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Impacts of Vegetation and Precipitation on Throughfall Heterogeneity in a Tropical Pre-Montane Transitional Cloud Forest

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ABSTRACT

Precipitation throughfall (TF) plays an important role in the water balance of tropical forests. This study used 164 gauges to quantify precipitation and TF variability in a tropical pre-montane transitional cloud forest on the Caribbean slope of the Cordillera Tilarán, Costa Rica, to identify the ecological and meteorological drivers of this variability. Daily TF measurements were taken from 28 June to 17 July 2012 and 12 June to 16 July 2013, for a total of 39 precipitation events. The total mean TF was 87.9 percent and TF at individual gauges ranged from 22.7 percent to 245.7 percent. Leaf area index (LAI) was calculated above each gauge using hemispheric photography for a mean study-site LAI of 7.7. There was no statistically significant relationship between LAI and TF. However, the amount of TF was positively correlated with precipitation intensity, while the variability of TF was negatively correlated with precipitation intensity. Our calculations indicate that at least 61 gauges are required to obtain mean TF estimates with less than 5 percent error. This study demonstrates that TF is highly spatially heterogeneous due to multiple compounding effects.

Abstract in Spanish is available in the online version of this article.

Key words: Costa Rica; leaf area index; precipitation; throughfall; transitional cloud forest.

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Heterogeneous hydrologic processes impact ecosystem function and services, and in some locations, the amount of water available for consumption, irrigation, and hydroelectric power generation (*e.g.*, Keim *et al.* 2005, Levia & Frost 2006, Roth *et al.* 2007, Zimmermann *et al.* 2007, Levia *et al.* 2011). The hydrology of tropical forests can be quite complicated due to the temporal delay and spatial redistribution of precipitation by the process of interception (Loustau *et al.* 1992, Germer *et al.* 2006, Levia & Frost 2006, Staelens *et al.* 2006, Roth *et al.* 2007, Levia *et al.* 2011). Throughfall (TF) is precipitation that falls through a forest canopy or comes in contact with the canopy and, after some time delay relative to the occurrence of precipitation, falls to the forest floor (Levia *et al.* 2011). Throughfall is separated into two types based on the manner of descent: water that reaches the forest floor without coming in contact with any foliage is considered free TF, and water that contacts foliage and drips down is release TF (Levia & Frost 2006). Spatial redistribution of water occurs as rain falls through the canopy, as water runs off leaves at drip points, or flows down stems, resulting in significant small-scale heterogeneity (Loustau *et al.* 1992, Staelens *et al.* 2006). Measurements of TF and its heterogeneity are important; for example, variations in TF lead to irregular concentrations of water in the forest, which results in a non-uniform spatial distribution of moisture, organic matter, and nutrient cycling in the soil (Roth *et al.* 2007). Additionally, TF measurements provide a basis for calculating interception loss of incoming water (Roth *et al.* 2007). Previous studies estimate that TF ranges from 60 to 95 percent of gross precipitation in tropical regions (Lloyd & Marques 1988, Crockford & Richardson 2000, Bruijnzeel *et al.* 2004, Germer *et al.* 2006, Levia & Frost 2006, Llorens & Domingo 2007, McJannet *et al.* 2007, Vernimmen *et al.* 2007, Zimmermann *et al.* 2007, Berger *et al.* 2008, Brauman *et al.* 2010). This large range in estimated percent TF (TF%) indicates that there is a high degree of variability, and potential uncertainty in quantifying TF. Various studies have determined the minimum number of gauges needed to estimate TF within 5 percent or 10 percent of the mean (Helvey & Patrick 1965, Czarnowski & Olszewski 1970, Kimmins 1973, Masukata *et al.* 1990, Rodrigo & Àvila 2001, Carlyle-Moses & Price 2003, Carlyle-Moses *et al.* 2004, Holwerda *et al.* 2006). Most of these studies consider a sample size of 30 gauges to be sufficient in estimating TF. However, as described in Rodrigo and Àvila (2001), most of these studies were conducted in temperate forests.

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Previous studies have investigated variability in precipitation and TF in rain forests and cloud forests (*e.g.*, Zimmermann *et al.* 2007, Wullaert *et al.* 2009). Elevation and canopy cover play an important role in controlling the spatial variability of precipitation and TF (*e.g.*, Goovaerts 2000, Germer *et al.* 2006, Zimmermann *et al.* 2009, Zimmermann & Zimmermann 2014). Variations in vegetation species, size, and structure can result in channeling of rainfall, drip points, and localized sheltering in the lower canopy. These incongruities produce spatially heterogeneous patterns of TF (Germer *et al.* 2006, Roth *et al.* 2007, Hopp & McDonnell 2011). Wullaert *et al.* (2009) argue that any meteorological influence on the spatial variability of TF is inconsequential. However, Zimmermann *et al.* (2010) conclude that it is impossible to disregard the influence of meteorological parameters on TF. Thus, there are differing opinions regarding the drivers of TF variability. Furthermore, the precipitation–canopy–TF relationships are probably scale-dependent, with previous studies applying varying gauge densities. To date, no clear picture emerges that allows for a definitive assessment of TF variability.

Here, we apply a large number of regularly spaced fixed rain gauges at varying densities and under differing canopies to determine if there is a consistent relationship between precipitation, canopy density, and TF.

METHODS

STUDY SITE.—This study was conducted at the Texas A&M University Soltis Center for Research and Education in San Isidro de Peñas Blancas, Costa Rica (Fig. S1). The Soltis Center is located on the Caribbean slope of the Cordillera Tilarán of Costa Rica and is adjacent to the Monteverde Cloud Forest Reserve. The mean annual precipitation in this forest is approximately 4500 mm/yr. Mean monthly rainfall varies from 136 mm in February to 512 mm in November. Typically the wettest months occur from May to December and the drier months are January to April. The diurnal cycle of precipitation at the study site is similar to most other land areas in Central America, with convective precipitation typically starting in the early afternoon and continuing into the evening as the weather systems mature (Small *et al.* 2007, Biasutti *et al.* 2012, Rapp *et al.* 2014). Throughfall was measured in and around a 2.2-ha watershed at 455 m asl. The elevation difference in this easterly-facing catchment is 120 m, with slopes ranging from 12° to 55°.

One novelty of this study of TF variability is that it is undertaken in a transitional forest. The Soltis Center is situated between lowland tropical forests (*e.g.*, La Selva) and montane cloud forests (*e.g.*, Monteverde), each with their unique characteristics. At slightly higher elevations than the Soltis Center, tropical montane forests are biologically diverse ecosystems that depend on frequent immersion by clouds and mist in addition to orographic precipitation and the capture of this moisture by vegetation. At slightly lower elevations than the Soltis Center, lowland and lower montane forests are primarily controlled by temperature, not fog (Bruijnzeel 2004). The Soltis Center includes 100 ha of forest that transitions between fog-controlled and temperature-controlled, depending on climate conditions (Holdridge 1967). Therefore, this study area provides a critical linkage between the entire range in elevation and disturbance gradients investigated in previous studies focusing on ecohydrology in Costa Rica's tropical wet and cloud forests (*e.g.*, Clark *et al.* 1998, Loescher *et al.* 2002, Bruijnzeel 2004) and thus enhances understanding of tropical ecohydrology.

GAUGE LAYOUT.—TF was measured following the approach of Zimmermann *et al.* (2007). We installed a total of 164 Tru-Chek® Direct-Reading Rain Gauges at a height of 1 m above the ground. These wedge-shaped gauges measure from 0.1 mm to 150 mm of precipitation and are 33 cm long with a 36.3 cm^2 opening. Gauges were deployed using the fixed-gauge method commonly used in tropical locations (*e.g.*, Scatena 1990, Cavelier *et al.* 1997, Clark *et al.* 1998, Schellekens *et al.* 2000). This method involves placing gauges at fixed sites for the duration of the study. Four networks were deployed to evaluate microscale variations in TF (Fig. S1). We installed three of these gauge networks (sites 1, 2, and 3) in the forest, each with 36 gauges in a 6 × 6 grid of 2 m spacing to cover an area of 100 m^2 (Fig. S1). We selected these sites so that they provided a representative sampling of the terrain, vegetation, and canopy density in the watershed. We located a control site in a clearing at the edge of the forest. The control site had 35 gauges in a 7 × 5 grid, also covering an area of 100 m^2, to monitor for spatial heterogeneity in precipitation. A more spatially extensive network (site 4) of 21 gauges spaced 10 m apart covered an area of approximately 1600 m^2. Site 3 was nested within this extensive network. Overall, we placed 129 gauges in the forest and placed 35 at the control site. Each of these networks was also equipped with a portable Onset HOBO weather station recording at 5-min intervals to provide precipitation and TF event timing, duration, and intensity. We also used data from a permanent 10-m meteorological observation site, located immediately adjacent to the control site in our study. We mounted the tipping-bucket precipitation gauges on the Onset HOBO weather stations at a 2 m height above the ground to avoid shielding by the station itself, while the tipping-bucket gauge at the meteorological tower is at the 1-m level.

We used a *post-hoc* Monte Carlo sampling method to validate the robustness of our sample size as well as simulate the alternate roving gauge sampling method applied in other studies. We randomly selected gauges and calculated the estimated mean TF utilizing bootstrap sampling with replacement, which simulates an array of roving gauges. The number of gauges that was selected varied from 1 to 128 and the randomized selection method was applied 10,000 times for each unique number of gauges.

TF MEASUREMENTS.—From 28 June to 17 July 2012 and 12 June to 16 July 2013, we recorded precipitation (control site) and TF (forest sites) amounts daily at all gauges, typically during the morning hours. When data collection every 24 h was not possible, we collected data at the next possible 24-h interval. Measurements were delayed if precipitation was occurring at the usual time of measurement; we instead collected data after the rain event had ended. Following Staelens *et al.* (2006), if a 24-h period received less than 1 mm of rain, we did not define or include that period as an 'event' in our analysis. These 'events' thus reflect the precipitation and throughfall for the day and night preceding measurements.

We analyzed the TF data using both mean and percent TF. Percent TF is calculated relative to mean precipitation for all 39 events from the control-site gauges. We analyzed the overall variability of mean and percent TF for each gauge for all 39 events using the coefficient of variation (CV). At each site, we plotted the gauge CV value at the location of the corresponding gauge, and obtained a spatial pattern by interpolating the variability using the natural neighbor interpolation method (Sibson 1981) in MATLAB. Additionally, we calculated the CV and percent TF of each site for each event.

SITE CHARACTERISTICS.—We characterized the forest stand within a ~20-m radius of each network. We measured approximately 20 trees representative of each study site, including only trees with a diameter at breast height (dbh) of >3 cm. Table 1 shows the dbh, height, and species of this sampling of representative trees in each network. The most common tree species was *Calophyllum brasiliense*, which accounted for nearly 15 percent of the trees. Site 1 had the greatest variety of trees, with 19 unique species identified. This site had some of the largest trees in our networks (mean dbh = 78.5 cm), including the largest tree in the watershed (*Ceiba pentandra*, 239 cm dbh). Tree height ranged from 4.8 m to 36.6 m. Site 2 had 20 trees within a 20-m radius from the center of the gauge network. There are a variety of tree species, with 20 percent identified as *Carapa guianensis*. Another 20 percent of the trees were standing but dead, possibly due to a potential lightning strike prior to our field campaign. Other trees in the stand included *Cordia cymosa*, *Genipa americana*, and *Colubrina spinosa*. Site 2 generally had the smallest trees (mean dbh = 25.2 cm). The mean tree height was 14.6 m and 12 of the 20 trees had a dbh <21 cm. Site 3 had a number of larger trees, including the second largest tree (genus *Pouteria*), with a dbh of 196 cm. Over 20 percent of the trees were *Carapa guianensis* and 20 percent were unidentifiable or dead. The mean dbh (55.1 cm) indicates that, in general, the trees at this site were of intermediate size relative to the other sites. A characterization of site 4 was not conducted, as the center of site 4 is represented by nested site 3.

CANOPY DENSITY THROUGH HEMISPHERIC PHOTOGRAPHY.—We determined canopy density above each gauge using hemispheric photographs taken with a fish-eye lens on a Nikon D3200 digital camera, mounted and horizontally leveled at gauge height. We obtained photographs once per gauge for the study period, under entirely overcast yet dry conditions to minimize the anisotropy of the sky radiance (Zimmermann *et al.* 2009). We analyzed photographs in Delta-T Devices HemiView v. 2.4 software and estimated leaf area index (LAI) above each individual gauge. Following the methodology of Zimmermann *et al.* (2009), we calculated LAI at a range of zenith angles to better characterize

TABLE 1. *Stand characteristics and summary statistics for each forest site.*

Site	Species	DBH (cm)	Height (m)
1	*Acacia centralis*	59	29.2
	Brosimum guianensis	93	27.1
	Carapa guianensis	26.5	6.3
	Ceiba pentandra	239	15.7
	Cestrum racemosum	21	4.9
	Chimarris parviflora	163	24.0
	Colubrina spinosa	56	9.2
	Ficus tonduzii	52	9.9
	Guarea, sp. unknown	62	9.5
	Hyeronima alchorneoides	119.2	15.0
	Inga coruscans	127	36.4
	Koanophyllon hylonoma	35.7	6.1
	Koanophyllon hylonoma	37.8	3.3
	Lauraceae, sp. unknown	98.5	14.7
	Lonchocarpus, sp. unknown	99.5	23.3
	Otoba novogranatensis	78	10.2
	Otoba novogranatensis	99.9	12.7
	Phyllanthus skutchii	118	17.2
	Prestoea decurrens	20	4.8
	Sphaeropteris brunei	41.2	6.7
	Vochysia guatemalensis	57	15.8
	Unknown	23.5	6.7
2	*Brosimum,* sp. unknown	15.7	13.0
	Carapa guianensis	13.8	16.1
	Carapa guianensis	12.5	8.6
	Carapa guianensis	17.4	8.5
	Carapa guianensis	12.6	11.9
	Chimarris parviflora	49	14.8
	Colubrina spinosa	16.2	12.4
	Cordia cymosa	31.7	15.4
	Cordia cymosa	8	5.4
	Ficus tonduzii	20.7	18.7
	Genipa americana	30.3	20.7
	Guatteria recurvisepala	21	11.9
	Hampea appendiculata	51.3	21.4
	Lacmellea panamensis	32.4	31.0
	Rubiaceae, sp. unknown	13.3	15.0
	Socratea exorrhiza	8.8	3.5
	Dead	49	25.3
	Dead	16.1	10.5
	Dead	39.3	14.7
	Dead	44	12.5
3	*Apeiba membranacea*	99	19.2
	Carapa guianensis	21.6	9.1
	Inga coruscans	35.5	9.0
	Carapa guianensis	81	22.1
	Otoba novogranatensis	40.2	11.5
	Inga coruscans	29.5	11.1
	Carapa guianensis	63	15.1

(continued)

Table 1 *(continued)*

Site	Species	DBH (cm)	Height (m)
	Protium panamense	26.5	8.6
	Marila pluricostata	47.2	7.2
	Pouteria, sp. unknown	196	20.0
	Carapa guianensis	38.5	10.4
	Chimarris parviflora	65	11.1
	Annonaceae, sp. unknown	49	10.5
	Otoba novogranatensis	18.8	4.9
	Ocotea, sp. unknown	102.5	20.3
	Pausandra trianae	20.3	6.4
	Dead	27.9	3.5
	Unknown	26.1	5.4
	Unknown	49	15.7
	Unknown	65	20.2

Site	Summary statistics	DBH (cm)	Height (m)
1	Mean	78.5	14.0
	Standard deviation	53.3	9.0
	Range	99.2	31.6
2	Mean	25.2	14.6
	Standard deviation	14.5	6.5
	Range	43.3	27.5
3	Mean	55.1	12.1
	Standard deviation	41.5	5.8
	Range	80.2	18.6

potential TF and quantify canopy cover. As Zimmermann *et al.* (2009) used the LAI at the zenith angle with the best correlation with their TF measurements, we found and used 2.5° as the optimum LAI zenith angle value for our TF measurements.

Precipitation intensity.—We analyzed the effect of rainfall intensity to determine its potential influence on TF variability. Rainfall intensity was calculated following the approach of Sato *et al.* (2011), where the total amount of rainfall for a given event was divided by the duration, as measured by the tipping-bucket gauges located at each site. Based on the rainfall intensities from all events, we defined a threshold for distinguishing high- and low-intensity events, similar to the methods used in Sato *et al.* (2011) and Staelens *et al.* (2006).

RESULTS

Precipitation events.—We sampled a total of 39 rainfall events during two field seasons. Of these events, 13 occurred between 18 June and 18 July 2012. An additional 26 events were sampled between 12 June and 16 July 2013. The events ranged from 1.2 mm to 101.2 mm. In accordance with Staelens *et al.* (2006), precipitation events <1 mm were excluded. Table 2 shows the characteristics of each event. The cumulative precipitation depth was 660.8 mm. The CV of the accumulated data was 0.01 and the standard deviation was 0.15 mm. The maximum difference between gauge measurements at the control site was 0.65 mm.

Throughfall variability.—Based on the 39 events, the total mean TF was 87.9 percent (with respect to the control-site mean). Accumulated TF at individual gauges ranged from 22.7 percent to 245.7 percent. The variability of TF at sites 1–4 is shown in Fig. 1A–D. The differences in TF between sites were not statistically significant. The greatest spatial variability of TF occurred at site 2, where the CV of all the events was 0.36 and the standard deviation was approximately twice as large as the standard deviation at the other sites. The overall TF at this site was 90.2 percent, ranging from 22.7 percent to 245.7 percent of the total precipitation. The large variability at site 2 is predominantly driven by a single gauge (Fig. 1B), which received 245.7 percent of the incident precipitation over the study period. Direct field observations showed that this gauge was under an active drip point during most events. Site 4 (extensive network) exhibited the second greatest overall variability (CV = 0.29). Throughfall varied from 30.3 percent to 139.4 percent, with the lowest TF occurring at a gauge located under a large leaf, as observed in direct observation of the gauge. The accumulated data at site 1 and site 3 both had a CV of 0.21. Throughfall at site 1 ranged from 55.3 percent to 145.6 percent and from 25.5 percent to 116.0 percent at site 3.

Canopy cover and leaf area index.—The mean LAI of all forest sites was 7.7 (SD = 3.8). There is not a statistically significant relationship between LAI and TF (Fig. 2). This is largely due to the fact that locations with similar LAI values may have different configurations of leaf type, wood cover, orientation of foliage and branches, and other differences that may form shelter points and drip points. The maximum LAI at site 1 was 12 and the minimum LAI was 1.8 (SD = 2.6). The gauges with the maximum and minimum LAI were both within 7 percent of the mean TF percentage, indicating that low or high LAI above a gauge did not influence TF. Site 2 had the greatest range of LAI, with three gauges exhibiting LAI of over 20 and three data points below 1. The standard deviation at this site was 5.6, which was the largest standard deviation of LAI of all the sites.

The highest maximum LAI values were associated with a wide distribution of TF percentages. For example, the maximum LAI at site 3 was 18.8, and the minimum value of that site was 4.2; despite this difference in LAI, both of these values were observed at gauges receiving a relatively high TF percentage. The standard deviation of LAI values at site 3 was 2.3. Site 4 was similar to site 3, as expected, due to the nesting of site 3 within site 4. The maximum LAI at site 4 was 15.1, and the lowest LAI at the site was 3.3. The maximum LAI at site 4 was 15.1, and the lowest LAI at the site was 3.3. Despite a large difference in LAI, these two gauges only differed by 13 percent TF, which is a relatively small difference considering that the TF ranged by over 109 percent at this site overall. The distribution of LAI with total TF (%) for each gauge further suggests that no relationship exists between these two factors (Fig. 2).

TABLE 2. *Precipitation event characteristics.*

Event	Date	Precip. (mm)	Mean Intensity (mm/h)	Mean TF (%)	CV (%)	Hours between events (h)	3-D antecedent precip. (mm)
1	6/18/2012	8.9	4.6	65	60	65	43
2	6/19/2012	2.0	3.1	42	109	16	9
3	6/21/2012	13.7	15.0	103	45	49.	11
4	6/22/2012	8.4	12.6	106	38	22	16
5	6/28/2012	9.7	19.3	94	39	144	23
6	6/29/2012	10.7	4.3	83	40	9	19
7	7/3/2012	4.3	5.2	81	45	38	21
8	7/5/2012	12.2	5.6	91	40	40	25
9	7/10/2012	1.0	3.1	140	47	36	27
10	7/11/2012	5.3	7.1	89	53	26	18
11	7/13/2012	16.3	7.5	83	40	39	19
12	7/17/2012	3.1	5.2	108	48	41	23
13	7/18/2012	4.6	6.9	109	53	18	25
14	6/12/2013	55.5	11.3	93	48	Unavailable	24
15	6/13/2013	7.4	4.4	92	70	Unavailable	63
16	6/14/2013	44.8	14.2	87	52	Unavailable	67
17	6/15/2013	101.2	10.0	88	33	20	108
18	6/16/2013	30.5	36.6	89	38	13	153
19	6/17/2013	1.7	4.1	124	68	12	177
20	6/18/2013	4.1	12.4	76	60	26	133
21	6/19/2013	56.0	23.2	95	36	20	36
22	6/20/2013	20.8	13.1	90	60	18	62
23	6/21/2013	2.3	6.8	72	55	12	81
24	6/22/2013	15.3	12.3	99	66	15	79
25	6/24/2013	1.2	7.3	90	62	41	38
26	6/26/2013	30.0	21.2	85	39	25	17
27	6/27/2013	34.0	9.7	92	57	8	32
28	6/28/2013	2.8	4.1	85	78	11	65
29	6/30/2013	28.1	5.6	89	70	41	37
30	7/1/2013	16.0	5.6	100	87	13	31
31	7/3/2013	1.4	3.2	70	170	21	44
32	7/4/2013	24.4	19.5	88	39	24	17
33	7/9/2013	24.7	29.6	90	41	2	26
34	7/10/2013	18.1	8.0	88	56	33	110
35	7/11/2013	18.9	11.3	90	52	13	133
36	7/12/2013	4.0	4.9	102	208	6	127
37	7/13/2013	5.5	5.0	69	76	13	62
38	7/15/2013	6.9	8.3	74	82	19	41
39	7/16/2013	5.4	5.9	76	100	46	10

INFLUENCE OF PRECIPITATION ON THROUGHFALL VARIABILITY.—Site-averaged TF was used to compare the magnitude of each event with TF variability across the sites. The range of site-averaged TF (%) for each event was found to decrease as the total precipitation received in a single event increased (Fig. 3). The range of TF (%) of different events shows that TF (%) at different sites varies more during precipitation events of relatively low total accumulation. For example, TF percentages over 150 percent and as low as 30 percent were both recorded for small events. Throughfall nears 90 percent during greater precipitation events (Fig. 3). The average coefficient of variation, analyzed as the site CV per event, decreased as the magnitude of precipitation in each event increased ($R^2 = 0.23$, $P < 0.05$, Fig. 4). A series of *t*-tests at a number of different precipitation break points, considering all events, showed that the threshold between high and low precipitating events was 10 mm. Performing a *t*-test on the CV of each event using all the TF gauges yields significantly different (95%-level) CV values for values less than 10 mm versus values

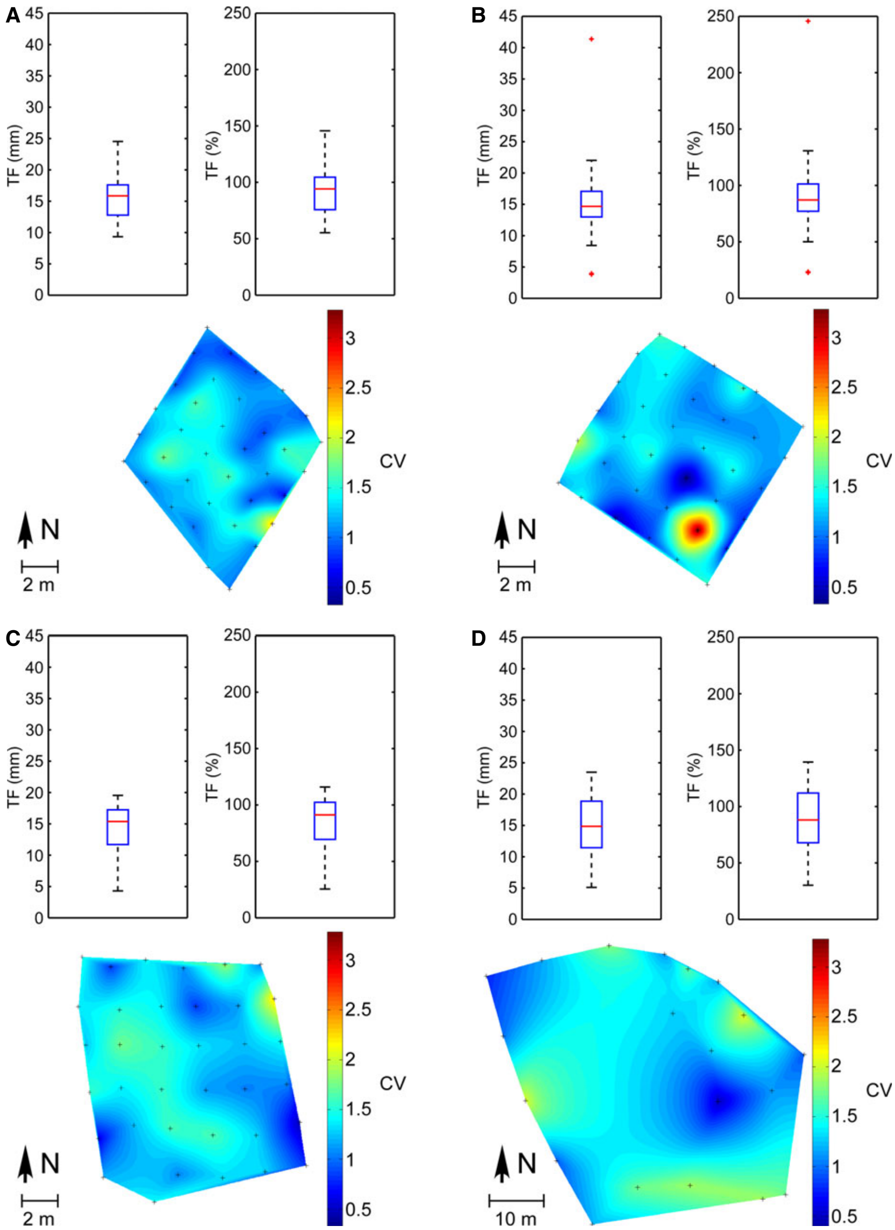

FIGURE 1. Site characteristics including mean TF (mm), mean TF (%), and spatial CV variability based on 39 events for: (A) site 1, (B) site 2, (C) site 3, and (D) site 4.

greater than 10 mm. A *t*-test over the site-averaged CV yields a *P*-value <0.001. Therefore, the spatial variability in TF associated with the smaller precipitation events (<10 mm) is significantly different than that for larger precipitation events (>10 mm). Although there are significant differences between large and small events, when relating LAI and TF within small and large events, there is not a significant relationship.

The average intensity of precipitation was calculated by dividing the total rainfall from a single event by the amount of time it rained during that event (based on data collected with HOBO weather stations). The coefficients of variation for all of the events were compared with the average event intensity to determine how precipitation intensity influences TF variability at each site. We observed a negative correlation between CV and intensity, with increased precipitation intensity associated with a decreased TF variability ($R^2 = 0.18$, $P < 0.05$, Fig. 5). A frequency distribution of intensity showed an apparent threshold at 7.5 mm/h, and we found the difference in intensities above and below this threshold to be statistically significant ($P < 0.001$, $N = 156$) when performing a *t*-test on the CV of each site. Therefore, we defined a low-intensity event as ≤7.5 mm/h and a high-intensity event as >7.5 mm/h. After separating the two classes of average intensity, results show that high-intensity events generally receive a higher mean percentage TF than low-intensity

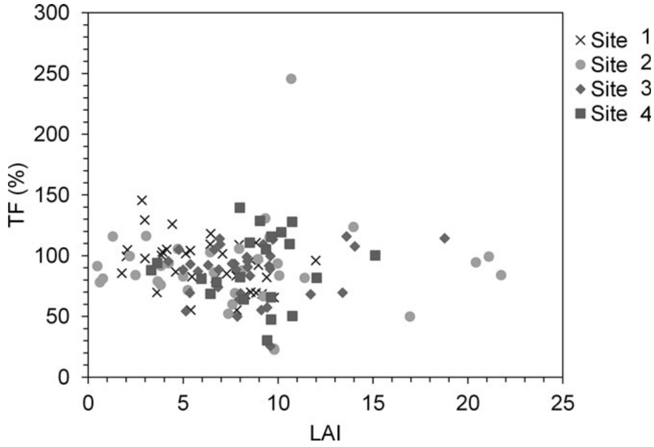

FIGURE 2. Total TF (%) at each gauge versus LAI at all sites under the canopy (N = 129 gauges).

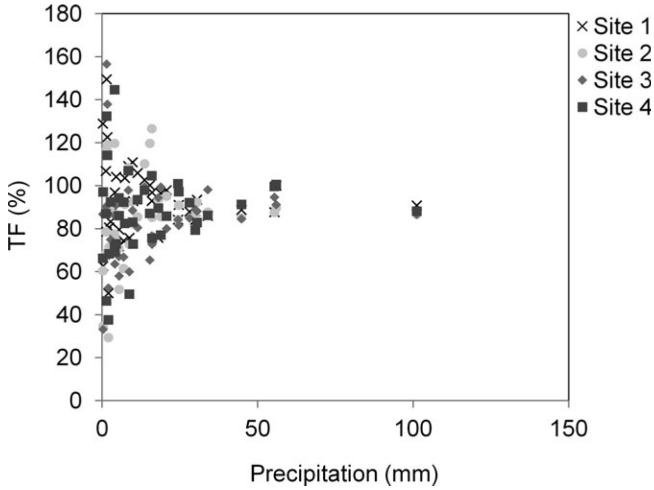

FIGURE 3. Throughfall (%) plotted against event precipitation (N = 156).

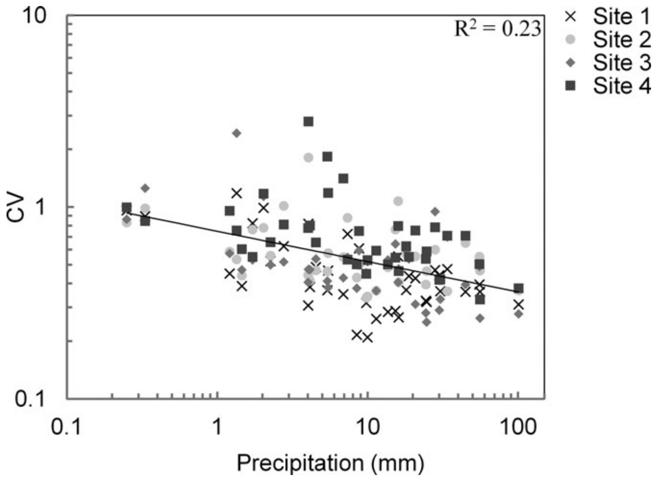

FIGURE 4. Coefficient of variation (CV) of TF at each site for each measured precipitation event (N = 156) plotted against precipitation from the control site. The best fit line is significant at $P < 0.05$.

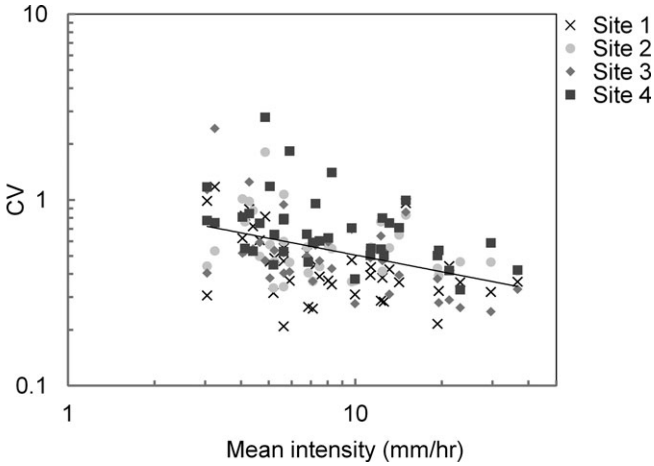

FIGURE 5. Coefficient of variation of TF at each site for each measured precipitation event (N = 156) compared with the mean rainfall intensity (mm/h). The best fit line is significant at $P < 0.05$.

events (Fig. S2). High-intensity precipitation events yield approximately 90 percent TF, whereas low-intensity events show approximately 85 percent TF. Sites 1 and 2 show the largest TF (%) disparity between events of high and low intensity.

Previous studies suggest the use of at least 30 gauges in measuring TF (*e.g.*, Czarnowski & Olszewski 1970, Rodrigo & Àvila 2001, Carlyle-Moses & Price 2003, Carlyle-Moses *et al.* 2004, Holwerda *et al.* 2006). Based on our Monte Carlo bootstrapping analysis, we determined that 30 gauges would have produced a mean TF estimate within 9 percent of our fixed-gauge estimate, showing that a larger number of gauges would be required for accurate estimations of TF in this transitional forest. We selected gauges from all sites, as the differences between sites were not statistically significant. We further find that 61 roving gauges would have been required to achieve a mean TF estimate within 5 percent of the fixed-gauge estimated mean in this study forest, while 125 roving gauges would have been required to estimate TF within 1 percent of the fixed-gauge estimated mean. The distributions of mean bias error values for 61 and 30 randomly selected gauges are plotted along with their 2.5th and 97.5th percentiles in Figure S3 to demonstrate the difference in accuracy using different sample sizes. Given that our study used >120 gauges, we have high confidence in our estimates of mean event TF for this forest.

DISCUSSION

Influence of canopy.—This study demonstrated that TF in a pre-montane tropical transitional forest is very heterogeneous, which is consistent with the conclusions of previous studies (Lloyd & Marques 1988, Beier & Hansen 1993, Whelan & Anderson 1996, Zimmermann *et al.* 2009, Macinnis-Ng *et al.* 2014). It is clear that the vegetation influences how water moves through the canopy and that while TF is generally less than precipitation, certain arrangements and shapes of vegetation can create drip points that result in TF greatly exceeding precipitation.

Previous research has shown that as LAI increases, TF decreases (*e.g.*, Whelan & Anderson 1996, Burghouts *et al.* 1998, Llorens & Gallart 2000, Loescher *et al.* 2002, Nadkarni & Sumera 2004). For example, Scatena (1990) found that TF in the Tabonuco forest in Puerto Rico was higher under canopy gaps, because a smaller canopy surface correlates with a smaller amount of water intercepted. Similarly. Bellot and Escarre (1998) also found a correspondence between high LAI and low TF values. However, Gomez-Peralta *et al.* (2008) compared LAI with rainfall interception at two sites and found a statistically significant relationship at just one of the sites. Overall, results of studies attempting to relate canopy cover or vegetation characteristics to throughfall have been inconsistent (Marin *et al.* 2000, Loescher *et al.* 2002, Keim *et al.* 2005), and one study Loustau *et al.* (1992) found the effect of stem spacing on TF to be negligible.

We also did not find strong relationships between LAI and TF in this study, based on our observations of individual gauges. Observations suggested that the canopy structure leads to preferential routing or channeling of water within the canopy, which can play an important moderating role. Our results, in conjunction with results of previous studies, suggest that areal estimates of LAI are perhaps not sufficient to characterize TF at this watershed scale. The location of a single large leaf in a dynamic canopy can considerably alter TF at the microscale when influenced by dynamic meteorological conditions. The lack of a consistent relationship between LAI and TF in our study suggests that the LAI is not the sole driver of TF variability. Instead we found evidence that TF variability is probably influenced by hydrologic routing and drip points, the sources of which are not evident in measurements of LAI. Zimmermann *et al.* (2009) suggest that variability caused by water dripping from large leaves is a potential cause of TF outliers during small precipitation events, which our results support. Future work should make use of other canopy metrics accounting for canopy complexity and hydrologic routing to determine the influence of vegetation on TF at this scale. Many other elements of canopy conditions can affect TF, such as antecedent canopy wetness (Zimmermann *et al.* 2008). To explore this, we analyzed TF variability (both TF percent and variability) separately based on two canopy wetness approximations: hours between events, and 3-d antecedent precipitation (Zimmermann *et al.* 2008). However, no significant relationships were observed (not shown), possibly due to sample size limitations.

We found that vegetation and its influence on TF is dynamic. The temporal variability of TF can be illustrated by examining the observations from a single gauge. For example, the TF (%) at one of the gauges was approximately 78 percent throughout most of the study. However, after a large vine above this gauge shifted, the gauge collected 77 mm of TF from a 4-mm event (1952% TF). The use of a fixed-gauge network allows us to characterize the spatial and temporal variability in TF that results from dynamic vegetation processes (*e.g.*, creation of a new drip point). Gauges that received the lowest amounts of TF were typically under large leaves or dense vegetation. For example, one gauge at Site 2 that received consistently low TF (22.7%) was located under a large leaf, which was observed to shelter the gauge during precipitation events. Some gauges received more TF during high-intensity events, while other drip points were more active during low-intensity events. It was also observed that some drip points were consistently active during the first 2 wk of the second field season, but then became more sporadic. The number of active drip points seems to decrease with an increasing amount of time between rainfall events, indicating that a wetter canopy may be more favorable to the formation of drip points. However, analysis of the throughfall variability in correspondence with the 3-d antecedent wetness did not support this hypothesis.

Influence of precipitation on TF.—This study has shown that as precipitation increases, TF variability decreases. For example, an event that received only 1.4 mm had a CV of 2.43 at site 3 while our largest event (101.2 mm) had a CV of 0.28 at the same site (Fig. 4). Our results support previous studies showing that events with more precipitation result in less variability in TF (Scatena 1990, Bouten *et al.* 1992, Loustau *et al.* 1992, Rodrigo & Àvila 2001, Staelens *et al.* 2006, Llorens & Domingo 2007, Sato *et al.* 2011, Zimmermann & Zimmermann 2014). As the amount of precipitation increases, TF at all sites tends toward 88 percent of the total rainfall. This agrees with the findings by Germer *et al.* (2006) and Zimmermann *et al.* (2007), who recorded 79 percent and 89 percent TF in tropical forests, respectively. Levia *et al.* (2011) reported 91 percent TF in a tropical rain forest in Brazil, which is also similar to our findings. In comparison, TF in temperate forests ranges from approximately 61 percent to 84 percent in both coniferous and deciduous forests combined (Levia *et al.* 2011). An explanation for the higher TF in the tropics is that raindrop sizes are typically larger because the rainfall intensity is higher (Calder 1996). All sites had more TF during the higher intensity events. Low-intensity events averaged 5 percent less TF than the high-intensity events.

We also examined the influence of rainfall intensity on TF variability. Loustau *et al.* (1992) and Levia *et al.* (2011) found that the variability of TF was greater in storms of lesser intensity than in storms of greater intensity; this finding is supported by our study. Brandt (1990) showed that the momentum of a raindrop decreases as drop size and rainfall intensity decrease. Therefore, when drops are smaller, they will more easily be redistributed by the canopy, resulting in more spatial heterogeneity than if the drops penetrate the canopy as free or release TF.

CONCLUSIONS

Our findings suggest that the spatial and temporal patterns of TF are complex and dynamic in tropical transitional forests. Our use of high-density sampling demonstrated that TF variability is negatively correlated with precipitation intensity. However, we found no evidence of a statistically significant correlation between LAI and TF or TF variability regardless of the size of the precipitation event. The lack of a consistent relationship between LAI and TF suggests that using spatially averaged canopy metrics such as LAI is not sufficient for characterizing TF variability at this scale. Antecedent canopy conditions, including hours between precipitation events and 3-d antecedent precipitation, also did not significantly correlate with TF variability. Instead we found evidence that other factors such as drip points have an important influence on TF variability. We recommend future studies to analyze the fine-scale heterogeneity of TF and temporal variability of TF.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Location of the study sites and gauges within the watershed.

FIGURE S2. Mean TF for low- and high-intensity events compared for each site.

FIGURE S3. Histogram of mean bias error.

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