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Evaporation from a tropical rain forest, Luquillo Experimental Forest, eastern Puerto Rico

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Abstract. Evaporation losses from a watertight 6.34 ha rain forest catchment under wet maritime tropical conditions in the Luquillo Experimental Forest, Puerto Rico, were determined using complementary hydrological and micrometeorological techniques during 1996 and 1997. At 6.6 mm d^{-1} for 1996 and 6.0 mm d^{-1} for 1997, the average evapotranspiration (ET) of the forest is exceptionally high. Rainfall interception (E_i), as evaluated from weekly throughfall measurements and an average stemflow fraction of 2.3%, accounted for much (62–74%) of the ET at 4.9 mm d^{-1} in 1996 and 3.7 mm d^{-1} in 1997. Average transpiration rates (E_t) according to a combination of the temperature fluctuation method and the Penman-Monteith equation were modest at 2.2 mm d^{-1} and 2.4 mm d^{-1} in 1996 and 1997, respectively. Both estimates compared reasonably well with the water-budget-based estimates (ET $-$ E_i) of 1.7 mm d^{-1} and 2.2 mm d^{-1}. Inferred rates of wet canopy evaporation were roughly 4 to 5 times those predicted by the Penman-Monteith equation, with nighttime rates very similar to daytime rates, suggesting radiant energy is not the dominant controlling factor. A combination of advected energy from the nearby Atlantic Ocean, low aerodynamic resistance, plus frequent low-intensity rain is thought to be the most likely explanation of the observed discrepancy between measured and estimated E_i.

1. Introduction

The recognition that tropical rain forest destruction can have serious hydrological and climatic implications (reviewed by *Bruijnzeel* [1990] and *Gash et al.* [1996]) has prompted a number of investigations into tropical forest evapotranspiration. Evapotranspiration (ET) represents an important component of the water balance of tropical lowland rain forest and therefore constitutes a major determinant of the amounts of water draining from such environments. With very few exceptions, however [*Calder et al.*, 1986; *Shuttleworth*, 1988], the available estimates of tropical forest ET are based on the catchment water budget technique [*Bruijnzeel*, 1990; *Malmer*, 1993; *Lesack*, 1993; *Jetten*, 1994; *Abdul Rahim et al.*, 1995]. This method is notoriously prone to errors associated with ungauged subterranean transfers of water into or out of the catchment and may therefore produce relatively unreliable estimates of ET, unless the catchment is demonstrably watertight [*Ward and Robinson*, 1990]. The problem is illustrated by the contrasting results obtained for various small forested catchments in central Amazonia whose reported apparent annual ET ranges from 1120 mm [*Lesack*, 1993] to 1675 mm [*Leopoldo et al.*, 1982] despite similar climatic and geological conditions. Similarly, annual water-budget-based estimates of ET for lowland and hill dipterocarp rain forests on granitic substrates in Peninsular Malaysia, receiving over 2000 mm of rain annually without a pronounced dry season, vary from about 1000 mm [*Low and Goh*, 1972] to almost 1800 mm [*Abdul Rahim and Baharuddin*, 1986].

Such methodological problems prevented *Bruijnzeel* [1990] in his review of tropical rain forest water use from finding distinct differences in ET for the three major rain forest blocks of West Africa, Amazonia, and Southeast Asia. In addition, *Bruijnzeel* [1990] ascribed ET totals that were well above 1400–1500 mm yr^{-1} to problems with catchment leakage rather than to specific climatic conditions favoring high evaporation [cf. *Richardson*, 1982].

Shuttleworth [1989] advanced the idea that compared to mid-continental sites, tropical deforestation was likely to have greatest effect on river flow (though not necessarily climate) at continental edge and island locations. He based this contention on a comparison of the micrometeorology of a rain forest in central Amazonia [*Shuttleworth*, 1988] and a spruce plantation in Wales, United Kingdom [*Shuttleworth and Calder*, 1979], as well as on the reported contrast in rainfall interception (E_t) by lowland rain forests in central Amazonia [*Lloyd and Marques-Filho*, 1988] and West Java, Indonesia [*Calder et al.*, 1986]. Unfortunately, the latter comparison was limited by markedly different methodologies for the estimation of E_t which rendered the argument inconclusive.

However, since the late 1980s a number of rainfall intercep-

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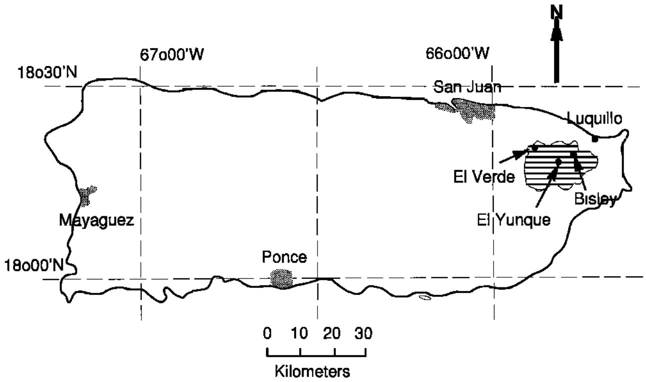

Figure 1. Map of Puerto Rico showing the location of the study site within the Luquillo Experimental Forest (indicated by the hatched area).

tion studies conducted in tropical forests located at continental edges and islands receiving high rainfall totals (>3000 mm yr^{-1}) have confirmed the possibility of very high E_i under such "maritime" tropical conditions [*Bruijnzeel*, 1988; *Scatena*, 1990b; *Dykes*, 1997; *Cavelier et al.*, 1997; *Clark et al.*, 1998]. None of these studies used above-canopy climatic observations and continuously recording throughfall equipment which could have helped to explain the inferred high rates of interception. Therefore the actual mechanisms and their relative importance were not identified. Neither has the dry-canopy evaporation component of ET (transpiration, E_t) been studied at these locations, and so the limits of forest ET under wet maritime tropical conditions remain to be explored [*Richardson*, 1982; *Malmer*, 1993; *Waterloo et al.*, 1999].

Arguably, a good way to resolve some of the methodological problems referred to above is to combine hydrological and micrometeorological process studies. The present study aimed to evaluate the magnitude of ET and its components under the wet maritime tropical conditions prevailing in the Luquillo Experimental Forest (LEF), eastern Puerto Rico, through a combination of catchment hydrological, geophysical, throughfall, and micrometeorological measurements. Earlier work in the LEF [*Scatena*, 1990b] had already suggested very high interception losses (up to 40% of incident rainfall on an annual basis), adding further interest to the determination of a potentially extreme value for total ET. This paper reports results for ET and its main components as obtained during 2 years of observations in the 6.43 ha Bisley II catchment in the Tabonuco forest zone of the LEF. *Schellekens et al.* [1999] present the results of a comparative application of various rainfall interception models.

2. Study Area

The Bisley II catchment is situated at 18°18'N, 65°50'W at an elevation of 265–456 m above sea level (asl) (Figure 1). The area is steep and dissected with sharp divides, steep stream gradients, and bowl-shaped valleys. Slopes in excess of 45% (24°) cover more than 50% of the catchment. The 0.8- to 1.0-m-deep clayey soils that have developed in the underlying thick-bedded tuffaceous sandstones and indurated siltstones are strongly leached Ultisols [*Scatena*, 1989]. Nonweathered bedrock is found at depths greater than 15 m below the level of the stream channel, regardless of position within the catchment [*Van Dijk et al.*, 1997]. Overlying the fresh bedrock is a zone of weathered rock of very low permeability (<2 mm d^{-1}).

The climate is maritime tropical (type A2m according to the Köppen classification), with the northeasterly trade winds bringing about 70% of the annual rainfall of 3530 mm ± 22.6% (as measured at the nearby long-term rainfall station at El Verde, 450 m asl; see Figure 1 for location) in association with tropical waves, depressions, and cyclones. Rainfall is distributed fairly evenly throughout the year, with May and November being relatively wet and January–March being relatively "dry" (Figure 2). Rainfall at El Verde is delivered as numerous (267 rain days per year), relatively small (median daily rainfall 3.0 mm) storms of low intensity (<5 mm h^{-1} [*Brown et al.*, 1983; *García-Martinó et al.*, 1996]). Further information on rainfall characteristics is given in section 4.1.

The seasonal variation in mean monthly temperatures in the Bisley area is about 3.5°C, ranging from ~24°C in December–February to about 27.5°C in July–August. Seasonal variation in average daily relative humidity levels is small (84–90%). Average monthly wind speeds in the lower reaches of the LEF are <2 m s^{-1} but vary between 2 and 5 m s^{-1} around exposed summits at higher elevations. Average incoming solar radiation in the lowlands adjacent to the LEF (Cape San Juan) ranges from 13.8 MJ m^{-2} d^{-1} in December to 26.0 MJ m^{-2} d^{-1} in the summer months. At 1000 m elevation these amounts are roughly halved [*Brown et al.*, 1983]. Reference open-water evaporation [*Penman*, 1956] in the Bisley area is estimated at ~1100 mm yr^{-1} [*Holwerda*, 1997].

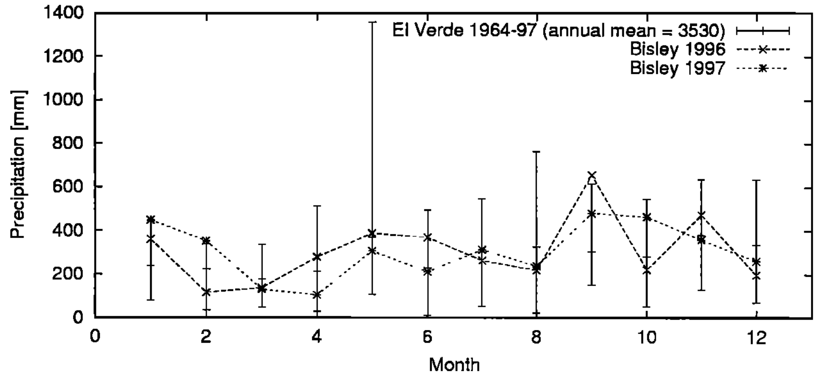

Figure 2. Monthly rainfall at Bisley in 1996 and 1997 compared with long-term means at El Verde (450 m above sea level, 1964–1997). The bars represent recorded minimum and maximum values for the respective months.

The Tabonuco forest is one of the four chief vegetation types found in the Luquillo Mountains, the others being Colorado, palm, and dwarf forests [*Wadsworth and Bonnet*, 1951; *Brown et al.*, 1983]. The Tabonuco forest has an irregularly shaped, 20–25 m upper canopy, an understory of palms and woody vegetation, and ground level herbs and shrubs. It occupies the lower reaches of the Luquillo Mountains (below 600 m). Both the structure and composition of the vegetation vary with topographic composition and aspect relative to the trade winds [*Lugo and Scatena*, 1995]. The average leaf area index (LAI) of mature Tabonuco forest is between 6 and 7 but may range between 12.1 on ridges and 1.95 in dark ravines and riparian valleys [*Odum et al.*, 1970a]. In September 1989 the Bisley area was severely impacted and nearly completely defoliated by Hurricane Hugo [*Scatena et al.*, 1993]. However, by 1996 when the present study was initiated, the LAI, canopy interception, and forest biomass were again similar to prehurricane conditions [*Scatena et al.*, 1996; *Holwerda*, 1997].

3. Methods and Instrumentation

3.1. Methods

The catchment water balance equation for the evaluation of ET [*Ward and Robinson*, 1990] reads as follows:

$$P = Q + \mathrm{ET} + \Delta S + \Delta G + L, \tag{1}$$

where P is the precipitation input, Q is the amount of streamflow leaving the catchment, ΔS and ΔG are the changes in soil moisture and ground water storages over the period of measurement, respectively, and L is the leakage into or out of the catchment (all expressed as millimeters of water). The results of a geophysical survey [*Van Dijk et al.*, 1997] strongly suggested that the catchment is watertight; that is, no significant amounts of water leave the catchment by some ungauged pathway. Consequently, L in (1) was assumed negligible. A stage-discharge relationship developed for the culvert at the outlet of the catchment [*Scatena*, 1990a] was used to obtain discharge after converting the logger readings to water levels at the culvert entrance. Water level records were corrected for changes in stream bed geometry when necessary.

An estimate of ΔS was made by comparing the precipitation totals of the 2 weeks preceding the beginning and end of the water balance period. To estimate ΔG, discharge levels at the start and end of the water balance period were inserted into a master recession curve consisting of two superimposed linear reservoirs [*Hall*, 1968] for which the coefficients were determined via nonlinear regression [*Marquardt*, 1963]:

$$Q_t = Q_1 K_1^t + Q_2 K_2^t, \tag{2}$$

where

Q_t discharge at time t [mm 5 min^{-1}];
Q_1 initial discharge of reservoir 1 [mm 5 min^{-1}];
Q_2 initial discharge of reservoir 2 [mm 5 min^{-1}];
K_1 recession constant of reservoir 1 [dimensionless];
K_2 recession constant of reservoir 2 [dimensionless];
t times [days].

Furthermore, the change in groundwater storage between two points on the recession curve (Q_0 and Q_t) can be calculated according to

$$\Delta G = \frac{\partial Q}{\partial t} = \frac{Q_t - Q_0}{\ln K_1} + \frac{Q_t - Q_0}{\ln K_2}. \tag{3}$$

Total ET is made up of rainfall interception (E_i, evaporation from a wet canopy), transpiration (E_t, evaporation from a dry canopy), and evaporation from the soil/litter layer (E_s). The latter term proved very small for the El Verde forest [*Odum et al.*, 1970b] with only 3.5% of the radiation reaching the forest floor [*Odum et al.*, 1970a]. In the present study, however, E_s is included in the estimate of E_t (see below). Amounts of E_i were derived by subtracting throughfall (TF) and stemflow (SF) from incident rainfall (P). Stemflow was not measured during the present study. Instead, an average value of 2.3% of P, as obtained by *Scatena* [1990b] before the forest was disturbed by Hurricane Hugo, was adopted.

The magnitude of E_t was evaluated using the temperature variance (TVAR) method [*Tillman*, 1972; *De Bruin*, 1982] during dry canopy conditions in combination with the simplified energy balance equation [*Brutsaert*, 1982]. Assuming that all available energy (A) is used either to warm up the air (sensible heat flux (H)) or for evaporation (latent heat flux, $\lambda E = \lambda E_t$), while neglecting various small storage terms [*Brutsaert*, 1982] and equating A to net radiation (R_n), E_t can be derived from

$$\lambda E_t = \lambda E = R_n - H, \tag{4}$$

where λE is the latent heat flux [W m^{-2}], R_n is net radiation [W m^{-2}], and H is the sensible heat flux [W m^{-2}]. Net radiation (R_n) was estimated using a regression equation that was modified from that of *Shuttleworth et al.* [1984] for a lowland rain forest in central Amazonia. To represent the difference in albedo between the forest at Bisley and the Amazonian forest, measurements of incoming and reflected solar radiation ($R_s\downarrow$ and $R_s\uparrow$) at Bisley were used to estimate the coefficient of the equation. The offset (representing the net longwave component) was left unaltered:

$$R_n = 0.88 R_s\downarrow - 35, \tag{5}$$

where R_n and $R_s\downarrow$ are again expressed in W m^{-2}.

The TVAR method evaluates the magnitude of H under dry unstable atmospheric conditions from the standard deviation of rapid temperature fluctuations [*Tillman*, 1972; *De Bruin*, 1982] using the following equation:

$$H = \rho c_p \left[\left(\frac{\sigma_T}{C_1}\right)^3 \left(kg\,\frac{z}{T}\right) \frac{\left(1 - C_2 \frac{z}{L}\right)}{-\frac{z}{L}} \right]^{1/2}, \tag{6}$$

where

ρ density of dry air [kg m^{-3}];
c_p specific heat of air at constant temperature T [J kg^{-1} K^{-1}];
σ_T standard deviation of temperature fluctuations [K];
g acceleration due to gravity [m s^{-2}];
z height above the surface [m];
T air temperature [K];
z/L stability parameter [dimensionless];
k von Kármán's constant, 0.41 [dimensionless];
C_1, C_2 empirical constants (2.9 and 28.4, respectively [*De Bruin et al.*, 1993]) [dimensionless].

Under unstable atmospheric conditions, z/L equals the Richardson number (Ri). In the case of free convection ($Ri < -1$), (6) can be simplified to [*Vugts et al.*, 1993]

$$H = 1.075\rho c_p \sigma_T^{3/2}\left(\frac{kgz}{T}\right)^{1/2}. \quad (7)$$

Combining (7) and (4) enables the determination of λE and thus E_t from rapid dry-bulb temperature fluctuations measured at a single level. When measuring above a forest, however, it is necessary to replace z by $(z - d)$ in (7), where d is the zero plane displacement [*Thom*, 1975]. A value of d of 17.2 m ($0.86h_v$, where h_v is vegetation height in meters [*Shuttleworth*, 1989]) was used throughout the calculations. When both wet- (σ_q) and dry-bulb temperature fluctuations are known, a Bowen ratio (β) approach can be applied [*Vugts et al.*, 1993]:

$$\beta = \frac{C_p \sigma_T}{\lambda \sigma_q}. \quad (8)$$

Assuming that the spectra for temperature and humidity are the same, the use of the Bowen ratio approach should not produce an underestimation of H as a result of the frequency losses associated with the use of thermocouples [*Moore*, 1986; *Van Asselt et al.*, 1991].

For those periods for which no thermocouple data were available, E_t was computed with the Penman-Monteith equation [*Monteith*, 1965]:

$$\lambda E = \frac{\Delta A + \rho C_p \mathrm{VPD}/r_a}{\Delta + \gamma(1 + r_s/r_a)}. \quad (9)$$

For wet canopy conditions, (9) reduces to (10):

$$\lambda E = \frac{\Delta A + \rho C_p \mathrm{VPD}/r_a}{\Delta + \gamma}, \quad (10)$$

where

- λE latent heat flux [W m^{-2}];
- A available energy [W m^{-2}];
- Δ slope of the temperature-vapor pressure relationship at temperature T [Pa K^{-1}];
- γ psychrometric constant [Pa K^{-1}];
- VPD vapor pressure deficit [Pa];
- r_a aerodynamic resistance [s m^{-1}];
- r_s surface resistance [s m^{-1}].

Values for the surface resistance parameter (r_s, in s m^{-1}) during selected hourly periods were derived using the corresponding TVAR-based estimates of E_t in an inverse application of the Penman-Monteith equation [*Shuttleworth*, 1988]:

$$r_s = \frac{\rho c_p}{\gamma}\frac{\mathrm{VPD}}{\lambda E} + r_a\left(\frac{\Delta A}{\gamma \lambda E} - \frac{\Delta}{\gamma} - 1\right). \quad (11)$$

The aerodynamic resistance (r_a) is normally obtained by (12) [*Thom*, 1975]:

$$r_a = \frac{\left(\ln\frac{z-d}{z_0}\right)^2}{k^2 u_{(z)}}, \quad (12)$$

where

- z measurement height above the ground surface [m];
- d zero plane displacement height [m];
- z_0 roughness length [m];
- $u_{(z)}$ wind speed at height z [m s^{-1}].

The ratio $0.06h_v$ for the roughness length (z_0) of the forest in central Amazonia [*Shuttleworth*, 1989] was also applied in the present case.

3.2. Instrumentation

A 25.3-m scaffolding tower situated at 335 m asl on the eastern water divide of the catchment was instrumented to monitor above-canopy climatic conditions at 26 m. Incoming shortwave radiation (350–1100 nm) was measured by a Li-Cor LI-200X pyranometer. Air temperature and humidity were determined using a Vaisala HMP35C probe which was protected against direct sunlight and precipitation by a model 41002 radiation shield. The accuracy of the humidity sensor was typically better that 2%, whereas a long-term stable precision of less than 1% per year was stated by the manufacturer. Both the temperature and humidity were regularly calibrated against readings with an Assmann psychrometer. Two fast-response dry-bulb thermocouples and one wet-bulb thermocouple (chromel − constantane wire type with 0.127-mm diameter [*Tillman*, 1972]) were used to measure rapid fluctuations in air temperature between May 5 and July 9, 1996 (66 days), for use in the TVAR method to derive sensible heat fluxes. Wind speed and direction were measured with a Met-One 014A Wind Set. A Texas Instruments tipping bucket rain gauge (TE525LL-L with 0.254 mm per tip) recorded precipitation. An adjacent totalizing rain gauge serving as a backup was emptied every week. All climatic data were stored in a Campbell Scientific Ltd. 21X data logger and retrieved weekly for further processing. The thermocouples were sampled every 2 s, whereas the other instruments were sampled every 5 s. Precipitation data were stored at 5-min intervals. Averages of wet- and dry-bulb temperatures, their standard deviations, and correlation coefficients were calculated every 5 min to avoid trends in the standard deviations. These were, in turn, averaged over 30-min periods and stored in the data logger. All other climatic data were stored at hourly intervals. Above-canopy climatic data (hourly measurements) were available for the whole of 1996 and 1997. Additional measurements of incoming and reflected shortwave radiation were made between June 11, 1997, and June 16, 1998, using a Kipp and Zonen model CM-7 type albedometer.

Throughfall (TF) was recorded continuously between May 5 and July 9, 1996 (66 days), using three flat-bottomed, sharp-rimmed steel gutters (6 × 300 cm) placed at a steep angle to minimize splash out. Each gutter was equipped with a 180-L capacity tipping bucket with logger system. To minimize wetting and drying losses, the gutters were cleaned and sprayed with a silicone solution every week. In addition, TF was measured with 20 randomly placed but nonroving collectors (143 cm^2 surface area) which were emptied every week throughout 1996 and 1997. These fixed gauges have been in operation since June 1987 [*Scatena*, 1990b]. A roving gauge technique [*Lloyd and Marques-Filho*, 1988] had been adopted in the beginning, but when an initial comparison of the performance of the fixed and roving gauges did not reveal significant differences, only the fixed network was maintained [cf. *Brouwer*, 1996]. The gutters and gauges were distributed throughout the catchment. The 5-min TF records obtained with the gutters were converted to areal averages every time the manual gauges were emptied, using a weighting procedure based on the relative magnitude of the surface areas of the respective gauge types.

Stream water levels were recorded at 5-min intervals by a

Table 1. Statistical Parameters for 80 Rainfall (*P*) and Throughfall (TF) Events at Bisley During the Period May 5 to July 9, 1996

	Size		Duration		Intensity	
	P, mm	TF, mm	*P*, day:hours:min	TF, day:hours:min	*P*, mm h^{-1}	TF, mm h^{-1}
Mean	10.7	4.8	00:03:34	00:04:41	3.0	1.0
Range	0.2–227.7	0.0–91.0	00:00:10–00:20:25	00:00:05–00:20:55	0.2–13.8	0.0–4.5
Median	3.3	1.4	00:02:25	00:03:16	1.9	0.4
Total	852.3	387.3	11:22:15	15:15:37		

Druck Ltd. PDCR-830 pressure transducer (1.5-mm accuracy) connected to a CTL data logger. Manual measurements using a staff gauge were made daily to check for instrumental drift. A nearly complete record of daily discharge totals was available for 1996 and 1997 (International Institute for Tropical Forestry, unpublished data, 1998).

4. Results

4.1. Rainfall Characteristics

Total amounts of rainfall recorded at Bisley in 1996 and 1997 were 3687 and 3480 mm, that is, slightly above (1996) and similar to (1997) the long-term mean of 3530 mm yr^{-1} for El Verde. During the 66-day period of detailed micrometeorological observations in 1996 a total of 852 mm of rain was received, distributed over 80 events. Events were separated by a dry period of at least 3 hours which was the time considered to dry the canopy completely. The average intensity of these events was 3.0 mm h^{-1}, and the average storm size was 10.7 mm, with an average duration of 3 hours and 34 min (Table 1). However, the results were influenced considerably by an extreme event (estimated return period > 5 years) occurring on May 13, 1996, during which 227.7 mm was delivered over a period of almost 21 hours (Table 1) of which more than 120 mm fell in 3 hours. Because of their rather skewed frequency distributions (Figures 3a and 3b), the median values of storm size and duration, and (with them) rainfall intensity, were markedly lower than the average values (Table 1). Some 65% of the storms were ≤5 mm (Figure 3a), but owing to their small size their overall contribution to the total was much smaller (~12%, Figure 3c). On average, small storms also had a lower intensity compared to larger storms (compare Figures 3a and 3b). The diurnal distribution of rainfall occurrence and amount is shown in Figure 4. Although more rain falls during the day, rainfall occurrence is higher during the night and early morning. This indicates the prevalence of small, low-intensity storms during the latter periods as opposed to the larger events that tend to occur mainly during the day.

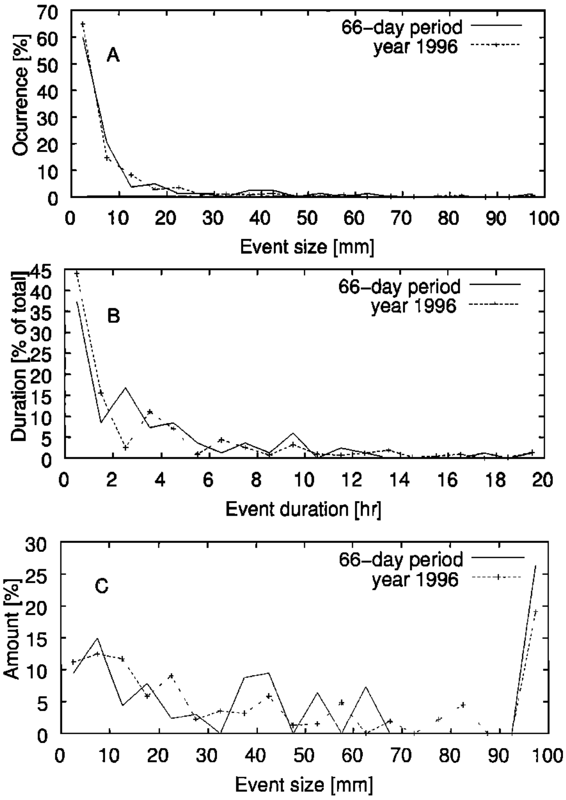

Figure 3. Frequency distributions of (a) rainfall, (b) event duration, and (c) the relative contribution to total rainfall by differently sized events at Bisley during the whole of 1996 and during the 66-day period of intensive measurements in May–July 1996.

4.2. Throughfall Characteristics

Throughfall totals for 1996 and 1997 amounted to 1814 and 2036 mm, respectively, corresponding to 49 and 59% of gross precipitation, respectively. At 45% of *P* the relative amount of TF determined between May 5, 1996, and July 9, 1996, (period of continuous recording) represents one of the lowest values measured between March 1996 and March 1998 (Figure 5).

The May–July 1996 TF data set was subdivided into daytime and nighttime events. Table 2 lists the properties of the 54 storms that could be used in a day/night comparison (i.e., a subset of those shown in Table 1). Storms that crossed the day/night boundary were excluded, as were storms larger than

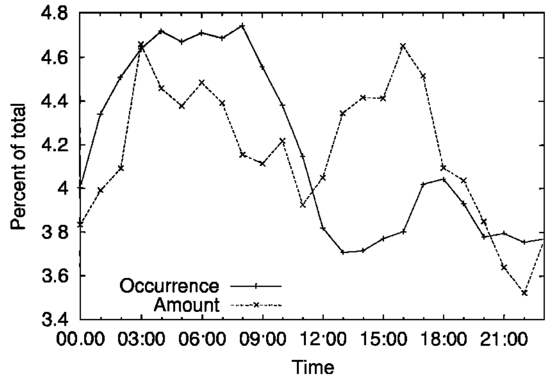

Figure 4. Diurnal distribution of relative amounts and occurrence of rainfall at Bisley in 1996 and 1997.

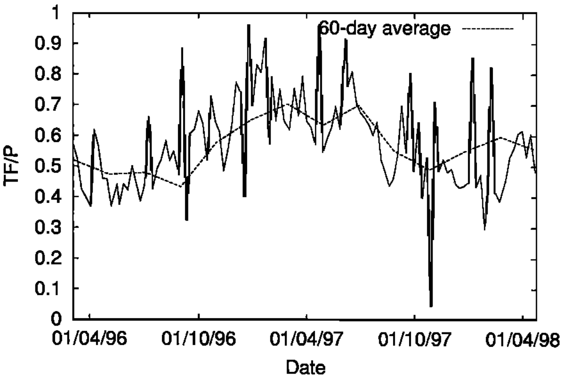

Figure 5. Seasonal variation in relative amounts of weekly throughfall at Bisley between March 1996 and March 1998.

15 mm so as to make the two subsets more comparable. As shown in Figure 6, there was no significant difference in the relationship between TF and P for daytime and nighttime conditions. Also, at least for storms ≤15 mm, the TF/P ratio was remarkably constant and apparently independent of storm size (Figure 6). However, on a longer timescale the TF/P ratio does vary (Figure 5). The implications of these observations is discussed in section 5.3.

4.3. Catchment Water Balance

The amounts of water leaving the catchment as streamflow during the 66-day period of detailed TF and micrometeorological measurements and 1996 and 1997 as a whole were 278, 1267, and 1301 mm, respectively, corresponding to 32, 34, and 37% of P for the respective periods (Table 3). The changes in groundwater storage (ΔG in (1)) for the observation periods were evaluated by determining the values of the constants in (3) using streamflow data for the May–July 1996 period. Application of (3) yielded negligibly small values for ΔG in all cases, that is, 0.06 mm for the 66-day period in 1996, −0.04 mm for 1996, and 0.03 mm for 1997. Changes in soil water storage (ΔS in (1)) were estimated by comparing precipitation totals during the 2 weeks preceding the start and end of the respective periods. Because the amounts of rainfall were found to be comparable in all cases (namely, 128 and 115 mm for the May–July 1996 period; 146 and 113 mm for 1996; and 129 mm and 122 mm for 1997), ΔS was also assumed negligible. In addition, runs with a soil moisture model [*Schellekens*, 2000] confirmed this contention. Because deep leakage (L in (1)) had been proven to be negligible as well [*Van Dijk et al.*, 1997], (1) simplifies to

$$\mathrm{ET} = P - Q. \tag{13}$$

Table 2. Statistical Parameters of Rainfall Events During the Period May 5 to July 9, 1996, Separated by Daytime or Nighttime Occurrence

	Night[a]		Day[b]	
	P	TF	P	TF
Mean	3.4	1.2	5.6	1.7
Median	2.9	0.8	5.3	1.5

All values in millimeters.
[a]Number of nighttime storms, 32.
[b]Number of daytime storms, 22.

Application of (13) yields a value for ET of 574 mm (8.70 mm d^{-1}) for the 66-day period in 1996, whereas ET totals for 1996 and 1997 were estimated at 2420 mm (6.61 mm d^{-1}) and 2179 mm (5.97 mm d^{-1}), respectively (Table 3).

4.4. Evaporation Components

4.4.1. Water-budget-based estimates of rainfall interception and transpiration. Rainfall interception losses (E_i) were derived from

$$E_i = P - (\mathrm{TF} + \mathrm{SF}). \tag{14}$$

Applying a constant stemflow fraction of 2.3% [*Scatena*, 1990b] yielded the following values of E_i for the 66-day period in 1996, the whole of 1996, and 1997: 444 mm (52.1% of P), 1788 mm (48.5%), and 1364 mm (39.2%), respectively. By further subtracting the values of E_i from the corresponding ET totals, an estimate of transpiration (E_t) was obtained. This resulted in values of 130 mm (2.0 mm d^{-1}) for the May–July 1996 period, 632 mm yr^{-1} (1.7 mm d^{-1}) for 1996, and 815 mm yr^{-1} (2.2 mm d^{-1}) for 1997 (Table 3).

4.4.2. Transpiration according to the TVAR method. A total of 509 hours of thermocouple data was selected from the climatic record, during which the canopy was dry and net radiation (R_n) intensity was ≥50 W m^{-2}, for use in the temperature variance (TVAR) method (7). The selection criterion of 50 W m^{-2} as representing intervals with free convection is somewhat on the low side considering the roughness of the forest. However, because an increase in the threshold value to 150 W m^{-2} influenced the results only marginally (giving an increase in total E_t of 2%), the criterion was maintained at 50 W m^{-2}. A comparison of H derived from (7) and (8) indicated an underestimation of H when using (7) of 32%, close to the theoretical estimate of 30% for frequency losses expected under the conditions prevailing at Bisley [cf. *Moore*, 1986]. A correction factor for frequency losses of 1.32 was therefore applied to H as estimated from the dry-bulb temperature fluctuations. Combining the resulting values for hourly sensible heat fluxes with corresponding amounts of R_n, E_t including evaporation from the soil was estimated using (4). The application of (4) assumes that heat storage in trees as well as the soil heat flux is negligible. The small fraction of incoming radiation that reaches the forest floor in Tabonuco forest (3.5% [*Odum et al.*, 1970a]) indicates that the soil heat flux must be negligible. To evaluate the heat storage in the vege-

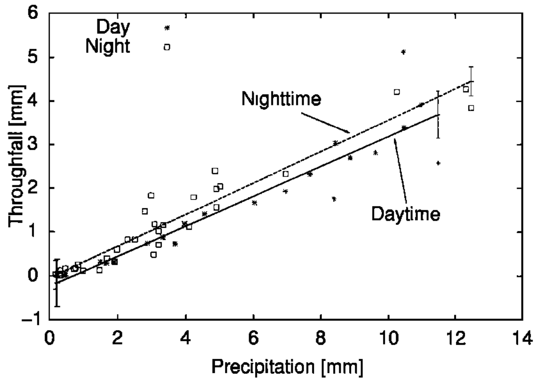

Figure 6. Relationships between incident rainfall and throughfall for daytime and nighttime conditions at Bisley between May 5 and July 9, 1996.

Table 3. Total Evapotranspiration (ET), Transpiration (E_t), and Rainfall Interception (E_i) for the Bisley Forest as Determined With Different Methods During a 66-Day Period in May–July 1996 and the Years 1996 and 1997 With Amounts of Rainfall (P), Streamflow (Q), Throughfall (TF), and Stemflow (SF) Added for Comparison

	Period								
	May–July 1996			1996			1997		
Water Balance Component	Millimeters	Millimeters per Day	Percent of Precipitation	Millimeters	Millimeters per Day	Percent of Precipitation	Millimeters	Millimeters per Day	Percent of Precipitation
Rainfall	852	12.9	100	3687	10.1	100	3480	9.50	100
Throughfall	388	5.90	44.9	1814	4.96	49.2	2036	5.59	58.5
Stemflow	20	0.30	2.30	85	0.25	2.30	80	0.20	2.30
Streamflow	278	4.21	32.1	1267	3.46	34.4	1301	3.56	37.4
Evapotranspiration-WB[a]	574	8.70	67.4	2420	6.61	65.6	2179	5.97	62.6
Evapotranspiration-PM[b]	192	2.91	22.5	1039	2.84	28.2	1146	3.14	32.9
Transpiration-WB[c]	130	1.97	15.3	632	1.73	17.1	815	2.23	23.4
Transpiration-PM[d]	151	2.28	17.7	817	2.29	22.2	858	2.35	24.6
Interception-WB[e]	444	6.73	52.1	1788	4.88	48.5	1364	3.74	39.2
Interception-PM[f]	41	0.62	4.81	221	0.60	5.99	287	0.79	8.25
Interception-WBPM[g]	403	6.11	47.3	1532	4.19	41.6	1218	3.34	35.0

[a] Catchment water budget (WB) method (13); value for 1997 extrapolated from 359 days of runoff observations, annual value for 1996 extrapolated from 275 days.
[b] Penman-Monteith (PM) method (9) and (10); extrapolated from 324 days of climatic records in 1996 and 300 days in 1997.
[c] Water budget method ($E_{t\mathrm{WB}} = P - Q - (P - \mathrm{TF} - \mathrm{SF})$).
[d] Penman-Monteith method (9).
[e] Water budget method ($E_{i\mathrm{WB}} = P - \mathrm{TF} - \mathrm{SF}$).
[f] Penman-Monteith method (10).
[g] $E_{i\mathrm{WBPM}} = P - Q - E_{t\mathrm{PM}}$.

tation, the approach of *Meesters and Vugts* [1996] was followed which uses daily average wind speeds in combination with biomass and hourly temperature data to estimate heat storage in stems. Maximum hourly heat storage was 12.1 W m^{-2}, while the minimum was -8.6 W m^{-2}. Incorporating changes in heat storage in the determination of E_t using the TVAR method resulted in a 2.4% reduction, indicating that heat storage in trees can, indeed, be neglected at Bisley. The average value of E_t derived in this way for the selected hours amounted to 2.75 mm d^{-1} (range 0.5–4.5 mm d^{-1}, Figure 7), corresponding to a total dry canopy evaporation over a 52-day period of 143 mm.

4.4.3. Evaporation according to the Penman-Monteith equation. Before the Penman-Monteith equation (9) could be applied to compute E_t for those days for which no thermocouple data were available, aerodynamic and surface resistances to evaporation (r_a, r_s) needed to be evaluated. Values of r_a were initially derived with (12) during periods of approximately neutral stability [*Thom*, 1975]. The resulting average diurnal pattern of r_a is shown in Figure 8. An average value of ~20 s m^{-1} was estimated. Inserting the values of E_t obtained for 52 days with the TVAR method into (11) produced the average diurnal pattern of r_s shown in Figure 9. The average

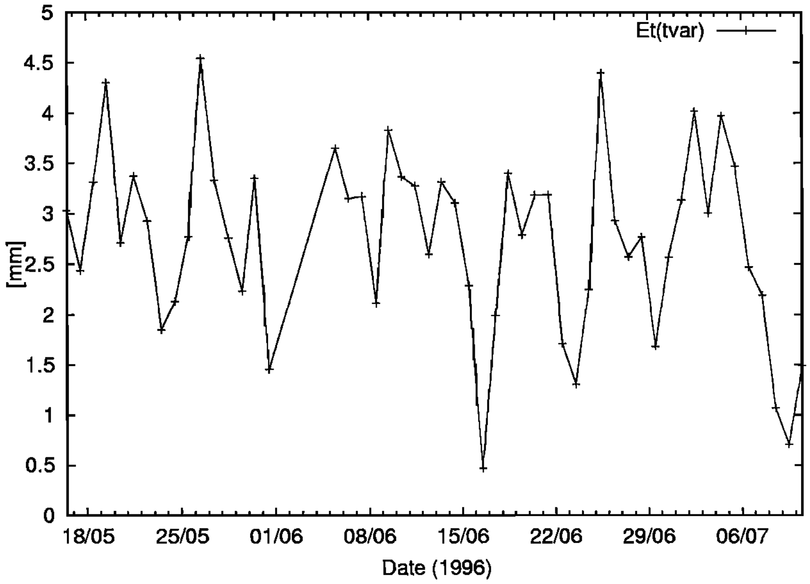

Figure 7. Daytime transpiration totals at Bisley as determined using the temperature variance (TVAR) method between May and July 1996.

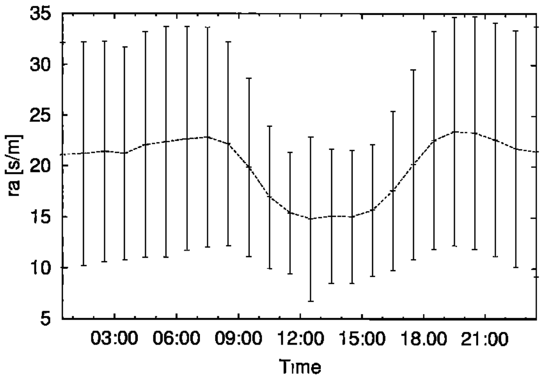

Figure 8. Average diurnal course of the aerodynamic resistance (r_a) of the Bisley forest in 1996 and 1997. Vertical bars represent corresponding standard deviation around the mean.

daytime value of r_s was determined at 58 s m^{-1}. To extend our estimates of r_s to other days as well, hourly values of r_s were regressed against corresponding hourly ambient climatic variables, notably $R_s\downarrow$, VPD, air temperature (T), and wind speed (u), as follows ($r^2 = 0.52$ and $n = 509$):

$$r_s = \exp(0.6251 - 0.0019R_s\downarrow + 0.1550\ \mathrm{VPD} + 0.2247T - 0.5699u). \qquad (15)$$

Equation (15) is valid for daytime ($R_n > 50$ W m^{-2}) periods with dry canopy conditions.

Daytime totals of dry canopy evaporation (E_t) were computed by inserting the appropriate values for r_s and r_a into the Penman-Monteith equation (9). The resulting E_t totals for the 66-day period in May–July 1996 ("calibration period") and the years 1996 and 1997 amounted to 171 mm (2.6 mm d^{-1}), 888 mm yr^{-1} (2.4 mm d^{-1}), and 961 mm yr^{-1} (2.6 mm d^{-1}), respectively. As such, the Penman-Monteith-based estimates of E_t were 16% (May–July 1996), 29% (year 1996), and 5% (1997) higher than the corresponding catchment water-budget-based estimates (Table 3). Expressed as a percentage of corresponding rainfall totals, the difference between the two estimates of E_t amounted to 5%, 7% and 4%, respectively (Table 3). Hourly rates of wet canopy evaporation ($r_s = 0$ [*Monteith*, 1965]) were computed with (10) and summed to total values for the three periods. Adding the resulting totals of 41 mm, 221 mm, and 287 mm to the corresponding totals of E_t derived earlier yielded Penman-Monteith-based estimates of total ET of 192 mm (2.9 mm d^{-1}), 1039 mm (2.8 mm d^{-1}) and 1146 mm (3.1 mm d^{-1}) for the 66-day period in May–July 1996 and the years 1996 and 1997, respectively (Table 3). As such, the estimates of ET obtained with the Penman-Monteith equation are much lower than those derived from the catchment water balance, mainly because of the contrast in the respective values estimated for wet canopy evaporation/rainfall interception (Table 3).

5. Discussion

5.1. Rainfall and Throughfall Characteristics

At 3.0 mm h^{-1} the average rainfall intensity at Bisley is lower than the values reported for a number of lowland equatorial sites (5–10 mm h^{-1} [*Bruijnzeel and Wiersum*, 1987; *Lloyd et al.*, 1988; *Noguchi et al.*, 1996]) and only a little higher than the values characteristic of the maritime climates of more temperate latitudes (1.75–2.1 mm h^{-1} [*Gash et al.*, 1980; *Pearce et al.*, 1980]).

Relative amounts of throughfall (TF) in the Bisley forest rank as some of the lowest recorded for tropical lowland rain forest (typically 70–90% of incident rainfall [*Bruijnzeel*, 1990]). *Read* [1977] observed a similarly low TF value (50%) in a lowland forest near the Caribbean coast of eastern Panama, whereas values of 55–62% have recently been reported for a number of montane forests in Central and South America [*Cavelier et al.*, 1997; *Clark et al.*, 1998; *Ataroff*, 1998]. However, the latter are likely to be caused primarily by the presence of abundant mosses and other epiphytes on branches and trunks

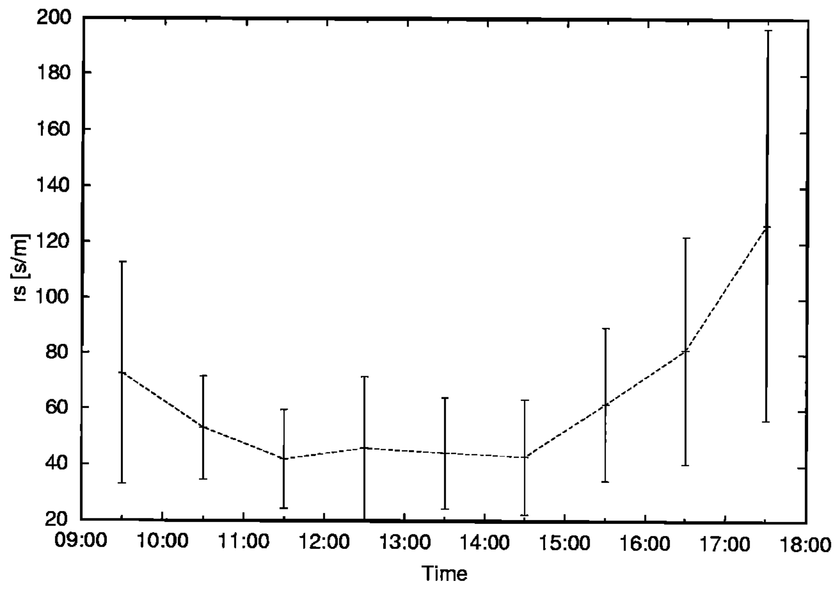

Figure 9. Average diurnal course of the surface resistance (r_s) of the Bisley forest based on an inverted application of the Penman-Monteith equation for 52 days between May 17 and July 10, 1996. Vertical bars represent standard deviation around the mean.

which increases the canopy's capacity to intercept and store precipitation [*Veneklaas and Van Ek*, 1990], whereas the estimate for the lowland Panamanian forest was based on measurements made with only one throughfall trough. *Jackson* [1971] already noted that TF is notoriously difficult to estimate accurately, mostly because of the large spatial variability. *Lloyd and Marques-Filho* [1988] suggested that this is even more true for lowland tropical rain forest with its high species diversity and proposed a roving technique to reduce the sampling error. The forest at Bisley differs from the Amazonian forest, however, in that the trees are smaller and species diversity is considerably lower [*Scatena*, 1989]. In addition to being distributed throughout the catchment (instead of being concentrated in a small plot), the total area of the gauges and gutters employed in the present study was considerably larger than the area in the study by *Lloyd and Marques-Filho* [1988] in central Amazonia. Consequently, we would expect the present error in estimated TF to be smaller than the 11% predicted for a nonroving setup with 20 gauges by *Lloyd and Marques-Filho* [1988].

As shown in Figure 5, the seasonal variation in the TF/*P* ratio at the study site is considerable, with relatively low values in the "summer" months (down to ~0.45) and higher values during the "winter" and "spring" period (up to ~0.70). Seasonal changes in rainfall, radiation, and temperature are thought to be the main contributors to this variation.

Interestingly, a separate analysis of daytime and nighttime events did not reveal a significant difference in the TF/*P* ratio for daytime and nighttime conditions (Figure 6). *Asdak et al.* [1998] observed a similar phenomenon for a lowland rain forest in central Kalimantan, Indonesia. Working in more temperate environments, both *Pearce et al.* [1980] and *Dunin et al.* [1988] reported significant wet canopy evaporation during nocturnal events for *Nothofagus* and *Eucalyptus* forests in southern New Zealand and southeast Australia, respectively. At the New Zealand site, where rainfall was both high (annual total 2610 mm) and often of long duration, nighttime evaporation even made up 50% of the total wet canopy evaporation loss [*Pearce et al.*, 1980]. As will be discussed in more detail in section 5.3, such observations strongly suggest that radiant energy alone is not sufficient to maintain such high wet canopy evaporation [cf. *Shuttleworth and Calder*, 1979]. Although the simple linear regression shown in Figure 6 does not do justice to the complexity of the interception process, Figure 6 suggests that the same applies to the Bisley situation.

5.2. Catchment Water Balance and Evaporation Components

At 2420 and 2179 mm yr^{-1} the evapotranspiration (ET) totals for the Bisley forest for 1996 and 1997, respectively, derived with the catchment water budget technique (Table 3) represent some of the highest values ever obtained for lowland tropical rain forest [*Bruijnzeel*, 1990, Table 1]. It is also higher than the 1707 mm yr^{-1} derived for the entire elevational range in the LEF by *García-Martinó et al.* [1996] but compares well with the 1860–2154 mm yr^{-1} found by *Odum et al.* [1970b] for the Tabonuco forest at El Verde and recent water-budget-based estimates for the entire Rio Mameyes watershed (17 km^2, of which the Bisley II catchment is part) for 1996 (2337 mm yr^{-1}) and 1997 (2134 mm yr^{-1}) by *Larsen and Concepción* [1998]. Although water budget estimates of ET can have wide error margins because of the accumulation of errors in the individual components of the water balance equation (1) [*Lee*, 1970], these are likely to be limited in the present case. Not only must the catchment be considered watertight [*Van Dijk et al.*, 1997], but also the changes in groundwater and soil moisture storages (ΔG and ΔS in (1), respectively) were shown to be negligible. The errors in the remaining terms, precipitation (P) and streamflow (Q), are estimated at 5 and 10%, respectively, at the most, suggesting the overall error in ET to be about 12%, that is 70 mm, 290 mm, and 260 mm for the May–July 1996 period and the years 1996 and 1997, respectively.

Part of the high value derived for E_t, and thus for total ET, may be attributed to our simple estimate of SF as a constant fraction of P [*Scatena*, 1990b]. This assumption might not be valid for large high-intensity storms [*Waterloo*, 1994]. Assuming the error in rainfall and throughfall measurements to be about 5% [*Gash et al.*, 1980], the error in measured interception loss (at 45% of gross rainfall) would be 16%. A second argument for the validity of the high ET totals obtained for the Bisley forest concerns the reasonable agreement between the water-budget-based values of ET and the sum of the micrometeorological (Penman-Monteith) estimates of E_t plus measured E_i (~7%, Table 3). Accepting therefore the high values for ET at Bisley, further inspection of Table 3 shows that the bulk of the total evaporation consists of wet canopy evaporation (E_i), namely, 57% for 1997 and 65% in 1996. As shown in Table 4, the magnitude of the dry canopy component of ET (E_t) at Bisley is quite comparable with results obtained for other lowland rain forests, confirming once more the importance of E_i at the study site.

Several possible sources of error can be identified for the present application of the temperature variance method. First, the Monin-Obhukov similarity theory requires measurements to be made high enough above the vegetation, preferably outside the roughness layer. However, it is equally important that the terrain should be as homogeneous and level as possible to avoid advection. Frequency losses caused by the use of relatively slow sampling thermocouples and the employed sampling procedures represent another source of error. Such losses depend on the diameter of the thermocouple wire, wind speed, and measurement height [*Moore*, 1986; *Van Asselt et al.*, 1991]. Taking into account the prevailing wind speeds at Bisley, an underestimation of the sensible heat flux of as much as 30% may be obtained in this way [cf. *Moore*, 1986]. In a study above a palm forest in the LEF (at 700 m) and at a lowland forest site about 45 km to the west, M. K. van der Molen (personal communication, 1999) found no significant differences between sensible heat flux estimates above these forests made at several heights (with $z - d$ ranging from 4.7 to 15.7) and concluded that the performance of the temperature variance method does not depend on the position in the roughness sublayer in these locations. Similar findings were obtained by *Vugts et al.* [1993] above a pine forest in Fiji. When comparing the TVAR-based results with simultaneous eddy correlation measurements (using a sonic anemometer) at the lowland site, an underestimation of the sensible heat flux by the TVAR method of up to 35% was found (M. K. van der Molen, personal communication, 1999). These findings are in line with our Bowen ratio-based estimate (using both wet- and dry-bulb thermocouples), which yielded a correction factor of 1.32 for the sensible heat flux (H), as derived with dry-bulb thermocouple temperature fluctuation measurements only.

In his review of evaporation from tropical rain forests, *Bruijnzeel* [1990] suggested an average value of about 1400 mm

Table 4. Evaporation Components for Selected Tropical and Warm Temperate Forests

Location and Source[a]	Type[b]	P	ET	E_i	E_t	E_i/E_t
Queensland, Australia, 1	1	4035	1420	1010	420	2.40
Puerto Rico, 2	1	3685	2420	1790	630	2.84
Puerto Rico, 3	1	3480	2180	1365	815	1.67
Fiji, 4	1	2015	1740	365	1375	0.27
Fiji, 5	1	2015	1540	355	1185	0.30
Sipitang, East Malaysia, 6	2	3945	1835	870	965	0.90
Jamaica, 7	2	3745	2000	710	1290	0.55
French Guyana, 8	2	3725	1440	560	880	0.64
West Java, Indonesia, 9	2	2850	1480	595	885	0.67
Peninsular Malaysia, 10	2	2775	1555	640	915	0.70
Eastern Brazil, 11	2	1819	1365	220	1145	0.19
Western Amazonia, Peru, 12	3	3065	1535	470	1065	0.44
Guyana, 13	3	2480	1485	345	1135	0.30
Central Amazonia, Brazil, 14	3	2390	1225	245	980	0.25
Sapulut, East Malaysia, 15	3	2370	1440	290	1150	0.25
Tai, Ivory Coast, 16	3	1995	1415	265	1150	0.23
South Island, New Zealand, 17	4	2610	1100	650	350	1.86
Plynlimon, Wales, United Kingdom, 18	4	2035	865	530	335	1.58

Evaporation values (mm yr^{-1}) are rounded off to the nearest 5.

[a]Sources: 1, *Gilmour* [1975]; 2, this study (1996); 3, this study, 1997; 4, *Waterloo et al.* [1999], 6-year-old pines; 5, *Waterloo et al.* [1999], 15-year-old pines; 6, *Malmer* [1993]; 7, *Richardson* [1982]; 8, *Roche* [1982]; 9, *Calder et al.* [1986]; 10, *Abdul Rahim et al.* [1995]; 11, *Hölscher et al.* [1997]; 12, *Elsenbeer et al.* [1994] and R. A. Vertessy, personal communication, 1998; 13, *Jetten* [1994]; 14, *Shuttleworth* [1988] and *Lloyd and Marques-Filho* [1988]; 15, *Kuraji and Paul* [1994]; 16, *Collinet et al.* [1984] and *Hutjes et al.* [1990]; 17, *Pearce and Rowe* [1979] and *Rowe* [1979]; and 18, *Calder* [1990].

[b]Type codes: 1, Coastal and island sites, outer tropics; 2, continental edge, equatorial; 3, continental, equatorial; and 4, coastal sites, temperate latitude.

yr^{-1} for forests not subjected to significant water stress, ascribing the occasionally reported outlier (e.g., 2000 mm yr^{-1} for a submontane forest on the leeward site of Jamaica [*Richardson*, 1982]) to catchment leakage (something which was not entirely ruled out by Richardson herself (J. H. Richardson, personal communication, 1988)). However, since 1990 there have been several studies that have also obtained high evaporation totals (>1700 mm yr^{-1}, Table 4), both in equatorial areas with high rainfall (e.g., Sipitang, East Malaysia [*Malmer*, 1993]) and in the more seasonal outer tropics (leeward Viti Levu, Fiji [*Waterloo et al.*, 1999]) (see Table 4). To these can be added the recent estimates for the entire Rio Mameyes catchment [*Larsen and Concepción*, 1998] and the present study. Such results seem to confirm the original finding of *Richardson* [1982], although her explanation ("high rainfall and breezy conditions") is not necessarily valid for the other high-evaporation sites as well. As shown in Figure 10a, annual totals of ET for lowland tropical forests increase with rainfall, although the scatter is considerable, particularly for rainfall exceeding 3500 mm yr^{-1}.

Interestingly, for a given rainfall, values of ET observed for forests located on islands in the outer tropics (e.g., Fiji, Jamaica, and Puerto Rico, 18° north or south, "type 1") tend to be higher than those for forests situated closer to the equator (0–10° north or south). The latter group may be subdivided into "continental edge" ("type 2") and "midcontinental" locations ("type 3"). The scatter in ET values is primarily due to the very large variation in intercepted rainfall (range of 220–1790 mm yr^{-1}, Table 4 and Figure 10b), whereas the variability in dry canopy evaporation is generally less pronounced (range of 630–1375 mm yr^{-1}, Table 4 and Figure 10c) leaving the exceptionally low value derived for NE Queensland [*Gilmour*, 1975] aside for the moment, which may be related to an overestimation of the stemflow component. It should be noted, however, that with a few exceptions (Fiji, Brazil, and Java) most of the estimates of E_t listed in Table 4 were derived by subtracting interception losses from overall ET. As such, they should be treated with caution. Nevertheless, an interesting pattern emerges when plotting the ratio E_i/E_t against rainfall (Figure 10d). At the low end of the rainfall spectrum ($P <$ 2000 mm yr^{-1}), rainfall interception typically makes up 20–25% of the total evaporation, regardless of site location in terms of proximity to the ocean or the equator (i.e., types 1, 2, or 3). However, rainfall interception becomes gradually more important when annual rainfall exceeds a value of ~2500–2700 mm yr^{-1}, both in the absolute sense (Figure 10b) and relative to E_t (Figure 10d). Also, for similar amounts of rainfall above this "threshold" of 2500–2700 mm yr^{-1}, both absolute and relative values of E_i tend to be somewhat higher for "type 2" locations (equatorial continental edge sites) than for "type 3" locations (midcontinental sites). In turn, values for "type 1" locations (maritime outer tropical sites) exceed those for "type 2" locations (Figures 10b and 10d). Interestingly, two temperate maritime sites with high rainfall but lower absolute values of ET and E_i (Plynlimon, Wales, United Kingdom and NW tip of the South Island of New Zealand, Table 4) exhibit very similar values for E_i/E_t (Figure 10d), confirming the importance of intercepted rainfall in both humid tropical and temperate maritime settings [e.g., *Pearce et al.*, 1980; *Calder*, 1990]. Such findings lend further credibility to the high values presently found for E_i and ET in Puerto Rico.

5.3. Wet Canopy Evaporation: Inferred Rates and Possible Explanations

The evaporation data for the Bisley forest presented in the preceding sections represent some of the highest values reported for lowland tropical rain forest (Table 4). Averaged over the two years 1996 and 1997, the total ET loss was approximately 42% higher than the evaporation equivalent of the total net radiant energy input (R_n). The contrast becomes

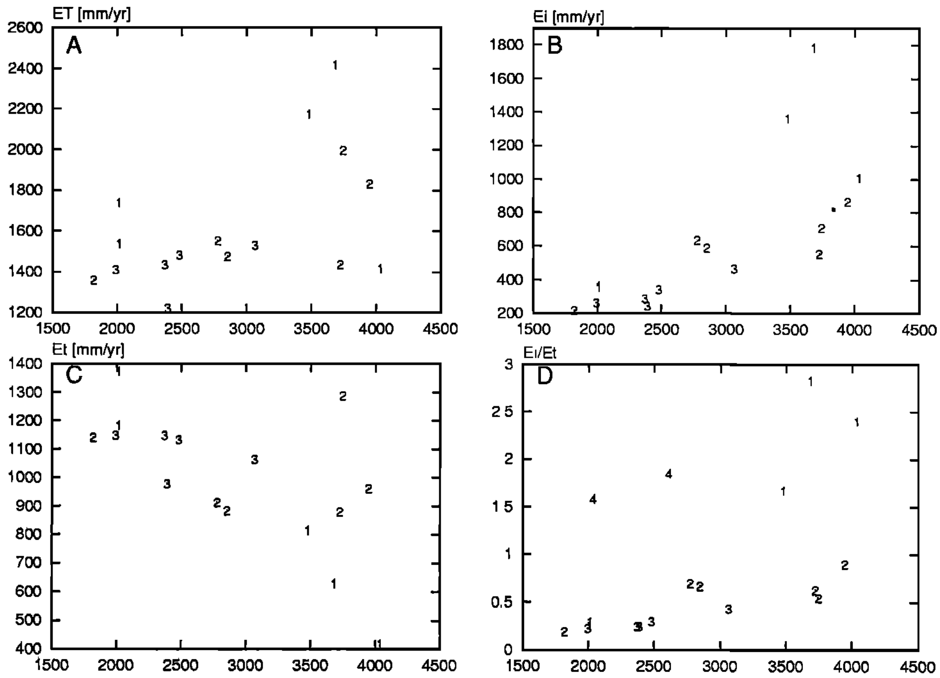

Figure 10. Annual precipitation versus (a) annual evapotranspiration (ET), (b) interception (E_i), (c) transpiration (E_t), and (d) the E_i/E_t ratio for the forests listed in Table 4 ("type 4" locations not included in Figures 10a–10c).

even larger when considering evaporation from a wet canopy. The observed annual rainfall interception totals of 1788 and 1364 mm for 1996 and 1997, respectively, correspond to average evaporation rates from a wet canopy (E_w) of 0.93 and 1.13 mm h^{-1}, respectively. The latter far exceed the evaporation equivalents of the corresponding net radiant energy inputs, namely, 0.10 and 0.11 mm h^{-1}, respectively, suggesting that at Bisley for wet canopy conditions, typically only about 10% of the required energy is supplied in the form of radiant energy. A similar, though less extreme, case has been documented by *Shuttleworth and Calder* [1979]. Here the canopy of a spruce plantation at Plynlimon, Wales, United Kingdom, was shown to receive typically only 20% of its total energy input during wet canopy conditions in the form of radiant energy, whereas the average annual ET loss from the forest exceeded the total radiant energy input by about 12% [*Shuttleworth and Calder*, 1979]. The maximum value of forest ET under wet temperate conditions is generally thought to be limited by the amount of advected energy available to evaporate intercepted rainfall from the wetted, aerodynamically rough forest canopy [*Shuttleworth and Calder*, 1979; *Calder*, 1998]. Conversely, under humid tropical conditions *Calder* [1998] considered forest ET to be limited primarily by radiation totals. Present findings suggest that this is most probably not the case at Bisley. High values of E_w (0.5–0.8 mm h^{-1} [*Bruijnzeel and Wiersum*, 1987; *Dykes*, 1997; *Waterloo et al.*, 1999]) have also been inferred from rainfall and throughfall measurements at other maritime tropical locations, but much lower values (typically about 0.2 mm h^{-1} or less [*Lloyd and Marques-Filho*, 1988; *Hutjes et al.*, 1990; *Asdak et al.*, 1998; *Waterloo et al.*, 1999]) are usually calculated from above-canopy climatic measurements using (10). Similarly, *Gash et al.* [1980] derived an average value of 0.13 mm h^{-1} for E_w in the case of the Plynlimon spruce forest referred to earlier when using the climate data, whereas a value of 0.24 mm h^{-1} was inferred from measured interception.

The origin of the energy needed in surplus of the radiant energy is still largely a matter of speculation. Advected warm air from the nearby Atlantic Ocean is a likely source [cf. *Shuttleworth and Calder*, 1979], although, unlike the situation in Wales, wind speeds in the study area are rather low (typically 1.1–2.3 m s^{-1} [*Holwerda*, 1997; *Schellekens et al.*, 1998]). Another possible energy source is heat released upon condensation of water vapor in the air above the forest. The latter possibility seems to find support from the observation that larger rainfall events are accompanied by higher E_i (i.e., the TF/*P* ratio is independent of storm size, Figure 6), suggesting a positive feedback of rainfall amount (and thereby condensation) on the magnitude of E_i.

Accepting that the presently measured E_w requires the total available energy A in (10) to be much higher than measured R_n also has consequences for the magnitude of r_a. Typical daytime values of r_a at Bisley as computed with (12) were about 18 s m^{-1} versus about 22 s m^{-1} at night when wind speeds are slightly lower (Figure 8) [*Holwerda*, 1997; *Schellekens et al.*, 1998]. The values for r_a can be compared with the r_a that would be required to match the measured and predicted rainfall interception (i.e., E_i calculated from (14) and (10)). Assuming that $A = \lambda E_w$, (10) can be rearranged to give

$$r_a = \frac{\rho C_p \mathrm{VPD}}{\gamma \lambda E_w}. \tag{16}$$

The resulting average value for r_a was 2.1 s m^{-1}, a very low value. *Asdak et al.* [1998] obtained an average value of 3.2 s m^{-1} for a forest in central Kalimantan, Indonesia (where similarly low wind speeds prevail), using a similar method. *Calder* [1977] derived an optimum value of 3.5 s m^{-1} for the Plynlimon forest referred to earlier (versus a theoretical value of

5.4 s m^{-1} using (12) at an average wind speed of 3.75 m s^{-1} [*Calder*, 1990]). Even when taking into account the sensitivity of r_a (and thus E_w) as determined with (12) to variations in the magnitude of z_0 [*Gash et al.*, 1980], particularly at high values of d/h_v, the latter parameters would have to be reduced to unrealistically low values to bring the outcome of (12) into agreement with (16). However, the outcome of (16) is sensitive to errors in VPD, especially under highly humid conditions [*Gash et al.*, 1980]. Lowering the relative humidity at Bisley during rainfall by 2% to an average value of 97.2% (VPD is 79 Pa) raised the inversely determined r_a to 3.2 s m^{-1}, which is very similar to the values suggested by *Asdak et al.* [1998] and *Calder* [1990]. However, given the very low wind speeds at Bisley, this is not nearly enough of a change to make the results from (12) and (16) comparable; to do so, unrealistically low values for the relative humidity during precipitation would be needed.

Thus the question of how the r_a at Bisley can be so low compared to values predicted by (12) remains. *Calder* [1990] drew attention to the possibility of enhanced upward transport of evaporated moisture by gusts and eddies, even during neutral or stable conditions, although he added that the "extent to which these gusts are associated with thermal- or humidity-driven plumes, local topography or other factors is still unknown." More recently, *McNaughton and Laubach* [1998] showed that such enhanced upward moisture transport increases with a relative increase of the standard deviation of wind speed compared to the mean wind speed. This confirms the contention of *Calder* [1990] that gusts may, indeed, be important, and although further study of the instantaneous wind data is needed, it is probable that gusts are relatively important because of the low mean wind speed. In addition, the aerodynamic roughness of the Bisley forest may be increased further by its very irregularly shaped canopy as a result of hurricane damage in the past [*Scatena et al.*, 1993]. Further work is necessary to improve our understanding of the transport mechanism of evaporated moisture under conditions of low wind speed during rain events. Clearly, such transport at Bisley is much more efficient than suggested by (12).

An alternative approach to match measured and predicted rainfall interception totals was followed by *Calder et al.* [1986] when an application of the Rutter model of rainfall interception [*Rutter et al.*, 1971] underestimated measured E_i by more that 50% in a secondary lowland rain forest in West Java, Indonesia. Apart from optimizing the value for r_a to 5 s m^{-1} and modifying the wetting and drainage functions of the Rutter model, *Calder et al.* [1986] proposed the use of much larger values for the canopy storage capacity (S) (up to 4–5 mm) than the 0.75–1.3 mm that have usually been obtained for tropical forests using more traditional techniques [e.g., *Jackson*, 1975; *Lloyd et al.*, 1988; *Asdak et al.*, 1998]. However, to match measured E_i totals at Bisley with those predicted by the analytical model of rainfall interception [*Gash*, 1979; *Gash et al.*, 1995], using above-canopy climatic parameters and (10) would require an optimized canopy storage capacity of ± 20 mm. In addition, the application of such an unrealistically high value for S produced a pattern of E_i that differed markedly from the measured one. Conversely, optimizing for E_w gave a near-perfect fit with observed daily totals. A further discussion of the performance of various interception models using the Bisley data set was given by *Schellekens et al.* [1999].

6. Conclusions

Although values of transpiration (evaporation from a dry canopy (E_t)) for the Bisley forest in eastern Puerto Rico are within the "low to normal" range for lowland tropical rain forests, those for intercepted rainfall (evaporation from a wet canopy (E_i)) are exceptionally high (up to 50% of incident precipitation (P)). As a result, annual values of total evapotranspiration (ET) in eastern Puerto Rico are also very high (2180–2420 mm).

Several factors are believed to be responsible for these observations, including (1) the frequent occurrence of rainstorms of low intensity associated with frontal activity; (2) a highly effective net upward transport of evaporated moisture from the wetted canopy driven by the release of heat upon condensation, probably aided by (3) the proximity of the site to the warm waters of the Atlantic Ocean which may act as a source of advected energy brought in by the trade winds; and (4) a comparatively low aerodynamic resistance due to the broken-up character of the forest as a result of hurricane damage and its location in highly dissected terrain.

Comparison of the present results with those obtained for other tropical island and continental locations suggests that high ET losses may well be a distinct feature of near-coastal locations. The Penman-Monteith evaporation model failed to predict the observed high values for E_i unless the value of r_a was reduced to 2.1 s m^{-1}, a very low value. Further research is needed (and intended), especially on (1) the proper quantification of the aerodynamic characteristics of lowland rain forest subject to hurricane disturbance and (2) the elucidation of the nature of the large amounts of additional nonradiant energy required for sustaining the observed high evaporation rates.

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