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Forest Ecology and Management 255 (2008) 1915–1925

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a Panamanian plantation

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Received 11 May 2007; received in revised form 8 December 2007; accepted 10 December 2007

Abstract

Tree canopies partition rainfall into temporary canopy storage, throughfall and stemflow. Knowledge of this partitioning process is needed to predict the hydrological effects of the large areas of tree plantations that are being established in the tropics. In this study, we compared throughfall, stemflow and interception in four Neotropical and one exotic tree species growing in selection trials in the Republic of Panama. We sought to answer four questions: (1) Are there interspecific differences in total throughfall and stemflow, and throughfall and stemflow for a range of rainfall depths?, (2) How do crown traits influence interspecific differences in throughfall?, (3) Does the spatial heterogeneity of throughfall differ among species? and (4) How do species affect litter biomass and other variables that influence rainfall erosivity? Rainfall depth mediated interspecific differences in throughfall and stemflow, the relative importance of crown traits in the interception process, and spatial heterogeneity of throughfall. Total throughfall was between 10.9 and 16.2% less in *Acacia mangium* than *Gliricidia sepium*, *Guazuma ulmifolia*, *Ochroma pyramidale* or *Pachira quinata*. Increasing rainfall also changed relative quantities of throughfall and stemflow among species. For example, throughfall was similar in *Gliricidia* and *Acacia* for small rain events, but increased more rapidly in *Gliricidia* with increasing rainfall depth. Interspecific differences in throughfall were driven, in part, by canopy traits. Leaf area index (LAI), crown depth and crown openness all affected throughfall from smaller storms, but live crown length was the only significant predictor of throughfall in storms that were deeper than 20 mm. The spatial heterogeneity of throughfall beneath individual tree canopies increased with rainfall depth, but was always lower in *Gliricidia* than in *Acacia*, *Ochroma*, or *Pachira*. High litter biomass and cover in *Acacia* and *Ochroma* relative to other species would be likely to buffer the erosive effects of raindrop impacts. These complex interactions between rainfall and species traits may affect local hydrology, and may need to be explicitly considered in reforestation projects in the seasonal tropics.

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Keywords: Throughfall; Stemflow; Canopy traits; Neotropical tree species; *Acacia mangium*; Plantation forestry; Hydrological impacts

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1. Introduction

1.1. Rainfall interception by trees

Tree canopies modify raindrop trajectories by partitioning the incident rainfall into throughfall and stemflow. A proportion of the incident rainfall is intercepted by, and retained temporarily on leaf surfaces, branches and stems. Some of this intercepted rainfall subsequently evaporates by a process known as ‘‘wet-canopy evaporation’’ or ‘‘interception-loss’’ (I_c). A second fraction, throughfall (T) either falls from foliage as ‘leaf-drip’ or passes directly through small gaps in the canopy as ‘direct throughfall’. A third component is channeled down side branches to the main stem as ‘stemflow’ (S) (Crockford and Richardson, 2000; Chappell et al., 2001). These components are linked by the following relationship:

$$I_c = P_g - T - S \tag{1}$$

where P_g stands for gross rainfall.

The species composition of vegetation cover and changes in land use affect the balance between throughfall, stemflow, interception and evapotranspiration (Brandt, 1987; Bonell, 1999; Douglas, 1999; Crockford and Richardson, 2000; Bruijnzeel, 2004,). These variables are modified by canopy cover, canopy architecture, and tree age in broadleaved and coniferous forests (e.g. Huber and Iroumé, 2001; Pypker et al., 2005), and agroforestry systems (Schroth et al., 1999). Leaf

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doi:10.1016/j.foreco.2007.12.025

shape, orientation and size (Calder, 2001; Nanko et al., 2006), branch angle, leaf area index (LAI) and canopy gap fractions all play roles in rainfall partitioning (Crockford and Richardson, 2000; Johnson and Lehmann, 2006). Stemflow is influenced by canopy volume and area (Martinez-Meza and Whitford, 1996), and the angle at which branches join main stems (Iida et al., 2005). Bark roughness and absorptivity further modify stemflow by affecting the storage capacity of main stems and branches, which may exceed that of small branches and foliage combined (Herwitz, 1985; Liu, 1998; Llorens and Gallart, 2000; Levia and Herwitz, 2005).

1.2. *Role of plantations in local hydrology*

Forest plantations and agroforestry are increasingly seen as viable land use alternatives on deforested and degraded lands in the tropics (Evans, 1999; Lamb, 1998; Cusack and Montagnini, 2004). If established over wide areas, tree plantations are likely to produce major alterations in watershed- and landscape-scale hydrology. Reforestation of whole watersheds generally leads to reduced dry season water flows (Jackson et al., 2005; Scott et al., 2005; Sun et al., 2006). Relative to grass cover or cropland, tree cover increases rainfall interception (e.g. Dunisch et al., 2003), but improves the infiltration of water into the soil, and limits evaporation from the soil (Wallace et al., 2005). Raindrop erosivity is also reduced because litter inputs directly protect the soil surface and improve soil structure (Wiersum, 1985; Brandt, 1987; Mapa, 1995; Putuhena and Cordery, 1996).

Planted trees might improve soil moisture and overall water yields if improved infiltration and reductions in soil evaporation were to exceed any additional losses due to evapotranspiration (Scott et al., 2005). Most interception studies in the tropics have, however, been done in unmanaged or lightly managed natural forests with multiple species and canopy layers (Chappell et al., 2001; Germer et al., 2006). By contrast, *Pinus* and *Eucalyptus* are the most frequently investigated genera in plantation-based interception studies (reviewed in Scott et al., 2005). Our knowledge of rainfall interception among tropical broadleaved tree species in plantation is derived from isolated studies of *Acacia auriculiformis* A. Cunn. (Wiersum, 1985), teak (*Tectona grandis* L.f.) (Calder, 2001), *Carapa guianensis* Aubl. (Dunisch et al., 2003), shade coffee plantations (Hairiah et al., 2006), and agroforestry systems (e.g. Imbach et al., 1989; Schroth et al., 1999). As the area of tropical plantations expands, and the number of species being grown in plantations increases, more studies of the effects of tropical plantations on rainfall interception and other aspects of local hydrology are needed.

1.3. *Objectives and research questions*

The purpose of our research was to investigate interspecific differences in the dynamics of throughfall and stemflow among plantation-grown tropical trees. Five species were chosen for study based on differences in their trunk and branch architecture, leaf size and arrangement and crown morphology. Data on throughfall and stemflow were collected from individual trees over 2 months to answer four questions: (1) Are there interspecific differences in total throughfall and stemflow, and throughfall and stemflow for a range of rainfall depths?, (2) How do crown traits influence interspecific differences in throughfall?, (3) Does the spatial heterogeneity of throughfall differ among species? and (4) How do species affect litter biomass and other variables that influence rainfall erosivity?

2. Methods

2.1. *Site descriptions*

Our study was conducted in an experimental multi-species tropical forest plantation located in Soberania National Park (SNP), Republic of Panama (9°10′N, 79°35′W). The natural vegetation in SNP is lowland tropical moist forest, in which annual rainfall, averaged over the period 1966–2003, was 2127 mm yr^{-1} with a 4-month dry season in which less than 100 mm of rain fell in each month (Autoridad Nacional del Ambiente, unpublished data). Most rain events are short but intense storms, with occasional longer events of moderate intensity. The topography of the planted area comprises rolling hills with slopes of up to 48% interspersed with occasional moist swales.

The plantation was established by the Project for Reforestation Using Native Species (PRORENA), a joint project of the Smithsonian Tropical Research Institute (STRI) and Yale Tropical Resources Institute (TRI). It comprises a series of species selection trials intended to demonstrate the feasibility of using native and exotic trees to restore forest cover to degraded agricultural land. At SNP, 63 native and exotic species pre-selected for their restoration potential, timber value, fodder production, live fencing and fruit production were planted between 2003 and 2005. Each specie was planted in three replicate monocultures of 20 trees in each of three randomized complete blocks at 3 m × 3 m spacing. At 2 years of age, half the trees in each plot were thinned to avoid crown competition, increasing inter-tree spacing to 6 m × 6 m.

2.2. *Species selection*

Tree species chosen for the measurement of throughfall and interception were selected on the basis of obvious differences in crown architecture, leaf size and arrangement and stem morphology (Table 1, Fig. 1). In addition to these morphological criteria, the crowns of neighboring trees had to be in contact, or nearly so, and only plots that had attained an average crown closure of 60% or greater were chosen for study. This metric was estimated by looking upwards through a 10 × 10 grid of 2 cm squares drawn on clear plastic and estimating closure by the grid at four random points. The species chosen were *Acacia mangium* Willd., *Gliricidia sepium* Jacq., *Guazuma ulmifolia* Lam., *Ochroma pyramidale* Swartz, and *Pachira quinata* (Jacq.) W.S. Alverson. All of these trees (hereafter described by their genus names only) have

Table 1
Morphological characteristics of five tree species chosen for study

Species	Family	Leaves	Stems and branches
Acacia mangium Willd.	Fabaceae	Phyllodes[a], alternate and spiral around branches	Single stem, monopodial, plagiotropic branches
Gliricidia sepium Jacq.	Fabaceae	Pinnately compound, 8–12 leaflets	Multiple stem, branching from base, orthotropic branches
Guazuma ulmifolia Lam.	Sterculariaceae	Simple, alternate, lanceolate	Single stem, sympodial trunk, orthotropic to plagiotropic branching
Ochroma pyramidale Swartz	Bombacaceae	Simple, alternate	Single stem, monopodial,
Pachira quinata (Jacq.) W.S. Alverson	Bombacaceae	Palmately compound, 7 lanceolate leaflets	Single stem, monopodial trunk, plagiotropic branches

[a] Phyllodes are modified petioles or stems.

commercial or traditional multipurpose value, and are increasingly being planted across Central America by forestry companies and farmers. Large plantations of *A. mangium* have also been established in reclamation projects and for commercial purposes in parts of its native range in southeast Asia (Kuusipalo et al., 1995).

2.3. Field measurements

2.3.1. Crown characteristics and the understory

Each specie was represented by a sample of three individuals, each of which was chosen from separate plots. We measured the height, live crown length, crown width, diameter at breast height (dbh), and diameter at stemflow gauge height on each individual at the beginning of the study. Tree height and live crown length were estimated using a clinometer at 10 or 15 m from the base of the tree. Crown diameter was measured along the longest crown axis and perpendicular to this axis using a metric tape. These measurements were subsequently used to estimate canopy area using the formula for an ellipse. Tree diameters were measured to the nearest millimeter with a metric diameter tape.

Leaf area index for each tree was measured with an Accupar PAR-80 ceptometer (Decagon, Inc, Pullman, Ill). The ceptometer was matched to an external quantum sensor (LI-COR Inc., Lincoln, NE) for simultaneous above- and below-canopy readings. The ceptometer's 80 quantum sensors were divided into four groups of 20 to allow for local non-randomness in the distribution of canopy elements. Zenith angle was calculated automatically from latitude and longitude

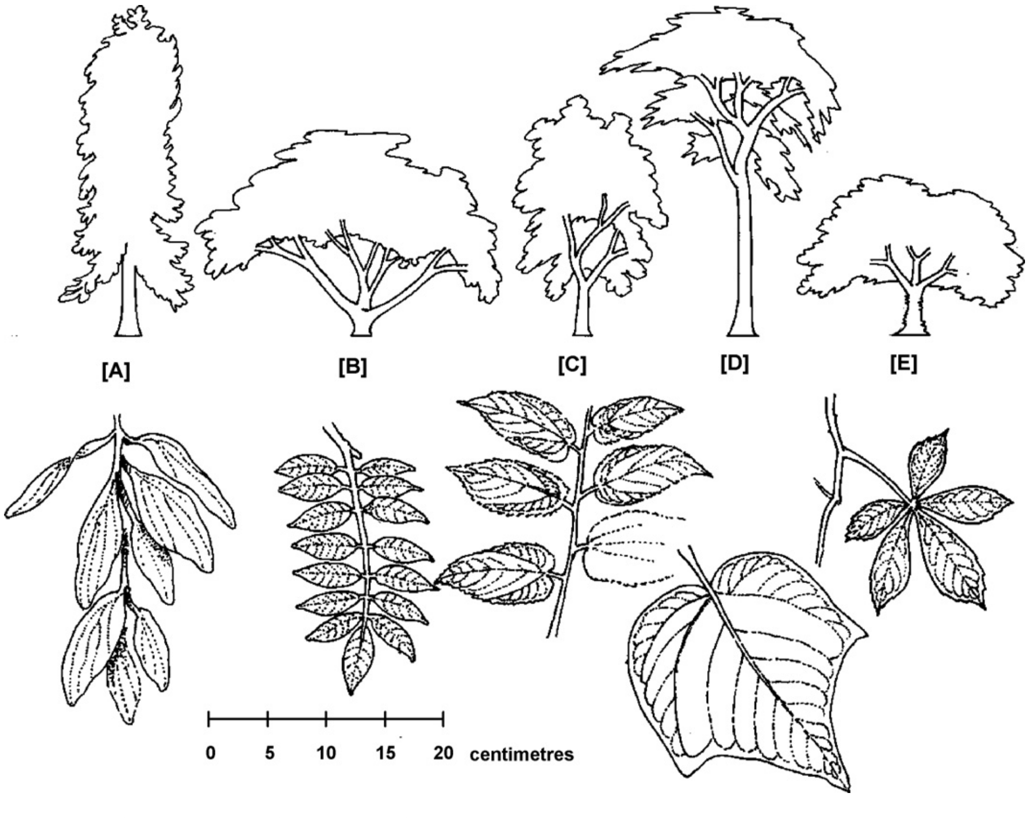

Fig. 1. Basic morphology and leaf characteristics of 3-year-old subject tree species: [A] *Acacia mangium*, [B] *Gliricidia sepium*, [C] *Guazuma ulmifolia*, [D] *Ochroma pyramidale* and [E] *Pachira quinata*. Trees and leaves are drawn approximately to scale relative to each other. Drawing by Andrew Park.

information provided to the instrument. The canopy angle distribution parameter (χ) was calculated for individual trees using the expression:

$$\chi = \frac{\ln \tau_0}{\ln \tau_{90}} \tag{2}$$

where τ_0 is the proportion of light seen vertically through a clump of foliage and τ_{90} is the proportion of light to shade seen horizontally (Decagon Devices, 2003). A transparent grid of 100 2 cm × 2 cm squares was used to obtain estimates of τ_0 and τ_{90}. The grid was held in front of the observer, about 30 cm from the eyes, so that it approximately filled the field of vision. Four estimates were made for each tree, inserted into the equation, and the average χ was then programmed into the ceptometer. Eight LAI readings were taken under each of the 15 subject trees. For each reading, the ceptometer was positioned with the wand facing outwards from the tree trunk, about midway between the trunk and the drip line of the canopy. Successive readings were taken at angles of approximately 45° from each other.

Canopy openness was averaged from four digital fisheye photographs taken at a height of about 60 cm at four cardinal points around each tree. Photographs were taken with a Nikon Coolpix 4500 equipped with a Nikon FC-E8 fisheye attachment. Individual photographs were analyzed using Gap Light Analyzer (GLA) software (Frazer et al., 1999) using 36 azimuth and 20 zenith regions. The ‘‘Gap Fraction’’ utility was used to calculate the ratio of open sky pixels to total pixels integrated across zenith regions. We then calculated openness as the percentage of open sky in the zenith regions between 0° (directly overhead) to 45°. This angle was selected to reflect the probable limits to the angle of incidence of falling raindrops impacting on our tree canopies.

Leaf litter was collected from ten 0.041 m^2 quadrats randomly placed beneath each tree. The samples were dried for 72 h in a drying oven and were then weighed to the nearest tenth of a gram. Litter depth in each quadrat was also estimated using a metric tape and averaged out of three random measurements to the closest 0.1 cm. Litter cover is thought to be one of the major variables limiting the erosivity of rainfall, since raindrops may still achieve terminal velocity when dripping from leaves high in the canopy (Wiersum, 1985; Calder, 2001).

2.3.2. Throughfall and stemflow

Rainfall in the open was measured using a tipping-bucket automated rain gauge (Spectrum Technologies, Plainsfield, Illinois) with a bucket capacity of 0.3 mm, which recorded rainfall in 5 min intervals. Throughfall was measured using improvised rain gauges made from 1 US gallon capacity bleach bottles and plastic funnels (avg. diameter = 21.2 cm). Twelve gauges were placed beneath each tree. These were established in three concentric rings of four gauges at 33%, 67% and 100% of the crown width to permit the sampling of different crown densities. The position of the first gauge in each ring was determined by taking a random compass bearing centred upon the tree trunk. The other three gauges in each ring were placed at angles of 90 and 180° from the first one. Each bottle was secured to a 1/4 in. diameter metal stake to keep it upright.

Stemflow was measured using collars constructed from flexible aluminum foil plates that were fitted around the entire circumference of the tree trunk. Each stemflow collar was sealed to the trunk using all weather silicon caulking, and doubly secured on the underside of the collar with duct tape. A 1 cm aperture PVC hose led from the stemflow gauge to a lidded bucket (approximately 16 l capacity). Collars were placed at heights of approximately 0.5 m from the base of the tree, depending on the species and stem arrangement. In the case of *Gliricidia*, in which each individual had between four and six stems, two stemflow gauges were established around separate stems selected at random.

Throughfall and stemflow were measured each morning. A discrete rain event was held to be one that occurred with at least seven daylight hours between individual storms. Direct observation confirmed that this amount of time was sufficient to evaporate residual water from tree crowns. Measurements were taken between July 23rd and September 20th 2006.

2.4. Statistical analysis

Throughfall per tree for each rain event was estimated as the average of the throughfall collected from all 12 gauges. Stemflow volume was divided by crown area to yield depth of stemflow per tree (Gómez et al., 2002). For *Gliricidia*, stemflow was estimated by multiplying the measured stemflow depth by following ratio: sum of circumferences of stems with gauges divided by sum of circumferences of all stems. Question 1 (Are there interspecific differences in throughfall and stemflow?) was investigated using analysis of variance (ANOVA) and linear regression. An ANOVA was calculated on interspecific differences in the percentage of the total rainfall for the study period that became throughfall. Linear regressions of gross rainfall depth on throughfall and stemflow were calculated on log-transformed data to reduce heteroscedacity among residuals. Regression slopes were then compared using a *t*-test for the difference between two slope coefficients. If slope coefficients were statistically equal (parallel slopes), we tested whether slopes coincided or occupied different elevations in the regression graph (Zar, 1996, Ch. 18), and therefore had different intercepts. Dunn–Sidak corrections were applied to the significance levels returned by these interspecific comparisons to allow for Type I error inflation in multiple tests.

The potential influence of crown traits on percent throughfall (Question 2) was tested with multiple linear regressions on the pooled tree population. Canopy traits used to predict throughfall were LAI, percent crown openness, and live crown depth. Because rain events with different depths are likely to vary in the ways that they interact with canopy traits, separate regressions were performed on the following storm size categories ($\leq$5, $>$5–20, 20–30 and $>$30 mm). Multiple regressions were performed on untransformed data, since exploratory analyses showed residuals to be normally distributed with no heteroscedacity in the data.

To answer Question 3 (Does the spatial heterogeneity of throughfall differ among species?), we first calculated variance-mean ratios for the throughfall contributions of all 12 rain gauges beneath individual trees for each rain event. The variance–mean ratio is often used as a measure of overall spatial randomness. Because the variance equals the mean under a Poisson distribution, values close to 1 indicate spatial randomness, while those much larger or smaller than 1 indicate relative clustering or randomness, respectively (Greig-Smith, 1983). Here, we use it to measure the influence of leaf size and distribution on the variability of throughfall collected in individual gauges. These ratios were log transformed and regressed against log-transformed gross rainfall with statistical comparisons of slope coefficients as described above.

Finally, to answer Question 4 (how do species affect litter and soil surface variables?), we used one-way ANOVAs to explore interspecific differences in litter biomass, litter cover and the proportion of bare ground. All statistical tests were performed in SPSS 12.0 or SPSS 14.0 (SPSS Inc., USA, 1989–2005).

3. Results

3.1. Species characteristics

Significant interspecific differences ($P \leq 0.05$) were found for overall height, live crown length and LAI, but not for crown openness or crown area (Table 2). *Acacia* (mean height 10.1 m), *Ochroma* (mean height 11.5 m) were at least 2.4 m taller than the other three species. *Gliricidia*, *Guazuma* and *Pachira*, whose mean heights ranged from 5.1 to 7.7 m, were also significantly different in height. *Acacia* had an average live crown length of 9.2 m, which contrasted with two short-crowned trees (*Gliricidia* and *Pachira*) and those with intermediate live crown lengths (*Guazuma* and *Ochroma*). *Acacia* and *Pachira* had the highest LAIs (2.51 and 2.38, respectively), while *Gliricidia* and *Guazuma* had intermediate values (1.86 and 1.75, respectively), and *Ochroma* had a low LAI of 1.25.

3.2. Rainfall, throughfall and stemflow

3.2.1. Gross rainfall

During the study period, 32 rainfall events were identified as being available for analysis (Fig. 2). These events delivered 699.2 mm of rain with average and median depths of 21.9 mm and 14.2 mm, respectively. Rainfall lasted between 5 and 595 min, with 5-min intensities that ranged from 0.3 to 13.7 mm. The smallest and largest events delivered 0.3 and 87.5 mm of rain, respectively. Nine additional rain events were removed from analysis due to measurement errors, rest days, or because rain recommenced before daily measurements were complete.

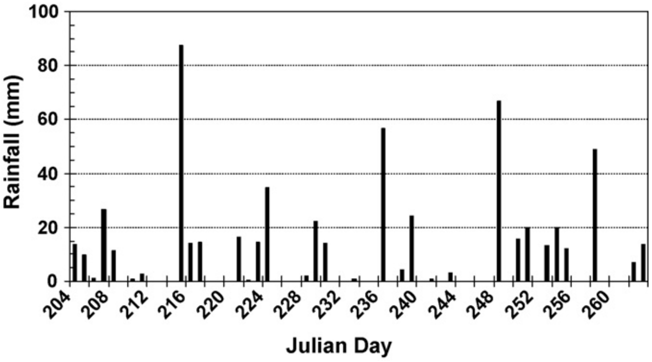

Fig. 2. Rainfall depth arranged by Julian Day.

3.2.2. Throughfall and stemflow

Throughfall totals were calculated on 31 rain events for 11 out of 15 trees, and 30 events in the remaining four. Occasional rain events were omitted from analysis due to measurement uncertainties. Average total throughfall ranged from 73.1% (*Acacia*) to 89.3% (*Guazuma*) from (Table 3). Interspecific differences in total throughfall expressed as a percentage of rainfall were significant ($F_{4,10} = 7.876$, $P = 0.004$). *Acacia* transmitted between 10.9 to 16.2% less throughfall than the other species ($P \leq 0.004$). All other interspecific differences in percent throughfall were smaller than 5.2%, and were non-significant.

Average total stemflow varied from 0.9 to 2.7% of the total rainfall. During some of the larger rain events, however, the stemflow containers of several trees overflowed. Measurement errors necessitated the deletion of records from several trees for other rain events. Stemflow was therefore measured over 14–26 rain events (Table 3), leading to large interspecific differences in the gross rainfall depths for which stemflow was calculated. We therefore restrict our analysis of total stemflow depth to the reporting of descriptive statistics. Total rainfall interception, calculated only for events in which both throughfall and stemflow were recorded, ranged from 9.2% of gross rainfall for *Guazuma* to 25.6% for *Acacia*.

Linear regressions of gross rainfall versus throughfall were highly significant ($0.988 \leq r^2 \leq 0.994$, $P \leq 0.002$; see

Table 2
Canopy and stem traits for the five subject species with mean ± standard deviation

Species	Height (m)	Live crown length (m)	Crown area (m^2)	LAI ($m^2\ m^{-2}$)	Canopy openness (%)
A. mangium	10.1 (0.95) a	9.2 (1.25) a	18.0 (6.82) a	2.51 (0.45) a	20.6 (2.83) a
G. sepium	7.7 (1.35) b	3.9 (3.09) b	30.3 (6.55) a	1.86 (0.32) b	24.9 (2.53) a
G. ulmifolia	6.8 (0.75) c	4.8 (1.10) c	18.1 (2.26) a	1.75 (0.20) b	26.6 (2.36) a
O. pyramidale	11.5 (0.38) a	7.7 (0.50) c	39.7 (18.93) a	1.25 (0.61) c	35.3 (12.75) a
P. quinata	5.1 (0.25) d	3.5 (1.03) b	21.7 (5.28) a	2.38 (0.25) a	27.3 (10.54) a

Means followed by different letters are significantly different (least significant difference (LSD), $P \leq 0.05$).

Table 3
Summary of mean total rainfall, throughfall, stemflow and interception for five tropical tree species

	A. mangium	*G. sepium*	*G. ulmifolia*	*O. pyramidale*	*P. quinata*
Throughfall					
Total rainfall (mm)	653.6	632.5	688.0	665.8	665.8
Total throughfall (mm)	478.4 (52.27)	549.7 (9.05)	614.2 (34.33)	560.0 (62.14)	582.7 (14.23)
Percent throughfall	73.1 (2.93) a	86.9 (1.43) b	89.3 (4.99) b	84.0 (5.77) b	87.7 (3.41) b
Stemflow					
Total rainfall (mm)[a]	158.1	255.1	264.2	269.6	232.6
Total stemflow (mm)	4.1 (2.65)	3.6 (1.09)	6.0 (0.92)	2.4 (1.32)	3.1 (1.13)
Percent stemflow	2.7 (1.98)	1.5 (0.21)	2.3 (0.28)	0.9 (0.58)	1.3 (0.26)
Percent Interception[b]	25.6 (7.87)	13.5 (0.50)	9.2 (5.93)	15.7 (9.24)	11.2 (4.02)

Percent throughfall figures separated by different letters are significantly different (LSD, $P \leq 0.05$).

[a] Stemflow calculated on between 14 and 26 rain events.

[b] Interception calculated only for rain events in which both throughfall and stemflow occurred.

Table 4). Histograms and quantile–quantile (QQ) plots of regression residuals were normally distributed with no apparent heteroscadicity. Furthermore, no temporal trends in residuals were observed in scatterplots of the temporal sequence of rain events and unstandardized regression residuals. When slopes were compared, significant differences were found between *Acacia* and *Gliricidia* ($P < 0.001$), and between *Gliricidia* and *Ochroma* ($P = 0.002$). *Gliricidia* had a similar intercept to *Acacia*, but transmitted more throughfall as rain event depths increased ($P \leq 0.0051$, Fig. 3a). Throughfall was lower in *Acacia* than in the other species across the full range of rainfall depths ($P \leq 0.0064$). Minor differences in intercept were observed between *Guazuma* and *Pachira*, and between *Ochroma* and *Guazuma*. Back-transformation of the log-transformed data allowed us to calculate the rainfall needed to saturate the canopy before throughfall would occur in each specie. Thresholds were 0.28 mm (*Acacia*), 0.23 mm (*Gliricidia*), 0.13 mm (*Guazuma*), 0.11 mm (*Ochroma*) and 0.17 mm (*Pachira*).

Linear regressions of gross rainfall versus stemflow depth were also significant ($0.386 \leq r^2 \leq 0.733$, $P \leq 0.001$). Residuals were normally distributed and no temporal trends in stemflow were apparent. The slope coefficient for *Ochroma* was significantly smaller than those for *Acacia*, *Gliricidia* and *Guazuma* ($P \leq 0.0051$, Table 4, Fig. 3b). Similarly, *Guazuma* had a steeper slope of stemflow with rainfall than did *Pachira*. Of the species pairs whose slope coefficients were not significantly different, *Acacia* transmitted more stemflow than *Gliricidia* throughout the rainfall range tested ($P \leq 0.0085$). The slope for *Gliricidia* was lower than that for *Guazuma* for all rainfall depths greater than 0.35 mm. Saturation thresholds for stemflow were larger in every species than those for throughfall. Thresholds were 1.19 mm (*Acacia*), 1.82 mm (*Gliricidia*), 1.62 mm (*Guazuma*), 1.43 mm (*Ochroma*) and 1.78 mm (*Pachira*). The variability of stemflow among individuals of the same species was, however, greater than the variability of throughfall (Fig. 3b). Statistical comparisons of stemflow regression coefficients and the thresholds calculated from them should therefore be interpreted with caution.

3.3. Throughfall–crown trait relationships

The relative importance of different crown traits as predictors of percent throughfall depended on rainfall depth. All regressions were highly significant, ($P \leq 0.001$), although the relatively low *r*-squared values showed unmeasured variables to account for much of the variability in percent

Table 4
Regression coefficients for gross rainfall versus throughfall and stemflow (standard errors of coefficients in parentheses)

Species	Intercept	Slope	R^2	*F*	d.f.	*P*-value
Throughfall						
A. mangium	−0.104 (0.011) a	0.974 (0.009) a	0.992	5392.9	1, 88	<0.001
G. sepium	−0.093 (0.012) abc	1.022 (0.010) b	0.991	6610.3	1, 89	<0.001
G. ulmifolia	−0.057 (0.010) b	1.002 (0.008) ab	0.994	6581.3	1, 89	<0.001
O. pyramidale	−0.044 (0.013) c	0.975 (0.011) a	0.988	6472.4	1, 88	0.002
P. quinata	−0.068 (0.011) b	1.007 (0.010) ab	0.992	7528.1	1, 88	<0.001
Stemflow						
A. mangium	−0.055 (0.020) ac	0.165 (0.022) ac	0.581	57.99	1, 48	<0.001
G. sepium	−0.048 (0.013) b	0.115 (0.014) ab	0.525	70.4	1, 77	<0.001
G. ulmifolia	−0.072 (0.013) a	0.172 (0.013) c	0.733	183.6	1, 67	<0.001
O. pyramidale	−0.027 (0.012) b	0.070 (0.011) b	0.386	40.8	1, 65	<0.001
P. quinata	−0.051 (0.012) bc	0.115 (0.012) ac	0.624	94.8	1, 57	<0.001

Different letters following the standard errors for slope coefficients indicate significantly different slopes (Dunn–Sidak adjusted *alpha* = 0.0051). Intercept standard errors followed by different letters indicate parallel but non-overlapping slopes (Dunn–Sidak adjusted *alpha* = 0.0064 for throughfall and 0.0085 for stemflow).

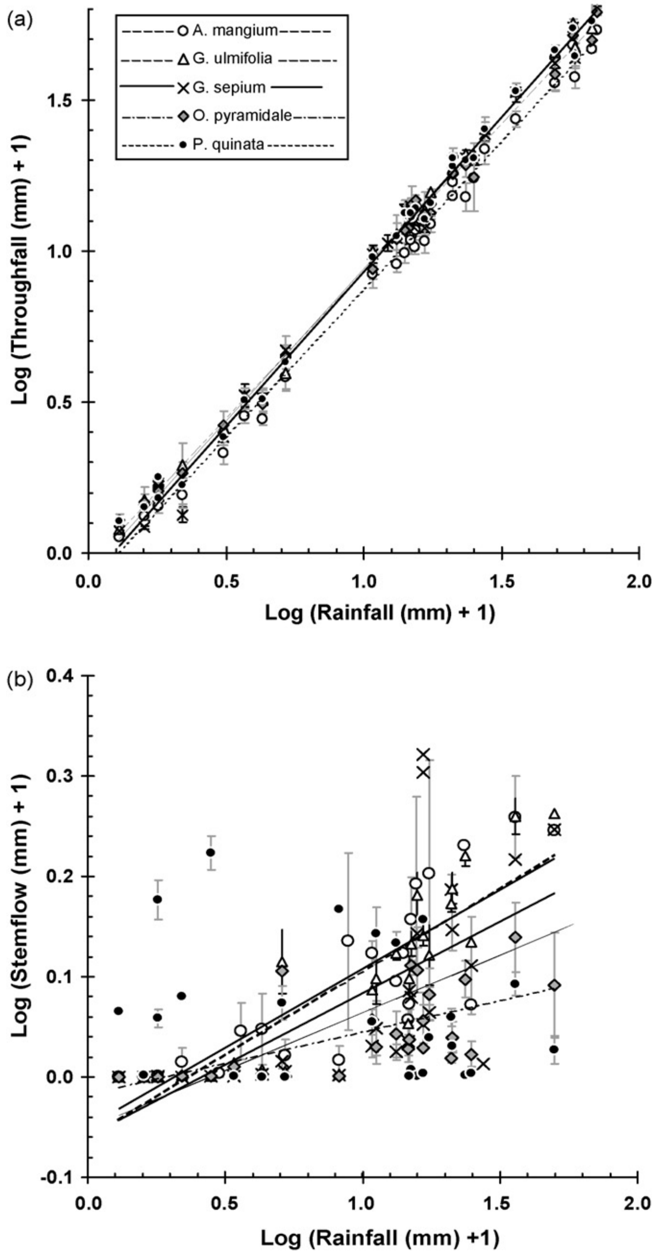

Fig. 3. (a) Average throughfall and (b) average stemflow for the five tree species. Values are averages per rain event. Error bars are standard errors for each rain event, and lines represent predicted throughfall or stemflow from regression equations.

throughfall ($0.164 \leq r^2 \leq 0.653$, Table 5). As expected, the coefficients for LAI and live crown length were negative while those for crown openness were always positive (Table 5). Every crown trait affected throughfall in the ≤5 mm and >5–20 mm rainfall depth categories, but live crown length was the only statistically significant variable in the >20–30 mm and >30 mm classes ($P \leq 0.001$). Two distinct trends in the magnitude of the regression coefficients were observed. First, slope coefficient for crown openness declined consistently with increasing rainfall depth. Second, coefficients for live crown length became increasingly negative (from −1.578 to −2.207) with greater rainfall depth.

3.4. Spatial heterogeneity of throughfall

Variance–mean ratios became significantly larger as rainfall depth increased in every species ($0.339 \leq r^2 \leq 0.639$, $P < 0.001$; Table 6). They varied from a 0.009 beneath *Gliricidia* for a 0.8 mm rain event to a 19.6 under *Pachira* for a 57.7 mm event. These figures illustrate a general transition from relatively regular (or even) to highly clumped distributions of throughfall as rainfall depths increased. Regression slopes were not significantly different, but *Acacia*, *Ochroma* and *Pachira* showed greater throughfall heterogeneity than *Gliricidia* at all rainfall depths ($P \leq 0.0051$), with *Guazuma* showing an intermediate degree of variation.

3.5. Soil surface characteristics

Significant interspecific differences were found in leaf litter biomass and percent litter cover, but not in percent bare ground or litter depth (Table 7). *Acacia* and *Ochroma* had higher litter biomasses than *Gliricidia*, *Guazuma* and *Pachira* ($P \leq 0.05$). *Acacia* also had significantly more litter cover than *Gliricidia* and *Pachira* ($P \leq 0.040$), while *Ochroma* had more litter cover than *Pachira* ($P = 0.006$).

4. Discussion

4.1. The role of canopy traits

Although interspecific differences in throughfall were relatively small, total throughfall and throughfall for individual rain events were significantly lower in *Acacia* than in the other four species (Question 1, Fig. 3a). Stemflow tended to be higher in *Acacia* than other species, although interspecific differences in regression slopes showed the relationship of stemflow to rainfall depth to be a complex one (Fig. 3b).

Differences in the throughfall–rainfall relationship appear to have been driven by species canopy traits (Question 2). The relative influence of crown length, LAI and canopy openness varied with rainfall depth (Table 5), and probably reflected the operations of fine scale variables that were not directly measured in our study. Leaf shape and orientation, branch angle, and bark roughness all modify the partitioning of rainfall to throughfall and stemflow (Hutchinson and Roberts, 1981; Herwitz, 1987; Crockford and Richardson, 2000). Leaf size (Calder, 2001; Nanko et al., 2006) and the vertical layering of canopies (Brandt, 1987) strongly affect throughfall drop size and terminal velocity.

High variance-mean ratios of throughfall beneath *Acacia*, *Ochroma* and *Pachira* were probably caused by the relatively large size and coarse-grained distribution of leaves in these species. *Ochroma* has some of the largest leaves among Neotropical trees, and throughfall heterogeneity in this specie could be attributed to the tendency of rain drops to coalesce into localized throughfall streams on large leaves (Calder, 2001; Nanko et al., 2006). *Acacia* phyllodes are arranged in whorls around stems, which may lead to similar localization of throughfall. By contrast, the small pinnate leaves of *Gliricidia*

Table 5
Results of linear regressions of crown trait effects on percent throughfall, divided into four rainfall depth classes

Rainfall	Variable	Coefficient	S.E.	*P*-value	R^2	*F*	d.f.	*P*-value
$\leq$5 mm	Intercept	87.322	(5.437)	<0.001	0.164	29.02	3, 55	<0.001
	LAI ($m^2\ m^{-2}$)	−3.858	(1.477)	0.009				
	Crown length (m)	−1.578	(0.244)	<0.001				
	Crown openness (%)	0.343	(0.105)	<0.001				
>5–20 mm	Intercept	95.989	(5.880)	<0.001	0.314	23.60	3, 148	<0.001
	LAI ($m^2\ m^{-2}$)	−4.690	(1.610)	0.004				
	Crown length (m)	−1.689	(0.265)	<0.001				
	Crown openness (%)	0.227	(0.114)	0.049				
20–30 mm	Intercept	88.336	(8.759)	<0.001	0.353	9.98	3, 55	<0.001
	LAI ($m^2\ m^{-2}$)	−2.575	(2.378)	0.477				
	Crown length (m)	−1.770	(0.393)	<0.001				
	Crown openness (%)	0.282	(0.169)	0.061				
>30 mm	Intercept	105.784	(8.484)	<0.001	0.316	12.47	3, 81	<0.001
	LAI ($m^2\ m^{-2}$)	−3.931	(2.265)	0.086				
	Crown length (m)	−2.206	(0.380)	<0.001				
	Crown openness (%)	−0.018	(0.162)	0.911				

Table 6
Regression coefficients for gross rainfall vs. throughfall variance–mean ratio (standard errors of coefficients in parentheses)

Species	Intercept	Slope	R^2	*F*	d.f.	*P*-value
A. mangium	−0.064 (0.033) a	0.360 (0.027) a	0.639	171.4	1, 88	<0.001
G. sepium	−0.138 (0.057) b	0.344 (0.047) a	0.339	52.3	1, 89	<0.001
G. ulmifolia	−0.137 (0.044) ab	0.400 (0.036) a	0.561	126.4	1, 89	<0.001
O. pyramidale	−0.044 (0.044) a	0.376 (0.036) a	0.510	106.1	1, 88	<0.001
P. quinata	−0.084 (0.044) a	0.401 (0.036) a	0.551	119.5	1, 88	<0.001

Intercept standard errors followed by different letters indicate parallel but non-overlapping slopes (Dunn–Sidak adjusted *alpha* = 0.0051).

are likely to produce fine-grained patterns of leaf surface and open space, leading to a less heterogeneous distribution of throughfall at all rainfall depths (Fig. 4, Question 3).

High rainfall interception by forest canopies is frequently associated with high LAIs (e.g. Marin et al., 2000). In our study, however, live crown length was the only significant constraint on throughfall under rain events that were $\geq$20 mm deep. Although one might expect LAI and crown length to be correlated, no such relationship existed among our study species ($R = -0.047$).

Crown length could potentially influence throughfall independently of LAI in several ways. First, short-term storage of rainfall might be enhanced because of reduced evaporation in the interiors of long crowns. Second, for a given LAI, leaves distributed across long canopies may have more of their surface area available to intercept raindrops than those that occupy a restricted vertical space, where overlapping leaf surfaces may be in contact. High numbers of branches emerging from the main stems of long crowns also enhance water storage, especially in heavy rains (Herwitz, 1985). Finally, Dietz et al. (2006) suggest that high rates of evaporation of intercepted rainfall from tall trees lead to low throughfall. This hypothesis depends on long canopies having greater "roughness" (Cionco, 1972) than short ones. If this were the case, high evaporation would be the product of high rates of turbulent exchange with the atmosphere in tall canopies relative to short trees with similar LAIs.

Rough bark may store more water, and therefore generate less stemflow than smooth bark (Herwitz, 1985; Crockford and Richardson, 2000). The opposite appeared to be true in our

Table 7
Comparison of selected understory variables

Species	Litter biomass (g 0.25 m^{-2})	Bare ground (%)	Litter cover (%)[a]	Litter depth (cm)[a]
A. mangium	249.6 (105.85) a	5.0 (5.30)	72.4 (10.47) a	1.6 (0.30)
G. sepium	48.6 (5.96) b	15.7 (16.60)	45.3 (15.81) b	0.9 (0.21)
G. ulmifolia	43.3 (10.96) b	24.9[a]	32.6[a]	2.6[a]
O. pyramidale	237.5 (107.97) a	10.1 (5.41)	63.6 (4.43) a	1.5 (0.63)
P. quinata	31.4 (23.81) b	25.6 (6.76)	26.4 (12.66) b	0.9 (0.19)

Figures separated by different letters are significantly different (LSD, $P \leq 0.05$).

[a] Only one sample collected for *G. ulmifolia* in these categories.

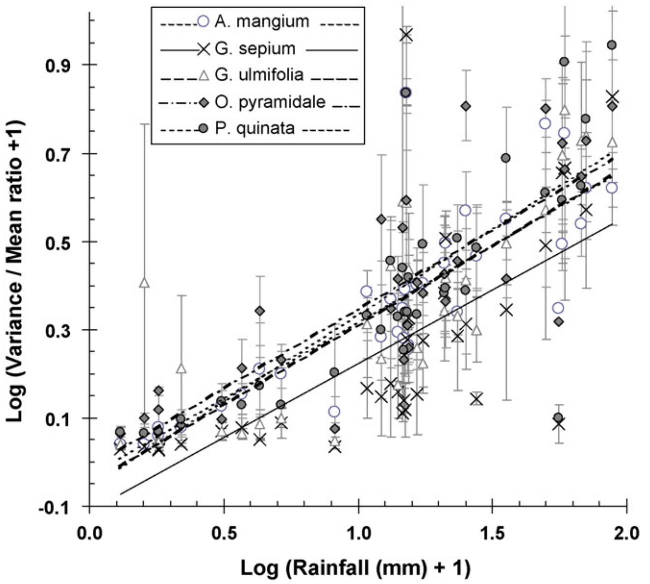

Fig. 4. Average variance–mean ratios for each rain event. Error bars are standard errors for each rain event, and lines represent predicted throughfall or stemflow from regression equations.

study (see also Marin et al., 2000). *Ochroma*, which had smooth bark, generated smaller quantities of stemflow than trees with rough bark (e.g. *Acacia*) or interconnected thorns (*Pachira*). Differences in leaf arrangement and branch angle may have negated any effects of bark roughness among our species. The phyllodes of *Acacia*, for example, are angled down into their stems, which would tend to channel water towards stemflow. Leaves of *Ochroma*, *Pachira* and *Gliricidia* hang away from their stems, and may therefore channel water towards throughfall. Interspecific differences in bark absorptivity, which were not measured in our study, also have a strong role in determining stemflow volumes (Liu, 1998; Levia and Herwitz, 2005).

4.2. Comparisons with other studies

Throughfall percentages in our study (73.1–87.7%) were in the mid- to high end of the ranges recorded for natural forests. In natural forests, throughfall values as low as 27% (matorral) or as high as 96% (African moist forest) of incident rainfall are not uncommon (Levia and Frost, 2006). Extremes of 16 and 115% are recorded for *terra firma* Amazonian rain forest (Germer et al., 2006). Among the data available for plantations, throughfall percentages for *Gliricidia*, *Guazuma*, *Ochroma* and *Pachira* occupied the mid-range reviewed by Scott et al. (2005). Throughfall in *Acacia* was similar to the low (70.0–73.5%) figures recorded for plantations of *Pinus caribaea* and *P. elliotti* in the same review. Our throughfall figures also fell in the lower end of the range reported for several agroforestry systems (Jackson, 2000; van Dijk and Bruijnzeel, 2001).

Our stemflow figures (0.9–2.7%) were close to or lower than the median value of 2.66% reviewed by Johnson and Lehmann (2006). Intraspecific differences in stemflow were far greater than those of throughfall in our study (Fig. 3b). High stemflow variability appears to be common (Crockford and Richardson, 2000; Marin et al., 2000). Stemflow percent may also increase with rainfall depth. With these facts in mind, it should be noted that our stemflow data were biased towards smaller rain events, since the largest events caused overflow from the available collectors. Higher rates of stemflow may have been recorded, had we been able to collect data from the largest rain events.

Storage thresholds for throughfall (0.17–0.28 mm) in our species were relatively low compared to other studies. Throughfall thresholds as low as 0.04 mm in temperate forest (Price and Carlyle-Moses, 2003), or as high as 1.55 mm in humid tropical forest have been recorded (Marin et al., 2000). Herwitz (1985) derived rainfall storage thresholds two to four times higher than those in our study. These were attributed to high LAIs in old growth rain forest trees (up to 20 m^2 m^{-2}), and the increase in woody surface relative to crown area with tree age.

4.3. Management implications

The re-establishment of partial tree cover in agroforestry systems reduces surface runoff, erosion and soil evaporation relative to cropland alone. These protective functions of tree cover must be balanced against interception losses (Wallace et al., 2005), and the large amount of water transpired by many fast growing trees (Scott et al., 2005).

A. mangium might be the best of the five species to plant if the primary goal of reforestation is to limit erosion. *Acacia* intercepted more rainfall than other species, and its long crown meant that raindrops would, on average, have a shorter distance to fall than was the case for *Ochroma* or *Gliricidia*. Throughfall from *Acacia* might therefore have lower kinetic energy, and cause less erosion than throughfall from other species. *Acacia* also maintained a higher biomass and cover of leaf litter than the other species (Question 4), which also buffers raindrop impacts (Wiersum, 1985; Putuhena and Cordery, 1996), and improves infiltration (Mapa, 1995; Hairiah et al., 2006). On the other hand, the greater volume of water intercepted by *Acacia*, together with its apparent lack of stomatal control (Scott et al., 2005) may produce high rates of evapotranspiration, increasing the risk that plantations of this specie could reduce dry season water flows.

If used in agroforestry systems, or as nurse tree to foster natural regeneration, semi-deciduous trees such as *Gliricidia* may be an optimal choice. Three-year old *Gliricidia* had wide canopies and low LAIs (1.86), which should allow other species to establish beneath them. Furthermore, *Gliricidia's* relatively low variance–mean ratio meant that throughfall would be more evenly distributed than it would beneath other species. Such ‘‘smoothing out’’ of throughfall has the potential to reduce throughfall kinetic energy, and reduces the potential for rill initiation (Keim and Skaugset, 2003).

Acknowledgements

The authors wish to acknowledge the hard work of the numerous investigators, administrators, and technicians who maintain and monitor the PRORENA plantations. We thank the Smithsonian Tropical Research Institute for providing logistic support to us throughout our stay in Panama. Andrew Park's research was funded by a University of Winnipeg startup grant, and Jessie-Lee Cameron was funded by a University of Winnipeg major grant. The editorial and scientific advice of two anonymous reviewers is also gratefully acknowledged.

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