Second International Colloquium on
Hydrology and Water Management in the Humid Tropics

Water Budgets of Two Upper Montane Rain Forests of Contrasting Stature in the Blue Mountains, Jamaica

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ABSTRACT

The water budgets of a relatively tall (7-12 *m*, PMull) and a stunted tropical montane forest (5-8 *m*, MMor) spaced <30 *m* apart at c. 1820 *m* in the Blue Mountains, Jamaica, were determined over 1995 using complementary hydrological and micro-meteorological techniques. Rainfall (*P*) amounted to 3060 $mm\ yr^{-1}$, and cloud water interception was estimated at 1.4 and 3.4 % of incident rainfall in the tall and the stunted forest, respectively. Net precipitation (throughfall + stemflow) amounted to 86 and 78 % of gross precipitation (2630 and 2380 *mm*), giving a rainfall interception (E_i) of 430 and 680 *mm* (14 and 22 % of annual P), respectively. At 13 and 18 % of rainfall, the stemflow fractions in both the tall and the stunted forest were exceptionally high. Transpiration (E_t) was calculated using the Penman-Monteith equation and meteorological observations above low regenerating forest vegetation at nearby (< 150 *m*) Bellevue Peak (1849 ma.s.l.). Average E_t for the 233 days for which a complete meteorological record was available was 1.52 $mm\ d^{-1}$ (maximum 4.4 $mm\ d^{-1}$). Over 1995, E_t was estimated at 1.39 $mm\ d^{-1}$ or 509 $mm\ yr^{-1}$ (16.6 % of *P*) for the vegetation at Bellevue Peak and for the stunted MMor forest. For the taller-statured PMull forest E_t was estimated at 1.7 $mm\ d^{-1}$ or 620 $mm\ yr^{-1}$ (20.3 % of *P*). Adding E_i and E_t gave about 1050 and 1190 $mm\ yr^{-1}$ for total forest evaporation (*ET*) in the taller and the stunted forest, respectively.

Drainage was computed with a one-dimensional SVAT model and equalled 2032 $mm\ yr^{-1}$ in the taller forest vs. 1857 $mm\ yr^{-1}$ in the stunted forest. Corresponding changes in soil moisture storage were small (-20 and +14 *mm*). Modelling the influence of drought on forest stature indicated that dry periods would have to exceed ca. 40 and 14 days to generate possible water stress (soil moisture tensions ≤ -100 *kPa*) in the taller and the stunted forest, respectively, whereas ca. 18 and 6-12 dry weeks (depending on the horizon) would be required to reach permanent wilting point (soil moisture tensions ≤ -1.58 *MPa*).

In conclusion: (i) Differences in net precipitation inputs between the two sites are insufficient to explain the contrasts in stature and physiognomy between the taller and the stunted forest; (ii) The estimated transpiration rates are comparable to those reported for tall montane forests that experience little to no cloud; this is supported further by the

small amounts of cloud water intercepted by the two forests; (iii) The stunted forest appears to be slightly more sensitive to drought than the taller forest but the long dry periods required to cause significant soil water stress are unlikely to happen under the prevailing rainfall regime.

1 INTRODUCTION

Tropical montane forests are under increasing anthropogenic pressure (Doumenge *et al.*, 1995) and fears have been expressed that the loss of headwater forests subject to frequent cloud incidence (so-called tropical montane cloud forests (TMCF) (Stadtmüller, 1987) may adversely affect the water supply to densely populated lowlands, particularly during rainless periods (Stadtmüller, 1987; Zadroga, 1981; Brown *et al.*, 1966). However, although TMCFs are known to receive additional inputs of water via intercepted cloud water, these amounts of `horizontal precipitation' are extremely variable, both in time and space (Brown *et al.*, 1996; Bruijnzeel & Proctor, 1995; Bruijnzeel, 1999). Similarly, whilst water use by TMCF is allegedly low, reliable information on the subject is extremely scarce. Estimates of transpiration E_t are mostly based on catchment water budgets in which forest water uptake is evaluated by subtracting amounts of rainfall interception from total evapotranspiration ET (Bruijnzeel & Proctor, 1995).

Also, montane cloud forests may show considerable differences in stature, ranging from tall (up to 30 *m*; (Steinhardt, 1979)) to stunted (down to 2-3 *m* (Howard, 1968)). A host of hypotheses have been advanced to explain such differences in stature and many of these involve a hydrological element. Persistent waterlogging, occasional drought on shallow soils, climatically reduced water uptake, and severe leaching of the substrate have all been suggested as a potential cause of forest stunting on wet tropical mountains (Bruijnzeel & Proctor 1995).

Within the framework of a comparative study of the causes of forest stunting the components of the water budgets of two nearly adjacent upper montane rain forests of contrasting stature in the Blue Mountains of Jamaica were studied between 1 January 1995 and April 1996. The shorter-statured forest (main canopy height 5-8 *m*) of the two was situated at 1824 *m a.s.l.* on an exposed ridge top and was classified as a 'moderately-developed' Mor forest. The taller-statured forest (7-12 *m*) was located 30 *m* away on an almost level section of the NW slope of the same ridge at an elevation of 1809 *m a.s.l.* and was classified as a 'poorly-developed' Mull forest (PMull). The adjectives 'poorly-' and 'moderately-developed' refer to the relative position of the sites within a sequence of montane forest types previously recognized by Grubb & Tanner (1976), Tanner (1977) and Hafkenscheid (2000).

The present paper reports on the water budgets of the two forests over the year 1995. A detailed discussion of the climatic conditions in 1995 as measured at 1849 *m a.s.l.* on nearby (< 150 *m*) Bellevue Peak has been given by Hafkenscheid *et al.* (2000).

2 STUDY AREA

A detailed description of the structural, floristic and soil characteristics of the two study forests (PMull and MMor) has been given by Hafkenscheid (2000). Summarizing, the PMull forest plot (area 300 m^2) has a main canopy height of 7-12 *m* and an estimated LAI of 5.0 $m^2 m^{-2}$. Tree density of this forest type is 4400 trees per ha of which 570 trees per ha have multiple trunks. For the MMor forest (area 240 m^2) the corresponding values are 5-8 *m*, 4.1 $m^2 m^{-2}$, 6040 trees ha^{-1}, and 1040 trees ha^{-1} with multiple trunks, respectively. Despite these structural differences, the two forests exhibit a large overlap in species.

The soils of the MMor forest (Folic histosol) and the PMull forest (Dystric cambisol) differ markedly. In the PMull, a discontinuous ectorganic horizon (< 4 cm) overlies a leached clayey mineral soil, with increasing amounts of weathered andesitic parent material with depth and the mass of fine roots gradually decreasing with depth. Key soil physical parameters are listed in Table 1. Topsoil porosity (*ca.* 80 % in the Ah horizon) decreases to *ca.* 60 % in the subsoil. Median values of saturated hydraulic conductivity (K_{sat}) range from 10.1 $m\,d^{-1}$ in the Ah-horizon to 0.24 $m\,d^{-1}$ in the Bh-Bw1 to < 1 $cm\,d^{-1}$ in the Bw2 horizon.

The soil in the MMor is characterized by a thick high-surface root mat and accumulation of slowly decomposing acid mor humus (thickness ≤ 50 *cm*) above a shallow soil profile (≦ 70 *cm*). The MMor soil is also highly leached but more acid (pH_{CaCl2} < 4.0) and less clayey than the PMull soil, with andesitic parent material occurring in the subsoil. Porosity of the MMor subsoil is slightly higher than in the PMull. K_{sat} decreases again with depth. Media n values K_{sat} range from *ca.* 18.5 $m\,d^{-1}$ in the Ah-Bh to *ca.* 1 $m\,d^{-1}$ in the BC horizon.

Table 1: Variations with depth of soil texture (clay<2μm silt 63ì*m*<sand 2*mm*<gravel, %), bulk density (BD, $g\,cm^{-3}$), saturated hydraulic conductivity (K_{sat}, $m\,d^{-1}$), porosity (%), volumetric water content (è, $cm^3\,cm^{-3}$) at water tensions of -10 *kPa* (pF: `field capacity'), -100 *kPa* (pF), and -1.58 *MPa* (pF: `permanent wilting point') and amounts of plant available water (PAW, $è_{pF2}$-$è_{pF4.2}$, $cm^3\,cm^{-3}$) at the PMull and MMor forest sites.

Forest	Horizon	Depth [cm]	clay	silt	sand	gravel [%]	BD [$g\,cm^{-3}$]	K_{sat} [$m\,d^{-1}$]	Porosity [$cm^3\,cm^{-3}$]
PMull	Ah	0-14	28.7	40.3	31.0	0.0	0.44	13.8	0.79
	Bh	14-38	22.6	21.9	53.8	1.7	0.84	0.23	0.68
	Bw1	38-65	7.3	6.7	46.0	40.0	0.98	0.24	0.64
	Bw2	65-82	18.6	20.2	49.1	12.1	1.07	0.01	0.61
			θ_{pF2}	θ_{pF3}	$\theta_{pF4.2}$	PAW			
	Ah	0-14	0.455	0.227	0.099	0.356			
	Bh	14-38	0.523	0.336	0.190	0.333			
	Bw1	38-65	0.512	0.310	0.160	0.352			
	Bw2	65-82	0.552	0.362	0.180	0.372			
MMor	Ah	0-5	21.4	24.0	51.3	3.3	0.39	89.9	0.78
	Bh	5-10	6.4	6.0	36.2	44.4	0.54	23.4	0.78
	Bw	10-35	4.1	3.0	48.4	44.5	0.61	13.7	0.75
	BC	35-≅70	5.2	4.1	51.2	39.5	0.81	1.4	0.63
			θ_{pF2}	θ_{pF3}	$\theta_{pF4.2}$	PAW			
	Ah	0-5	0.369	0.210	0.109	0.260			
	Bh	5-10	0.399	0.206	0.094	0.305			
	Bw	10-35	0.358	0.190	0.090	0.268			
	BC	35-≅70	0.411	0.204	0.087	0.324			

3 METHODOLOGY

3.1 General

For a vegetated surface subject to mist or low cloud, the equation for the water balance over a given period of time reads:

$$P + CW = E_i + E_t + E_s + R + D + \ddot{A}S \qquad (1)$$

where P is incident rainfall, CW cloud water interception, R surface runoff (overland flow), D drainage, and $\ddot{A}S$ the change in soil moisture storage. The evaporation terms E_i, E_t, and E_s represent the losses via intercepted precipitation (evaporation from a wet canopy), transpiration (evaporation from a dry canopy) and evaporation from the soil and litter complex, respectively. Their sum equals total evapotranspiration (ET). All components of the water budget are expressed in *mm* of water for the chosen time interval. E_s is generally very small in tropical rain forests (Jordan & Heuveldop, 1981; Roche, 1982) and can be neglected therefore. Here E_s is included in the estimate of E_t (see below). Surface runoff was never observed (which is expected given the high permeability of the soils). As such, Equation 1 reduces to:

$$P + CW = E_i + E_t + D + \ddot{A}S \qquad (2)$$

The different forest types of the study area occur in small patches along and around narrow ridge tops (Grubb & Tanner, 1976; Hafkenscheid, 2000). This precluded the use of the catchment water balance approach in which streamflow (equalling R+D in Equation 1) is monitored and ET evaluated by subtracting streamflow from P+CW (Ward & Robinson, 1990). Although Equation 1 can be solved in principle on a plot basis as well, the estimation of the drainage component is notoriously difficult because of the large spatial variability of the hydraulic conductivity of forest soils (Cooper, 1979; Davis *et al.,* 1996). Therefore, use is often made of alternative techniques to determine E_t, such as micro-meteorological (Shuttleworth, 1988) or plant physiological methods (Roberts, Hopkins & Morecroft, 1999). The mosaical character of the vegetation in the study area precluded the application of micro-meteorological techniques to evaluate E_t separately per forest type because the fetch requirements of such techniques could not be met (Thom, 1975). Therefore, a combination of hydrometeorological and plant physiological methods was envisaged initially for the determination of E_i and E_t, respectively, per plot.

Unfortunately, the Greenspan sapflow gauges that were used on a series of nine sample trees of variable diameters in each plot could not cope with the humidity of the prevailing climate and failed to give any useful results and an alternative strategy had to be followed. Along with the continuous measurement of basic climatic variables (temperature, humidity, global and net radiation, wind speed and direction) above the freely exposed short (*ca.* 3 *m*) regenerating forest vegetation of similar floristic composition on Bellevue Peak (1849 *m a.s.l.*; lateral distance to the two forest plots < 150 *m* towards the NE), a set of thin-wire thermocouples was used to measure rapid fluctuations in temperature. From the latter, an estimate of E_t can be derived (Vugts *et al.*, 1993; Waterloo *et al.*, 1999). It was recognized from the outset that there would be differences in aerodynamic roughness and, especially, surface resistance between the vegetation at Bellevue Peak and each of the two study plots. As such, the estimates of E_t presented in the following for the regenerating forest at Bellevue Peak must be considered a first approximation of the water uptake of the mature forests of the plots. In the following the methodology used to quantify E_i, E_t, D and ΔS will be described whereas details of the instrumentation are given in part 4 ('RESULTS').

3.2 Interception loss

Rainfall interception (E_i) was evaluated as the difference between incident rainfall and the sum of throughfall (*Tf*) and stemflow (*Sf*). Because the latter was measured on a 3-4 day basis, the analytical model of rainfall interception developed by Gash (1979) and modified later by Gash, Lloyd & Lachaud (1995) was used to generate a daily record of both *Tf* and *Sf* of the forest structural parameters required by the analytical model. the canopy saturation value S, stemflow coefficient p_t and trunk capacity S_t were derived using the methods of Jackson (1975) and Gash & Morton (1978), respectively. The free throughfall coefficient p, *i.e.* the gap fraction of the forest canopy, was derived using ceptometer measurements of photosynthetic active radiation above and below the respective canopies.

3.3 Transpiration

Daily values of E_t were evaluated using the Penman-Monteith equation (Monteith, 1965):

$$\lambda E = \frac{\Delta A + \rho Cp.VPD / r_a}{\Delta + \gamma(1 + r_s / r_a)} \qquad (3)$$

where λE is the latent heat flux (Wm^{-2}), A the amount of available energy (Wm^{-2}), Δ the slope of the saturation vapour pressure curve at air temperature T ($Pa\,K^{-1}$), γ the psychrometric constant ($Pa\,K^{-1}$), C_p the specific heat of air ($J\,kg^{-1}K^{-1}$), ρ the density of air (kg m^{-2}), VPD the vapour pressure deficit (Pa), r_a the aerodynamic resistance ($s\,m^{-1}$) and r_s the surface resistance. For wet canopy conditions the surface resistance r_s reduces to zero, which allows Equation 3 to be simplified to:

$$\lambda E = \frac{\Delta A + \rho Cp.VPD / r_a}{\Delta + \gamma} \qquad (4)$$

The aerodynamic resistance r_a was calculated from wind speed observations above the regenerating forest at Bellevue Peak assuming a logarithmic wind profile and neutral stability conditions according to Thom (1975):

$$r_a = \frac{\left(\ln\left[\frac{z-d}{z_0}\right]\right)^2}{k^2.u} \qquad (5)$$

where z is the observation height above the ground surface (m), d the zero-plane displacement height (m), z_0 the roughness length (m), k is the dimensionless von Kármán's constant (0.41) and u the wind speed as measured at height z ($m\,s^{-1}$). Considering the short stature of the vegetation at Bellevue and the dissected nature of the terrain, d was set at 0.6 times the canopy height h (3.0 m) or 1.8 m. Wind profile data used in the analysis were restricted to wind speeds in excess of 3 $m\,s^{-1}$ at the lowest level (5.9 m) and to wind directions between 40° and 160° to avoid non-neutral atmospheric conditions and fetch limitations. Finally, wind speeds as measured at 5.9 m were converted to those expected at 3.5 m level (where most other climate parameters were measured) using a logarithmic wind profile (Thom, 1975). Values of z_0+d were derived for 3742 half-hourly periods with (near) neutral atmospheric stability and adequate fetch using the graphical method proposed by Thom (1975). An average value of 2.25 m was obtained, giving a value of z_0 of 0.45 m (0.15 times the vegetation height at Bellevue Peak). Converting wind speeds measured at 5.9 m to those predicted by the logarithmic wind profile for 3.5 m reduces Equation 5 to:

$$r_a = \frac{10.51}{u_{3.5}} \tag{6}$$

The resistance parameter r_s was evaluated by an inverse application of the Penman-Monteith equation, a method that requires independent estimates of λE (Monteith, 1965). These were obtained by solving a simplified energy budget equation. Assuming that (i) amounts of advected energy and various small physical and biochemical storage terms are small (and therefore negligible); and (ii) the resulting available energy (R_n-G) is used either for warming up the ambient air or for evapotranspiration (Brutsaert, 1982) we can write:

$$R_n - G = H + \lambda E \tag{7}$$

where R_n is the net radiation flux density (Wm^{-2}), G the soil heat flux density (Wm^{-2}), H the sensible heat flux density (Wm^{-2}), λE the latent heat flux of vaporization (Wm^{-2}) and λ the latent heat of vaporization ($J\,kg^{-1}$). R_n and G were measured directly as part of the meteorological observations at Bellevue Peak (Hafkenscheid *et al.*, 2000). The sensible heat flux H was obtained using the temperature variance method (Tillman, 1972; De Bruin, 1982). Under dry unstable atmospheric conditions, H is related to near-surface turbulent fluctuations in air temperature, the intensity of which is described by the standard deviations (σ_T) of high-frequency measurements of the air temperature T (K).

As this procedure is restricted to periods during which the forest canopy is dry, λE refers to transpiration E_t as well as to evaporation from the litter surface E_s. Next, the values for $\lambda E = E_t + Es$ obtained using the temperature variance method were employed in an inverse application of the Penman-Monteith equation and inserting measured climatic conditions:

$$r_s = \frac{\rho C_p}{\gamma}\frac{VPD}{\lambda E} + r_a\left(\frac{\Delta(R_n - G)}{\gamma\lambda E} - \frac{\Delta}{\gamma} - 1\right) \tag{8}$$

The resulting half-hourly values of r_s were subjected to a multiple-regression analysis and related to corresponding ambient climatic variables to permit solving of the Penman-Monteith equation during periods for which thermo-couple data were not available.

3.4 Drainage and soil moisture storage

Because soil water tension profiles were only measured at 3-4 day intervals, the one-dimensional Soil-Vegetation-Atmosphere-Transfer (SVAT) model VAMPS (Schellekens, 1996) was used for the computation of daily values of D and ΔS. The soil water module of VAMPS was adapted from the soil water simulation model SWATR (Feddes, Kowalik & Zarasny, 1978). Water fluxes in the unsaturated zone are calculated by solving an adapted ψ_m-based form of the numerical solution of the basic Richards equation for unsteady unsaturated flow (Richards, 1931) as described by Feddes, Kowalik & Zarasny (1978) and Belmans, Wesseling & Feddes (1983).

Soil moisture retention curves (ψ_m - θ relationships) needed to solve the basic equation for unsaturated flow (Richards, 1931) as used in VAMPS were derived using undisturbed soil cores (100 cm^3; typically 5-8 per horizon). The ψ_m - θ relationships were established using the porous medium *cum* pressure-membrane technique (Black et al., 1965; Stakman, 1973) Saturated hydraulic conductivities (K_{sat}) were measured with an ICW permeameter, using falling- and constant-head approaches for samples of low and high permeability, respectively (Kessler & Oosterbaan, 1973). Unsaturated conductivity $K(\psi_m)$ was derived from measured saturated conductivity and the relations between soil water content, suction head and $K(\psi_m)$ using the so-called Van Genuchten equations (Genuchten, 1980).

The upper 80 cm of the mineral soil profiles of the PMull and MMor forest plots were subdivided into 80 sub-layers of 1 cm each to enable the adequate simulation of the rapid fluctuations in top soil water tension ψ_m that are known to occur in the study area (Kapos & Tanner, 1985). Active rooting depths of 60 and 30 cm were assigned to the PMull and MMor soils, respectively (Elbers, 1996). Free drainage at the profile bottom was assumed in this study. The net precipitation record generated with the analytical model of rainfall interception and the estimates of E_t as computed with Equation 3 were taken to represent the amounts of water added to or extracted from the soil water reserve on a daily time step. Water uptake by the roots would start to deviate linearly from the potential rate indicated by Equation 3 whenever ψ_m<-100 kPa ('limiting point', pF; Landsberg (1986)) whereas transpiration stopped entirely at ψ_m<-1.58 MPa ('permanent wilting point', pF). An initial profile for ψ_m with depth was generated by interpolating the values measured at four depths on 1 January 1995 over the 80 sub-layers.

The ψ_m values predicted by the VAMPS model were calibrated against values measured by 3-4 tensiometers in each of the four principal soil horizons during the 208 day record for which continuous estimates of E_t were available (1 January - 27 July 1995). To obtain optimum agreement between predicted (mean values for 5 sub-layers of 1 cm each around a soil horizon's centre) and measured values of ψ_m, the magnitude of the saturated hydraulic conductivity (K_{sat}) was adjusted. The optimisations were restricted to a single parameter only for reasons of transparency and because values of K_{sat} in forest soils can be grossly underestimated when using small cores (Davis *et al.*, 1996).

3.5 Instrumentation

Rainfall (P, mm) at Bellevue Peak was measured above the vegetation at 3.5 m with a tipping bucket cum logger system (resolution 0.44 mm) backed by two manual gauges (100 cm^2 orifice) placed in a nearby clearing. The auto-recorded data were stored at 5 *min* intervals; manual gauges were read every 3-4 days. From 21 July 1995 onwards, a manual rain gauge was also operated above the canopy of the MMor forest.

Amounts of cloud water intercepted by a forest are bound to differ from those estimated with a simple standard fog gauge (Schemenauer & Cereceda, 1994; Hafkenscheid, Bruijnzeel & de Jeu, 1998). Therefore, although Grünow-type fog gauges (Russell, 1984) were installed above the vegetation at Bellevue Peak and the MMor forest, cloud water intercepted by the two forest plots was estimated as all throughfall that did not originate from rainfall. The underlying assumption is that all *Tf* recorded after the last registration of *P* had to be generated by *CW* after applying a threshold of 2 *h* to eliminate contributions by residual rainfall-induced crown drip. It is recognized that amounts of *CW* obtained in this way will represent minimum estimates.

Throughfall (*Tf*) was measured in the MMor and PMull forests with tilted (30^0) stainless steel gutters (400 times 4 *cm*) equipped with a tipping bucket cum logger device (0.3 *mm* per tip) in combination with twelve manual gauges (100 cm^2 orifice; 3-4 day sampling intervals) that were randomly relocated after each sampling (Lloyd & Marques-Filho, 1988). An areal average *Tf* volume was obtained by a weighting procedure that took the relative areas of the two types of gauges into account. The gutters were cleaned every 3-4 days and regularly treated with a Teflon® solution to prevent blockage by organic debris and to minimize wetting losses. In each plot, twelve trees, representing a range in species and diameter classes, were fitted with rubber collars connected to 22.5 litre containers to measure *stemflow* (*Sf*). Gauges were emptied simultaneously with those for *Tf* while dividing the *Sf* volumes by the projected area of the corresponding tree crowns enabled their expression in mm of water.

The meteorological mast at Bellevue Peak was in operation from 1 January 1995 until 4 April 1996, with the exception of 28 July-21 October 1995, 16 November-15 December 1995 and 30 December 1995-16 January 1996 when parts of the equipment were damaged by excessive moisture (1996) or lightning strikes (1995). To improve the seasonal representativity of the data, the present chapter is restricted to the observations made in 1995.

Net radiation (R_n, Wm^{-2}) was measured with a net radiometer (Radiation and Energy Balance Systems Inc.) placed at 5.9 *m* on an arm extending 1.5 *m* from the mast in such a way as to avoid shading of the instruments. Net soil heat fluxes (G_s, Wm^{-2}) were determined with a soil heat flux plate (Middleton & Co.) placed underneath a *ca.* 5 *cm* thick litter layer. Care was taken to avoid disturbance of the litter layer during installation. Air temperature (T, ^oC) and relative humidity (*RH*, percentage of saturation) were measured at 3.5 *m* with a precision thermometer (Campbell Sci. HMP 35AC) and Vaisala capacitative humidity sensor after 60 *s* of forced ventilation at approximately 2 $m\,s^{-1}$. Both sensors were placed in a Gill-type radiation shield to protect them against direct insolation and rainfall. The thermometer had an accuracy of 0.1^oC. The accuracy of the *RH* sensor was typically better than 2 % whereas a long-term stable precision of less than 1 % was stated by the manufacturer. Relative humidity readings in excess of 100 %, as were recorded sometimes during periods of prolonged wetness, were set at 100 %. Both *T* and *RH* sensors were calibrated regularly against readings made with an Assmann psychrometer. Wind direction was measured using a potentiometer windvane (Vector Instruments, W200P) placed at 12.5 *m*. Wind speeds were determined at three heights (5.94, 7.65, and 10.1 *m*) using three-cup anemometers (Vector Instruments, A101M/L), supported by arms (0.5 *m*) orientated towards the prevalent wind direction (ESE). The sensors had a stalling speed of 0.15 $m\,s^{-1}$ and an accuracy of 1-2 %. All instruments were sampled at 30-second intervals except for the *T* and *RH* probes (every 5 min). A fast-responding dry-bulb thermo-couple (chromel-constantane wire type; 12.7

μm wire thickness; Tillman, 1972) was used for the registration (0.5 *Hz*) of rapid fluctuations in air temperature at 5.9 *m* (2.9 *m* above the forest canopy) to derive the sensible heat flux *H*. Thermocouple data were pre-processed over 5-min intervals to avoid trends in standard deviation values. All data were processed by a Campbell 21X data logger system. Averages and standard deviations were calculated over 30-min periods and stored using a solid-state memory.

Soil water tensions ψ_m were determined at three sites within each forest, with a total of 14 tensiometers per plot distributed over the principal soil horizons (8 in the top horizons, 6 in the subsoil horizons) and read at 3-4 day intervals (*i.e.* the same as for the measurements of throughfall and stemflow). A needle cum pressure transducer system was used that was accurate to the nearest centimeter, up to tension values of *ca.* -0.9 *MPa* (*pF*; air entry value).

4 RESULTS

4.1 Rainfall and cloud water deposition

Rainfall input over the year 1995 at Bellevue Peak amounted to 3060 *mm*, *i.e.* about 7 % above the estimated average annual rainfall for the research area (2850 *mm*; Hafkenscheid, 2000) and *ca.* 25% above the long-term mean annual rainfall record for nearby Cinchona (2277 $mm\,yr^{-1}$; 1901 - 1990; J. R. Healey, *personal communication*). Amounts observed at Bellevue Peak and above the MMor forest did not differ significantly and the latter will not be considered further. Rainfall was unevenly distributed over the year: October and November were wetter than normal (> 450 *mm* each); a secondary peak that normally occurs in May and June was absent. The generally dry February - March period, on the other hand, was distinctly wetter than usual (Figure 1). Over 1995, the automated equipment identified 327 separate events distributed over 205 days with rain in excess of 0.44 *mm*, with an average of 14.9 *mm* per rain day. A total of 71 dry periods of 24 hours or more were recorded (mean duration: 2.3 days; 160 days in total) of which 51 (72 %) were of less than 48 hours duration. The longest continuously dry period lasted 11 days (27 March to 6 April). Average values for storm size, duration and intensity were 9.41 *mm*, 02:13 *h*, and 5.12 $mm\,h^{-1}$ (weighted mean 4.2 $mm\,h^{-1}$), respectively. The highly skewed frequency distributions of these parameters however requires the use of median rather than mean values: 1.78 *mm* , 0:40 h, and 2.36 $mm\,h^{-1}$.

Net cloud water deposition (*CW*) at the MMor plot in the form of *Tf* during rain-free periods totalled 93 *mm*. This amount equalled 3.4 % of the rainfall associated with the preceding storms. For the PMull plot the corresponding values read 31 *mm* and 1.4 % of *P*, respectively. Extrapolating these percentages to a one-year period, gives amounts of 43 $mm\,yr^{-1}$ for the shorter-statured but more exposed MMor. Both estimates must be considered conservative because the forest intercepts an unknown amount of fog during rainfall.

4.2 Throughfall, stemflow and derived estimates of rainfall interception.

Total throughfall (*Tf*) amounted to 2233 *mm* in the taller-statured PMull forest and was 1821 *mm* in the stunted MMor forest. These values correspond to *ca.* 73 % and 60 % of the associated rainfall. The corresponding amounts of stemflow (*Sf*) were 399 and 559 $mm\,yr^{-1}$, respectively, or 12 % and 18 % of *P*. Automatically recorded *Tf* data were available for 257 and 307 days in the PMull and MMor forest, respectively. The correlation between the continuously recorded and the spatially averaged manual *Tf* data (3-4 day periods) was modest ($r^2 \leq 0.75$), largely as a result of high spatial variability in *Tf*, presumably because of frequently occurring drip points .

Measured interception losses (E_i) amounted to 428 *mm* (14.0 %of *P*) in the PMull *vs.* 680 mm (22.2 % of *P*) in the MMor forest. The high interception estimated for the stunted MMor forest is surprising and largely due to its low *Tf* fraction because the *Sf* fraction is very high.

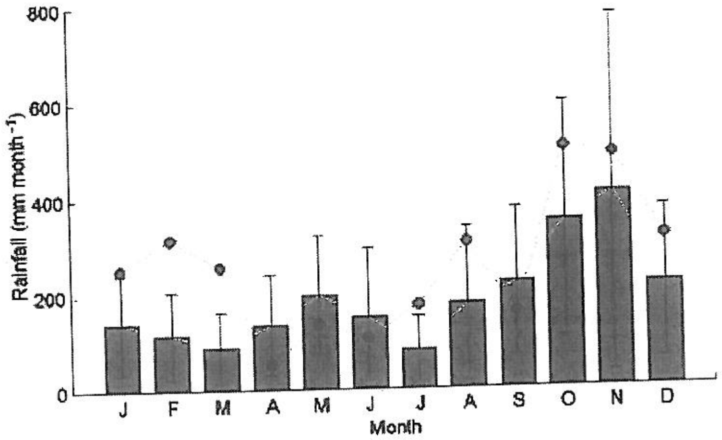

Figure 1: Long-term (1901-1990) average monthly rainfall (bars) at Cinchona (1500 m a.s.l.; J. R. Healey, *personal communication*) and monthly totals at Bellevue Peak (1849 m a.s.l.) in 1995 (dots). Vertical lines represent one standard deviation from the mean.

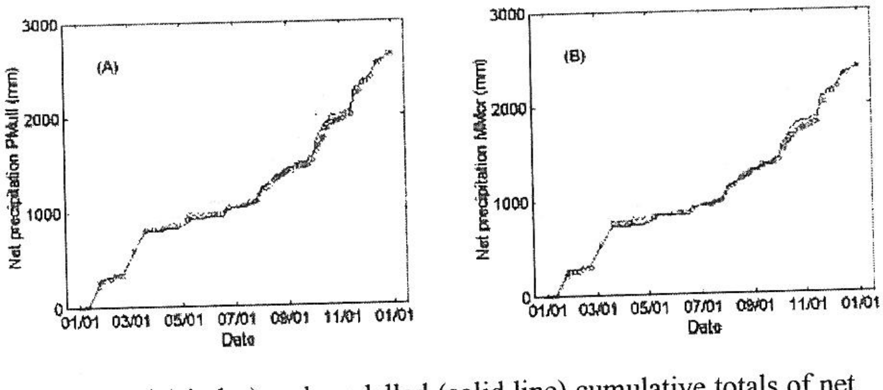

Figure 2: Observed (circles) and modelled (solid line) cumulative totals of net precipitation (*Tf*+*Sf*) over 365 days comprising 94 periods of manual sampling in the PMull (A) and MMor (B) forest, respectively. Gross precipitation (dotted line) has been added for comparison.

Table 2 lists the values of the four forest structural parameters (p, S, p_t, and S_t) that were used in the analytical model of rainfall interception, along with the average and median rainfall intensities and the rate of evaporation from a wet canopy (Equation 4). The larger stature and LAI of the PMull forest are reflected in the higher values of the canopy and trunk storage capacities whereas the MMor forest has a higher gap fraction (p) and a higher stemflow coefficient (p_t). Figure 2 shows the measured amounts and optimised model predictions of net precipitation ($Tf+Sf$) over 1995 for the PMull and MMor forests. Using the average value of 0.15 $mm\ h^{-1}$ for E_{wet} as calculated with Equation 4 in the analytical model overestimated the measured E_i by 52 mm (1.7 % of P) in the PMull forest but gave an underestimation of 247 mm (-8.1 % of P) in the MMor forest. Optimising the value of E_{wet} to match measured and modelled net precipitation totals gave a value of 0.11 $mm\ h^{-1}$ for the PMull forest (*i.e.* 40 % lower than the previous estimate of 0.15 $mm\ h^{-1}$) but required a 230 % increase to 0.36 $mm\ h^{-1}$ for the MMor forest. We will return to this discrepancy in the discussion.

4.3 Transpiration

Calculations of E_t using the Penman-Monteith equation (Equation 3) require knowledge of the diurnal patterns of the aerodynamic- (r_a) and surface-resistance (r_s) parameters. The average diurnal pattern of r_a at Bellevue Peak (based on 253 days of wind speed observations) mirrors the pattern of lower wind speeds during the day and maximum wind speeds at night (Hafkenscheid *et al*, 2000). Values for r_a increase during the day to a mid-afternoon maximum of *ca.* 39 ± 22 $s\ m^{-1}$ followed by a rapid decrease in the late afternoon to a minimum and rather constant nocturnal value of 19 ± 15 $s\ m^{-1}$ (Figure 3).

Inverse application of the Penman-Monteith equation to derive values of r_s (Equation 8) requires independent observations of the latent heat flux (evapotranspiration) λE. Using the temperature variance method in combination with the energy budget (Equation 7), λE of the forest at Bellevue Peak was derived for 411 half-hourly periods with dry canopy conditions and R_n > 100 Wm^{-2}. The corresponding totals of net radiation (R_n), soil heat flux (G), and sensible heat flux (H) amounted to 264.7, 3.6 and 128.5 $MJ\ m^{-2}$, respectively, giving a total λE of 132.6 $MJ\ m^{-2}$ (equivalent to 54.0 mm of water given a mean value for λ of 2.46 $MJ\ kg^{-1}$). The average hourly rate of λE was 0.26 ± 0.16 $mm\ h^{-1}$ (maximum 0.72 $mm\ h^{-1}$). The average diurnal pattern of r_s derived from these 411 half-hourly values of λE by solving Equation 8 is shown in Figure 4. Values of r_s are lowest in the early morning (09:00 AM) and increase steadily during the remainder of the day to reach values ≥ 100 $s\ m^{-1}$ in the night.

Table 2: Forest structural and climatic parameters used in an application of the analytical rainfall interception model for the MMor and PMull forests: the mean (R_i) and median intensities of precipitation, the mean evaporation rate from a saturated canopy (E_{wet}), the storage capacities of the canopy (S) and trunks (S_t), the coefficients of free throughfall (p) and stemflow (p_t), and the amounts of P necessary to saturate the canopy (P_s).

Forest	R_i	R^{median}	E_{wet}	p	S	p_t	S_t	P_s
		$mm\ h^{-1}$			-	mm	-	mm
PMull	5.12	2.36	0.154	0.05	1.57	0.15	0.39	2.0
MMor	5.12	2.36	0.154	0.13	1.30	0.20	0.20	2.2

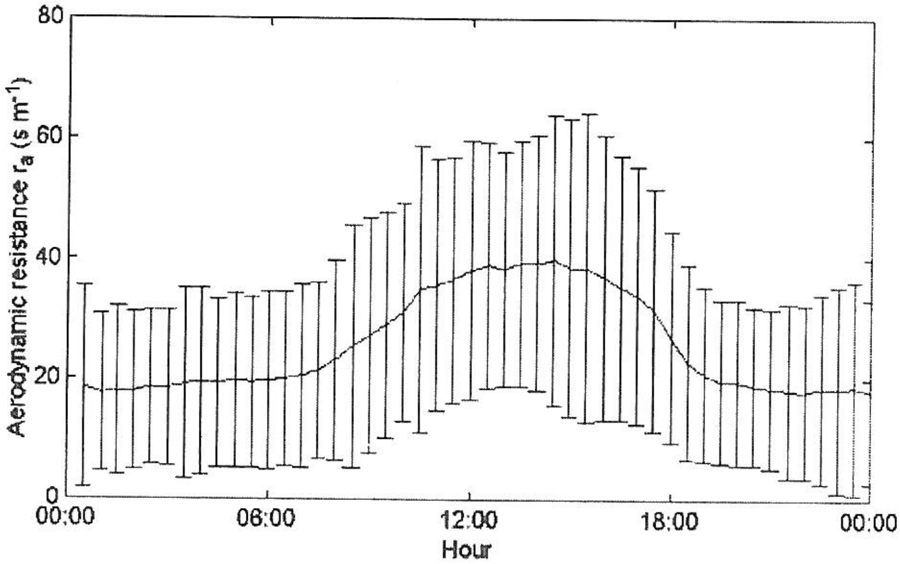

Figure 3: Average diurnal pattern of the aerodynamic resistance r_a for the vegetation on Bellevue Peak based on 253 days of wind speed observations between 1 January and 31 December 1995. Vertical bars represent ± one standard deviation.

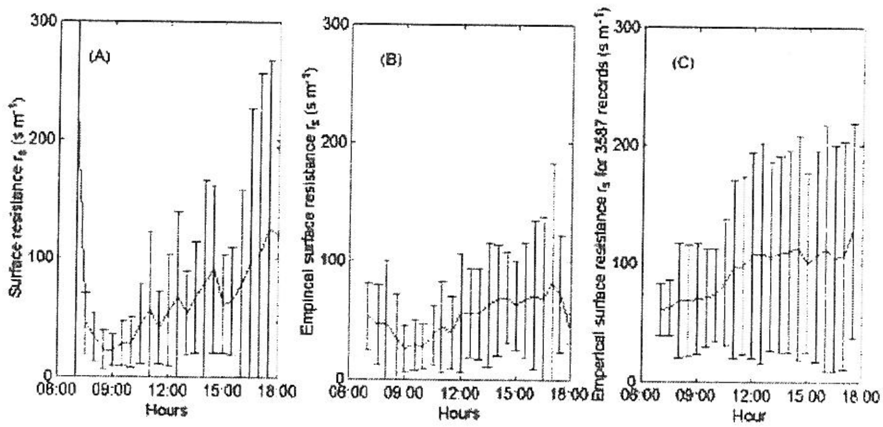

Figure 4: Average diurnal patterns of the surface resistance r_s for the regenerating vegetation at Bellevue Peak based on (A) solving Equation 8 for 411 half-hourly records; (B) solving Equation 9 for the same data set and (C) solving Equation 9 for all 3587 half-hourly periods between 1 January and 31 December 1995 with a dry canopy, R_n > 100 Wm^{-2}, and functional instrumentation. Vertical bars represent ± one standard deviation

To enable the extension of the above values of r_s to periods for which no thermocouple data were available, they were subjected to a multiple-regression analysis with ambient climatic variables, notably net radiation (R_n, Wm^{-2}), vapour pressure deficit (VPD, kPa), temperature (T, K) and wind speed at 3.5 m($u_{3.5m}$, $m\,s^{-1}$) . The resulting empirical relationship (n = 411, r^2 = 0.67) reads:

$$r_s = e^{-5.853-0.004.R_n-0.018.VPD+0.635.T-0.198.u_{3.5m}} \quad (9)$$

Equation 9 was applied to all 3587 half-hourly records during which the canopy could be assumed to be dry and R_n > 100 Wm^{-2}. During much of the day the resulting average pattern for r_s (shown in Figure 4B) corresponds reasonably well with that derived using Equation 8 (Figure 4A) but large deviations occur in the early morning and in the late afternoon, when the TVAR-based estimates of r_s are higher. The associated standard deviations are so large that the differences are non-significant. The predicted average diurnal pattern of r_s for all 3587 dry half-hourly periods of above-canopy climatic observations to which Equation 9 could be applied (*i.e.* not during rainstorms or within 2 hours after storms > 1 *mm*; see section on rainfall) is displayed in Figure 4C. Although the mean daytime values for r_s are generally higher compared to the previous predictions, the resulting pattern is very similar and was used in the remainder of the computations of ëE.

Next, daily totals of E_t were calculated using Equations 3 and 9 for the same dry daytime hours. For periods characterized by a fully wetted canopy, r_s was set to zero and transpiration was assumed to have ceased (Monteith, 1965; Rutter, 1975). It is recognized that the use of a 2-hour threshold period for the canopy to dry up is arbitrary and may be conservative given the estimates of S and E_{wet} in Table 2. The computations were therefore repeated using a stop/go principle, with r_s for wet conditions using values of r_s as predicted by Equation 9 immediately after rainfall had stopped. The effect of applying a threshold proved to be small (see below).

Equations 3 and 9 could be used on 233 days (n = 3587 half-hourly periods) for which there was a complete climatic record to compute daytime *ëE*, the sum of which represents the evaporation from a dry canopy or transpiration (E_t). The total transpiration for this 233 *day*-period amounted to 354 mm or 1.52 ± 0.73 $mm\,d^{-1}$ (maximum 4.36 $mm\,d^{-1}$; median 1.48 $mm\,d^{-1}$). Extrapolated to a period of 365 days would give an approximate annual E_t of 555 mm. Applying the stop/go principle without the use of a threshold period to allow the canopy to dry up, gave a total E_t for the 233 days of 363 *mm* (1.56 ± 0.70 $mm\,d^{-1}$), suggesting that the effect of applying a threshold period of 2 h is indeed small (*c.* 2.5 %).

For 71 days in 1995 wind speed data were unavailable. Daily E_t values (in $mm\,d^{-1}$) were related to the remaining climatic variables (mean daytime R_n (Wm^{-2}), T (^oC), and RH (%)) using a multiple-regression analysis:

$$E_t = 8.90 + 0.005.R_n - 0.213.T - 0.058.RH \quad (10)$$

Using daytime (06:00-18:00 h) means of VPD rather mean values of RH did not improve on the coefficient of correlation. Total E_t over the 304 days for which estimations could be made with reasonable reliability (by solving Equation 3 and Equation 10 for 233 and 71 days, respectively) amounted to 430 *mm* (equivalent to 516 $mm\,yr^{-1}$), or 1.41 ± 0.72 $mm\,d^{-1}$ (median: 1.35 $mm\,d^{-1}$). For the remaining 61-*day* gap (Figure 5), average values of 1.85 $mm\,d^{-1}$ and 1.03 $mm\,d^{-1}$ were adopted for the E_t of the 20 remaining dry- and 41 rainy days (P > 0.44 *mm*), respectively.

The averages for dry and wet days were based on values obtained for 141 wet and 163 dry days during 1995. In the absence of climatic data collected at other locations in the vicinity of the study area that could have been used to help fill the remaining 61-*day* gap in the meteorological records, average values of 1.85 $mm\ d^{-1}$ and 1.03 $mm\ d^{-1}$ were adopted for the E_t of the 20 remaining dry days and 41 days with rain ($P > 0.44$ *mm*), respectively. These latter averages for dry and wet days were based on values obtained for 141 wet and 163 dry days during 1995. Following this procedure an annual E_t of 509 *mm* (1.39 ± 0.67 $mm\ d^{-1}$) was estimated for 1995.

The average reference open-water evaporation total according to Penman (1956) for the 365-*day* period was 3.0 ± 1.2 $mm\ d^{-1}$ (Hafkenscheid *et al.*, 2000). Dividing the 1.4 $mm\ d^{-1}$ *obtained* for E_t (304 days) by the 3.0 $mm\ d^{-1}$ open-water evaporation E_0 ($n = 318$ days) gives an E_t:E_0 ratio of 0.47. This value is typical for montane forests that experience little or no cloud (Bruijnzeel and Proctor, 1995). Using the stop/go principle referred to earlier, total E_t for the 365 days amounted to 526 *mm*. This represents an increase of 3.3 % compared to the computations in which a 2-h threshold period was applied to storms > 1 *mm*. Not surprisingly, the effect was most pronounced on wet days for which average E_t of 1.11 $mm\ d^{-1}$ was obtained when no threshold was applied *vs.* 1.03 $mm\ d^{-1}$ for the computations using a 2-hour threshold period.

In the absence of direct estimates of E_t for the PMull and MMor forests themselves, the value obtained for the regenerating forest at Bellevue Peak (509 $mm\ yr^{-1}$) may be used as a starting point. Although it is recognized that extrapolating the Bellevue Peak results to the two older forests has its limitations, no statistically significant differences were found in the weighted mean $\delta^{13}C$ concentrations in leaves collected in a series of mature sun leaves from four forests of gradually increasing stature in the study area, including the PMull and MMor forests (Hafkenscheid, 2000). This suggests a comparable gas exchange capacity (including water vapour) at the leaf level for these forests (Ehleringer, 1993). In addition, no significant differences were found in terms of stomatal size and density and photosynthetic capacity (Hafkenscheid, 2000; Tanner & Kapos, 1982; Aylett, 1985). Such findings suggest that differences in transpiration rates, at least per unit of leaf area, between forests of contrasting stature in the study area may well be limited and therefore will be determined mainly by differences in leaf area index (LAI). Although the LAI of the regenerating forest at Bellevue Peak is unknown, visual evidence suggests that it is similar to the LAI of the MMor (*c.* 4 $m^2 m^{-2}$) but smaller than that of the PMull. The LAI of the MMor and PMull forests were estimated at 4.1 and 5.0 $m^2 m^{-2}$ (Hafkenscheid, 2000). Taking the E_t value derived for the forest at Bellevue Peak (509 $mm\ yr^{-1}$) to represent that of the MMor forest, and adding the amount of intercepted rainfall E_i (680 *mm*), gives an estimated annual total evaporation (*ET*) of 1189 *mm* (Table 3). Taking the difference in LAI into account, the E_t for the PMull becomes about 620 $mm\ yr^{-1}$ (1.7 $mm\ d^{-1}$) and the *ET* about 1050 $mm\ yr^{-1}$ (Table 3). The values derived for the PMull forest in particular must therefore be considered as approximations only.

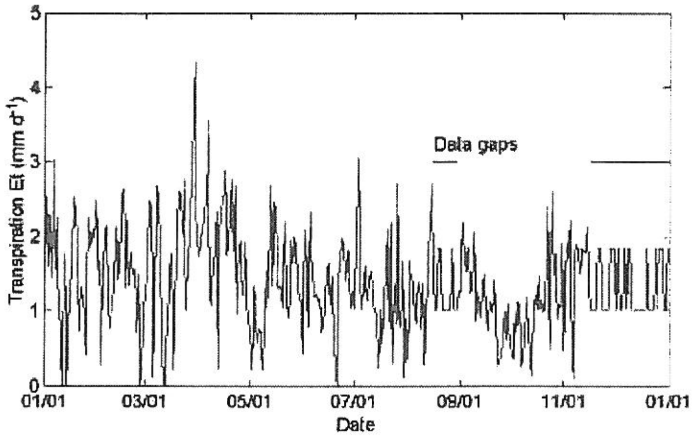

Figure 5: Daily transpiration totals for 1995 above regenerating forest vegetation at Bellevue Peak as determined with the Penman-Monteith evaporation model (233 days) and a multiple-regression equation (Equation 10) between daily transpiration totals and pertinent climatic variables (71 days). Mean values for rainy and dry days (41 and 20 days; 1.02 vs. 1.85 $mm\ d^{1}$) were used to estimate rates for the remaining gaps in the data (61 days).

4.4 Soil water dynamics

The soil water tension values ($\varnothing_m$) predicted by the VAMPS model are compared with actually measured values in the four main horizons of the PMull and MMor soils in Figure 6 and Figure 7, respectively. Apart from a consistent underestimation of moisture depletion from the thin uppermost soil horizon (Ah), the predicted patterns of $\varnothing_m$ generally resemble those observed in the field. As indicated by Figures 6 and 7, the soil underlying the MMor forest plot showed a higher sensitivity to drought than that of the PMull forest plot. Predicted values of $\varnothing_m$ in the PMull soil never fell below -40 *kPa* at any depth but got below -60 *kPa* in the Ah and Bh horizons of the MMor soil during six days in April 1995 (including a predicted minimum $\varnothing_m$ of -80 *kPa* in the Ah-horizon on 28 April. The lowest value of $\varnothing_m$ observed in the field was -76 *kPa* (MMor Ah-horizon, 11 June 1995; Figure 6).

Table 3: Annual amounts of rainfall (*P*), cloud water (*CW*), net precipitation (P_{net}), rainfall interception (E_i), transpiration (E_t), total evapotranspiration (*ET*), changes in soil water storage (ΔS), and drainage (*D*) beyond a 80 cm soil column in the PMull and MMor forests. Percentages of gross precipitation are given in parentheses.

Forest	*P*	*CW*	P_{net}	E_i	E_t	*ET*
PMull	3060	43 (1.4)	2632 (86)	428 (14)	620 (20.3)	1048 (34.2)
MMor	3060	104 (3.4)	2380 (78)	680 (22)	509 (16.6)	1189 (38.8)

Forest	ΔS	*D*
PMull	-20 (0.7)	2032 (66.4)
MMor	14 (0.5)	1857 (60.7)

The total amount of water draining beyond a depth of 80 *cm* was calculated at 2032 $mm\ yr^{-1}$ (66.4 % of P or 5.6 $mm\ d^{-1}$ on average) for the PMull plot vs. 1857 (60.7 % of *P* or 5.1 $mm\ d^{1}$ on average) for the MMor plot. Overall the changes in soil water storage (ΔS) in the two soil profiles were small: -20 *mm* (< 0.7 % of *P*) for the PMull soil column and +14 *mm* (< 0.5 % of *P*) for the MMor soil column (Table 3). It should be noted that the estimated contributions by *CW* were not taken into account in the model computations because the observed net precipitation totals already included net amounts of *CW*. As such, the computed soil water tensions and drainage amounts can hardly have been affected. Although the soil water dynamics in the two forest sites can be modelled reasonably well with VAMPS, it is difficult to assess the uncertainty associated with the outcome. However, considering the moderately successful simulation of soil water depletion patterns in the two forest plots in 1995, VAMPS was used to predict the number of days without precipitation that would be required to reach $\o_m$ values of -100 *kPa* (pF, 'limiting point' where soil water stress starts to affect transpiration; (Landsberg, 1986) and -1.58 *MPa* (pF, 'permanent wilting point' where the vegetation starts to die) in an attempt to assess the relative sensitivity of the two forests to drought. The model was run with zero precipitation input and a constant transpiration rate of 1.83 $mm\ d^{-1}$ for the MMor forest and 2.23 $mm\ d^{-1}$ for the PMull as observed during dry days in the dry season (April-July) until a value of $\o_m$=-100 *kPa* was reached. The simulations started with an average $\o_m$ profile as typically observed during the dry season (April-July). In the PMull profile a value of -100 *kPa* was reached after 37, 43, and 56 days for, successively, the Ah/Bh, Bw1 and Bw2 horizons, whereas 117, 134, and 248 days were required to reach the permanent wilting point in the Ah, Bh, and Bw1 horizons (0-65 *cm*). Conversely, in the MMor soil profile, a value of pF was already reached after only 13, 16, and 58 rainless days throughout the Ah-Bh-Bw horizons (0-35 *cm*) while permanent wilting point would be reached after approximately 40, 80, and 220 rainless days, respectively. The shallow rooting depth in the MMor profile (Elbers, 1996) prevented the BC-horizon (35-80 *cm*) from attaining values of $\o_m$ -120 *kPa* within a one-year dry period.

5 DISCUSSION

5.1 Net rainfall and rainfall interception

At 73 % and 60 % of incident rainfall, the relative amounts of throughfall (*Tf*) observed in the PMull and MMor forests during 1995 are rather different and, at first sight, contrary to expectations on the basis of the observed contrasts in gap fraction (0.37 *vs.* 0.24; Table 2) between measurements of below-canopy PAR levels (5 % *vs.* 13 % of incoming PAR; (Hafkenscheid *et al.*, 2000)) and LAI. However, the very low *Tf* value obtained for the MMor forest is partly explained by the very high stemflow (*Sf*) percentage (18.3 % *vs.* 13.0 % for the PMull site), bringing the sum of *Tf* and *Sf* to 86 % and 78 % for the PMull and MMor forest, respectively.

In a recent assessment of the hydrological characteristics of tropical montane forests (Bruijnzeel, 1999) three classes were distinguished: (i) tall forest that is little affected by fog or low cloud (*Tf* typically 65-80 %; *Sf* < 1 %); (ii) mossy forest of intermediate stature and variable cloud incidence (Tf 55-130 %; *Sf* usually < 1 % but occasionally up to 10 %); and (iii) stunted ridge-top upper montane forest subject to frequent cloud (*Tf* 90-125 %; *Sf* 5-10 %). Comparison of the Jamaican results with the ranges reported for the respective forest types highlights a unique combination of high stemflow (typical for short-statured cloud-ridden forest) and low throughfall (typical for tall forest or epiphyte-laden forest of intermediate stature (Bruijnzeel, 1999). Such findings once more suggest that adverse edaphic rather than adverse climatic conditions must be held responsible for the occurrence of short-statured forest in the study area (Hafkenscheid, 2000). Interestingly, a high stemflow percentage has also been reported for so-called lowland heath forest on infertile white sands in Amazonia (Jordan, 1978), which has a number of physiognomic conditions in common with low-statured montane forests (Whitmore, 1998). However, our stemflow data should be interpreted with care because of their high spatial and temporal variability. Although variations in tree diameter and species were taken into account, errors are inevitably introduced when converting measured volumetric data to mm of water because of the difficulties associated with estimating the projected areas of the crowns of sample trees. A comparison of patterns of measured amounts of *Sf* with those predicted by the analytical model of interception over 1995 revealed that deviations did occur during a few storms (> 50 *mm*) when several individual trees carried extreme volumes of *Sf* (R. L. L. J. Hafkenscheid, *unpublished*).

The lack of agreement between measured rainfall interception values and differences in forest physiognomy (the stunted MMor forest has both the lowest LAI and the highest E_i) increases even further if contributions via cloud water interception are taken into account: from *ca.* 250 *mm* (rainfall only) to *ca.* 315 *mm* (rainfall plus cloud water; Table 3). This unexpected result, plus the discrepancy in optimised values for evaporation from a wet canopy between the two forest plots may well be related to errors in the measurements of net rainfall. Taking the total annual amounts of *Tf* caught by each of the 12 moving gauges per forest as an individual sample gave coefficients of variation of 5.8 % for the PMull forest and 10.3 % for the MMor.

The required number of gauges (RNG) for accurate estimates of throughfall volumes (*e.g.* a 95 % confidence interval) can be calculated following (Kimmins, 1973):

$$RNG = \frac{t^2 \times CoV^2}{c^2} \qquad (11)$$

where t is the *student's*-t value for a desired confidence interval, c, expressed as a percentage of the mean. Solving Equation 11 for the observed CoV's (5.8 % for the PMull, 10.3 % for the MMor) and t = 2.18 (95 % confidence interval (Spiegel, 1972)) suggests that 7 and 20 gauges would be required to obtain reliable *Tf* measurements for the PMull and MMor forest, respectively. It can be concluded therefore that 12 gauges were sufficient to sample *Tf* adequately in the PMull forest but quite insufficient in the MMor forest. These computations do not take into account any error in the measurements of the stemflow component. Because the readings of individual stemflow gauges depend on species, size and shape of the trees to which they are attached it is not possible to assess the error associated with the stemflow measurements.

5.2 Transpiration

Quantitative information on water uptake (E_t) in tropical montane forests is scarce and mostly based on catchment water budgets, *i.e.* obtained by subtracting amounts of intercepted rainfall from total evapotranspiration *ET*. In view of the potentially large cumulative errors associated with such estimates the absence of any trends in the values of E_t or *ET* with elevation is not surprising (Bruijnzeel, 1990; Bruijnzeel & Proctor, 1995). Bruijnzeel & Proctor (1995) suggested water-balance based values for E_t of 510-830 $mm\,yr^{-1}$ for tall montane rain forests that are little affected by fog and low cloud *vs.* 250-310 $mm\,yr^{-1}$ for (shorter-statured) mossy forests subject to frequent fog incidence. Therefore, at 509 $mm\,yr^{-1}$ (Table 3) the annual transpiration total derived for the regenerating forest at Bellevue Peak falls in the lower part of the reported range for (tall) montane forests below the main cloud belt and greatly exceeds values observed for 'true' cloud forest. This observation agrees with the small amounts of cloud water interception (1.4-3.4 % of annual P) that were derived for the PMull and MMor forests, respectively.

Compared to 'true' upper montane cloud forests, the high transpiration figure found in the present study becomes more pronounced when expressed as the ratio to the reference open-water evaporation (E_0) according to Penman (1956). The E_t:E_0 ratio reported for several tall montane forests experiencing little to no cloud ranges from 0.47-0.56 (Bruijnzeel & Proctor, 1995) and exactly span the presently obtained value of 0.47 (E_t $mm\,d^{-1}$, E_0 $mm\,d^{-1}$ for the regenerating forest at Bellevue Peak (and probably the MMor) and the 0.57 (E_t) for the PMull forest.

Much lower E_t:E_0 ratios (0.22-0.25) have been reported for short-statured summit forests on cloud-affected coastal mountains of comparatively low elevation (700-1015 m) in South-east Asia (Bruijnzeel et al., 1993; Hafkenscheid, 1994) and Puerto Rico (Holwerda, 1997). Interestingly, these seemingly consistent ratios were obtained under quite contrasting evaporative conditions and rainfall regimes. Corresponding values of E_0 varied between 1.9 $mm\,d^{-1}$ at the Puerto Rican site and 3.6-4.9 $mm\,d^{-1}$ at the Southeast Asian sites. Also, rainfall and cloud incidence at the latter locations occur mainly in the afternoon (Hafkenscheid *et al.*, 2000) but falls largely at night and in the early morning in Puerto Rico (Schellekens *et al.*, 1998).

Such contrasts further support the contention that the forests of the present study cannot be regarded as 'true' cloud forests, *i.e.* characterized by high cloud water interception and low transpiration (Stadtmüller, 1987). It remains to be seen, however, whether the rates of E_t derived above the regenerating vegetation at Bellevue Peak apply equally to the older-growth forests. On the other hand, as indicated earlier, no systematic differences were found in the δ^{13}C values for the leaves of seven principal tree species in four forest plots of gradually decreasing stature on increasingly acid soils in the study area, including the PMull and MMor sites (Hafkenscheid, 2000). Given the fact that δ^{13}C values are determined by the ratio of intercellular and atmospheric partial CO_2 pressures, the observed similarity in values for tall and stunted forest could imply a comparable gas exchange capacity, including for water vapour. This, together with the close correlation between atmospheric saturation deficits and foliar δ^{13}C concentrations (Kitayama *et al.*, 1998), the presumably identical ambient climatic conditions and partial CO_2 pressures experienced by the nearly adjacent PMull and MMor forests, and the absence of significant inter-site differences in stomatal density and size (Hafkenscheid, 2000) all suggest that contrasts in transpiration rates per unit leaf area between the different forest types in the study area are probably limited. Additional studies of water uptake in the PMull and MMor forests are required to confirm to what extent extrapolation of the results obtained at Bellevue Peak to the two forests was justified. In view of the difficulties encountered with operating heat pulse velocity equipment at the study sites due to the prevailing high humidity levels, future studies could consider employing isotope injection techniques (Calder, 1992; Dye, Olbrich & Calder, 1992) as an alternative. Finally, the LAI of the forest at Bellevue Peak will need to be known as well to further assess the degree of discrepancy in E_t between young and old-growth forests in the area.

5.3 Evapotranspiration

The annual estimates of evaporation (ET) for the PMull and MMor forests listed in Table 3 (1050 and 1190 $mm\ yr^{-1}$, respectively) must be considered preliminary in view of the extrapolation of the transpiration results for the regenerating forest at Bellevue Peak to the forest plots. Not surprisingly in view of the rather high values obtained for E_t (510-620 $mm\ yr^{-1}$), the presently derived annual totals for ET fall in the range reported for tall montane forest not affected by cloud (Bruijnzeel, 1999). It is of interest to note that elsewhere in Jamaica, Richardson (1982) established a value of 2000 $mm\ yr^{-1}$ for the ET of a rain-forested catchment at 775-1265 ma.s.l. using the water balance technique. Although this value may have been influenced by deep leakage (J. H. Richardson, *personal communication* to L. A. Bruijnzeel) there are several recent studies of forest evaporation at mostly wet maritime tropical locations that have also reported much higher values of ET (1770-2400; (Malmer, 1993; Waterloo *et al.*, 1999; Schellekens *et al.*, 2000) than the 1300-1500 mm normally found for lowland rain forest (Bruijnzeel, 1990). However, it cannot be concluded from such observations that the presently derived high evaporation totals could also have been obtained because of the specific climatic conditions prevailing at the study site. The high E_i totals reported for other wet maritime locations (Puerto Rico, East Malaysia) were largely caused by high rainfall interception (Malmer, 1993; Schellekens *et al.*, 2000) whereas in the present case E_t is equally important (Table 3).

5.4 Soil water regime

As shown in Figure 6 and Figure 7, the soils of the study sites were never waterlogged and only occasionally experienced high, but not critical, soil water tensions. Although montane forest on shallow soils has been reported to be dying following severe drought (Lowry, Lee & Stone, 1973; Werner, 1988), Bruijnzeel *et al.* (1993) demonstrated that an extreme drought in East Malaysia did not cause increased leaf shedding in forests frequently enveloped in clouds, whereas forests below the cloud zone were significantly affected. Similarly, a severe drought occurring in 1993-1994 in Puerto Rico did not affect soil moisture levels in stunted 'elfin' cloud forest (F. N. Scatena, *personal communication*). The rejection by Bruijnzeel *et al.* (1993) of regular soil water deficiency as a major factor governing the distribution of low-statured montane forest is also supported by the work of Kapos & Tanner (1985) in the study area where, during 1.5 years of soil water observations in Mor and Mull forests, topsoil water tensions always remained above $-1.50\ MPa$, and therefore did not reach the permanent wilting point. More importantly, soil water tensions in Mull forest soil were consistently higher than in Mor soils.

The simulations with the VAMPS model indicated that in the more shallow MMor soil tensions below $-100\ kPa$ (pF = 3) may be expected down to a depth of 25 cm after 58 rainless days (16 days for the top 10 cm) whereas the permanent wilting point would be reached after approximately 220 dry days (80 days for the top 10 cm). Conversely, in the deeper PMull soil it would take 37-56 rain-free days to reach $\psi_m \leq -100\ kPa$ in the top 15 to 40 cm and 117-134 dry days to reach the wilting point (depending on soil horizon depth). Naturally, these results depend strongly on the adopted rates of water extraction (2.23 $mm\ d^{-1}$ for the PMull; 1.83 $mm\ d^{-1}$ for the MMor) which were based on the observations made for young forest on Bellevue Peak.

Examination of the historic rainfall data at nearby Cinchona (1500 *m a.s.l.*) indicates that long dry spells are rare, but possible. Between 1901 and 1990, 16 months with rainfall < 10 mm have been identified whereas two long dry periods occurred, *e.g.* 30 days in 1986 and 39 days in 1987 (J. R. Healey, *personal communication*). However, rainfall at Cinchona, which is situated in a more leeward position and at a lower elevation than the study plots, is probably lower than that at Bellevue Peak. During ordinary years severe soil water stress is probably absent and, as such, not important in determining stature and physiognomy of the forests in the study area. However, rare occasional droughts will primarily affect the forest growing on shallow Mor soils. Adverse effects of such long dry spells on the growth of the Mor type forest can therefore not be ruled out entirely

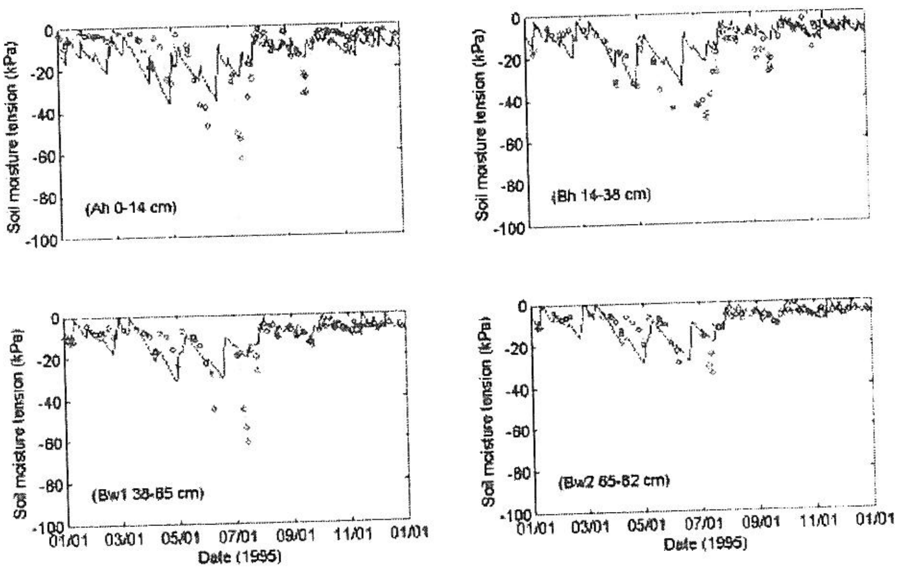

Figure 6: Observed (o) and predicted (solid line) values of soil moisture tensions (*kPa*) in the Ah (0-14 *cm*), Bh (14-38 *cm*), Bw1 (38-65 *cm*), and Bw2 (65-82 *cm*) horizons of the PMull forest soil in 1995.

As most observations of soil water dynamics and leaf water potential in upper montane forests indicate wet to very wet conditions, with little chance that the trees will ever experience severe soil water deficits (Lyford, 1969; Herrmann, 1971; Hetsch & Hoheisel, 1976; Dohrenwend, 1979; Bruijnzeel *et al.*, 1993), waterlogging and subsequent root anoxia have been advanced as contributing to the development of forests that are limited in growth. Dohrenwend (1979) in Venezuela and Santiago *et al.* (1999) in Hawaii reported clear negative relationships between montane forest stature, leaf area and the degree of soil saturation. However, persistent waterlogging is not necessarily a characteristic of all stunted tropical montane forests (Kapos & Tanner, 1985; Hafkenscheid, 1994). Despite the occasional occurrence of exceptional amounts of rainfall (*e.g.* more than 1200 *mm* in 5 days in February 1996), the soils in the study forests never became waterlogged because the high permeability of the soils prevented fully saturated conditions. In conclusion, waterlogging is not an important factor governing forest stature in the study area.

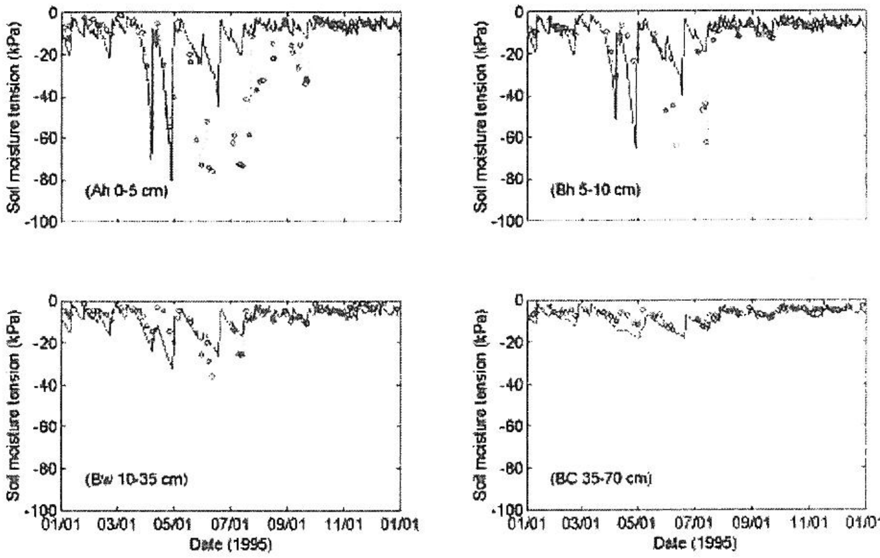

Figure 7: Observed (o) and predicted (solid line) values of soil moisture tensions (*kPa*) for the Ah (0-5 *cm*), Bh (5-10 *cm*), Bw (10-35 *cm*), and BC (35-≅ 70 *cm*) horizons of the MMor forest soil in over 1995.

6 CONCLUSIONS

Amounts of cloud water interception by the MMor and PMull forest are low and insufficient to play an important role in the overall forest water balance or explain differences in stature. The full implications of cloud water interception on leaf physiological behaviour, notably a reduction of transpiration and photosynthetic activity, are as yet unknown but there are indications that such effects are small, or at least not more pronounced in the stunted MMor forest than in the taller-statured PMull forest (Hafkenscheid, 2000). The relative magnitude of net precipitation (throughfall + stemflow) in the PMull and MMor forests (250 mm higher in the PMull) suggest that the depth of net precipitation in the low-statured MMor forest is likely to have been underestimated. However, the error associated with the measurements of *Tf* alone (± 6 % and 10 % of the mean in the PMull and MMor, respectively) cannot explain the discrepancy, implying that errors in the measurements of stemflow (notably in the MMor forest) are important as well. The specific physiognomy of Mor-type forest (numerous trees with multiple stems, gnarled appearance of trunks and branches festooned with mosses and epiphytes, etc.) probably demand a much higher number of *Tf* (and *Sf*) gauges than used in the present study (*cf.* Equation 11)

The estimated rates of transpiration (E_t) in the two forests are not particularly low and, judged against the overall atmospheric conditions, comparable to values reported for tall montane forests that experience little or no cloud. The current assumption that the E_t determined for the regenerating forest at Bellevue Peak represents transpiration in the MMor forest as well requires validation, for example by a rerun of the sapflow measurements (after redesigning the equipment) or by employing isotope injection techniques.

Soil characteristics prevent prolonged soil saturation in both the PMull and MMor forest; persistent water logging or root anoxia therefore cannot be an important factor governing the stature and physiognomy of these forests. Contrasts in soil water holding capacity and rooting depth (both less in the MMor) suggest that the MMor forest may be more sensitive to the effects of occasional drought (which are rare but do occur in the area) than the forests growing on the deeper Mull soils. However, simulation of the effects of prolonged dry spells on soil water levels and thus the long-term functioning of the forests suggested drought to have a minimal effect. Longer-term monitoring of soil water status in combination with weekly litterfall observations would be desirable to test this contention.

In conclusion: the present hydrological results and other data presented by Hafkenscheid (2000) suggest that unfavourable (non-physical) edaphic conditions (such as high acidity, excess aluminium, and low key nutrients) may be held responsible for the low above-ground productivity and stature observed in the more stunted forest types in the study area.

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