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Throughfall in a Puerto Rican lower montane rain forest: A comparison of sampling strategies

F. Holwerda [a,*], F.N. Scatena [b], L.A. Bruijnzeel [a]

[a] *Department of Hydrology and Geo-Environmental Sciences, Faculty of Earth and Life Sciences, Vrije Universiteit, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands*
[b] *Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA, USA*

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Summary During a one-year period, the variability of throughfall and the standard errors of the means associated with different gauge arrangements were studied in a lower montane rain forest in Puerto Rico. The following gauge arrangements were used: (1) 60 fixed gauges, (2) 30 fixed gauges, and (3) 30 roving gauges. Stemflow was measured on 22 trees of four different species. An ANOVA indicated that mean relative throughfall measured by arrangements 1 (77%), 2 (74%), and 3 (73%) were not significantly different at the 0.05 level. However, the variability of the total throughfall estimate was about half as high for roving gauges (23%) as for fixed gauges (48–49%). The variability of stemflow ranged from 36% to 67% within tree species and was 144% for all sampled trees. Total stemflow was estimated at 4.1% of rainfall, of which palms contributed about 66%. Comparative analysis indicated that while fixed and roving gauge arrangements can give similar mean values, least 100 fixed gauges are required to have an error at the 95% confidence level comparable to that obtained by 30 roving gauges.
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Introduction

On the basis of limited evidence, Shuttleworth (1989) hypothesized that because of relatively high levels of rainfall interception, tropical deforestation at continental edge and island locations is likely to have a greater effect on stream flow than deforestation in mid-continental sites. Since then an increasing number of interception studies conducted in tropical forests located at continental edges and islands suggest that interception may indeed be higher under 'maritime' climatic conditions (Scatena, 1990; Cavelier et al., 1997; Dykes, 1997; Clark et al., 1998; Schellekens et al., 2000). These high interception losses have been attributed variously to an orographic rainfall regime (i.e. frequent low intensity rains) (Scatena, 1990; Schellekens et al., 1999); advection of sensible heat from the nearby ocean (Dykes, 1997; Schellekens et al., 2000); high epiphyte loading (Cavelier et al., 1997; Ataroff, 1998), or a combination of these factors (Clark et al., 1998; Hölscher et al.,

* Corresponding author. Tel.: + 31 (0)20 5987332.
E-mail address: friso.holwerda@falw.vu.nl (F. Holwerda).

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2004). Nevertheless, it cannot be ruled out that some of the high interception estimates and variability between studies were caused by an underestimation of amounts of throughfall because of the use of a limited number of fixed gauges (Schellekens et al., 2000).

Lloyd and Marques (1988) demonstrated that the distribution of relative throughfall values was much broader for an Amazonian lowland rain forest (typically about 0–200% of rainfall) than for a temperate pine plantation forest (typically about 0–100% of rainfall). This broader distribution in lowland rain forest indicates that throughfall is increasingly concentrated at certain spots, or 'drip points', and consequently, more strongly depleted elsewhere (Shuttleworth, 1989). Because of this large spatial variation, measurements of throughfall in tropical rain forests are particularly prone to large sampling errors, especially if only a limited number of fixed gauges are used (Lloyd and Marques, 1988). Therefore, Lloyd and Marques (1988) recommended the frequent random relocation of gauges (i.e. roving gauge method) to increase the area sampled and so reduce the error.

In most studies of interception loss in maritime tropical locations, throughfall was measured using a fixed gauge arrangement (Scatena, 1990; Cavelier et al., 1997; Clark et al., 1998; Schellekens et al., 2000). A roving gauge approach has only been used occasionally (e.g. Dykes, 1997). In addition, only a few studies have reported the spatial variability of throughfall; for lower montane rain forests in Puerto Rico and Panama, individual gauge catch was found to range between 0–107% (Scatena, 1990) and 0–1000% (Cavelier et al., 1997) of incident rainfall, respectively. Similarly, the actual sampling error associated with throughfall measurements has been reported only sporadically (e.g. Clark et al., 1998), whereas in several studies (Cavelier et al., 1997; Dykes, 1997; Schellekens et al., 2000) the error was estimated using the equations derived by Lloyd and Marques (1988) for central Amazonian rain forest.

Therefore, comparatively little is known about the variability of throughfall in tropical forest under maritime tropical conditions, and requirements for adequate sampling of throughfall in these forests are poorly defined. This study measured throughfall using different gauge arrangements from November 2000 through November 2001 in the same Puerto Rican lower montane rain forest studied earlier by Scatena (1990) and Schellekens et al. (1999). Stemflow was also measured on trees of various species. The main objectives of this study were to assess the variability of throughfall and the errors associated with different gauge arrangements.

Study area

The study was conducted in the 6.4 ha Bisley 2 catchment, which is located at 18°19′N, 65°50′W at an elevation between 265 and 456 m in the Luquillo Mountains, northeastern Puerto Rico. The catchment is covered with Tabonuco-type rain forest consisting of 20–25 m high irregularly shaped trees with an understory dominated by palms, and ground level herbs and shrubs (Scatena and Lugo, 1995). There are 107 tree species in the catchment, and the three dominant species, *Dacryodes excelsa* (Tabonuco), *Prestoa montana* (a frequently occurring palm), and *Sloanea berteriana*, comprise 51% of the basal area, 49% of the stem density, and 57% of the importance value (Chinea et al., 1993). The average leaf area index of the forest was estimated at 6.4 (Odum et al., 1970).

The Bisley 2 catchment receives about 3000–4000 mm of rainfall per year (Scatena, 1989). Rainfall is distributed fairly evenly within the year. In general, May and November are the wettest months with about 385 mm each. The period January–March is relatively dry with 200 mm per month on average (Schellekens et al., 1999). Mean monthly temperatures in the area vary little throughout the year (24 °C in December–February vs. 27–28 °C in July–August), and seasonal variation in average daily relative humidity is small (84–90%) (Brown et al., 1983). Whilst hurricanes are common, mean daily wind speeds are generally low (1–2 m s^{-1}) and have little seasonal variation (Brown et al., 1983; Van der Molen, 2002). The forest was hit by hurricane Hugo in September 1989, which caused considerable damage to the forest (Scatena and Lugo, 1995). However, approximately one year after the hurricane throughfall approached pre-storm levels, and after five years aboveground biomass was 86% of the pre-hurricane value (Scatena et al., 1996).

Methods

Rainfall

Rainfall (P, mm) was measured with a Casella CEL tipping bucket rain gauge (400 cm^2 orifice, 0.10 mm per tip) and a totalizer rain gauge (100 cm^2 orifice) placed on a 24.2 m scaffolding tower situated at 335 m on the northern water divide of the Bisley 2 catchment. The recording rain gauge (25.7 m above the ground) was connected to a Campbell Scientific 21× data logger and 60 min totals were stored in an external storage module. The totalizer gauge (25.5 m above the ground) was read at the same time as the throughfall measurements, approximately every 2–3 days. Rainfall totals as measured with the recording gauge (P_{rec}) and the totalizer (P_{tot}) correlated very well ($P_{tot} = 1.01P_{rec} - 0.16$, $r^2 = 1.00$, $N = 28$). Rainfall data from the totalizing gauge were used in the present analysis.

Throughfall

Throughfall (TF, mm) was measured between November 2000 and November 2001 on the northern slope of the Bisley 2 catchment (directly to the south of the tower) using three different gauge arrangements (Table 1). For the first arrangement, a 139 m transect was outlined with numbered flags placed at 1 m intervals, representing 140 possible sampling positions. Next, 60 fixed gauges were placed by randomly selecting 60 from the 140 possible sampling positions. For the second and third arrangements, a separate 159 m transect was outlined. The 30 fixed gauges were distributed by randomly selecting 30 from the 160 possible sampling positions. For the roving gauge arrangement, the 160 sampling positions were divided into 30 groups of 5–6 neighbouring positions. Within each group, a gauge was placed by randomly selecting one from the 5–6 possible sampling positions. This procedure was repeated each time

Table 1 The three different arrangements of throughfall gauges used in the Tabonuco forest between 28 November 2000 and 5 November 2001

Arrangement	Number of gauges	Sampling method	Measurement period
1	60	Fixed	28 November 2000–9 March 2001
2	30	Fixed	16 March–6 July 2001
3	30	Roving	16 March–5 November 2001

the gauges were emptied, typically every 2–3 days. Each of the TF gauges had a 100 cm^2 orifice that was placed horizontally at 30 cm above the ground and held by steel holders.

Stemflow

Between 28 November 2000 and 5 November 2001, stemflow (SF, mm) was measured on 22 trees of four different species that were located in or adjacent to the throughfall-sampling transects. The sampled tree species were *Dacryodes excelsa* (Tabonuco), *Prestoa montana* (a frequently occurring palm), *Sloanea berteriana*, and *Cecropia peltata* (a pioneer species dominating gaps). At ca. 1.0–1.5 m from the ground, silicon tubing slit open lengthwise was attached to the stem in a spiral fashion. Any remaining spaces between tubing and stem were sealed with silicon sealant. For practical reasons, SF could only be measured on a limited number of trees at a given time. Therefore, once a good relationship between SF and rainfall *P* was obtained for a given tree ($r^2 > 0.70$), the gauge was relocated. The regression of SF volume (L) vs. *P* (mm) was used to calculate SF volume for each sampling interval to estimate the total SF volume for the entire study period for each sampled tree. Preferably, areal SF (mm) should be estimated using relationships between SF volume and tree diameter and information on tree size distribution in the forest (cf. Hanchi and Rapp, 1997). In the present study, however, SF data for a particular tree species were collected on trees of relatively uniform size (see Table 5). Therefore, relationships between SVR (total SF volume divided by total rainfall) and dbh (diameter at breast height) predicted unrealistic values for tree sizes outside the measured range. For example, the SVR to dbh relationship for *Dacryodes excelsa* yielded negative SF values for trees with dbh < ~22 cm, while that for *Prestoa Montana* predicted negative values for trees with dbh > ~18 cm. Hence, areal SF was estimated by multiplying mean SF volume per tree species by the density of stems per hectare equal or greater than 2.5 cm in diameter.

Results

Statistical analysis

Before performing statistical tests, the spatial distribution of throughfall TF was assessed using the 160 point measurements as obtained with the roving gauge method between 16 March and 5 November 2001 (arrangement 3, Table 1). Cumulative TF per position was divided by corresponding rainfall *P* and multiplied by 100 to give relative throughfall (TF/*P*, $N = 160$). These data were distributed over eight class intervals, each consisting of relative TF fractions of 25% width (Fig. 1a). Point TF ranged between 19% and 186% of rainfall, and mean and median TF/*P* were 71% and 67%, respectively (Table 2). Since the distribution of point TF was positively skewed, chi-square tests were used to determine how well the normal, log-normal, and the square-root normal theoretical distributions fitted the observed data (Table 2). The square-root normal distribution produced the best fit. Therefore, further statistical analysis was performed using this type of data transformation (cf. Lloyd and Marques, 1988). Mean TF, however, was calculated as the arithmetic mean of the non-transformed TF measurements, since this gives the best estimate of total

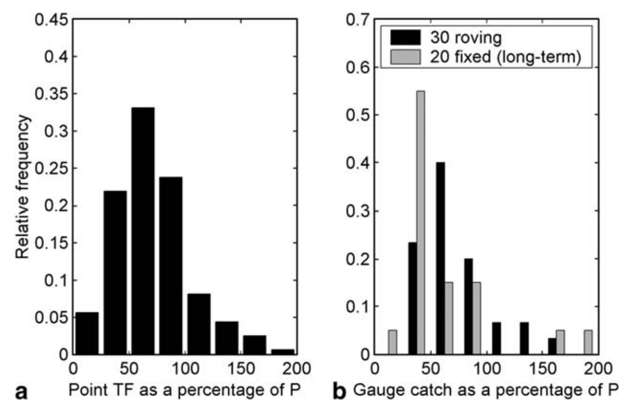

Figure 1 (a) Frequency distribution of point throughfall TF, expressed as a percentage of rainfall *P*, at 160 sampling positions in the Tabonuco forest between 16 March and 5 November 2001. (b) Frequency distribution of cumulative TF catch per gauge, expressed as a percentage of total *P*, for 20 fixed long-term gauges and 30 roving gauges of arrangement 3 during October 2001 in the Tabonuco forest (see Section 5.7 for further explanation).

Table 2 Some statistical parameters of relative throughfall (TF/*P*) at 160 sampling positions as obtained with 30 roving gauges in the Tabonuco forest between 16 March and 5 November 2001 (see also Fig. 1a), and the results of chi-square (goodness of fit) tests (see text for explanation)

Mean TF/*P* (%)	71 (range: 19–186)
Median TF/*P* (%)	67
Standard deviation SD (%)	34
Coefficient of variation CV (%)	48
Chi-square statistics χ^2	
χ^2 (no transformation)	15.9
χ^2 (log transformation)	10.4
χ^2 (square-root transformation)	3.0
Critical value of the 0.05 significance level	11.1

TF reaching the forest floor (Lloyd and Marques, 1988). Standard deviations SD, standard errors SE, coefficients of variation CV, and confidence intervals were also calculated using non-transformed data.

General comparisons between gauge arrangements

Total throughfall TF (330 mm) as measured with 60 fixed gauges (arrangement 1) was 77% of rainfall *P* (Table 3). The difference between relative throughfall TF/*P* as measured with 30 fixed gauges (74%) and 30 roving gauges (76%) was small. During the period 16 March–5 November 2001, total TF as measured with the 30 roving gauges (1324 mm) was 73% of *P* (1816 mm). Graphical analysis (Fig. 2) and a one-way analysis of variance test (ANOVA) showed that mean TF/*P* according to arrangements 1 (77%), 2 (74%), and 3 (73%) were not statistically different at the 0.05 significance level.

30 fixed vs. 30 roving gauges

For the period 16 March–6 July 2001, total throughfall TF measured using 30 fixed gauges (628 ± 302 mm) was not significantly different at the 0.05 level from that obtained with 30 roving gauges (642 ± 148 mm, Table 3). The correlation between mean TF per sampling occasion measured with 30 roving (TF_{rov}) and 30 fixed (TF_{fix}) gauges was strong ($TF_{rov} = 1.08TF_{fix} - 0.71$, $r^2 = 0.97$, $N = 56$, Fig. 3a). An ANOVA between the fixed and roving gauge TF data per sampling occasion (Table 4) indicated that the two methods gave a significantly different mean TF on only one sampling occasion (at the 0.05 level, but not at the 0.01 level). Patterns of cumulative TF as measured with the fixed and roving gauge methods also agreed very well (Fig. 3b). For both

Table 3 The three data sets used in the present analysis

Data set	1	2		3
Arrangement	60 fixed gauges	30 fixed gauges	30 roving gauges	30 roving gauges
Period	28 November 2000–9 March 2001	16 March–6 July 2001		16 March–5 November 2001
No. of observations (*N*)	54	56		102
P (mm)	430	845	845	1816
TF ± 1SD (mm)	330 ± 163	628 ± 302	642 ± 148	1324 ± 310
TF/*P* (%)	77	74	76	73
CV (%)	49	48	23	23
SE (mm)	21	55	27	57
95% confidence interval (mm)	288–372 (±42)	518–738 (±110)	588–696 (±54)	1210–1438 (±114)
Error (%)	13	18	8	9

TF is the arithmetic mean of the throughfall measurements per observation period (total TF), *P* the corresponding rainfall, TF/*P* the total throughfall in % of the total rainfall (mean relative throughfall). Also shown are standard deviation SD, coefficient of variation CV, standard error SE, 95% confidence interval (calculated using critical value z_c of 2.0), and the error at the 95% confidence level (in % of TF) of TF.

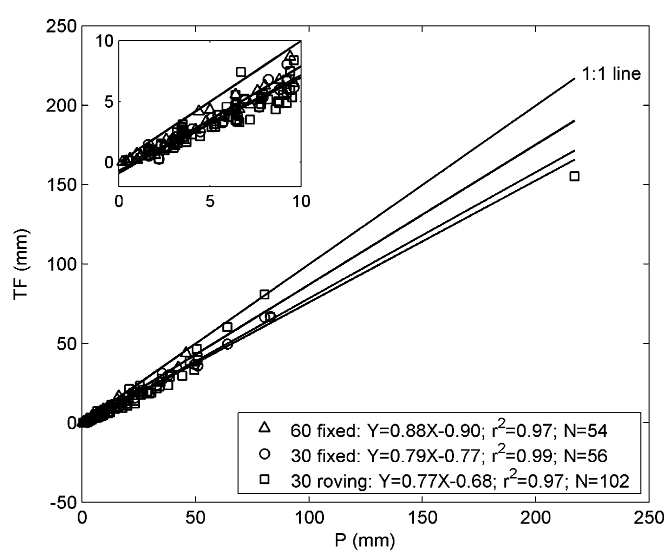

Figure 2 Mean throughfall TF per sampling occasion against rainfall *P* for 60 fixed gauges (28 November 2000–9 March 2001), 30 fixed gauges (16 March–6 July 2001), and 30 roving gauges (16 March–5 November 2001) in the Tabonuco forest. Also shown are the 1:1 line and the regressions of TF on *P*.

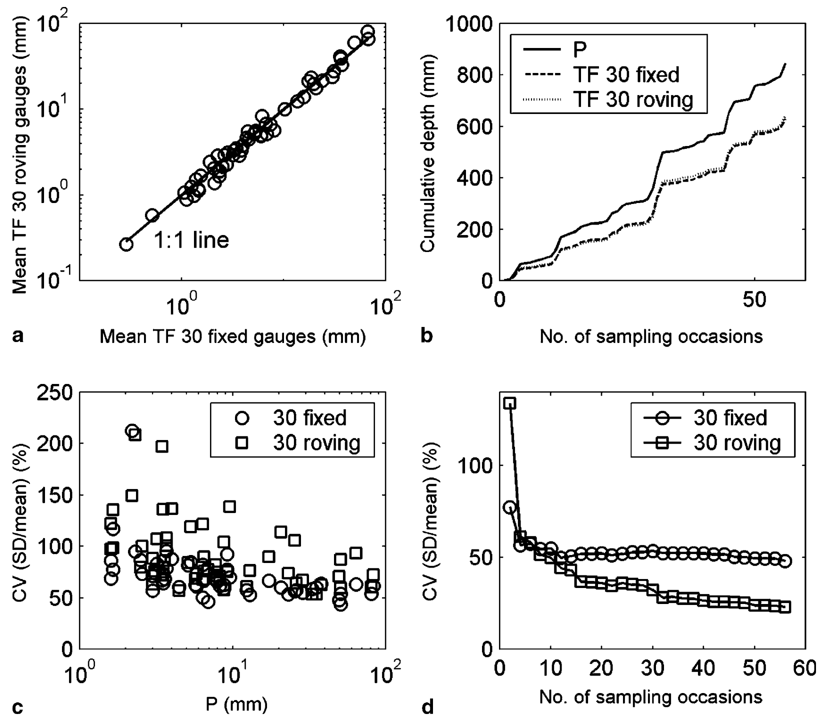

Figure 3 (a) Relationship between mean throughfall TF per sampling occasion according to 30 roving and 30 fixed gauges in the Tabonuco forest between 16 March and 6 July 2001; also shown is the 1:1 line. (b) Cumulative patterns of rainfall *P* and TF as measured using 30 fixed and 30 roving gauges between 16 March and 6 July 2001. (c) Relationship between the coefficient of variation CV of mean *TF* (per sampling occasion) against *P* using 30 fixed and 30 roving gauges between 16 March and 6 July 2001. (d) The CVs of total *TF* using 30 fixed and 30 roving gauges as a function of the number of sampling occasions used to calculate them between 16 March and 6 July 2001.

methods, the coefficient of variation CV (%) of mean TF (per sampling occasion) increased with decreasing rainfall *P* below about 10 mm; within the range $P = 0–10$ mm, the CV varied between about 50% and 150%. For $P > 10$ mm, the CV generally varied between 50% and 100%. Fig. 3d shows the CV of the fixed and roving gauge arrangements against the number of sampling occasions (calculated using the cumulative TF data per gauge). The CV of the fixed gauges decreased from about 80% to 60% over the first 4 samplings, then decreased from about 60% to 50% over the next 8 samplings, and remained nearly constant thereafter (being about 48% at the end of the measurement period, Table 3). Conversely, the CV of the roving gauges decreased asymptotically with the number of samplings, and was about 23% at the end of the measurement period (Table 3).

60 fixed gauges

Fig. 4a shows the coefficient of variation CV of mean throughfall TF against rainfall *P* using 60 fixed gauges (arrangement 1) between 28 November 2000 and 9 March 2001. As observed previously for arrangements 2 and 3, the CV increased with decreasing *P* below about 10 mm. Within the range $P = 0–10$ mm, the CV varied roughly between 50% and 550%, the highest CVs being associated with $P < 1$ mm. For $P > 10$ mm, the CV generally varied again be-

Table 4 Summary of one-way analysis of variance tests (ANOVA) performed on 56 samples of TF using 30 fixed and 30 roving gauges in the Tabonuco forest between 16 March and 6 July 2001 (i.e. the *F* statistic was calculated 56 times)

Rainfall amount (mm)	*N*	Mean *F*	Maximum *F*	$F > F_{.95}$[a]	$F > F_{.99}$[b]
0–2.5	7	0.74	1.91	0	0
2.5–5.0	14	1.12	4.58	1	0
5.0–10.0	18	0.73	2.96	0	0
10.0–20.0	3	0.39	0.52	0	0
>20	14	0.62	1.82	0	0
Total	56			1	0

The results were classified by rainfall amount. *N* is the number of samples.
[a] 4.01.
[b] 7.10.

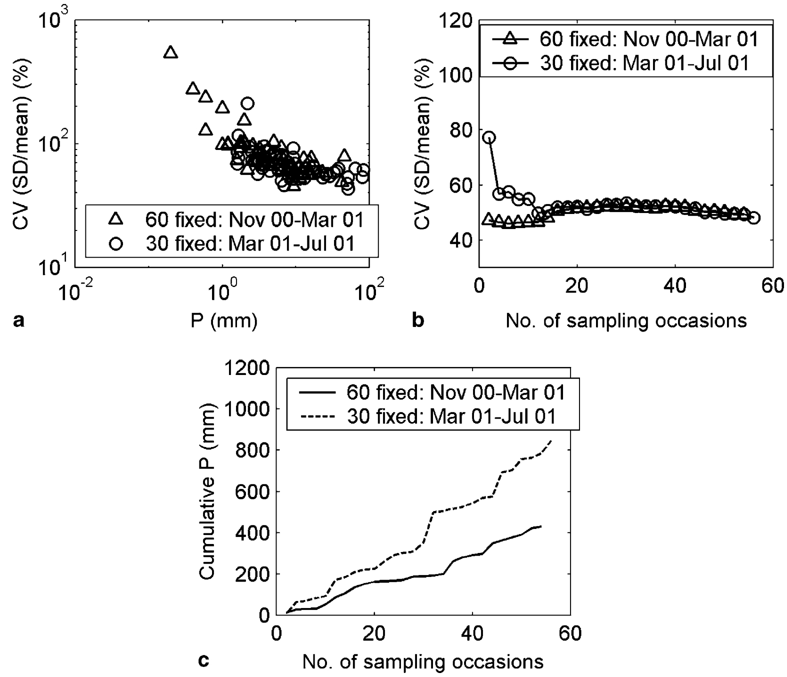

Figure 4 (a) Relationship between the coefficient of variation CV of mean TF (per sampling occasion) against rainfall *P* using 60 fixed gauges in the Tabonuco forest between 28 November 2000 and 9 March 2001; data for the 30 fixed gauges added for comparison (cf. Fig. 3c). (b) The CV of total TF using 60 fixed gauges as a function of the number of sampling occasions used to calculate it between 28 November 2000 and 9 March 2001; data for the 30 fixed gauges again added for comparison (cf. Fig. 3d). (c) Cumulative patterns of *P* for the periods 28 November 2000–9 March 2001 and 16 March–6 July 2001.

tween 50% and 100%. The CV of the 60 fixed gauges (calculated using the cumulative TF data per gauge) was typically ca. 50% (Fig. 4b, cf. Table 3). Total *P* for arrangement 1 (28 November 2000–9 March 2001) was about half that for the 30 fixed gauges of arrangement 2 (16 March–6 July 2001, Fig. 4c).

Stemflow

Total stemflow volumes SF (L) as well as volume per mm of rain (SVR) for each tree are listed in Table 5. The coefficient of variation CV of mean SF ranged from 36% for *Sloanea berteriana* to 67% for *Prestoa montana*. *Cecropia peltata* and *Dacryodes excelsa* had intermediate values of 50% and 59%, respectively. The CV of the mean SF of all trees ($N = 22$ trees) was 144%. *Prestoa montana* and *Cecropia peltata* were the tree species with the highest and lowest SVR, respectively. Total SF between 28 November 2000 and 5 November 2001 (excluding the period 10 March–15 March 2001) was estimated at 4.1% of the total rainfall *P* of 2246 mm in this period (Table 6). Palms (*Prestoa montana*) contributed about 66% of the total SF.

Discussion

Fixed vs. roving gauge arrangements

Over the same period, estimates of total throughfall TF using 30 fixed (628 ± 302 mm) and 30 roving gauges (642 ± 148 mm, Table 3) were not significantly different at the 0.05 level. Likewise, there were no significant differences between mean TF per sampling occasion for fixed and roving gauge arrangements (Table 4). Coefficients of variation CVs of mean TF per sampling occasion were also high for both gauge arrangements (typically about 50–100%, Fig. 3c). However, the CV of total TF based on roving gauges (23%) was about half that for the fixed gauges (48%, Table 3).

The reduction of the variation in the total TF estimate when using roving gauges can be explained as follows. Because each of the 30 roving gauges was randomly relocated between 5 and 6 possible sampling positions, TF was measured at 160 different points in the roving gauge arrangement compared to 30 points in the fixed arrangement. The distribution of relative TF at these 160 sampling points is shown in Fig. 1a. Mean relative TF was 71% with a standard deviation SD of 34% (Table 2). The chance of measuring a relative TF between 50% and 75% (about 33%) was much larger than measuring a relative TF between 150% and 175% (about 3%). Hence, with an increasing number of gauge relocations, the more extreme values were averaged out and variation between the gauges decreased. The positive effect of random relocation on TF variation between the roving gauges is also demonstrated in Fig. 3d. At first, the CV of the roving gauges decreased rapidly. However, with an increasing number of relocations CV asymptotically approached a minimum value of about 23% (cf. Table 3). Random relocation of the 30 gauges amongst all 160 possible sampling positions (instead of within groups of 5–6 positions) should have reduced the variation further.

Table 5 Total SF volume (L) per tree between 28 November 2000 and 5 November 2001 (except for the period 10 March–15 March 2001) as estimated from the regression of SF volume (L) on rainfall *P* (mm)

Species	Tree no.	dbh (cm)	*a*	*b*	r^2	SF (L)	SVR (L mm rain^{-1})
Dacryodes excelsa	1	32	0.43	−4.14	0.86	523	0.23
	2	54	0.63	−1.95	0.94	1129	0.50
	3	49	0.44	−3.12	0.92	619	0.28
	4	32	0.08	−0.69	0.89	95	0.04
	5	41	0.35	−3.65	0.73	405	0.18
	6	59	0.62	−5.72	0.86	763	0.34
Mean (±1SD)						589 (±348)	0.26 (±0.15)
CV (%)						59	59
Sloanea berteriana	1	17	0.29	−2.31	0.83	393	0.17
	2	20	0.27	−2.48	0.85	333	0.15
	3	14	0.28	−1.57	0.86	436	0.19
	4	24	0.13	−1.25	0.73	165	0.07
Mean (±1SD)						332 (±119)	0.15 (±0.05)
CV (%)						36	36
Prestoa montana	1	15	4.05	−3.94	0.97	8495	3.78
	2	16	3.03	−5.11	0.89	6045	2.69
	3	16	1.47	−2.95	0.81	2856	1.27
	4	15	2.41	−7.09	0.96	4393	1.96
	5	18	0.35	−1.49	0.77	588	0.26
	6	17	1.76	−0.55	0.73	3877	1.73
	7	15	4.87	−0.10	0.98	10942	4.87
	8	17	1.30	−0.67	0.84	2807	1.25
Mean (±1SD)						5000 (±3362)	2.23 (±1.49)
CV (%)						67	67
Cecropia peltata	1	21	0.07	−0.58	0.81	93	0.04
	2	24	0.14	−1.49	0.84	158	0.07
	3	19	0.13	−0.92	0.95	191	0.09
	4	18	0.14	−0.03	0.95	317	0.14
Mean (±1SD)						190 (±94)	0.08 (±0.04)
CV (%)						50	50
Mean of all trees (±1SD)						2074 (±2991)	0.92 (±1.32)
CV (%)						144	144

a is the slope of the regression, *b* is the *y*-intercept, r^2 is the coefficient of determination, and dbh is the diameter at breast height. The last column shows the stemflow volume ratio (SVR) defined as the total SF volume (L) divided by the total *P* of 2246 mm between 28 November 2000 and 5 November 2001 (except for the period 10 March–15 March 2001).

Using different numbers of fixed gauges

The data sets of gauge arrangement 1 (60 fixed) and arrangement 2 (30 fixed) are not directly comparable, as they cover different periods and rainstorms of different duration and intensity (Table 3, Fig. 4c). However, some qualitative observations can be made by comparing the coefficients of variation CVs of mean throughfall TF (per sampling occasion) using 60 and 30 fixed gauges (Fig. 4a). For $P > 10$ mm, the variation between 60 or 30 gauges was typically 50–100% in both cases. With decreasing rainfall *P* below about 10 mm, the CVs of mean TF increased regardless whether 60 or 30 gauges were used (Fig. 4a). The CVs of total TF for 30 and 60 fixed gauges were also very similar (nearly 50%, Fig. 4b, Table 3). Hence, the present results strongly indicate that increasing the number of fixed gauges from 30 to 60 would not greatly reduce the variability of the TF measurements in the Tabonuco forest.

Variation in cumulative throughfall

The spatial variability in throughfall TF between fixed gauges for individual sampling occasions (typically about 50–100%, Fig. 4a) was larger than the variability for cumulative totals (nearly 50%, Fig. 4b). The CV for the 30 fixed gauges decreased from about 80% to 60% in the first four samplings (Fig. 4b). This decrease was primarily associated with an event of about 26 mm occurring during the third

Table 6 Estimated SF per species in % of the total rainfall of 2246 mm between 28 November 2000 and 5 November 2001 (except for the period 10 March–15 March 2001) (column 5)

Species	Density[a] (stems ha^{-1})	SF (L $stem^{-1}$)	SF[c] (mm)	SF (%)
Dacryodes excelsa	97[b]	589	5.7	0.3
Sloanea berteriana	382	332	12.7	0.6
Prestoa montana	123	5000	61.5	2.7
Cecropia peltata	18	190	0.3	0.0
Other	743	–		0.5[d]
Total				4.1

[a] Taken from Scatena and Lugo (1995).
[b] Number of stems with dbh ⩾ 30 cm as estimated from the size class distribution given by Brown et al. (1983); *Dacryodes excelsa* with dbh < 30 cm were not used in the stemflow computations because no data were collected for this size class.
[c] Column 2 (stems ha^{-1}) multiplied times column 3 (L $stem^{-1}$) and divided by 10,000 to obtain units of mm.
[d] SF value for other species taken from Scatena (1990).

sampling period. Rainfall during the first and second sampling periods was less than 4 mm on both occasions. The CV for the 60 fixed gauges was less than 50% after the first two samplings for which corresponding rainfall totals were about 10 and 2 mm, respectively. Apparently, the variability between cumulative gauge totals decreases when one or more 'large' rainfalls (of about 10 mm or more) are included. This was examined further by calculating the spatial variability of monthly TF between December 2000 and June 2001 using the data of the fixed gauges (Table 7). Between December 2000 and June 2001, the average number of rain-days per month (22) was almost equal to the five-year mean (21). However, for all months except April 2001, rainfall was less than the five-year average; December 2000 and January 2001 were exceptionally dry. Furthermore, for most months the number of days with $P > 10$ mm was less than the five-year average. Nevertheless, despite these relatively dry conditions the variability of monthly TF was typically 50–55% (based on 30 and 60 fixed gauges) and thus very similar to the variability in total TF for the gauges over the 3–4 month sample periods discussed above (48–49%, Table 3, Fig. 4b). It is also very similar to the variability between 160 point measurements of relative TF (about 48%) as obtained with the 30 roving gauges between 16 March and 5 November 2001 (Table 2, Fig. 1). These results suggest that given the local rainfall pattern the spatial variability of TF in the Tabonuco forest over periods of one month or more will typically be about 50%, regardless of the number of storms with $P > 10$ mm.

'Towards the optimum throughfall sampling approach'

An often used criterion in throughfall TF measurement design is that the error in mean TF should not be larger than 5% or 10% (from the mean) at the 95% confidence level (Kimmins, 1973; Rodrigo and Ávila, 2001). Table 3 indicates that only the roving gauge arrangement produced estimates of TF with errors of less than 10% at the 95% confidence level (8–9%). Errors in the estimates of *TF* using 30 and 60 fixed gauges were 18% and 13%, respectively (Table 3). The number of fixed gauges required to make the 95% confidence interval of the mean TF equal to a pre-set (fixed) error (in % of the mean) can be estimated from the coefficient of variation CV using (Kimmins, 1973)

$$n = \frac{z_c^2 \times CV^2}{c^2} \tag{1}$$

Table 7 The coefficient of variation CV of monthly throughfall TF (based on 60 and 30 fixed gauges) between December 2000 and June 2001

Month	CV (%)	No. of rain-days	Mean[c]	Mean *P* per rain-day (mm)	Mean[c] (mm)	No. of days with $P > 10$ mm	Mean[c]	Monthly *P* (mm)	Mean[c] (mm)
December 2000	52[a]	24	24	5.8	13.3	5	8	140	340
January 2001	69[a]	17	25	6.5	11.3	2	10	110	291
February 2001	51[a]	27	14	5.6	9.0	7	5	151	193
March 2001	54[b]	15	18	7.7	11.0	3	6	116	194
April 2001	54[b]	24	19	10.9	9.9	9	5	261	187
May 2001	52[b]	22	19	10.2	16.7	5	6	225	330
June 2001	54[b]	23	23	8.9	10.5	4	8	205	247
Mean	55	22	21	7.9	11.7	5	7	173	253

Also shown are the number of rain-days per month, the mean rainfall *P* per rain-day (mm), the number of days with $P > 10$ mm, and monthly *P* (mm). Five-year means were added for comparison.
[a] Based on 60 gauges (arrangement 1, Table 1).
[b] Based on 30 gauges (arrangement 2, Table 1).
[c] Based on five years of daily rainfall data (1994, 1996–1999) as obtained from the Luquillo LTER data base (http://luq.lternet.edu).

in which n is the required number of gauges, z_c is the critical value of the 95% confidence level (2.0; Spiegel, 1988), and c is the pre-set error (in % of the mean). Given that the variability of TF for the Tabonuco forest is about 50% (Tables 3 and 7), 100 fixed gauges are needed for an error of 10%. This estimate only applies to gauges with orifice equal to that used in the present study (100 cm^2), because gauges with larger orifice will measure TF from a greater canopy area, which may decrease the spatial variability (Kimmins, 1973). Naturally, the use of 100 fixed gauges is very labour-intensive and, as demonstrated previously, random relocations of a much smaller number of gauges yields a similar level of accuracy (8–9% error in the overall TF estimate, Table 3) with less labour. Using roving gauges would therefore be a much better option, if the objective of the study is to determine mean TF over a considerable number of sampling intervals. If, however, the study is of short duration or concerns e.g. throughfall variability in relation to canopy or meteorological characteristics, it is better to use a large number of fixed gauges (cf. Kimmins, 1973).

The error was reduced to 8–9% (at the 95% confidence level) by randomly relocating 30 gauges within groups of 5–6 (possible) sampling positions (Table 3). Random relocations between all (160) possible sampling positions would have resulted in an even smaller error. The relocation schedule will depend mainly on the duration of the study. The current results suggest, however, that weekly relocation will do in a one-year study of TF (cf. Fig. 3d). Furthermore, Lloyd and Marques (1988) showed that sampling along 100 m transects yielded better estimates of TF than sampling in 20 m × 4 m area grids. A similar spatial dependence of TF was found by Loescher et al. (2002) for tropical lowland forest in Costa Rica, who recommended a spacing between gauges of >45 m to avoid bias in TF estimates caused by large tree crowns and gaps. Hence, to minimize effects of spatial dependence in tropical rain forests, TF sampling networks (either line transects or area grids) should be large enough to cover most of the variation in forest structure.

Comparison with other forests

At nearly 50%, the variability of throughfall TF in the Tabonuco forest is higher than generally found in non-tropical forests. For example, using 24 roving gauges in a plantation of Scots pine (Thetford Forest, Norfolk, England), Gash and Stewart (1977) found that the variability in TF was typically 20–24%. Similarly, using 94 fixed gauges in a 40-year old western hemlock-western red cedar forest (Southwestern British Columbia, Canada), Kimmins (1973) found the variability in TF to be 20–30%. In two Mediterranean holm oak forests (northeast Spain), Rodrigo and Ávila (2001) observed a variability of ca. 20% (using 32 gauges in each forest). However, the present result compares well with the findings of Lloyd and Marques (1988) in Amazonian lowland rain forest (Brazil). Lloyd and Marques (1988) measured TF at 494 sampling positions using 36 roving gauges over a one-year period. Mean relative TF was 91% with a standard error SE of 2.2%; according to this information, the variability of TF in their forest was about 50–55%. However, other studies of TF in tropical forest have reported smaller variation. Using 55 fixed gauges in tropical lowland forest (Costa Rica), Loescher et al. (2002) found a variability of TF of ca. 24%. Using 20 fixed gauges in tropical montane forest (Monteverde, Costa Rica), Clark et al. (1998) obtained a mean TF of 2068 mm with a SE of 132 mm, suggesting a CV of 25–30%. For somewhat drier evergreen mixed forests in Guyana, Brouwer (1996) found relative TFs of 83 and 85% with SEs of only 2% and 3%, respectively (using 20 fixed gauges in each forest type); the variability of TF in these forests was between 13% and 15%.

In these cited studies, types, numbers, and arrangements of gauges were different from those used in the present study. In addition, rainfall characteristics and duration of the measurements were not the same. Nevertheless, at ca. 50%, the variability of TF in the Tabonuco forest appears high compared to most other values reported for tropical forests, with the exception of the Amazonian forest studied by Lloyd and Marques (1988). At the same time, the Tabonuco forest differs from Amazonian rain forest in that the trees are shorter, smaller, and species diversity is considerably lower (Scatena, 1989). The high variability of TF in the Tabonuco forest may well reflect the effects of past hurricane damage. Hurricane Hugo (September 1989) was the most recent storm that passed directly over the study site and caused considerable damage to the forest, including windfall, breakage, and massive defoliation (Scatena and Lugo, 1995). Smaller-scale canopy disturbances were subsequently caused by hurricanes Bertha (August 1996), Hortense (September 1996), and Georges (September 1998). Consequently, the current canopy of the Tabonuco forest shows increased heterogeneity compared to canopies not disturbed by hurricanes, although overall leaf area index had returned to pre-hurricane values at the time of the observations (F. Holwerda, unpublished data). Furthermore, for a nearby palm-dominated forest at 900 m elevation the variability of TF was estimated at about 100% (Holwerda et al., in preparation). Since the understory of the Tabonuco forest consists mainly of palms (ca. 123 trees ha^{-1}, Table 6), these may also have contributed to the observed large variability of TF. However, detailed information on vegetation type and structure at each sampling position is required to confirm such sources of variation.

Stemflow

The results of the stemflow SF measurements show high variability within (36–67%) and between (144%) tree species (Table 5). Variability within a species is generally due to differences in crown size and shape and canopy position (Levia Jr and Frost, 2003). Variation between tree species results from species-specific differences in canopy structure (e.g. crown size, leaf area, leaf shape and orientation, and branch angle) and variation in bark type (Crockford and Richardson, 2000). For Tabonuco trees (*Dacryodes excelsa*), the relationship between SF volume ratio SVR and tree diameter was positive (SVR = 0.01dbh − 0.22, r^2 = 0.62, p = 0.06), indicating that SF yield increased with increasing crown size. The relationship of SVR to dbh was negative for palms (*Prestoa montana*) (SVR = −1.05dbh + 19.19, r^2 = 0.63, p = 0.02), possibly because old palms have smaller crowns and more epiphytic growth on their stems than young palms. The limitations of these two equations have already been hinted at in Section Stemflow. The SF value found for Tabonuco (0.3% of rainfall P, Table 6) is very similar to the value reported by Scatena (1990) for this species in the same area (0.26% of *P*). Palms (*Prestoa montana*) contributed about 66% to the total SF (cf. Lloyd and Marques, 1988). Palms have a relatively high leaf area, steep fronds emanating from a central stem with relatively smooth bark; these factors probably explain the high SF of this species. The fast-growing successional tree *Cecropia peltata* had the lowest SF (Tables 5 and 6). *Cecropia peltata* has comparatively low leaf area and small crown size, and direct interception of rainfall by the stem probably generated most of its SF. The SF value found for *Sloanea berteriana* (0.6% of *P*, Table 6) is about 3× the value reported by Scatena (1990) for a single large canopy tree of this species in the same area (0.2% of *P*).

At 4.1% of *P*, SF is an important component of the wet canopy water budget and higher than values found for most other tropical forests. For Amazonian rain forest, Lloyd and Marques (1988) determined SF at 1.8% of *P*. Tóbon-Marin et al. (2000) found values between 0.85% and 1.45% of *P* for four lowland rain forest types in the Colombian Amazon. However, since palms contributed about 66% to the SF in the Tabonuco forest, it cannot be excluded that such differences largely reflect differences in palm density.

Comparison with long-term throughfall measurements in the Tabonuco forest

Relative amounts of throughfall TF for the present study period (73—77%, Table 3) are higher than suggested by the long-term data set that has been collected in the Bisley forest (50—60%, Scatena, 1990; Schellekens et al., 2000). The long-term study started in July 1987 and collects TF weekly from 20 to 30 randomly placed but non-roving gauges made of one gallon plastic jugs fitted with 18 cm diameter funnels (254 cm^2 orifice, Scatena, 1990). During October 2001, the long-term gauges were emptied at the same time as the 30 roving gauges of arrangement 3. Table 8 shows that the 20 long-term gauges gave lower mean TF than the 30 roving gauges on all sampling occasions except for one (22 October 2001). For October 2001, total TF as measured with the long-term gauges (156 ± 118 mm) was about 18% lower than that obtained with the roving gauges (190 ± 76 mm, Table 8). These differences are probably not caused by the smaller number of long-term gauges (20) compared to roving gauges (30) or by the different sampling methodologies used (i.e. fixed vs. roving), because: (1) the 20 long-term gauges had a larger orifice (254 cm^2) and hence greater joint surface area (0.51 m^2) than the 30 roving gauges (100 cm^2 orifice, 0.30 m^2 total area); and (2) the present study revealed no systematic differences in mean TF when using (30) fixed or (30) roving gauges (Fig. 3a and b), although random gauge relocation reduced the variation in the total TF estimate (Fig. 3d). The frequency distribution of cumulative gauge catch, expressed as a percentage of total rainfall *P*, for the 20 long-term and 30 roving gauges also indicates that more of the 20 long-term gauges have a lower percent catch (Fig. 1b). While the range in relative TF as measured with the two arrangements was similar (0—200% of *P*), more than half (60%) of the long-term gauges received less than 50% of *P* (Fig. 1b). In contrast, only 23% of the roving gauges received less than 50% of *P* (Fig. 1b). One apparent reason for this is that over time understory plants like ferns have grown over some of the long-term gauges, causing drip to be led away from the funnels (F.N. Scatena, personal observation). On the other hand, the TF sampling positions for the roving gauges were marked out at 1 m intervals along a 159 m transect. It is unlikely that this approach did not include understory plants in representative manner; also, disturbance of these plants was minimized by placing the gauges at 0.5—1.0 m from the access trail. It can not be excluded, therefore, that the lower catch by the long-term gauges compared to the roving gauges was also related to differences in gauge design.

Table 8 Mean throughfall TF per sampling occasion as measured with the 30 roving gauges (TF_{RO}) and the 20 fixed gauges of the long-term network (TF_{LT}) during October 2001 in the Tabonuco forest

Sampling date	*P* (mm)	TF_{RO} (±SD) *N* = 30	TF_{LT} (±SD) *N* = 20	Difference (%)
4 October 2001	50.5	46.7 (±46.1)	32.4 (±19.5)	−31
5 October 2001	23.3	17.5 (±10.8)	13.3 (±9.2)	−24
9 October 2001	23.2	12.2 (±6.7)	12.1 (±12.3)	−1
10 October 2001	23	19.0 (±13.6)	15.4 (±9.5)	−19
16 October 2001	34	22.9 (±17.4)	18.7 (±16.0)	−18
17 October 2001	19	13.9 (±13.3)	10.4 (±8.0)	−25
19 October 2001	8.7	5.0 (±3.0)	4.9 (±3.9)	−2
20 October 2001	9.0	5.5 (±5.2)	4.4 (±3.8)	−20
22 October 2001	5.2	3.1 (±2.5)	3.3 (±3.3)	+6
23 October 2001	27.6	18.6 (±12.6)	18.1 (±14.3)	−3
29 October 2001	34.5	25.1 (±20.9)	22.7 (±22.4)	−10
Total (mm)	258	190 (±76)	156 (±118)	−18
95% confidence interval (mm)		162—218	104—208	
TF/*P* (%)		74	60	

Also given are rainfall *P* and the difference between TF_{RO} and TF_{LT} per sampling occasion, the 95% confidence interval of the total TF estimates, and relative amounts of TF (TF/*P*).

Derived rainfall interception

Throughfall TF as measured in the present study (73—77% of rainfall, Table 3) was much higher than suggested by the long-term data set that has been collected in the Tabonuco forest (50—60%, Scatena, 1990; Schellekens et al., 2000). Consequently, levels of rainfall interception loss based on the new measurements (19—23%) were about half the values derived from the long-term measurements (40—50%). Previous interception modeling studies in the same forest had difficulty to match the very high interception levels inferred from the long-term measurements, unless very high wet canopy evaporation rates were used (Schellekens et al., 1999). However, simulated interception rates using a modified Rutter-type model agreed very well with the presently measured values (Venneker and Holwerda, in preparation).

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