

Spatial variation of throughfall volume in an old-growth tropical wet forest, Costa Rica

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ABSTRACT. Throughfall volume and interception of bulk precipitation events were measured during individual rain events of differing magnitudes in a primary wet tropical forest at La Selva Biological Station, Costa Rica. The relationship between canopy structure and throughfall were examined to identify key sources of spatial variation. Geostatistical analyses were also used to examine the spatial variation in throughfall, spatial autocorrelation and to determine minimum distances for independence of collectors. Throughfall volume was collected from 56 ground-based (funnel-style) collectors. Throughfall was collected for 26 separate precipitation events during July and August 1998. Per cent cover, distance to nearest tree, distance to nearest leaf were also estimated for each collection point. A weak relationship was found with per cent cover ($r^2 = 0.11$). No relationship was found between throughfall and distance to the nearest leaf above the collector. Estimated interception was 1.88 mm ($r^2 = 0.94$) with increased variance as bulk precipitation increased. A range distance of 45 m was estimated from variograms, strongly suggesting that large tree canopies and gaps are the source of much of the spatial variance in throughfall volume. Interception was reduced by 19% if only spatially independent collectors were used.

KEY WORDS: Costa Rica, hydrological balance, interception, La Selva, throughfall, tropical wet forest, spatial variation

INTRODUCTION

Understanding how water and nutrients in aqueous solutions move through forested systems enhances our understanding of ecosystem-level processes such

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as energy partitioning, streamflow and productivity (Waring & Running 1998). This becomes particularly important when modelling these processes across spatial and temporal scales under different climate scenarios. Throughfall and canopy interception of rainfall are key elements in any forest hydrological and nutrient cycle. Quantification of throughfall and associated nutrient losses start with collection of throughfall volume that includes both 'free' throughfall and canopy drip, here, referred to collectively as throughfall. Interception, throughfall rates, and movement of nutrients are usually based on regression analyses, whose key assumption is independence of samples. However, spatial independence of collected throughfall is rarely established, nor is the assumption of spatial independence verified statistically.

Many studies have examined throughfall and interception through the use of models to explain water usage, storage and flow with little attention paid to spatial controls, for example physical models (Gash 1979, Liu 1992, Rutter *et al.* 1975, Ubarana 1996) empirical models (Massman 1983) and stochastic models (Calder 1986). Examining the sources of variation is key to understanding the spatial distribution and independence of throughfall, and has not received much attention in the literature. Rather, previous studies have focused on the variation in throughfall volume within each collector (Lloyd & Marques 1988) and have found that throughfall volume from an individual collector increased with distance from nearest tree bole (Beier *et al.* 1993). Many of these studies have been conducted in architecturally simple, even-age stands (Bruijnzeel & Wiersum 1987, Liu 1998) and have shown high within-collector variability (Lloyd & Marques 1988, McDowell 1998). Lloyd *et al.* (1988) demonstrated difficulty applying both the Gash (1979) and Rutter *et al.* (1975) models to tropical forests, which exhibited higher spatial variability than many temperate forests (Jackson 1971). Jackson (1971) called for large sample size to reduce error associated with high spatial variability. Whereas Lloyd *et al.* (1988) found better precision in their throughfall estimates with random placement of – and relocations of – collectors along a transect with 1-m intervals rather than a plot (20 × 4 m) with 1 × 1-m grids. They did not, however, attempt to identify specific controls on their sources of variability. Moreover, throughfall estimation assumes that canopies are locally uniform in distribution of leaf area and water retention properties. At what spatial scale does this occur? For this reason, identifying sources of spatial variability in throughfall volume from wet tropical forests can assist in the interpretation of model results, and increase both the precision and accuracy of direct methods of estimation. The objectives of this study were the following: to determine throughfall volume amounts and interception of bulk precipitation events in a wet tropical forest, to determine the spatial autocorrelation of throughfall, and to examine relationships between canopy structure and throughfall.

STUDY SITE

This study was conducted in concert with ongoing carbon balance studies (Projecto Carbono) at the La Selva Biological Station, Costa Rica

(10°26'N, 83°59'W, and elevation 80–150 m asl). In the Holdridge classification system, La Selva is wet tropical forest (Hartshorn & Peralta 1988). Annual bulk precipitation is *c.* 4000 mm y⁻¹ with no single month receiving less than 100 mm (Sanford *et al.* 1994). While the distribution of precipitation during both the wet and dry seasons is variable, the first 3 mo of 1998 were drier than the average, possibly due to the warm-phase of the El Niño Southern Oscillation, see Figure 1. Mean annual air temperature is *c.* 26 °C. The annual mean above-canopy wind direction is at 90° due to the attenuation of the NE surface winds with altitude. Stand structure is outlined in Table 1. While landscape variation of forest structure and above-ground biomass has been studied (Clark & Clark 2000), little is known concerning the distribution of leaf area, leaf size and shape in the tropics. Detailed information on this site is found in

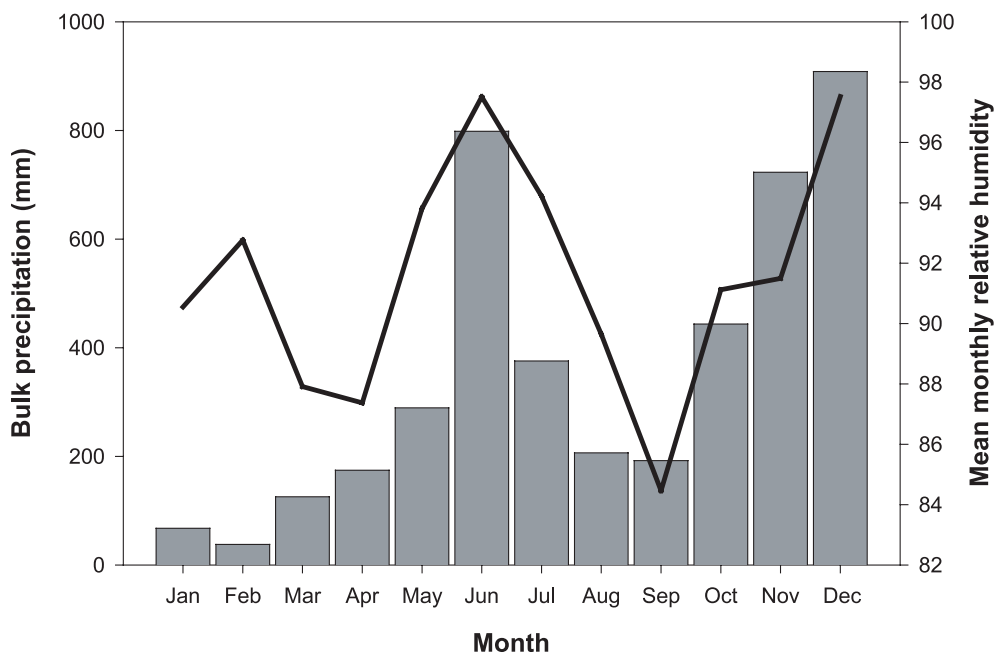


Figure 1. Monthly bulk precipitation (bars) and mean relative humidity (line) from La Selva Biological Station, Sarapiquí, Costa Rica for 1998. Relative humidity (RH) was measured using CS500 probe (Campbell Scientific, Logan UT) and calibrated against a sling psychrometer. Both rain gauge and RH sensor were co-located atop a 42-m tower.

Table 1. Elements of stand structure from an old-growth wet tropical forest at La Selva Biological Station, OTS, Sarapiquí, Costa Rica (10°26'N, 83°59'W).

Mean number of stems ¹	504 (± 94) ha ⁻¹ , ≥ 10 cm dia
Mean basal area ¹	23.6 (± 2.2) m ² ha ⁻¹
Mean above-ground biomass ¹	161 (± 18) Mt ha ⁻¹
Number of tree species	≈ 100 ha ⁻¹
Mean tree height	21 m
Emergent height	38–54 m

¹Data collected from (18) 0.5-ha plots, see Clark & Clark (2000).

Sanford *et al.* (1994), and on general climatology in Waylen *et al.* (1996) and Hastenrath (1988).

METHODS

Thirty-six collectors were placed on radial transects extending away from a centre at distances of 20 m, 40 m and 60 m to determine volumetric throughfall quantities (excluding stemflow) and canopy interception. Each transect was repeated every 30° to maximize the distance classes of the matched pairs (Figure 2). A tipping-bucket rain gauge (model TE-252, Texas Electronics) mounted on top of a meteorological tower in the centre of the collection area, measured incoming rainfall so that all collectors captured the same rain event. To test for spatial autocorrelation, an additional 20 collectors were laid out 5 m N and 5 m E of all the collectors in the NE quadrant (Figure 2).

Collectors consisted of funnels with a surface area of 95 cm² attached to 3.79-litre jugs. To prevent splash-out, a 30-mm-high PVC ring was fixed to the perimeter of each funnel. Each collector stood 0.37 m above the ground under differing canopy heights and plant structures. Throughfall was collected manually, and collectors were levelled and cleaned of litter after each rain event. A rain event was defined by periods of complete drying of the upper canopy after a period of bulk precipitation. Below-canopy leaves were also typically dry, even though the relative humidity was > 90%. Epiphytes and canopy root mats may have remained moist and not entirely dry. Typically, rain events occurred daily in the late afternoon after a morning of convective building of the boundary

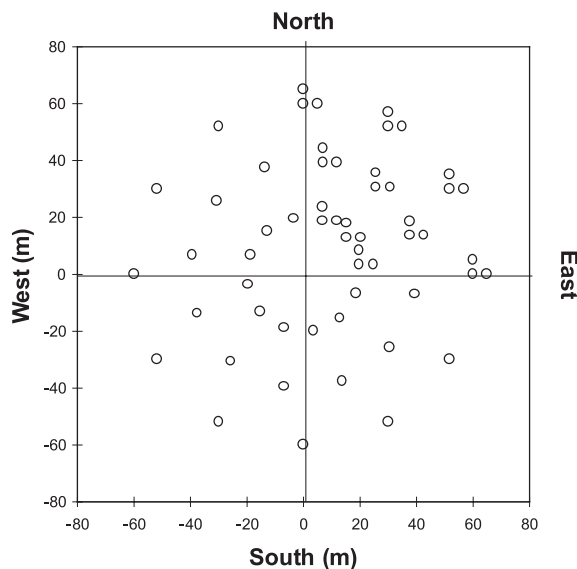


Figure 2. Radial layout of the throughfall collectors. Units are in metres.

layer, and often continued into the night. Evaporative losses from the canopy during a rain event were insignificant because it was assumed that air became saturated with water vapour soon after an event began (preconditions of high relative humidity, Figure 1), and much of the rain fell either during late afternoon or evening when the net radiation was low. Collections were made during the wet season and began on 7 July 1998 and ended on 14 August 1998.

Because variation in throughfall increased with both intensity and duration of the rainfall event, the data were log-transformed to homogenize the variance, Eqn 1.

$$\text{Log (L)} = a[\text{log (BP)}] + b \quad (\text{Eqn 1})$$

Where,

L = estimated mean throughfall, mm,
 BP = bulk precipitation, mm, and
 a+b = empirical coefficients.

Both interception and spatial variability were estimated from throughfall measurements. Data were regressed using Eqn 1 with interception estimated by the x-axis intercept where the y-axis is equal to zero. Interception defined here is the maximum 'free' water-holding capacity by the canopy, including the water more tightly held by arboreal soil and root mats. Stemflow was not measured, nor was any attempt made to estimate changes in interception over temporal scale, i.e. modelling changes in water-holding capacity. Minimal evaporation between collections was assumed because relative humidity was near 100% at ground level during the collection period and samples were stored in narrow-necked bottles.

Variograms were used to test for spatial autocorrelation in the throughfall data (for reviews of geostatistics see Goovaerts 1998, Trangmar *et al.* 1987, Webster 1985). Variograms are a geostatistical technique to detect spatial autocorrelation between mapped samples of a quantitative variable (e.g. throughfall). In a variogram, the averaged squared difference in the value of a variable between all pairs of points is computed across distance intervals (lag classes). The output is presented graphically as a plot of the average semi-variance versus distance class. The semi-variance will converge on total variance at distances for which values are no longer spatially autocorrelated (this is referred to as the range and is measured in units of distance). Thus, semi-variance takes on values from 0 to the total variability in the data set (i.e. the upper limit of semi-variance values will depend upon the units of measurement). Three parameters estimated from the variogram describe spatial autocorrelation in the data: the range, the sill (the sill is the asymptotic value of semi-variance at the range), and the y-intercept or nugget variance, which describes sampling error or variation at distances below those separating the closest pairs of samples. Empirical variograms were computed in Splus software (SPATIALSTATS package, Mathsoft Inc., Seattle WA) with 5-m lag

classes. The range, sill and nugget variance were estimated from theoretical models that were fitted to the empirical variograms using non-linear least squares methods. Two different functional models, spherical and Gaussian, were fitted to each variogram and the goodness-of-fit was assessed using the residual sum of squares. To assess the potential variability within each, and across all, event(s) the mean throughfall values from each collector were used. Variograms were constructed with a minimum of 20 pairs of collection points in each 5-m distance class (lag interval). The range distance (i.e. the distance beyond which samples are spatially independent) was estimated from the empirical variogram by fitting Gaussian and spherical theoretical models. Goodness-of-fit was assessed using the residual sum of squares.

To further explain the spatial variability of throughfall, descriptions of the canopy cover above collectors were made at each site. The distance to nearest vegetation directly above each collector was measured (measuring tape was used for distances < 2 m, optical rangefinder for distances > 2 m). Leaf area was estimated using a spherical densiometer because of ease and expense. Even though this technique may seem primitive to some, Englund *et al.* (2000) found good agreement between LAI values estimated by both spherical densiometry and hemispherical photography. These measurements were taken in each cardinal direction (N, E, W and S) above each collector, and averaged to obtain mean estimates. This technique was developed at La Selva Biological Station, and improves the precision of the estimate (see Englund *et al.* 2000).

RESULTS

For both mean and cumulative throughfall, samples separated more than 43 m apart (the range) were statistically independent (Figure 3). Interception was calculated both with the total dataset (Figure 4a), and with collectors ≥ 43 m apart (Figure 4b). Thus, estimated canopy interception was 1.88 and 1.54 mm ($r^2 = 0.94$, $P < 0.0001$ and 0.97 , $P < 0.0001$, respectively). A weak relation was

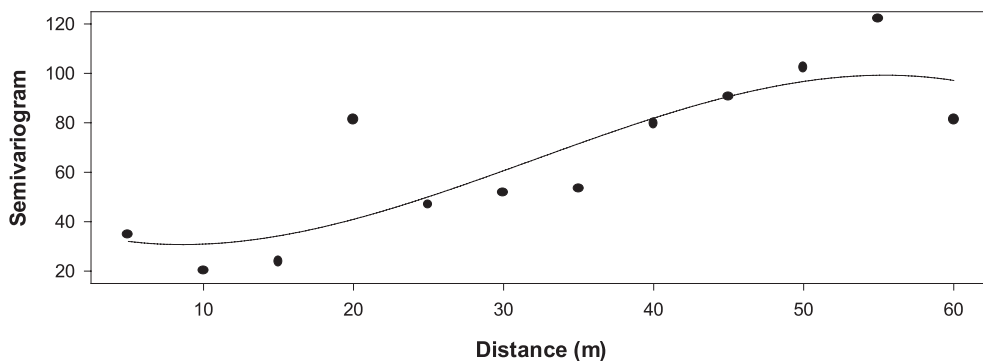


Figure 3. Semivariogram of mean throughfall volume and distance between collectors, range = 42.65, sill = 92.2 and nugget = 23.76.

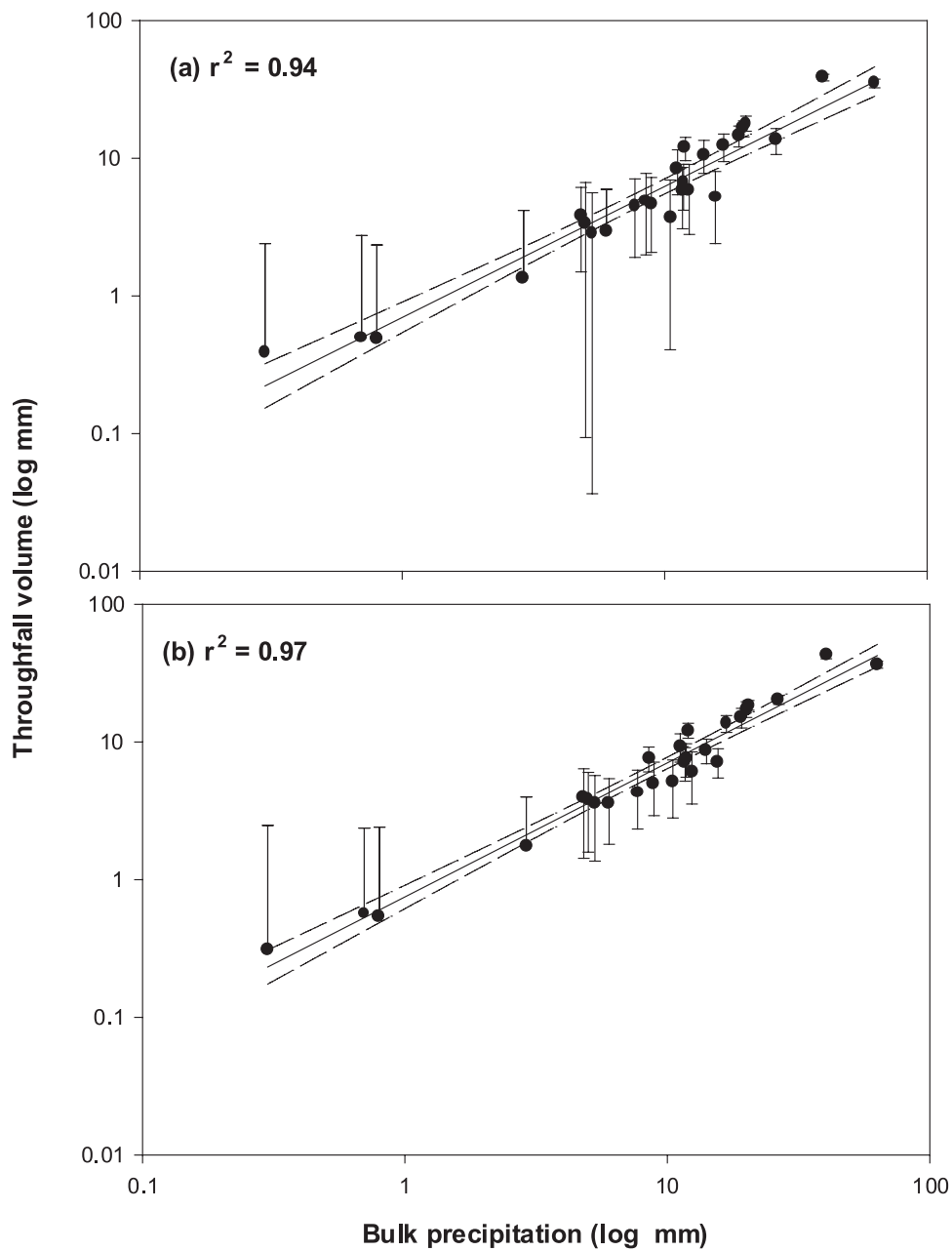


Figure 4. The relationship between bulk precipitation and mean throughfall averaged across all 26 rain events from (a) all collectors, $n = 56$, and (b) collectors ≥ 45 m apart, $n = 26$. Interception was 1.88 ($\log(L) = 0.952[\log(\text{BP})] - 0.157$) and 1.53 mm ($\log(L) = 0.974[\log(\text{BP})] - 0.127$), respectively. P-values for both slopes are < 0.0001 , and for the intercept 0.008 and 0.006, respectively. Error bars are ± 1 SD and dotted lines are 95% confidence intervals.

found between per cent canopy cover and throughfall volume (Figure 5, $r^2 = 0.11$, $P < 0.02$). The coefficient of variation among collectors was *c.* 24, which stabilized after 15 collectors (Table 2). No relationship was found between throughfall volume and distance to nearest leaf above the collector ($r^2 = 0.04$, $P = 0.19$) or distance to nearest plant ($r^2 = 0.002$, $P = 0.75$) with the nearest leaves and plants located in the understorey.

DISCUSSION

Numerous studies have estimated either canopy interception for hydrological budgets, or nutrient additions from wet deposition (Clark *et al.* 1998, Liu 1998,

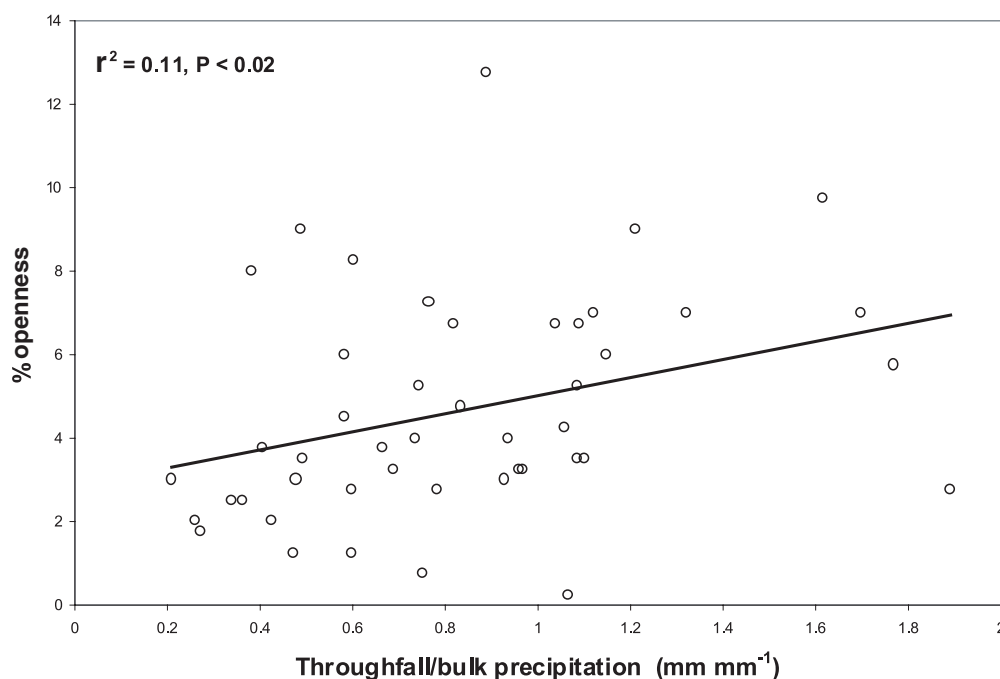


Figure 5. The relationship between the fractions of throughfall collected and per cent cover as determined by spherical densiometer.

Table 2. Changes in the coefficient of variation with increases in the number of collectors.

Number of collectors	Coefficient of variation
5	13.4
10	12.1
15	24.4
20	22.8
25	24.2
30	22.9
35	25.4
40	24.7
45	24.3
50	23.5
55	24.4

Lloyd *et al.* 1988). It is difficult to account for the inherent variability of interception and throughfall in scaling of these processes to the stand level, as evidenced in Table 2. To reduce the spatial variance, many previous studies have worked on relatively simple systems in terms of plant or canopy architecture.

Furthermore, determination of wet deposition rates in throughfall and interception estimates assume statistically independent samples from a random placement of collectors (Clark *et al.* 1998, Parker 1985). Independence should be estimated to better interpret the results from these studies. This study now provides a procedure by which independence can be determined in forested systems. For placement of collectors in this particular wet forest independence is achieved at 43 m. The significance of this distance becomes apparent when mapped spatially (Figure 6), and it appears to be due to large areas dominated either by individual tree canopies or by treefall gaps. This relationship likely holds true for other tropical wet forests with similar stand attributes, where treefalls are the major source of disturbance, and occur in similar density.

The influence of tree canopies and gaps was also found on light transmission at La Selva, Costa Rica. Independence was found to be 20 m for light interception as measured at 2 m in height (Clark *et al.* 1996). We expected the spatial variability of light to be greater than that of throughfall for several reasons. Because light interception (direct beam) decreases exponentially with height within forests (Beer-Lambert Law), the effect of the intercepting biomass on light is greater. Moreover, the frequency, duration and area of direct beam sunflecks lead toward increases in the spatial heterogeneity and variability,

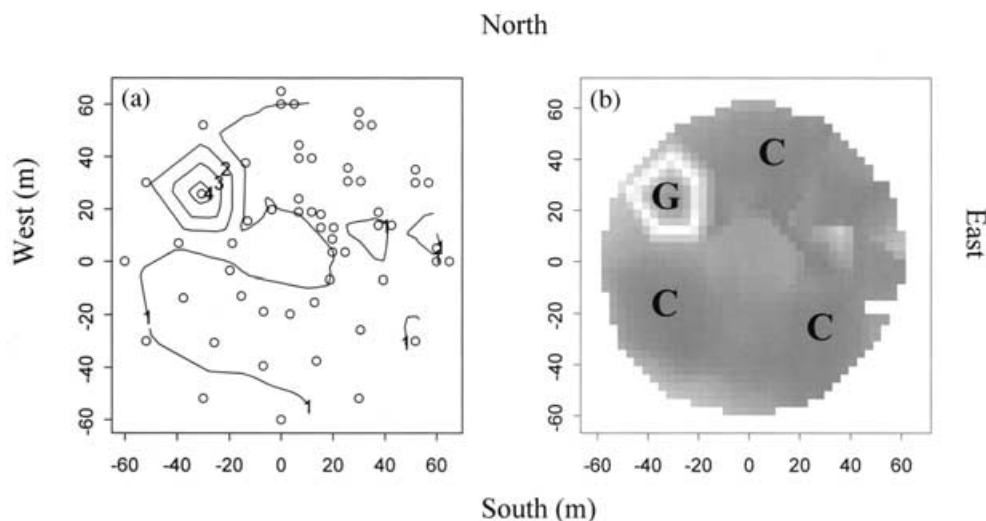


Figure 6. Variograms depicting mean throughfall volumes. In a), small circles show the location of Collectors and the numbers are means normalized by variance. In b), [G] signifies a gap was present with a horizontal distance >30 m, and [C] depicts specific tree crowns with minimum horizontal distance of 40 m. Darker pink indicates areas where throughfall << bulk precip, white – areas where throughfall < bulk precip, and blue – throughfall ≅ bulk precip. Axis units are in metres.

whereas throughfall volume is more dependent on the water-holding capacity of the intercepting biomass and is likely linear once canopy capacitance is filled. Thus, decreasing its spatial variability, assuming the horizontal distribution of biomass is uniform with height. Because the range for light and throughfall volume was more than double (20 m and 43 m, respectively), the variability in throughfall volume in a wet tropical lowland forest is more influenced by canopy architecture and the lack of overstorey (gaps) than light. A relationship was found between per cent cover and throughfall ($r^2 = 0.11$, $P = 0.02$) suggesting that interception is a function of ecosystem surface area (Waring & Schlesinger 1985) which in this case includes both leaf and epiphytic components. It is also important to note, that while epiphytic plants may not have contributed greatly to the attenuation of light below canopy, they may increase the ecosystem surface area substantially.

There is large variability in throughfall volume between collectors. Collection of throughfall in a single collector can exceed the bulk precipitation due to 'funneling', and likewise 'caps' above the collector can limit throughfall. Examination of the coefficient of variation shows that the variation in throughfall estimates stabilizes after 15 collectors, estimates of the mean are within 25% of the 'true' mean, and additional collectors do not contribute to precision of the mean (Table 2).

CONCLUSIONS

Spatial independence can be established for a wet tropical system where distance between collectors should be > 45 m. Canopy gaps and individual tree canopies influenced this distance. The variability in throughfall volume in a wet tropical lowland forest is more influenced by canopy architecture and the lack of overstorey (gaps) than light. When estimates were made from spatially independent collectors interception decreased by 19%. This result may not be significant, because 95% confidence intervals as estimated on a log-log plot increases greatly as the regression approaches the zero intercept. Interception was a function of ecosystem surface area estimated using LAI as a surrogate.

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