Journal of Hydrology 377 (2009) 71–79

Contents lists available at ScienceDirect

Journal of Hydrology

journal homepage: www.elsevier.com/locate/jhydrol

Spatial throughfall heterogeneity in a montane rain forest in Ecuador: Extent, temporal stability and drivers

H. Wullaert [a], T. Pohlert [a], J. Boy [a,b], C. Valarezo [c], W. Wilcke [a,*]

[a] *Earth System Science Research Center, Geographic Institute, Professorship of Soil Geography/Soil Science, Johannes Gutenberg University Mainz, Johann-Joachim-Becher-Weg 21, 55128 Mainz, Germany*
[b] *Institute of Soil Science, Leibniz University Hannover, Hannover, Germany*[1]
[c] *Universidad Nacional de Loja, Dirección General de Investigaciones, Ciudadela Universitaria Guillermo Falconí, Sector La Argelia, Loja, Ecuador*

ARTICLE INFO

Article history:
Received 6 May 2009
Received in revised form 24 July 2009
Accepted 2 August 2009

This manuscript was handled by
K. Georgakakos, Editor-in-Chief

Keywords:
Hydrologic cycle
Canopy structure
Spatial variability
Interception
Ecological niches
Rain gauge

SUMMARY

The drivers of spatial throughfall heterogeneity are still not fully understood. At an undisturbed forest site in the Ecuadorian Andes with ca. 2600 mm of annual rainfall we determined the accuracy of throughfall measurements by comparing Hellmann-type funnel gauges with troughs. At the same undisturbed and a managed, selectively-logged forest site we determined spatial variability of throughfall, temporal stability of spatial variability and the controls of spatial throughfall variability using a 4-year dataset in weekly resolution. There were no systematic differences between the collected volumes of funnel gauges and troughs. Based on the statistical distribution of annual throughfall volumes, a high number of 27 funnel-type rainfall collectors were required in the undisturbed forest and 20 in the managed forest to estimate throughfall with an error of 10% and a confidence interval of 95%. Spatial throughfall variability in the studied forests was high, markedly stable during 4 years and similar in six selected rain events suggesting that a stable canopy structure controlled throughfall variability. After mathematically eliminating the canopy influence, no meteorological variable had a significant effect on throughfall variability. We conclude that the high spatial variability of throughfall in the study forest, mainly controlled by a long-term stable canopy structure, contributes to the creation of different ecological niches which are a prerequisite for the enormous biological diversity of the north Andean forests.

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Introduction

Incident rainfall in forests is partitioned into throughfall, stemflow, and interception loss. Throughfall is the portion of rainfall reaching the forest floor as direct throughfall (without interception by the canopy), cascading through the canopy, and dripping from the crowns after temporal storage in the canopy. Throughfall in tropical montane rain forests ranges from 62% (Cavelier et al., 1997) to 97% (Chuyong et al., 2004) of incident rainfall. In general, it represents approximately four-fifths of incident rainfall (Levia and Frost, 2006). Water running down the trunks is referred to as stemflow but comprises a minor contribution to the water flux in a forest ranging from 0.1% (Veneklaas, 1990) to an exceptional 12.2% (Mamanteo and Veracion, 1985). In most tropical forests including the north Andean montane forest, stemflow does not exceed 2% of rainfall (e.g., Lloyd and Marques, 1988; Cavelier et al., 1997; Wilcke et al., 2001; Chuyong et al., 2004; Lilienfein and Wilcke, 2004). The difference between incident rainfall and the sum of throughfall and stemflow is interception loss.

Throughfall is known to show considerable spatial variability posing severe problems for representative sampling (Levia and Frost, 2006). Throughfall can be measured with troughs or with funnel gauges. Troughs have higher surface areas than funnel gauges allowing to be exposed to more drip points (Kostelnik et al., 1989) but funnel gauges can more easily be manifold replicated. Furthermore, the representativity of sampling can be improved by roving the samplers after each sample collection (Kimmins, 1973; Lloyd and Marques, 1988). There are a number of studies in which the sample size for representative measurement of throughfall was determined for temperate forests and a tropical lowland forest (Levia and Frost, 2006) but not yet for a tropical montane forest. To estimate throughfall volume with an error of not more than 10% with a 95% confidence interval, one needs 9–90 funnel gauges in a 30–40 year old coniferous stand in a temperate region (Kimmins, 1973) or 7–44 funnel gauges in a temperate hardwood forest (Houle et al., 1999).

Throughfall heterogeneity is influenced by canopy architecture. A higher epiphytic load of the canopy and certain leaf morpholo-

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* Corresponding author. Tel.: +49 6131 3924528; fax: +49 6131 3924735.
E-mail address: wolfgang.wilcke@uni-mainz.de (W. Wilcke).

[1] Present address.

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doi:10.1016/j.jhydrol.2009.08.001

gies can provide more drip points, leading to more throughfall variability (Fleischbein et al., 2005; Staelens et al., 2006). Several studies tried to relate throughfall variability with canopy cover and gauge position, such as distance from gauge to stem. While Robson et al. (1994) found that throughfall decreased with increasing distance from the tree stem in a beech forest in southern England, Beier et al. (1993) reported the reverse in a spruce forest in Denmark. Loustau et al. (1992) did not observe any correlation between throughfall volume and distance from tree stem in a maritime pine stand in France. Loescher et al. (2002) observed a weak relationship ($r = 0.33$) between percent plant cover and throughfall volume. In the study of Fleischbein et al. (2005), direct throughfall was negatively correlated with leaf area index. In a tropical rainforest in Kalimantan, Indonesia, interception losses decreased from 11% to 6% because of logging and throughfall volume increased correspondingly (Asdak et al., 1998). Thus, manipulations of the forest cover e.g., by improvement felling (i.e. logging of selected trees to improve growth of potential crop trees) are expected to have an impact on throughfall heterogeneity.

As throughfall influences local soil moisture (Schaap and Bouten, 1997) and carries directly plant-available nutrients to the soil, throughfall heterogeneity possibly creates a small-scale heterogeneity of ecological niches (Parker, 1983). Wilcke et al. (2002) demonstrated that soil nutrients are heterogeneously distributed in the organic layer of a tropical montane rain forest but were not able to offer a mechanistic explanation for this heterogeneity. Throughfall could contribute to explain the spatial variability of soil fertility if the spatial throughfall pattern was stable in the long run. Thus, temporal stability of spatial patterns is an ecologically important issue. A visual way to represent the stability of spatial variability in throughfall volume is by using so-called time-stability plots (Raat et al., 2002; Staelens et al., 2006). This technique was first applied by Vachaud et al. (1985) to describe soil water storage variability and transferred by Raat et al. (2002) to spatial throughfall variability. In a 3-month study in a tropical montane rainforest in Ecuador, Zimmermann et al. (2007) analysed five throughfall events and found that throughfall is spatially heterogeneous (mean coefficient of variation of 53%) and that throughfall patterns were stable during the monitored period.

In several studies it was shown that meteorological conditions influence spatial throughfall heterogeneity (Levia and Frost, 2006). Usually, increasing rainfall volume decreases the variability of throughfall within an event often until a threshold water input is reached after which the variability stabilizes (Llorens et al., 1997; Levia and Frost, 2006). Furthermore, rainfall event duration and intensity influence throughfall variability although observations are not consistent with respect to the direction of these effects. However, a separation of the effects of canopy properties and meteorological conditions was not attempted in any of the published studies.

Our objectives were to: (i) determine if throughfall volumes collected by troughs and funnel gauges differ from each other, (ii) quantify the spatial variability of annual throughfall in an undisturbed and a moderately thinned Ecuadorian tropical montane forest and derive the necessary number of funnel gauges for representative measurement, (iii) assess the temporal stability of the throughfall patterns for a period of 4 years and (iv) investigate into the meteorological controls of spatial throughfall heterogeneity after accounting for the influence of canopy properties. We hypothesized that: (i) troughs and funnel gauges collect the same throughfall volume, (ii) the variability of throughfall in an undisturbed tropical montane forest is high and is increased by thinning (iii) that throughfall patterns in the study forest are temporally highly stable even at the scale of several years, and (iv) that meteorological variables are important drivers of throughfall heterogeneity even after mathematical elimination of the canopy influence.

Materials and methods

Study area

The studied forest is located in south Ecuador on the eastern slope of the Cordillera Real of the Andes (i.e. the eastern cordillera) at an altitude between 1900 and 2000 m a.s.l. (3°58′S, 79°05′W), near the research station Estación Cientifica San Francisco in the deeply incised valley of the Rio San Francisco that drains into the Amazon. Our studied forest is located on the north-facing flank of the San Francisco valley. The vegetation of the study site is a Lower Montane Forest according to Bruijnzeel and Hamilton (2000). In the study area, more than 250 tree species have been identified so far with an above average abundance of the plant families Lauraceae, Melastomataceae and Rubiaceae. Most of the tree species are evergreen (Bendix et al., 2006). *Graffenrieda emarginata* (Melastomaceae) is one of the most common tree species. The high plant species diversity in the whole research area is also characterized by about 140 climber species, more than 400 angiosperm epiphytes, up to 98 vascular epiphytes species on single trees, 248 ferns and ferns allies and more than 525 bryophytes (Homeier et al., 2008). The forest has a mean canopy height of 18.9 m, and 80 trees – which were reaching the lower canopy – had a mean diameter at breast height (dbh) of 122 mm. Leaf area index ranges between 5.2–9.3 $m^2\ m^{-2}$ (Fleischbein et al., 2005).

Mean annual temperature in the research area is 15.2 °C. The coldest months are June and July, respectively, with a mean temperature of 14.4 °C; the warmest month is November with a mean temperature of 16.1 °C. The average temperature gradient between a meteorological station at 1952 m and another station at 2927 m a.s.l. is 0.61 °C per 100 m increase in elevation (Bendix et al., 2008). The distribution of the annual rainfall is unimodal with a maximum between April and September and without a dry season (Fleischbein et al., 2005), which is typical for eastern Andean slopes at altitudes between 1000 and 3600 m a.s.l. Mean annual rainfall is 2569 mm $year^{-1}$. During a 1468 day-period of meteorological observations at the meteorological station, 2971 rainfall events were registered. The events had a mean intensity of 0.41 mm h^{-1} and a mean duration of 9 h and 18 min. Events were separated by a dry period of at least 2 h, which was the time considered to dry the canopy completely. Seventy-three percent of the events had 0–2 mm of rain, 20% were larger than 2 mm and smaller than 10 mm, and only 7% were larger than 10 mm (Fleischbein et al., 2006). Horizontal rain in the study forest was small, accounting for <6% of the incident rainfall (Bendix et al., 2008). Mean humidity was 86% (with 90% continuously from April to June 2001) and 79% in November 2000. The mean speed of the mainly easterly winds for the period between April 1998 and April 2001 was 1.5 m s^{-1} with a maximum of 7.9 m s^{-1}.

Experimental design

Between May 2004 and May 2008, throughfall samples were collected in weekly intervals from three 20 m-long transects at lower slope position covering 10 altitudinal meter from 1900–1910, 1950–1960, and 2000–2010 m a.s.l. in a 9.1 ha large undisturbed microcatchment. We decided to collect rainfall samples in weekly intervals instead of sampling individual events because of the frequent slight rain events and because the rainfall samples are the basis for long-term nutrient budgets. Additionally, in the managed forest catchment which was ca. 12.1 ha large, throughfall samples were collected from three ca. 50 × 50 m large plots at 1875–2055 m a.s.l. where improvement fellings took place in June 2004. On the experimentally thinned site, all trees with dbh >0.20 m were registered out of a list of defined timber species,

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