



Throughfall heterogeneity in tropical forested landscapes as a focal mechanism for deep percolation



P. Zion Klos^{a,*}, Adina Chain-Guadarrama^{a,b}, Timothy E. Link^a, Bryan Finegan^b, Lee A. Vierling^a, Robin Chazdon^c

^a College of Natural Resources, University of Idaho, Moscow, ID, USA

^b Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica

^c Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

ARTICLE INFO

Article history:

Received 5 March 2014

Received in revised form 30 September 2014

Accepted 1 October 2014

Available online 12 October 2014

This manuscript was handled by Corrado

Corradini, Editor-in-Chief, with the

assistance of Xunhong Chen, Associate Editor

Keywords:

Throughfall

Soil water content

Deep percolation

Tropical forest

Roots

Hillslope processes

SUMMARY

Forest structure can both reduce and intensify precipitation inputs to the ground surface at fine spatial scales. Areas of localized input at the soil surface may have large effects on deep drainage because of the strongly nonlinear relationship between soil water content (SWC) and unsaturated hydraulic conductivity. We therefore explored the following questions: Does forest structure that creates high spatial heterogeneity in canopy throughfall also create associated deep percolation pathways capable of quickly moving water beyond the rooting zone? Or alternatively, do soil properties resulting from biological activity (e.g. root networks) reduce SWC heterogeneity created by the focused inputs from the canopy and eliminate the potential for these deep percolation pathways? We explored these questions by measuring spatial variation in both throughfall and SWC within 8 forested plots of the Sarapiquí region, Costa Rica where soil texture is relatively homogeneous within deep, clay-rich soils. A novel method that combined soil augering and frequency domain reflectometry was used to assess SWC profiles below the most extreme wet and dry throughfall locations within each plot. Findings revealed relatively homogeneous soil moisture within the surface root zone (0–90 cm depth) with SWC values of roughly 45%. Below the root zone, SWC heterogeneity increased, with the wettest throughfall sites having significantly ($\alpha = 0.05$) higher SWC than their paired driest throughfall end-members (by 2–15%). Below approximately 130 cm depth, SWC homogeneity was observed again. Physically-based modeling in HYDRUS-3D supports these findings and suggests processes that may explain these changes in SWC patterns observed with increasing depth, such as redistribution through macropores, focused deep-percolation, and lateral downslope flow, respectively. This is the first field-based study that explores the linkage between throughfall heterogeneity and focused deep-percolation, and therefore advances the integrated understanding of how the structure, diversity, and spatial heterogeneity of forests influence their hydrologic outputs.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Landscape conversion is occurring at unprecedented rates worldwide, with many forest systems being replaced by alternate land uses such as pasture or fields. As a consequence, landscape processes that are driven by the amount and type of vegetation cover, such as canopy interception and surface infiltration, can also

change dramatically. Previous work has found that forest patches increase infiltration relative to adjacent non-forested areas (Ludwig et al., 2005; Niemeyer et al., 2014). This may be due to several factors, including compaction and loss of macropore networks in non-forest soils (Trimble and Mendel, 1995). At a finer scale, another process linked to infiltration dynamics is throughfall, whereby plant canopies redistribute, reduce, and in some cases, locally increase precipitation at the ground (Levia and Frost, 2006). The focusing of throughfall has been found to be temporally consistent at time scales relevant to hillslope and watershed processes (Raaijmakers et al., 2002; Keim et al., 2005; Zimmermann et al., 2009). Theoretically, increased precipitation at specific locations under a vegetation canopy should create focused pathways for

* Corresponding author at: College of Natural Resources, University of Idaho, 875 Perimeter Drive MS 1133, Moscow, ID 83844-1133, USA. Tel.: +1 (920) 883 8617.

E-mail addresses: zion@uidaho.edu (P.Z. Klos), achain@catie.ac.cr (A. Chain-Guadarrama), tlink@uidaho.edu (T.E. Link), bfinegan@catie.ac.cr (B. Finegan), leev@uidaho.edu (L.A. Vierling), robin.chazdon@uconn.edu (R. Chazdon).

deep percolation due to the strongly nonlinear relationship between soil water content (SWC) and hydraulic conductivity (e.g. Van Genuchten, 1980). Modeling investigations have begun to incorporate this nonlinear relationship into throughfall and deep percolation processes at plot and hillslope scales relevant to streamflow generation, with previous results suggesting a large increase in downward deep percolation rate due to focused throughfall, ranging from 129% (Guswa and Spence, 2011) to 300% (Keim et al., 2008) relative to homogeneously distributed throughfall. Despite the strong theoretical basis and simulated examples, direct field measurements of combined throughfall and SWC patterns are lacking, and are therefore needed to assess the reality of this process's existence in forested landscapes.

In this study, we assess the role of heterogeneous throughfall in creating focused deep percolation pathways capable of facilitating the movement of water rapidly beyond the root zone using a combination of observational and simulated data. We explore two main questions: (1) Does forest structure that creates high spatial heterogeneity in canopy throughfall also create rapid deep percolation pathways? Or, alternatively, (2) do soil properties resulting from biological activity in the shallow soil, such as root development, homogenize these soil water inputs created by the focused canopy throughfall and eliminate the potential for focused deep percolation pathways below the surficial root zone? Beyond these questions, this study seeks to aid an interdisciplinary objective of understanding how biodiversity, and in particular structural diversity of forest canopies, impacts the movement and transfer of water through tropical forest systems. A companion study (Chain-Guadarrama et al., in preparation) addresses related questions regarding canopy structural and functional properties and their relationship to throughfall patterns across both old-growth and secondary tropical forests. In combination, these studies seek to understand the impacts of alternative forms of forest cover on the provisioning of water as an ecosystem service.

2. Materials and methods

2.1. Site description and throughfall collection

The study was located within the Sarapiquí region of Costa Rica, a lowland plain within a humid tropical climate on the windward side of the central Mesoamerican volcanic range. Soils in the region are uniform, deep (>5 m), clay-rich Ultisols, which are characterized by spatially uniform soil textures. Fluvial processes have created a hummocky topography with small high-relief hillsides up to 30° in slope. Additional detailed descriptions of the landscapes characteristics can be found in McDade et al. (1994) and Finegan and Camacho (1999).

Fieldwork was conducted over an 8-week period during the rainy season from July to September of 2011. Mean rainfall rates within the region during the study period were ~10 mm/day (Chain-Guadarrama et al., in preparation), produced by high-intensity convective storms that developed nearly every afternoon. Additional rainfall and throughfall metrics can be found in Section 3.2.

Fourteen 1-hectare forested plots (Fig. 1) were selected to measure throughfall spatial heterogeneity. Plots corresponded both to old- and secondary-growth forests encompassing a range of taxonomic and functional composition (Finegan et al., 1999; Chazdon et al., 2010). The secondary-growth forest ranged in age from roughly 20 to 50 years since abandonment. These 14 forest plots are characterized by high stem density and high species richness, with an average of 563 individuals ≥ 10 cm dbh per hectare, corresponding to an average basal area of 29 m² per hectare, with 98 tree and palm species represented. Heterogeneous stand structure and varying height classes of vegetation exist in these wet tropical

forests, particularly within the oldest forests where both taller stature and a greater rate of mortality and windfall of adult trees creates larger heterogeneity within the canopy (Guariguata and Ostertag 2001; Montgomery and Chazdon 2001). Secondary-growth forests in this region rapidly reach structural characteristics (basal area and stem density) of old-growth forests, with higher density of adult canopy palms (Guariguata et al. 1997). Leaf area index (LAI) values of secondary- and old-growth forest in this region have been estimated between 5.20 and 5.62 m² m⁻² (Tang et al. 2012), with canopy trees, lianas and palms accounting for 89% of total LAI (Clark et al. 2008).

Within each plot, 25 throughfall collectors were systematically placed 20 m apart in a gridded pattern to cover the entire spatial extent of the plot (Fig. 1); an additional reference collector was placed outside the plot in the nearest unobstructed clearing. Collectors were constructed as cylindrical low-density polyethylene ($A = 182$ cm²) containers similar to the traditional funnel-type collectors common for distributed throughfall sampling (Zimmermann and Zimmermann, 2014). Collectors were installed ~1 m above the ground surface so as to accurately measure throughfall variations created by the largest-order canopy size class and thus minimizing highly localized variations due to small (sub-meter) herbaceous understory vegetation. Throughfall was measured manually on a weekly basis during the experiment.

The methods and results for the throughfall work are further expanded in Chain-Guadarrama et al. (in preparation). This throughfall sampling scheme, combined with the complexity of the forest stands sampled, allowed for accurate measurement of total plot-level weekly throughfall within 5–15% relative error (Zimmermann and Zimmermann, 2014); had a relative error of under 5% been desired, approximately 100–200 collectors per one-hectare plot would have been needed.

2.2. Measurement of volumetric water content in soils

We measured SWC profiles within 8 of the 14 forest plots (not all 14 were measured due to equipment failure). Half of the 8 measured plots occurred within secondary-growth forests, while half occurred within old-growth forests. Within each plot, SWC profiles were measured adjacent to the throughfall collectors with wettest and driest throughfall measurements, as determined after at least one week of throughfall data collection. Vertical profiles of soil moisture were measured *in situ* by manual augering to access sequentially subjacent soil layers. Augered holes were 8 cm in diameter. At each location, the soil was tested for SWC, texture (Thien, 1979), and presence or absence of roots at 20 cm increments, starting at the surface and continuing down to either 60 cm below the deepest observed roots, or to the maximum depth capable with the auger (~280 cm). The SWC at each undisturbed soil depth layer was measured *in situ* with a portable frequency domain reflectometry (FDR) probe (Stevens Hydra Probe) over an integrated volume surrounding the 5 cm long sensing tines (Seyfried et al., 2005) prior to disturbing the layer in order to access the subjacent layers. Measurements occurred between rainfall events, usually in the mornings because the augered holes filled with rainfall during events. Each plot was only sampled once, with both the wettest and driest throughfall sites sampled on the same day for each plot to account for antecedent rainfall conditions specific to each plot. This novel method for *in situ* SWC measurement was implored because installing long-term SWC probes would have disturbed the sites, potentially creating artificial deep percolation pathways.

2.3. Physically-based modeling

To test the conceptual validity of the findings, HYDRUS-2D/3D was used in 2D mode to simulate water transport in the vadose

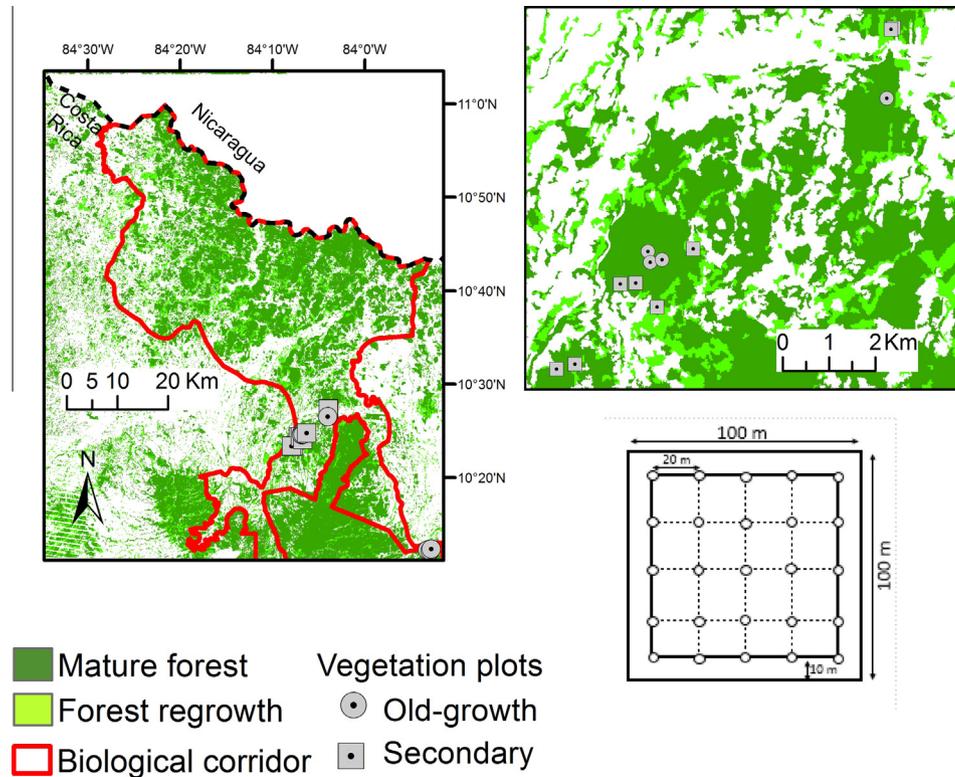


Fig. 1. Location of old-growth (circles) and second-growth (squares) forest study plots in the Sarapiquí Region of northeastern Costa Rica. Throughfall collectors ($n = 25$) were located within each 1 hectare plot following a gridded design; all collectors were 20 m apart, with a 10 m buffer from the plot border.

Table 1
HYDRUS-3D input parameters, all additional parameters were derived from HYDRUS default values unless mentioned below.

Model Run	Surface conditions			Upper root zone (0–0.9 m)			Lower soil (0.9–20 m)		
	Gap size (m)	Precipitation (mm/h)	Time step (h)	K_{sat} (mm/h)	SWC_{sat}	Particle size	K_{sat} (mm/h)	SWC_{sat}	Particle size
Clay-rich soil	43 ^b	0.45 ^c	1	2000 ^a	0.55 ^d	Sand ^c	2.0	0.58	Clay
Clay-rich soil, 20° slope	15	0.45 ^c	1	2000 ^a	0.55 ^d	Sand ^c	2.0	0.58	Clay
Sandy soil	43 ^b	0.45 ^e	1	2000 ^a	0.55 ^d	Sand ^c	297	0.43	Sand

^a Alaoui et al. (2011).

^b Loescher et al. (2002).

^c Coarse particle size to simulate macropore distribution by roots.

^d Maximum observed in field data.

^e Estimate of mean maximum daily throughfall during days with precipitation (see Table 2, equivalent to 101% throughfall).

zone under a series of cases to test variations in SWC patterns under different soil textures, precipitation regimes, and slope cases (Table 1). HYDRUS-3D was chosen since it uses Richards' Equation to simulate subsurface flow within variably saturated porous media (created by PC Progress S.R.O.). The default Genuchten–Mualem soil hydraulic model was used. The modeling domain was 200 horizontal meters by 30 vertical meters, additionally 50 m buffer zones of spatially invariant porous media extended the domain's parameters laterally beyond the zone of interest. There were no interactions with boundary conditions except at the air–soil interface and edges of the buffer zones. In all simulation domains, a high-hydraulic-conductivity shallow rooting zone layer simulated preferential flow by root pathways. K_{sat} for this upper high-hydraulic-conductivity rooting zone layer was determined from published work by Alaoui et al. (2011) who empirically found rates of K_{sat} in shallow forest soils dominated by preferential flow pathways, similar to the dense macropore networks observed within the near-surface soils of the sites within this study. The boundary between this upper high-hydraulic-conductivity rooting zone and the lower

soil, (i.e.: the root-zone/soil interface), was modeled as a discrete boundary. In reality, this boundary is likely not as discrete and is probably influenced by the presence or absence of unique macropores that facilitate the flow of water downwards, making the overall boundary continuous laterally, but somewhat variable in terms of its vertical depth and physical properties. To understand how extremes in canopy heterogeneity influence the creation of deep-percolation pathways, throughfall was modeled at the surface as sections of either mean maximum throughfall (101%) or no water input at the soil–air interface under a simplified canopy with a gap spacing of 43 m; this is the spacing of the largest overstory trees in the region (Loescher et al., 2002). To estimate the rate of maximum throughfall at the forest floor, the mean maximum daily throughfall rate was used to constrain the hydrologic inputs for the model (Table 1). The mean maximum daily throughfall rate was calculated by finding the collector with the highest maximum throughfall within each of the 14 forest plots for each week, and averaging those collector-level maximum throughfall values from all plots for all weeks of the study. This weekly mean maximum

throughfall rate (101%, Section 3.1) was then scaled to a daily rate by adjusting for the number of days (57, Section 3.1) out of the entire study (64, Section 3.1) when precipitation occurred. Using the total rainfall for the 64-day study period (612 mm, Section 3.1), the mean maximum daily throughfall rate for days when precipitation occurred was then applied to calculate the maximum daily rate of input at the forest floor (10.85 mm/day). Throughfall input was modeled for the duration of a 3-month wet season to isolate the effect of physical structure alone, with the influence of evaporation and transpiration not evaluated; their influence during the rainfall events that dominate the rainy season is assumed to be negligible because relative humidity approaches 100% such that there is a negligible vapor pressure deficit during events. The rate of input at the hourly scale to the forest floor was unknown, so both a continuous (24 h at 0.45 mm/hr, Table 1) and a concentrated on-off (3 h at 3.6 mm/h, then 21 h at 0 mm/h) application of water was modeled; the latter to more realistically simulate general temporal patterns resulting from convective storms common to the region.

Simplifications for forest cover and soil properties were used to simulate heterogeneous, focused input through two distinct soil types of highly differing hydraulic conductivity (clay and sand, Table 1). Also, the effect of slope (20°) was tested to explore the influence on flow and SWC at depth (Table 1). Additionally, the influence of smaller gap spacing at 15 m was evaluated because the secondary, regenerating forests in the region are unlikely to reach this larger ~43 m spacing until the trees mature. Initial SWC for all three modeled domains were evaluated at both field capacity and wilting-point (Table 1).

3. Results

3.1. Throughfall summary

Total rainfall over the region during the 64-day study period was 612.4 mm; 57 days had rain events resulting in a mean daily rainfall for event days of 10.74 mm/day. Mean throughfall (69%), mean maximum throughfall (101%), mean minimum throughfall (43%), and throughfall heterogeneity (coefficient of variation (CV): 0.32) were measured within the tropical forest sites (Table 2). Throughfall was heterogeneous over all study sites and no overland flow was observed within these forested sites during rainfall events.

3.2. Volumetric water content of soils

Volumetric SWC ranged from ~25–55% across all sites (Fig. 2). The deepest SWC measurement occurred at 280 cm below ground and bedrock was never encountered at any of the 8 plots where soil properties were measured. All plots had roots present to 40 cm depth. Roots generally occurred higher in the soil profile, except for one forest plot (Tirimбина 8) where they were observed at 280 cm. The lower boundary of the rooting zone, defined by a 50% presence versus absence threshold, occurred at ~90 cm depth (Fig. 2). Clay content was consistently above 75% for all samples

Table 2

Summary of throughfall (%) data collected across 14 forested-plots in the Sarapiquí region of Costa Rica during an 8-week period (Chain-Guadarrama et al., in preparation). Mean values (bold) followed by standard error with minimum and maximum values underneath.

Mean throughfall (%)	68.56 ± 1.34 (3.39, 153.14)
Throughfall heterogeneity (CV)	0.32 ± 0.01 (0.02, 1.49)
Mean maximum throughfall (%)	100.69 ± 2.16 (5.65, 232.92)
Mean minimum throughfall (%)	43.03 ± 1.15 (0.68, 109.48)

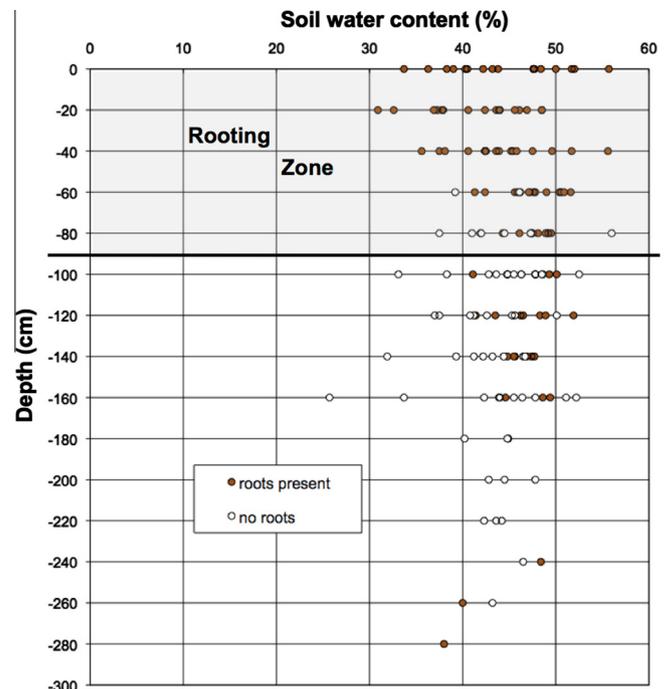


Fig. 2. Absolute SWC measurements from 16 augered sites within 8 tropical forested plots. Differences between presence (red circles) and absence of roots (white circles) are shown. Roots were observed in a majority of the samples to a depth of ~90 cm, from below which, root presence was in the minority and quickly declined. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

except at one augering site where a large portion of silt and sand was encountered at depths >140 cm, corresponding to lower SWC values (~24–35%, points excluded from Fig. 2).

Normalized SWC (Fig. 3, Table 3) was determined by taking the difference between the mean of the wettest and driest throughfall

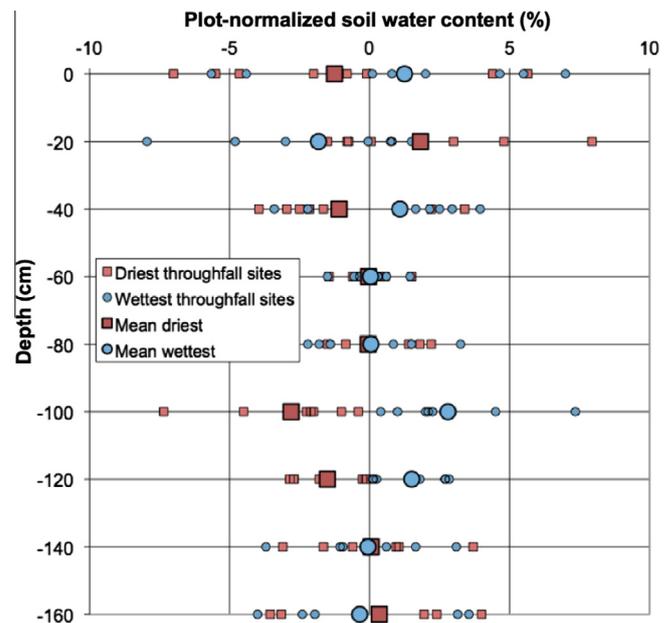


Fig. 3. Plot-normalized SWC from 8 tropical forested plots. Values normalized by the mean SWC between the wettest (blue) and driest (red) throughfall sites evaluated within each plot and at each depth individually. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Mean difference between the plot-normalized wettest and driest throughfall sites at each depth interval. No significant difference in normalized SWC was observed with the root zone from 0 to 80 cm depth. Immediately below this zone, there is a significant difference in the normalized SWC between throughfall extremes, with the wettest throughfall sites being uniformly wetter at 100 and 120 cm depth than the driest throughfall sites. This pattern disappears at 140 cm and below. *P* values calculated using a Student's *t*-test for paired data with a two-tailed distribution ($\alpha = 0.05$).

Depth (cm)	Mean difference (wettest–driest, SWC in %)	<i>P</i> value
0	2.5	0.27
20	–3.64	0.22
40	2.18	0.33
60	0.08	0.92
80	0.1	0.94
100	5.6	0.02
120	3.02	0.02
140	0.12	0.95
160	–0.7	0.79

site within each plot at each depth. For example, in Fig. 3 at 100 cm depth, paired wettest and driest samples ranged in SWC by a difference of 1–15%, with a mean difference of 6% between samples for the wettest throughfall sites versus the driest throughfall sites. Using a Student's *t*-test paired two-tailed distribution, *p*-values at each depth were calculated to evaluate the probability that the driest sites were similar in SWC to the wettest throughfall sites at each depth interval (Table 3). Clear patterns of SWC zonation occurred at different depths within the soil. There was no significant difference ($\alpha = 0.05$) in plot-normalized SWC within the rooting zone existing from 0 cm to 80 cm depth. Immediately below the rooting zone, at 100 cm depth, the wettest and driest throughfall sites were significantly different in SWC, with the wettest throughfall sites consistently having significantly higher SWC than the driest throughfall sites (5.6% mean relative difference in SWC). This trend continued to 120 cm depth across all sites, but disappeared at 140 cm and 160 cm, where no significant difference ($\alpha = 0.05$) between the wettest and driest throughfall sites could be detected (Fig. 3, Table 3).

3.3. Physically-based modeling

Here we present HYDRUS-3D simulations of SWC within (1) clay-rich soils, (2) sandy soils, and (3) clay-rich soils (20° slope) following the details highlighted in Table 1. Additional simulations that tested sensitivity to antecedent soil moisture conditions and hydraulic conductivity decrease with depth were completed, but revealed no distinct differences relative to the modeled results below and hence were omitted for brevity. Modeling of clay-rich soils (Fig. 4) revealed the formation of focused deep percolation pathways. These pathways corresponded spatially to focused throughfall inputs, with SWC increases at the root-zone/clay-soil interface. The increased SWC resulted in deep percolation pathways that were wider than the superjacent zone of throughfall input, due to the formation of saturated conditions atop the root-zone/clay-soil interface. After 3 months of rainy-season throughfall rates, the wetting front within the clay-rich zone reached a depth of 3 m. Maximum SWC within the deep percolation pathway was 58%, which corresponded to fully saturated conditions.

Within sandy soils (Fig. 5) formation of deep percolation pathways also occurred. These pathways corresponded spatially to the overriding heterogeneity in throughfall, but unlike the clay-rich soils with a slightly lower K_{sat} , a zone of higher SWC extending laterally beyond the location of the superjacent throughfall input, and being due to saturation at the root-zone/sand-soil interface, did not occur. Instead, only limited pooling of water occurred within an area approximately 5 cm above the root-zone/sand-soil interface and displayed no lateral migration (Fig. 5). Deep percolation pathways below the root-zone/sand-soil interface were relatively focused, and corresponded closely in width to the width of the superjacent throughfall input. Under 3 months of rainy-season rates of throughfall, the wetting front within the sandy soil reached a depth beyond the modeling domain. Within the deep percolation pathway the maximum SWC was 20%.

The presence of a moderately-steep 20° slope within clay-rich soils created focused input into the clay-rich soils initially (Fig. 6), but unlike the two horizontal simulations, these focused deep percolation inputs became homogenized at depth. Lateral down slope movement of water within the clay-rich soil produced

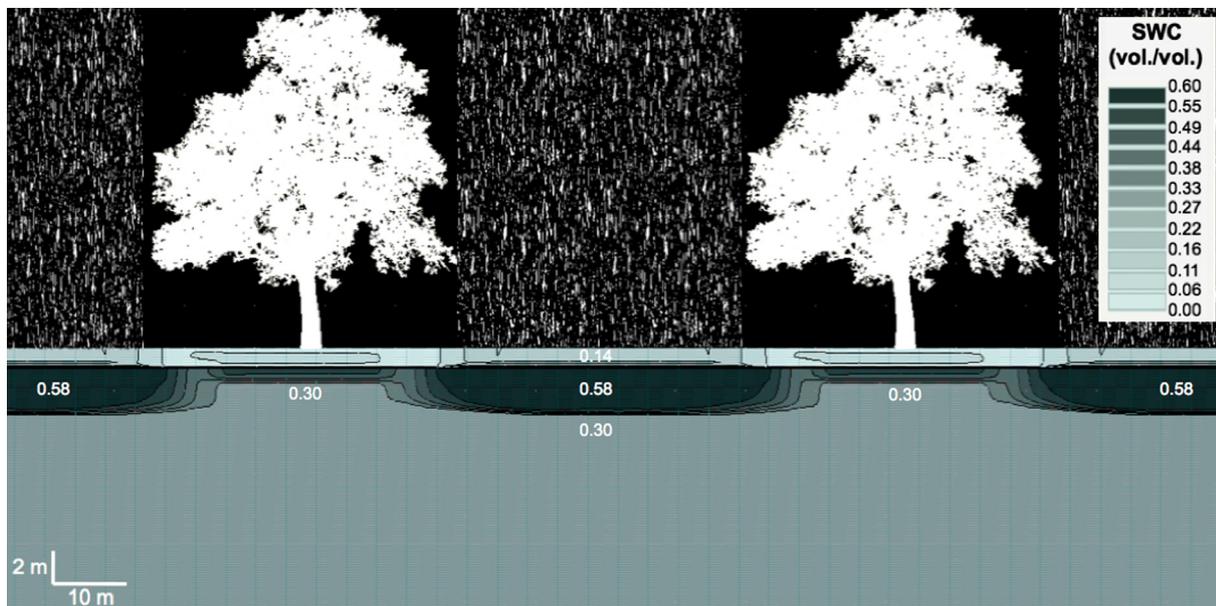


Fig. 4. HYDRUS-3D simulation of SWC within clay-rich soils underlying a surficial root zone. After 3 months of rainy-season throughfall rates, focused deep percolation pathways are present below the root zone and correspond spatially to overlying heterogeneity in throughfall. SWC (white numbers) for the specific regions of interest are indicated, as is the location of major nodes (thin lines) within the finite element mesh.

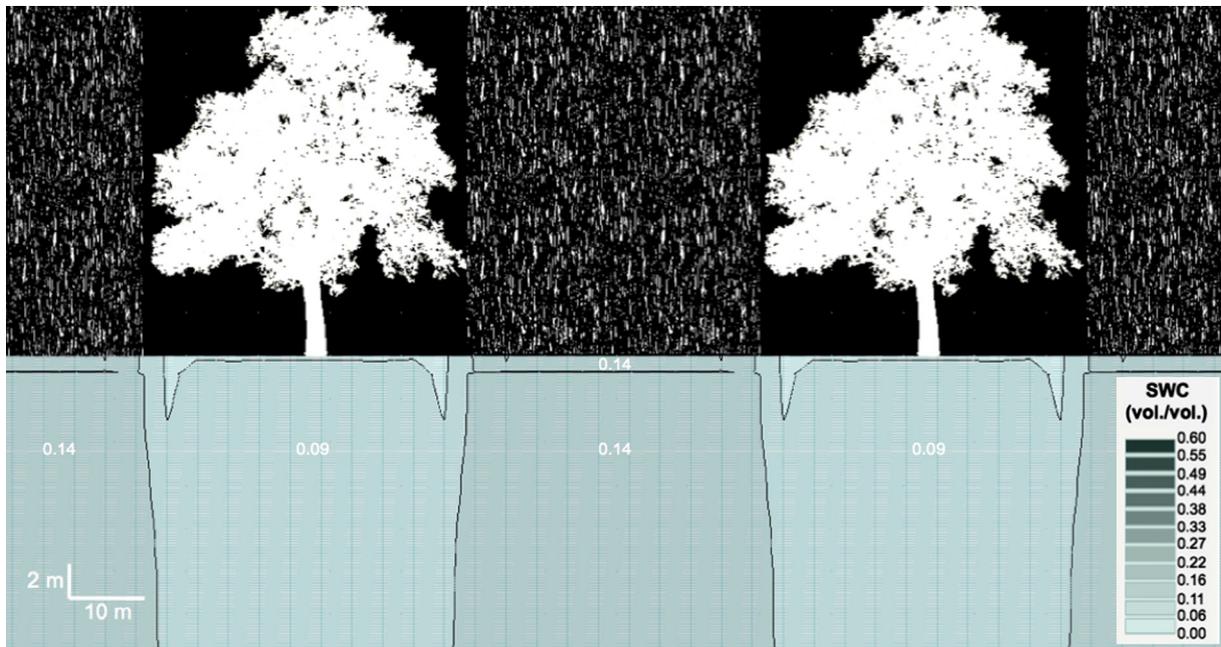


Fig. 5. HYDRUS-3D simulation of SWC within sandy soils underlying a surficial root zone; focused deep percolation pathways readily form during the 3 month simulation and correspond tightly to the spatial heterogeneity of throughfall. SWC (white numbers) for the specific regions of interest are indicated, as is the location of major nodes (thin lines) within the finite element mesh.

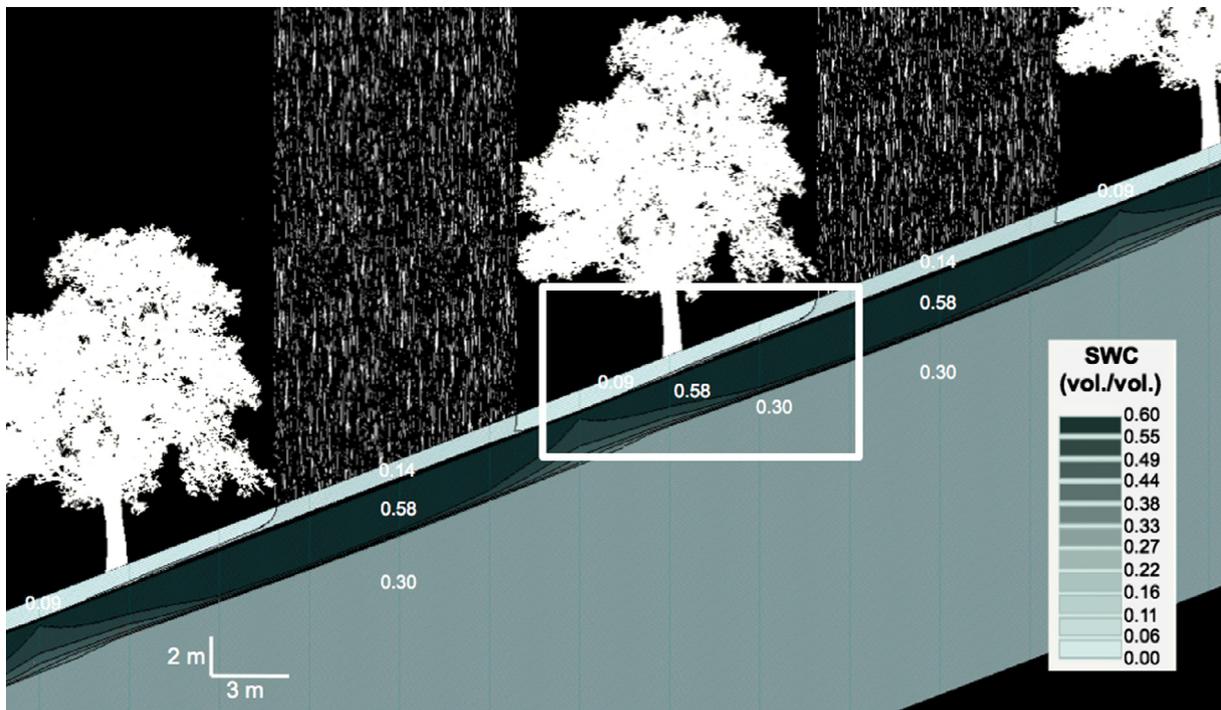


Fig. 6. HYDRUS-3D simulations of SWC within clay-rich soils on a 20° slope. After 3 months of rainy-season throughfall rates, focused deep percolation pathways within the lower clay-rich zone begin to homogenize (white box). SWC (white numbers) for the specific regions of interest are indicated, as is the location of major nodes (thin lines) within the finite element mesh.

this homogenization of SWC at depth. In addition, the transition to the less conductive layer at 90 cm, produced down slope migration of infiltrated water that created a more diffuse input into the deeper clay-rich zone. The wetting front within the clay-rich soil reached a depth of 2 m after 3 months of simulated rainy-season throughfall. Within these deep percolation pathways the maximum SWC was 58%.

Simulations using event-based 3-h input of daily maximum throughfall rates were conducted, but showed little difference from the 24-h continuous input scenario, except for greater subsurface SWC gradients at the edges of the deep percolation pathways and greater SWC within the pathways (Fig. 7, sand scenario comparison). This stronger and more defined deep percolation pathway under the event-based 3-h scenario (when compared to

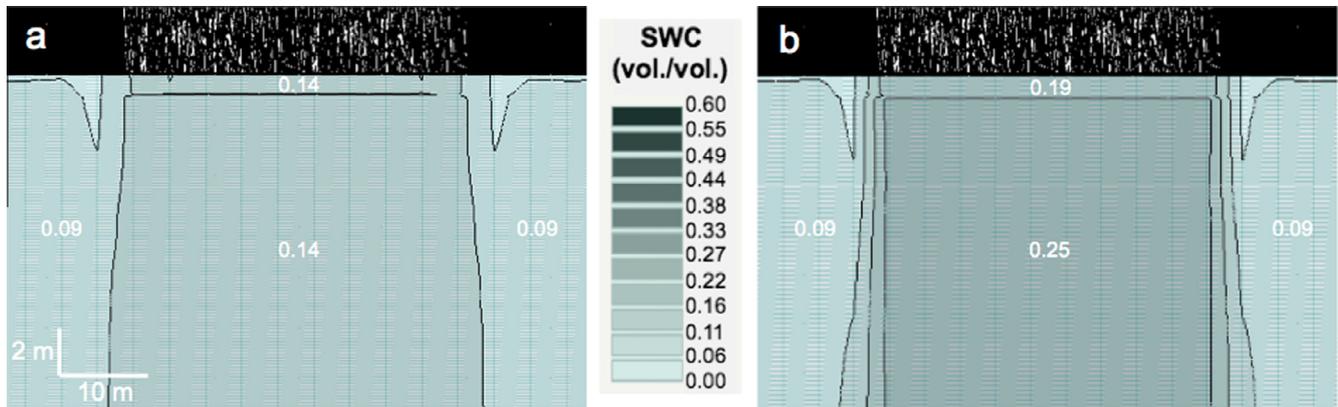


Fig. 7. A comparison of deep percolation pathways from HYDRUS-3D simulations using either (a) continuous (24 h at 0.45 mm/h) or (b) concentrated on-off (3 h at 3.6 mm/h, then 21 h at 0 mm/h) throughfall application (additional modeling parameters are the same as sandy soil in Table 1). SWC (white numbers) for the specific regions of interest are indicated, as is the location of major nodes (thin lines) within the finite element mesh.

the same daily input for the continuous 24-h scenario) suggests that the formation of deep percolation pathways is likely to occur under both event-based and continuous-event inputs, such as those modeled in Table 1 and Figs. 4–6.

4. Discussion

4.1. Throughfall heterogeneity and the formation of deep percolation pathways

We evaluated two questions about the processes controlling the connection of throughfall heterogeneity in forested landscapes and the formation of deep percolation pathways. In reference to these questions, it appears to be likely that throughfall heterogeneity, or more explicitly locations on the forest floor of relatively high throughfall versus locations of relatively low throughfall, produce focused deep percolation pathways, and that these deep percolation pathways extend beyond the root zone. These findings are based on both observed and modeled results. Observational field results suggest that within the main root zone from 0 to 80 cm, soil moisture is homogenized between events, but during the input event simulated in HYDRUS-3D, SWC becomes elevated subjacent to the focused throughfall sites and creates increased downward input beyond the root-zone, at the root-zone/intermediate-zone interface. This produces the observed uniformly higher plot-normalized SWC at 100 and 120 cm depths (Fig. 3, Table 3). Because all plots contain sloping topography, the influence of slope cannot be ignored, and may produce the reduced variability observed at depths exceeding approximately 140 cm (Figs. 3 and 6).

Although heterogeneous throughfall is found to persist as heterogeneous deep percolation through and beyond the root zone, from the process-level, these findings provide greater detail for a conceptual understanding of how these systems vary between times when precipitation is active or inactive (Fig. 8). During times of active precipitation (e.g. a storm event), homogenous rainfall is focused via the forest canopy into heterogeneous throughfall; this focused throughfall then enters the forest soils at higher rates than if the mean throughfall rate had been evenly distributed. These focused throughfall locations then create preferential deep percolation pathways that allow water to move faster through the root zone (relative to homogenous throughfall) and beyond the influence of roots (Guswa and Spence, 2011). Due to the influence of complex sloping terrain, the lateral movement of water then reduces the heterogeneity of these pathways as they progress down-slope (Fig. 8). Conversely, between precipitation events,

these focused deep-percolation pathways within the root zone rapidly homogenize by redistribution of water through preferential flow pathways (Table 3), likely caused by biological activity, similar to findings of other observational work in tropical forests (Niemeyer et al., 2014). This advance in process understanding should lead to improved hillslope and watershed simulation approaches in forested landscapes. The observational verification of these pathways now allows for more certainty as future research and modeling efforts incorporate these increased rates of deep percolation (e.g.: up to 129% (Guswa and Spence, 2011), or 300% (Keim et al., 2008)), associated with heterogeneous throughfall.

4.2. Considerations for discussion and suggestions for future research

The goals of the modeling were to evaluate the spatial variability of inputs during precipitation events, therefore evaporation and transpiration were not modeled in the HYDRUS-3D simulations, and only the *influence* that root networks have on hydraulic conductivity and not the preferential flow pathways themselves were simulated. In the observational component of the study, the effects of these evaporative processes were implicitly observed within the root zone (Fig. 3). Further research measuring or simulating evaporation and transpiration (using modeling platforms besides HYDRUS-3D) could help to elucidate additional process relationships present within the data. One example of the possible influence of evaporation and/or transpiration is the negative excursion in differences of plot-normalized SWC observed at 20 cm depth, where the overall wettest throughfall sites had drier surface layers relative to the driest throughfall sites by 3.6% SWC on average ($p = 0.22$, Table 3).

The scenarios simulated in this study evaluated only the extreme end-members of soil types (clay-rich and sandy soils). Findings suggested that although deep percolation pathways were more diffuse and laterally extensive within clay-rich soils, as opposed to sandier soils, they were still present and soil texture was not a factor limiting their presence or absence. Evaluating the influence of coarser soils may further enhance findings about SWC heterogeneity modeled in sandy soils and extend the length of the focused deep percolation pathways to even greater depths below the root zone in sloping terrain (assuming no difference in rooting depth). In addition, shallow fractured bedrock with high levels of hydrogeologic heterogeneity, and preferential flow occurring therein, may also confound these interpretations about the influence that canopy-derived throughfall focusing has on deep percolation. Within these highly heterogeneous, fractured dual

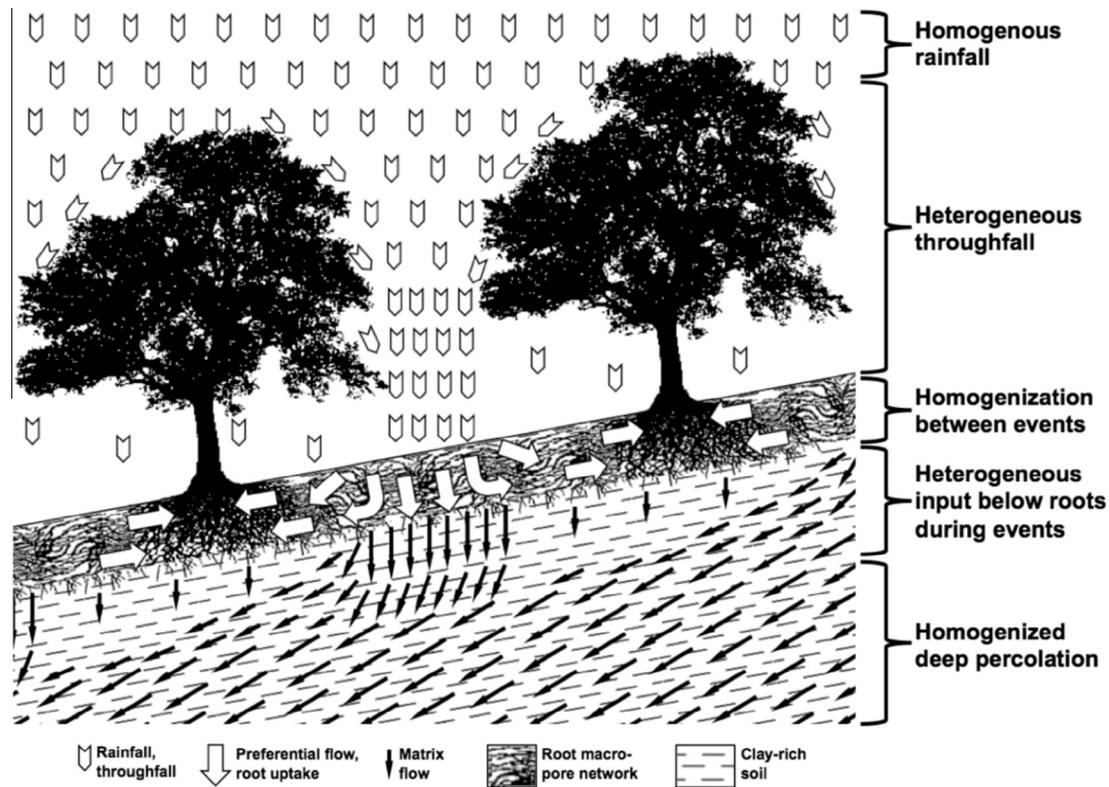


Fig. 8. A simplified conceptualization for the processes involved in the formation of focused deep-percolation pathways as water is transformed from precipitation to deep drainage within forested landscapes. Steeper slopes enhance the lateral homogenization of soil moisture observed at depth.

porosity systems downward flow is already enhanced by pre-existing, deep-running macropores, thus making the process of canopy-derived throughfall focusing potentially less influential. Future research should also focus on stemflow as another process that focuses soil water inputs that may likewise influence deep percolation and homogenization within the root zone. Previous studies in humid tropical forests found stemflow to be a minor component (only 0.2–8%; Scatena 1990; Cavelier et al., 1997; Ataroff and Rada 2000; Hölscher et al., 2004; Bryant et al., 2005; Fleischbein et al., 2005; Dietz et al., 2006; Germer et al., 2006; Holwerda et al., 2006; Germer et al., 2010; Holwerda et al., 2010; Ponette-González et al., 2010), but since the area over which the flow is input to the subsurface is proportionally smaller and extremely concentrated, it still may have potential to contribute to deep percolation and increased SWC. The impacts of stem flow may explain some of the homogenization observed within the upper root-zone, but is likely not a major component for deep percolation within the study locations since high throughfall sites were significantly correlated and conceptually linked to the locations of deep percolation at 100–120 cm depth (Fig. 3, Table 3).

The depth to groundwater and the height of the capillary fringe could also be evaluated in relation to the depth of homogenization for deep percolation. Though saturation within soil profiles was not observed at the study sites, the influence of the capillary fringe, and its extent within these clay-rich soils is unknown and could be a confounding factor. In the HYDRUS-3D simulations the entire subsurface was modeled with the assumption of existing entirely in the unsaturated zone. Within the field observations, it is unlikely that the capillary fringe or groundwater table was mistaken for the homogenization depth (~130 cm) since this would require a relatively uniform depth to groundwater across all sites. This uniform depth to groundwater is unlikely since the forested sites existed within complex terrain spanning a range of physiographic settings; including topographic highs, mid-slopes, and topographic lows.

5. Conclusions

This study evaluated the hypothesis that the focusing of throughfall by forest canopies can create correspondingly focused deep percolation pathways that transmit water beyond the root zone and into deep drainage. Field-based observations from 8 separate plots within humid tropical forests of Costa Rica suggest that this focusing occurs down to ~130 cm depth, but is homogenized between events within the root zone (which extends to ~90 cm depth). Based on simulations using HYDRUS-3D, it appears likely that the clay-rich soils and sloping terrain may be responsible for homogenization of these deep percolation pathways beyond ~130 cm. These findings provide field observations to support previously conceptualized ideas relating focused throughfall and deep percolation pathways (Keim et al., 2008; Guswa and Spence, 2011). Future physically-based hillslope and watershed modeling in forested landscapes may benefit from the inclusion or parameterization of this process, which can more than double the rate of deep percolation below the root zone when compared to an equivalent throughfall amount homogeneously distributed over the landscape (Keim et al., 2008; Guswa and Spence 2011). Additional observational and computational work is needed to evaluate the effects that variable evapotranspiration, coarser soil types (or fractured bedrock), stemflow, and water table depths may have upon deep percolation processes and rates within different climates and landscapes.

Acknowledgements

The authors would like to thank all the help, support, technical-expertise, and hospitality of the CATIE field technicians. Without their local floral and spatial knowledge, research would have been incredibly more difficult and much less enjoyable. Support was

provided to multiple authors by a diversity of Grants from the U.S. National Science Foundation, including a Graduate Research Fellowship Grant (2010100816), an Integrative Graduate Education and Research Traineeship Grant (0903479), a Chemical, Bioengineering, Environmental, and Transport Systems Grant (0854553), a Long Term Research in Environmental Biology Grant (0639393), and two grants (GEO-0452325 and GEO-1138881) supporting the DiverSus project in conjunction with the Inter-American Institute for Global Change Research (CRN 2015 and SGP-CRA2015). Additional support was also provided by Mexico's National Council of Science and Technology (CONACyT) to A. Chain-Guadarrama.

References

- Alaoui, A., Caduff, U., Gerke, H.H., Weingartner, R., 2011. Preferential flow effects on infiltration and runoff in grassland and forest soils. *Vadose Zone J.* 10, 367–377.
- Ataroff, M., Rada, F., 2000. Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. *AMBIO J. Human Environ.* 29, 440–444.
- Bryant, M.L., Bhat, S., Jacobs, J.M., 2005. Measurements and modeling of throughfall variability for five forest communities in the southeastern US. *J. Hydrol.* 312, 95–108.
- Cavelier, J., Jaramillo, M., Solis, D., De León, D., 1997. Water balance and nutrient inputs in bulk precipitation in tropical montane cloud forest in Panama. *J. Hydrol.* 193, 83–96.
- Chain-Guadarrama, A., Klos, P.Z., Casanoves, F., Finegan, B., Vierling, L., Chazdon, C., Link, T.E., The functional and structural characteristics of forest canopies drive distinctive throughfall patterns between old-growth and second-growth neotropical rain forests. *Ecol. Appl.* (in preparation)
- Chazdon, R.L., Finegan, B., Capers, R.S., Salgado-Negret, B., Casanoves, F., Boukili, V., Norden, N., 2010. Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. *Biotropica* 42, 31–40.
- Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A., Ryan, M.G., 2008. First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. *Ecol. Lett.* 11, 163–172.
- Dietz, J., Hölscher, D., Leuschner, C., 2006. Rainfall partitioning in relation to forest structure in differently managed montane forest stands in central Sulawesi, Indonesia. *For. Ecol. Manage.* 237, 170–178.
- Finegan, B., Camacho, M., 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988–1996. *For. Ecol. Manage.* 121, 177–189.
- Finegan, B., Camacho, M., Zamora, N., 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *For. Ecol. Manage.* 121, 159–176.
- Fleischbein, K., Wilcke, W., Goller, R., Boy, J., Valarezo, C., Zech, W., Knoblich, K., 2005. Rainfall interception in a lower montane forest in Ecuador: effects of canopy properties. *Hydrol. Process.* 19, 1355–1371.
- Germer, S., Elsenbeer, H., Moraes, J.M., 2006. Throughfall and temporal trends of rainfall redistribution in an open tropical rainforest, south-western Amazonia. *Hydrol. Earth Sys. Sci.*, 383–393.
- Germer, S., Werther, L., Elsenbeer, H., 2010. Have we underestimated stemflow? Lessons from an open tropical rainforest. *J. Hydrol.* 395, 169–179.
- Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M., Anderson, L., 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecol.* 132, 107–120.
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *For. Ecol. Manage.* 148, 185–206.
- Guswa, A.J., Spence, C.M., 2011. Effect of throughfall variability on recharge: application to hemlock and deciduous forests in western Massachusetts. *Ecohydrology* 5, 563–574.
- Hölscher, D., Köhler, L., Van Dijk, A.I.J.M., Bruijnzeel, L.A., 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *J. Hydrol.* 292, 308–322.
- Holwerda, F., Bruijnzeel, L.A., Muñoz-Villers, L.E., Equihua, M., Asbjornsen, H., 2010. Rainfall and cloud water interception in mature and secondary lower montane cloud forests of central Veracruz, Mexico. *J. Hydrol.* 384, 84–96.
- Holwerda, F., Scatena, F.N., Bruijnzeel, L.A., 2006. Throughfall in a Puerto Rican lower montane rain forest: a comparison of sampling strategies. *J. Hydrol.* 327, 592–602.
- Keim, R.F., Weiler, M., Jost, G., Tromp-Van Meerveld, I., 2008. Consequences of spatiotemporal redistribution of precipitation by vegetation for hillslope and runoff processes. Presentation, Am. Geophys. Union Ann. Meet.
- Keim, R.F., Skaugset, A.E., Weiler, M., 2005. Temporal persistence of spatial patterns in throughfall. *J. Hydrol.* 314, 263–274.
- Levia, D.F., Frost, E.E., 2006. Variability of throughfall volume and solute inputs in wooded ecosystems. *Progr. Phys. Geogr.* 30, 605–632.
- Loescher, H.W., Powers, J.S., Oberbauer, S.F., 2002. Spatial variation of throughfall volume in an old-growth tropical wet forest, Costa Rica. *J. Trop. Ecol.* 18, 397–407.
- Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., Imeson, A.C., 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86, 288–297.
- McDade, L., Bawa, K., Hespeneheide, H., Hartshorn, G., 1994. *La selva: Ecology and Natural History of a Neotropical Rain Forest*. University Chicago Press, Chicago.
- Montgomery, R.A., Chazdon, R.L., 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82, 2707.
- Niemeyer, R.J., Fremier, A.K., Heinse, R., Chávez, W., DeClerck, F.A.J., 2014. Woody vegetation increases saturated hydraulic conductivity in dry tropical Nicaragua. *Vadose Zone J.* 13.
- Ponette-González, A.G., Weathers, K.C., Curran, L.M., 2010. Water inputs across a tropical montane landscape in Veracruz, Mexico: synergistic effects of land cover, rain and fog seasonality, and interannual precipitation variability. *Global Change Biol.* 16, 946–963.
- Raat, K.J., Draaijers, G.P.J., Schaap, M.G., Tietema, A., Verstraten, J.M., 2002. Spatial variability of throughfall water and chemistry and forest floor water content in a Douglas fir forest stand. *Hydrol. Earth Syst. Sci.* 6, 363–374.
- Scatena, F.N., 1990. Watershed scale rainfall interception on two forested watersheds in the Luquillo Mountains of Puerto Rico. *J. Hydrol.* 113, 89–102.
- Seyfried, M.S., Grant, L.E., Du, E., Humes, K., 2005. Dielectric loss and calibration of the hydra probe soil water sensor. *Vadose Zone J.* 4, 1070.
- Tang, H., Dubayah, R., Swatantran, A., Hofton, M., Sheldon, S., Clark, D.B., Blair, B., 2012. Retrieval of vertical LAI profiles over tropical rain forests using waveform LiDAR at La Selva, Costa Rica. *Remote Sens. Environ.* 124, 242–250.
- Thien, S.J., 1979. A flow diagram for teaching texture-by-feel analysis. *J. Agronom. Educ.* 8, 54–55.
- Trimble, S.W., Mendel, A.C., 1995. The cow as a geomorphic agent – a critical review. *Geomorphology* 13, 233–253.
- Van Genuchten, M., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Sci. Soc. Am. J.* 44, 892–898.
- Zimmermann, A., Zimmermann, B., Elsenbeer, H., 2009. Rainfall redistribution in a tropical forest: spatial and temporal patterns. *Water Resour. Res.* 45, W11413.
- Zimmermann, A., Zimmermann, B., 2014. Requirements for throughfall monitoring: the roles of temporal scale and canopy complexity. *Agric. For. Meteorol.* 189, 125–139 (retrieved from Google scholar).