1997). On those occasions, the intercepted water limits transpiration and evaporation of intercepted water consumes energy that would otherwise be used for transpiration. Extrapolating our measurements from the relatively dry period of August (Fig. 3) would most likely overestimate the actual annual water use of our study stands. The other likely source of error in the estimated tree and stand transpiration may originate from the limited variation in microclimate, notably of air temperature, during the measurement period (Fig. 4). This limits the predictive value of the fitted Eq. (6) to short periods in proximity of the measured days, and/or to the days with very similar weather. For more contrasting conditions, more measurements are needed to verify the applicability and generality of the observed relationship of *A. mangium* transpiration to the microclimatic variables.

Land clearing and plantation establishment that avoids heavy mechanisms will always be a superior method with respect to the effect on soil properties (Bruijnzeel, 1996). Heavy mechanization affects runoff, surface erosion and topsoil properties that may decrease production and affect the water budget (Malmer and Grip, 1994). Our expedition measurements in the two stands that differ by their management history indicate those effects. In the absence of other differences acting on stand development, the observed differences in stand structure of the two studied stands may be an effect of changed soil parameters like compaction or/and erosion of the topsoil, which in turn predetermined tree and canopy water use assessed in this study. However, considerably more extensive investigation is needed to confirm these indications.

5. Summary

Acacia mangium is a fast-transpiring tree species with high daily water consumption. Tree level fluxes were strongly related to sapwood area. We observed indistinguishable stomatal control for this species, and a tight and linear response of measured sap flux to major climatic variables. No apparent limitation to water flux was observed, despite the high evaporative demand.

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