INFLUENCE OF CROWN TRAITS AND LEAF ARRANGEMENT ON RAINFALL INTERCEPTION, THROUGHFALL, AND STEMFLOW IN FIVE TROPICAL TREE SPECIES.

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Abstract

Tropical forest canopies intercept rainfall and partition the water into canopy storage (which is later evaporated), throughfall, and stemflow. Knowledge of this partitioning process is needed to predict the hydrological effects of establishing large areas of plantation forests on degraded farmland in the humid tropics. In this study, I compared throughfall, stemflow and canopy interception in four neo-tropical and one exotic tree species growing in plantation trials in the Republic of Panama. Research questions included: (1) Are there interspecific differences in the relationship between rainfall intensity and throughfall and stemflow?, (2) How does rainfall intensity interact with the distribution of throughfall beneath the tree?, (3) How do crown traits influence the depth of throughfall?, and (4) How do species affect litter biomass and other variables that influence rainfall erosivity? *Acacia mangium* intercepted approximately 13% more rainfall than the other four species. Interspecific differences in crown traits significantly influenced throughfall depth. Leaf area index, crown length, and crown openness all affected throughfall from smaller rainfall events. Only crown length consistently affected throughfall in rainfall events greater than 5 mm. Interspecific differences were found in leaf litter biomass, with *Acacia mangium* and *Ochroma pyramidale* having significantly more leaf litter around the tree than the remaining three species. This finding has potential consequences for erodibility, given that increased leaf litter biomass could provide soil cover to prevent erosion.

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1. Introduction

Tree canopies modulate the pathways followed by rainfall from the open sky to the ground. They modify the trajectories of falling raindrops by partitioning different proportions of the incident rainfall into throughfall and stemflow. Tree canopies will prevent a certain proportion of the rainfall from reaching the ground, because raindrops are intercepted and retained by leaves, branches, and stems. Some of this intercepted rainfall subsequently evaporates by a process known as "wet-canopy evaporation" or "interception-loss" (Chappell *et al.* 2001; Germer *et al.* 2005). A second fraction of intercepted rainfall is temporarily stored in the canopy, but will then drip from canopy surfaces as 'leaf-drip'. A third interception component may be channeled down side branches to the main stem as 'stemflow'. The remaining rainfall drops through small gaps in the canopy as 'direct throughfall' (Crockford & Richardson 2000; Chappell *et al.* 2001). Canopies also alter the spatial pattern of raindrop impacts on understory plants, leaf litter, and bare soil (Chappell *et al.* 2001). These relationships can be expressed as follows:

$$I_c = P_g - Th - Sf \qquad \text{Equation 1}$$

where I_c represents canopy interception, P_g stands for gross rainfall, Th represents throughfall (leaf drip plus direct throughfall) (Munishi & Shear 2005), and Sf represents stemflow (defined as precipitation intercepted by vegetative cover and channeled down the stem or major branches of such cover) (Calder 2001). Effective (net) precipitation can then be expressed as:

$$P_n = Th + Sf - I_L \qquad \text{Equation 2}$$

where P_n is net precipitation and I_L is interception by forest litter.

To summarize, canopy interception is measured as the difference between gross (above-canopy) and net (below-canopy) rainfall. Net rainfall is determined by summing the total of throughfall (canopy drip) and stemflow (Scatena 1990; Silva & Okumura 1996; Xiao *et al.* 1997; Murakami 2006).

The balance between throughfall, stemflow, interception and subsequent evaporation exerts a direct influence on local and regional hydrology and nutrient cycles. Understanding the mechanisms and magnitude of canopy interception is therefore critical to water resource management in natural forests and plantations. Interception losses are of major importance in influencing the water yield of forested areas (that is, the amount of water leaving the system as evaporation and amount that is absorbed into the soil) relative to deforested areas and other vegetative cover (Crockford & Richardson 2000, Gomez *et al.*). Sinun *et al.* (1992) has noted that widespread deforestation reduces evapotranspiration by 5 – 50%. Under certain conditions, therefore, regional precipitation patterns may be adversely affected (Calder 1976; Gash & Stewart 1977; Scatena 1990; Asdak *et al.* 1998).

At the regional and global scales, knowledge of interception and throughfall processes is needed to calibrate and validate the hydrological components of global circulation models (Lloyd 1990; Crockford & Richardson 2000). This knowledge is also required to characterize moisture distribution, soil erosion, and pollutant concentration and distribution in hydrological studies (Xiao *et al.* 2001).

Improved knowledge of canopy processes is allowing for better estimation of both the influence of forests on hydrology and the influence of hydrology (and meteorology) on forest function (Calder 2001). Keim and Skauget (2004) have suggested that researchers' interest in rainfall interception by forest canopies has primarily been stimulated by its importance as a determinant of evapo-transpiration. Evapotranspiration has been identified as the most important variable next to gross rainfall in understanding both forest hydrology and the irrigation of crops (Mohan & Arumugam 1996). Additionally, understanding spatio-temporal patterns in rainfall received beneath tropical forests is required for eco-hydrological modeling of soil-water status, river behaviour, soil erosion, nutrient loss, and wet-canopy evaporation (Chappell *et al.* 2001).

Canopy interception has been extensively studied in tropical and temperate forests at scales varying from that of individual trees to large stands (Rowe 1983; Crockford & Richardson 2000). Both coniferous and broadleaved species have been studied (Rowe 1983; Crockford & Richardson 2000). Most of these studies have, however, been conducted in unmanaged or lightly managed natural forests that support multiple species and canopy layers (Chappell *et al.* 2001; Germer *et al.* 2005). Other studies have been conducted in agroforestry systems (Schroth *et al.* 1999; Hairiah *et al.* 2006). In contrast, interception studies of individual species growing in forest plantations are rare. Rainfall interception parameters for plantation species are known only from isolated studies, for species such as *Acacia auriculiformis* A. Cunn. (Weirsum 1985), *Tectona grandis* L.f. (Calder 2001), *Carapa guianensis* Aubl. (Dunisch *et al.* 2003), and shade coffee plantations (Levia Jr.& Herwitz 2000).

1.1 The need for plantations

According to recent estimates, 350 million hectares of formerly forested pasture and cropland in the tropics is too degraded to support natural forest regeneration (I.T.T.O. 2005). Forest plantations and various forms of agroforestry are increasingly seen as viable land use alternatives on such land (Lamb 1998; Evans 1999; Cusack & Mantagnini 2004). Plantation forests differ from primary forests or naturally regenerated secondary forests in a number of ways. For example, plantation trees are generally planted in monocultures or simple mixtures whereas tropical forests contain hundreds of tree species. Plantations are usually planted in evenly spaced rows in contrast with the random or clumped growing positions of wild trees. Plantation canopies may also be more permeable to wind than the canopies of mature forests. Younger trees can also carry very large numbers of small branches, quite close to the ground. The result may be less channeling of water down the primary trunk of the tree, and more water drip off the branches themselves (consistent with low stemflow values from Crockford & Richardson 2000).

1.2. Study rationale and objectives

Canopy cover, tree species and tree age are known to affect canopy water storage and throughfall (Herwitz 1985; Pypker *et al.* 2005). However, few data exist to compare the roles played by species-specific canopy architectures, leaf sizes, and stem arrangements in modifying interception beneath a common rainfall regime. Recent literature indicates that crown size, leaf shape and orientation, branch angle, flow path obstructions, bark type, and canopy gaps all have individual roles in the partitioning of

rainfall (Crockford & Richardson 2000; Johnson & Lehmann 2006). Studies of desert shrubs show stemflow to be influenced by canopy volume and area (Martinez-Meza & Whitford 1996). Leaf size also impacts interception; compared to small leaves, water drops falling on large leaves tend to coalesce, thus concentrating throughfall (Nanko *et al.*2006).

The purpose of this project was to investigate throughfall, stemflow and interception in plantation-grown tropical trees that differ in their crown architectures and leaf arrangements. The tree species chosen included *Acacia mangium* Willd., *Gliricidia sepium* Jacq., *Guazuma ulmifolia* Lam., *Ochroma pyramidale* Swartz, and *Pachira quinata* (Jacq.) W.S. Alverson. All of these trees have commercial or traditional uses, and are increasingly being planted across Central America by forestry companies and farmers (PRORENA 2003). Extensive 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).

Five species were chosen for their marked differences in trunk and branch architecture, crown morphology, and leaf size and arrangements. Data on throughfall and stemflow were collected from individual trees over two months to answer the following questions: (1) Are there interspecific differences in the relationship between rainfall intensity and throughfall and stemflow?, (2) How does rainfall depth/intensity interact with the distribution of throughfall beneath the tree?, (3) How do crown traits influence the depth of throughfall?, and (4) How do species affect litter biomass and other variables that influence rainfall erosivity?

2. Methods

2.1 Site and plantation descriptions

This study was conducted in an experimental multi-species tropical forest plantation located in Soberania National Park (SNP), Republic of Panama (8°57′N, 79°30′W, Figure 1). The natural vegetation of the SNP is lowland tropical moist forest, and the area experiences pronounced rainy and dry seasons. Annual rainfall, averaged over the period 1966 – 2003 was 2127 mm per year with a four-month dry season (late-December to early-April) in which less than 100 mm of rain fell in each month (ANAM 2005). 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 (ANAM 2005).

The plantation was established and is maintained 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. Seedlings were planted in monocultures at 3 x 3 m spacing in plots of 20 trees. Three replicate monocultures of 20 trees of each species were established in each of three randomized complete blocks (PRORENA 2003).

In all, sixty-three native and exotic species pre-selected for their restoration potential, timber value, fodder production, live fencing and fruit production were planted

over a period of three years (2003 to 2005). Trees chosen for the measurement of throughfall and interception were selected from the 2003 planting. Because of their rapid growth, each plot from this planting was thinned to 50% of its original density in August 2005 to avoid crown competition.

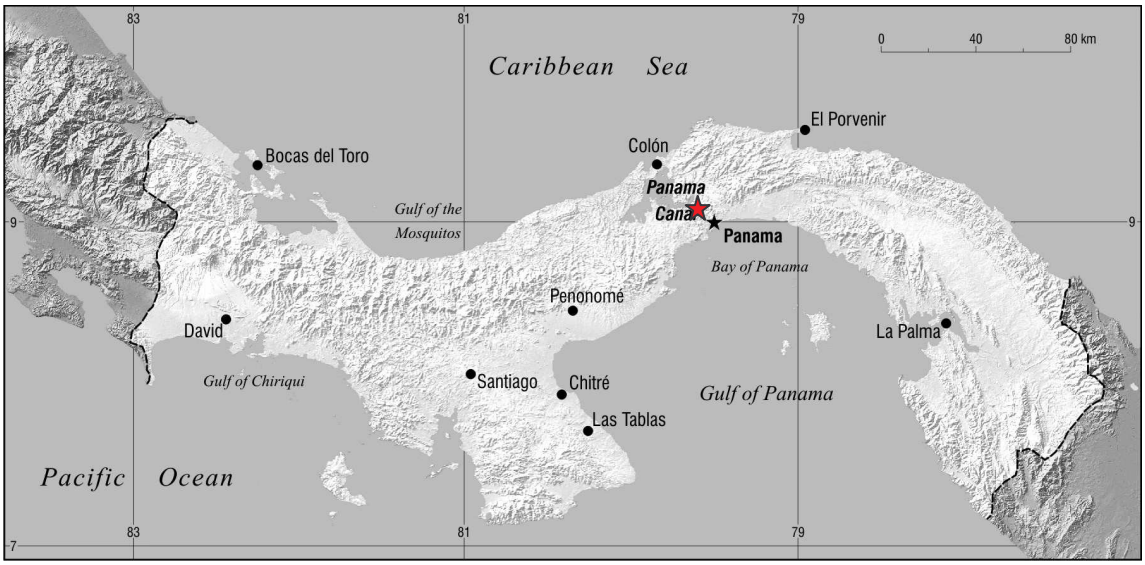

Figure 1: Map of the Republic of Panama, demonstrating the location of the study site in Soberania National Park, near Gamboa.

2.2 Tree selection

Throughfall and stemflow were measured in five tree species that were chosen due to differences in crown architecture, stem and branch morphology, and leaf size and arrangement (Table 1, and Figure 2). In addition to these morphological criteria, only species 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 x 10 grid of 2 cm squares drawn on clear plastic and estimating closure by the grid at four random points. The tree species chosen were *A. mangium, G. sepium, G. ulmifolia, O, pyramidale,* and *P.*

quinata. Three individuals of each of the five species that fit the crown closure criteria were chosen for this study (n=15 trees).

Table 1: Preliminary details of the five subject tree species from Soberania National Park, Republic of Panama.

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

Phyllodes are modified petioles or stems.

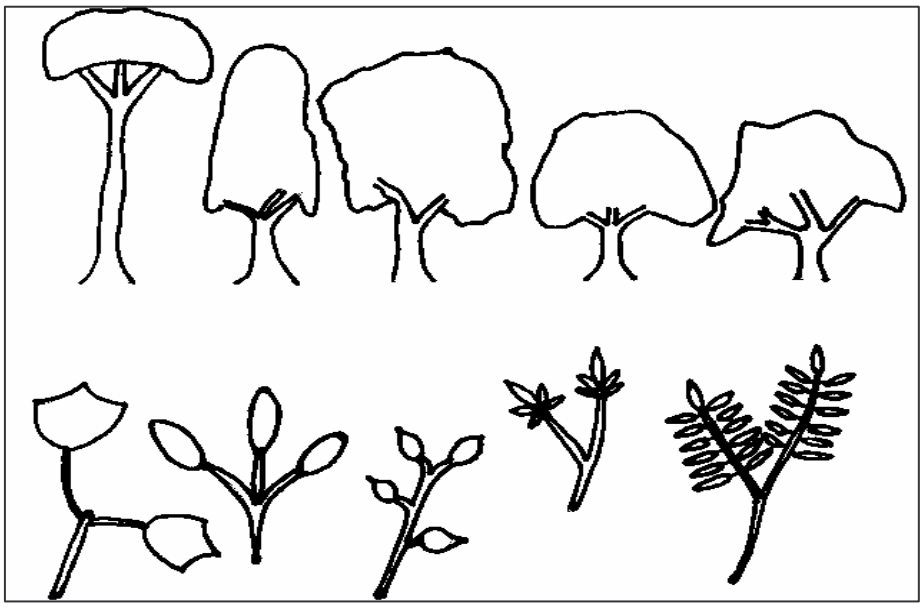

Figure 2: Profile drawings of the five subject tree species and their leaf arrangements, from left to right *Ochroma pyramidale, Acacia mangium, Guazuma ulmifolia, Pachira quinata* and *Gliricidia sepium.* The drawings approximate the relative size and shape of crowns and leaves as observed in the trees growing in Sobernia National Park, Panama. Scales are approximate.

2.3.1 Field measurements: Crown characteristics and the understory

The tree characteristics for interspecific comparisons were collected at the beginning of the experiment. Measurements included tree height, crown length and crown width measured across the longest crown axis and at right angles to it, diameter at breast height (dbh) and diameter at stemflow gauge height (approximately 0.5 m from the base of the tree). Tree height and crown length were estimated using a Suunto (Suunto, Langely, BC) clinometer at 10 m (or occasionally 15 m) from the base of the tree. Crown length was calculated by taking clinometer measurements at the top of the tree, base of the crown, and base of the tree. Crown width was measured along the longest crown axis and perpendicular to this axis using a metric tape and then averaged to receive a final value. Tree diameters were measured to the nearest millimetre with a metric diameter

tape. Additional data obtained from the plots were Leaf Area Index (LAI) measurements, crown openness estimations, and leaf litter samples.

Leaf area index (LAI) was measured with an AccuPAR PAR-80 ceptometer (Decagon, Inc, Pullman, USA). The ceptometer was matched to an external quantum sensor (LI-COR Inc., Lincoln, NB) for simultaneous above- and below-canopy readings. The ceptometer's 80 quantum sensors were further 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 information provided to the instrument. The canopy angle distribution parameter (χ) was calculated for individual trees using the expression:

$$\chi = \frac{\ln \tau_0}{\ln \tau_{90}} \qquad \text{Equation 3}$$

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 (see Decagon Application Note "Measuring χ Value", Frazer 1999). A transparent grid of 100 2 x 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 mid-way between the trunk and the drip line of the canopy. Successive readings were taken at angles of approximately 45 degrees 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^{o} (directly overhead) to 45^{o}. 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 using a 0.25 m^2 quadrat; 10 quadrats were randomly selected beneath each tree by tossing the quadrat square. Leaf litter was compared across species, based on collection from ten sub-samples per plot. The samples were dried for 36-72 hours in a drying oven and were then weighed to the nearest tenth of a gram. Percent ground cover underneath the trees was estimated using cover classes (% bare ground, % litter, % vegetation <30 cm, and % vegetation >30 cm). Litter depth was also estimated using a metric tape and an average was obtained from three random measurements to the closest 0.1 cm. Undergrowth was classified into the following morphospecies: lycopods, grasses, *Sacarum* sp., tall herbs, *Piper* sp., vines, and tree seedlings.

2.3.2 Field measurements: throughfall and stemflow

Throughfall was measured using improvised rain gauges constructed of 1 US gallon capacity Chlorox bottles and plastic funnels (avg. diameter = 21.2 cm). Twelve gauges were placed on the ground beneath each tree (36 per species, 180 gauges total). Three concentric rings of four gauges were established around each main stem to permit the sampling of different crown densities. Rings were set up at 30% of the crown width, 65% of the crown width, and beneath the drip-line (Figure 3 and Appendix A). 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 degrees from the first one. Funnels were placed in the mouths of the clorox bottles, and secured to ¼ inch diameter metal stakes with elastic bands (Figure 4 and Appendix A).

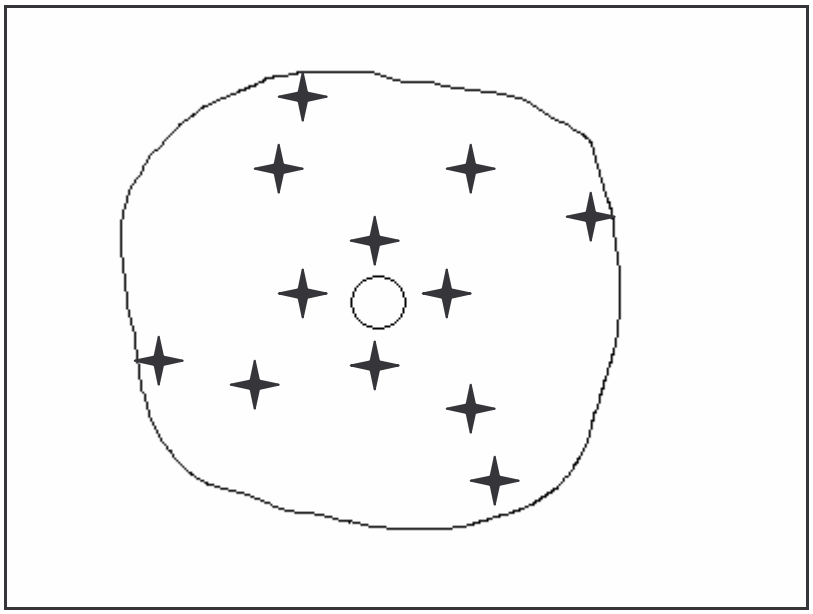

Figure 3: Plan view of throughfall gauge setup beneath the crown. Each gauge position is denoted by a four-point star. The inner ring consists of four gauges, each set at 30% of the crown width. The middle ring consists of four gauges, each set at 65% of the crown width. The outer ring consists of four gauges, each set at the dripline. The placement of the first gauge in each ring is determined by a random compass bearing at the trunk of the tree. The other three gauges in each ring were placed at angles of 90 and 180 degrees from the first one.

Throughfall was measured using the inner cylinder of an All-Weather Rain Gauge (Forestry Suppliers, Jackson, MS), which has an expanded scale calibrated for measuring rain to a precision of 0.2 mm. Rainfall in the open was measured using a tipping-bucket automated rain gauge (Spectrum Technologies, Plainsfield, Illinois), which recorded rainfall to a precision of 0.3 mm at five-minute intervals. Six improvised rain gauges were also placed in the open to compare rainfall estimates derived from these gauges and the tipping bucket gauge. Rainfall in the open was measured every day from the six funnel/bottle set-ups, and data was downloaded from the tipping-bucket gauge every 24 days using Specware software.

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 single 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 (Figure 4). One stemflow gauge was placed around the main trunks of single-stemmed species. In the case of *Gliricidia sepium*, which had multiple stems, two stemflow gauges were established around separate stems selected at random. Trunk diameters were measured at the stemflow gauge placement heights to provide a basis for stemflow measurement. Stemflow gauges were emptied and measured after each rainfall event. As with the throughfall and rainfall in the open measurements, the stemflow was emptied into a Forestry Suppliers rain gauge inner cylinder.

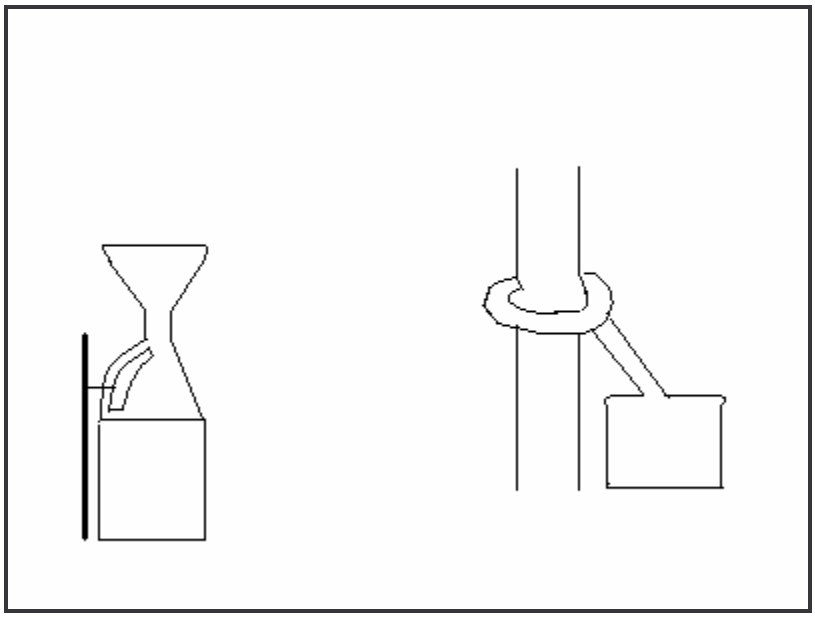

Figure 4: Diagram of throughfall gauge (right) and stemflow gauge. Throughfall gauges consisted of a plastic funnel attached to a 1 gallon (approximately 3.8 l) capacity Clorox bottle. These were attached to a metal stake in ground via elastic bands. Stemflow gauges were constructed of aluminum foil plates which were cut and molded to the trunk. Collars were attached with silicon caulking and secured at the base with duct tape. A hose led from the bottom of the collar to a 16 l (approximate capacity) plastic bucket at the base of the tree.

Throughfall and stemflow were measured each morning, with the exceptions of occasional rest days or occasions when storms occurred during the measurement period. A discrete rain event was considered 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. Gross rainfall, throughfall and stemflow measurements were taken between July 23rd and September 20th 2006. After allowing for rest days, days when measurements were interrupted by fresh storms and occasional incomplete collection of data, a total of 36 discrete rain events were defined.

2.4 Statistical Analysis

Throughfall per tree for each storm was calculated as the average throughfall from all 12 gauges. Throughfall averages for each concentric ring of gauges were also calculated. Stemflow volume was divided by crown area to yield depth of stemflow per tree (Gomez *et al.* 2002). Due to the limited capacity of the available stemflow containers, stemflow from a number of the trees overflowed in storms that generated more than 35 mm of rainfall. Data recording errors that resulted in biased measurements necessitated the deletion of records from several other trees for some storms. The stemflow data set was therefore substantially smaller than that for throughfall (n = 20 to 28 storms, depending on the species).

Linear regressions of rainfall versus throughfall and stemflow were used to determine if there were interspecific differences between rainfall depth/intensity and interception values. Raw data for gross rainfall and throughfall were log transformed to diminish heteroscedacity among residuals. Regression slope coefficients were compared using a *t*-test in order to determine the effect of the treatment (species) on the variable (throughfall). In the event that slope coefficients could not be separated statistically (parallel slopes), further testing occurred to determine whether they coincided or used different intercepts (Zar 1996).

Exploratory data analyses suggested that stemflow had a non-linear or even "broken-stick" relationship with rainfall. Thus, the curve-fitting function in SPSS was used to generate non-linear models, since no data transformation produced a satisfactory

linear model. In every case, r^2 was maximized by a power function relationship. The power curve is expressed as $Y = Bo * X^{B1}$, where Bo is the intercept and B1 is the slope coefficient. The power relationship is described as Ln (Y) = Ln Bo + Ln X. This provided a linear equation which was analyzed as for a normal linear regression.

A General Linear Model (GLM) Repeated Measures ANOVA was used to determine the interaction of rainfall depth/intensity with the throughfall heterogeneity beneath tree canopies (Objective 2). This procedure provides analysis of variance when the same measurement is made several times on each subject or case (Landau & Everitt 2004). In this analysis, storm size was divided into five categories (<5, 5-10, 10-20, 20-30, and >30 mm), which were used as repeated measures (within-subject) variables and ring position (30% of canopy width, 66% of canopy width, or drip-line) was nested within species. The final model repeated measures model was $Y_{ijk} = D_i + Sj + R_k(Sj) + D_i*Sj + Di*R(S) + \varepsilon_{ijk}$, where D represents the repeated measure of rainfall intensity, S is species, R(S) is ring nested within species, and Di*Ring(S) represents the interaction term.

The potential influence of species crown traits on percent throughfall (Objective 3) was tested with a multiple linear regression on the pooled tree populations. Canopy traits used to predict throughfall were LAI, percent crown openness, and crown length. Because rainfall events of different depth may vary in the ways that they interact with canopy traits, multiple regressions were performed on the same throughfall categories that were used in the nested ANOVA, as outlined above. Multiple regressions were

performed on untransformed data, since exploratory analyses showed residuals to be normally distributed and no heteroscedacity in the data.

Finally, one-way ANOVAs were used to explore interspecific differences in tree canopy traits and understory variables. All statistical tests were performed in SPSS 12.0 or SPSS 14.0 (SPSS Inc., USA, 1989-2005).

3. Results

3.1 Rainfall, throughfall and stemflow

3.1.1 Gross rainfall

The total rainfall at Soberania National Park from July 22 to September 19 2006 was 819.7 mm. During the study period, 29 storms were identified as distinct rain events available for analyses (Appendix B). Nine additional storms were also measured, but removed from analyses due to several factors including human measurement error and storms which fell over multiple days. The average depth for a rainfall event was 14.37 mm, with a range of duration from 5 minutes to 595 minutes and maximum five-minute intensities from 0.3 to 13.7 mm (see Table 3 for rainfall and interception summaries by species).

Table 2. Summary of mean total rainfall, throughfall and stemflow for five tropical tree species. Percent throughfall figures separated by different letters are significantly different (LSD, $P \leq 0.05$).

	A. mangium	***G. sepium***	***G. ulmifolia***	***O. pyramidale***	***P. quinata***
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
Total rainfall for stemflow (mm)	158.1	255.1	264.2	269.6	232.6
Total stemflow (mm)	4.1 (2.65)	3.8 (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)

3.1.2 Throughfall and stemflow

Acacia mangium intercepted significantly more rainfall than the other tree species, as seen in Table 2. This was supported statistically by the comparison of regression slopes (Figure 5). For stemflow, Table 2 suggested that *A. mangium* and *G. ulmifolia* produced the greatest stemflow depth, although this was not analyzed further due to time constraints. Measurement and equipment-related errors resulted in different numbers of storms being analyzed for each species for both throughfall and stemflow.

Thus, summary statistics in Table 2 were based on the total rainfall measured for each species and each variable.

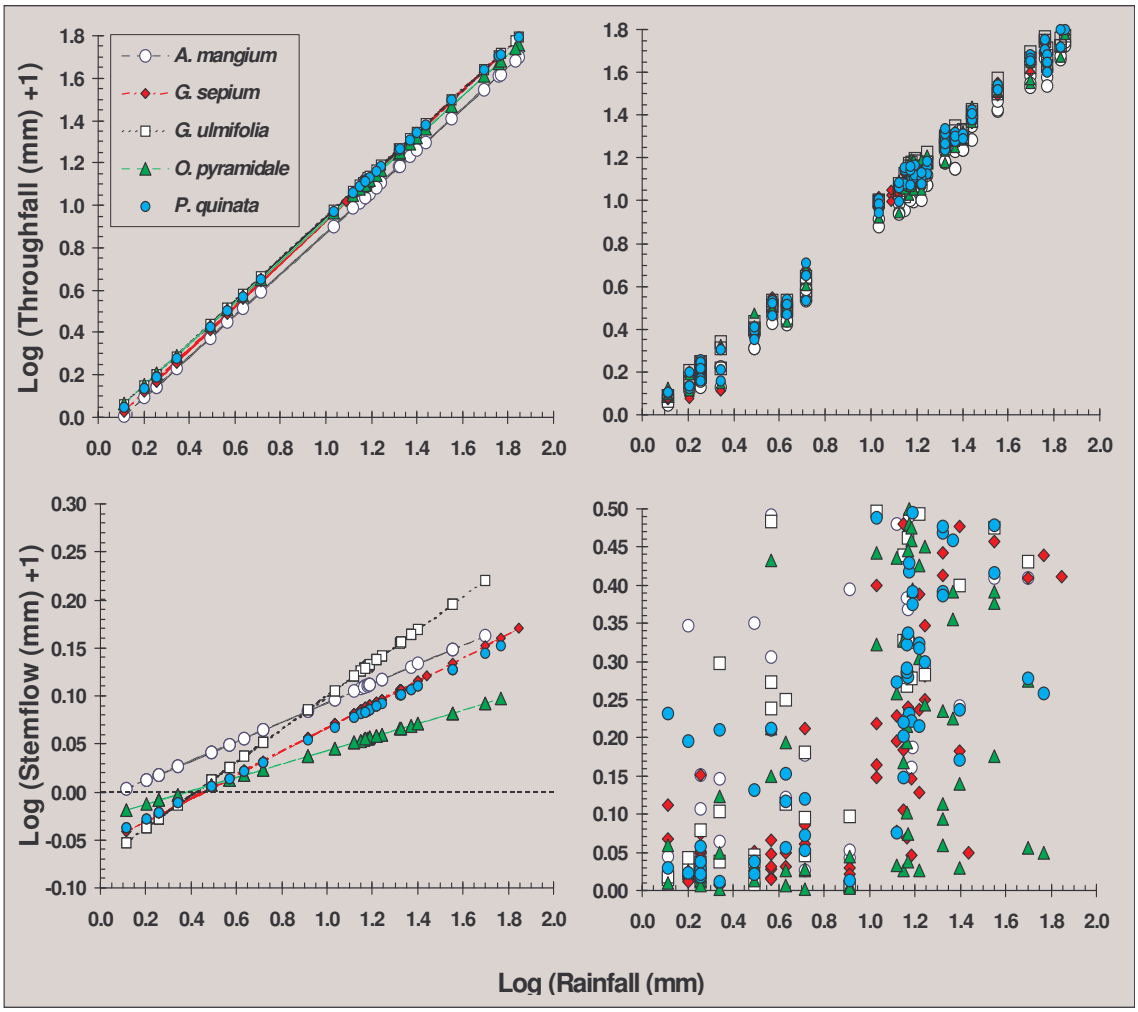

Figure 5: (a) Predicted and (b) actual values of rainfall versus throughfall, and (c) predicted and (d) actual values of rainfall versus stemflow for the five subject species.

All linear regressions of gross rainfall versus throughfall depth were highly significant ($P \leq 0.002$, $0.988 \leq r^2 \leq 0.994$, see Table 3). When slopes were compared,

significant differences were found between *A. mangium* and *G. sepium* (P <0.001), and between *O. pyramidale* and *G. sepium* (P =0.002). If slope coefficients are not different from each other, then there is the potential for them to be either coincident or parallel but at different heights (Zar 1996). Further *t*-tests were conducted to determine whether paired parallel slopes for different species coincided or not. Slopes indicate the overall relationship of each species with throughfall. Intercepts indicate amount of throughfall. Highly significant differences in slope heights were found between *A. mangium* and *G. ulmifolia*, *O. pyramidale*, and *P. quinata* (P<0.001). *Ochroma pyramidale* also differed significantly in slope height from *G. ulmifolia* and *P. quinata* (P<0.001).

Table 3: Regression coefficients for gross rainfall versus throughfall for individual species. Standard errors are shown in parentheses. Standard errors for Beta followed by different letters indicate significantly different slopes (Dunn-Sidak adjusted alpha=0.0051). Intercept standard errors followed by different letters indicate slopes that are parallel but at different heights (Dunn-Sidak adjusted alpha=0.0064).

Species	Intercept		Slope		r^2	*P*
A. mangium	-0.104	(0.011)a	0.974	(0.009)a	0.992	<0.001
G. sepium	-0.093	(0.012)a	1.022	(0.010)b	0.991	<0.001
G. ulmifolia	-0.057	(0.010)b	1.002	(0.008)ab	0.994	<0.001
O. pyramidale	-0.044	(0.013)c	0.975	(0.011)ac	0.988	0.002
P. quinata	-0.068	(0.011)b	1.007	(0.010)ab	0.992	<0.001

Much like the throughfall relationships, all non-linear regressions of gross rainfall versus stemflow depth were highly significant (P<0.001, $0.654 \leq r^2 \leq 0.865$, Table 4 and Figure 5).

Table 4: Regression coefficients for gross rainfall versus stemflow for individual species. Standard errors are shown in parentheses. Raw data was first fit to a Power curve and then linear regressions were ran on the linear equations that the Power fit yielded.

Species	Intercept		Slope		r^2	*P*
A. mangium	0.002	(0.001)	1.765	(0.157)	0.724	<0.001
G. sepium	0.001	(0.000)	1.816	(0.084)	0.860	<0.001
G. ulmifolia	0.001	(0.000)	1.943	(0.111)	0.820	<0.001
O. pyramidale	0.001	(0.000)	1.655	(0.149)	0.654	<0.001
P. quinata	0.002	(0.000)	1.661	(0.087)	0.865	<0.001

There were significant interspecific differences in throughfall depth among rainfall event depth categories ($F_{4,15}$=5.041, *P*=0.003, Table 5a). There was no difference among throughfall gauges placed in different sub-canopy positions (ring position) and throughfall depth ($F_{10, 30}$ = 1.126, *P* = 0.376). The low observed power for the effect of ring nested within species (0.465), which indicated a high probability of committing a Type II error, mitigated against finding significant differences in this variable (Table 5).

The multivariate tests in Table 5 address the effects of different rainfall depth classes measured across the same individual trees. Wilks' Lambda was used as the test of significance because it is an exact test and is in widespread use across many disciplines (Crichton 2000). The results indicated a difference in throughfall among the five different storm size categories ($F_{4,27}$ = 15473.124, *P* < 0.001). There was a significant storm depth x species interaction ($F_{16,83.124}$ = 2.966, *P* = 0.001), but no interaction was observed between storm depth and ring position nested within species ($F_{40, 104.236}$ = 1.395, *P* = 0.092), as shown in Table 6.

Table 5: Results from the Repeated Measures ANOVA tests of between-subjects effects to determine the interaction of storm size with distribution of throughfall. (alpha = 0.05)

Source	Type I Sum of Squares	df	Mean Square	F	*P*	Observed power
Intercept	244.977	1	244.977	22512.176	<0.001	1.000
Species	0.219	4	0.055	5.041	0.003	0.932
Ring(Species)	0.123	10	0.012	1.126	0.376	0.465

Table 6: Results from Wilks' Lambda multivariate testing indicating a non-significant interaction between rainfall and ring position under the canopy. (alpha = 0.05)

	Value	F	df	*P*	Observed power
Storm Class	0.000	15473.124	4	<0.001	1.000
Storm Class*Species	0.252	2.966	16	0.001	0.958
Storm Class*Ring (Species)	0.197	1.395	40	0.092	0.960

The significant interaction between rainfall category and species appears to have been driven by anomalous throughfall patterns in *O. pyramidale* (Figure 6). For the 5 – 10 mm storm category where there was only 1 storm, *O. pyramidale* let in a similar throughfall depth to *A. mangium*. This was not seen in any of the other storm classes; *O. pyramidale* usually allowed more throughfall than *A. mangium*, as did the other tree species. This is the probable reason for the significant result for the interaction between throughfall and species across rainfall categories. The interaction plot shown in Figure 6 is based on the estimated marginal means of the data, which represent predicted means from the ANOVA model without any experimental error.

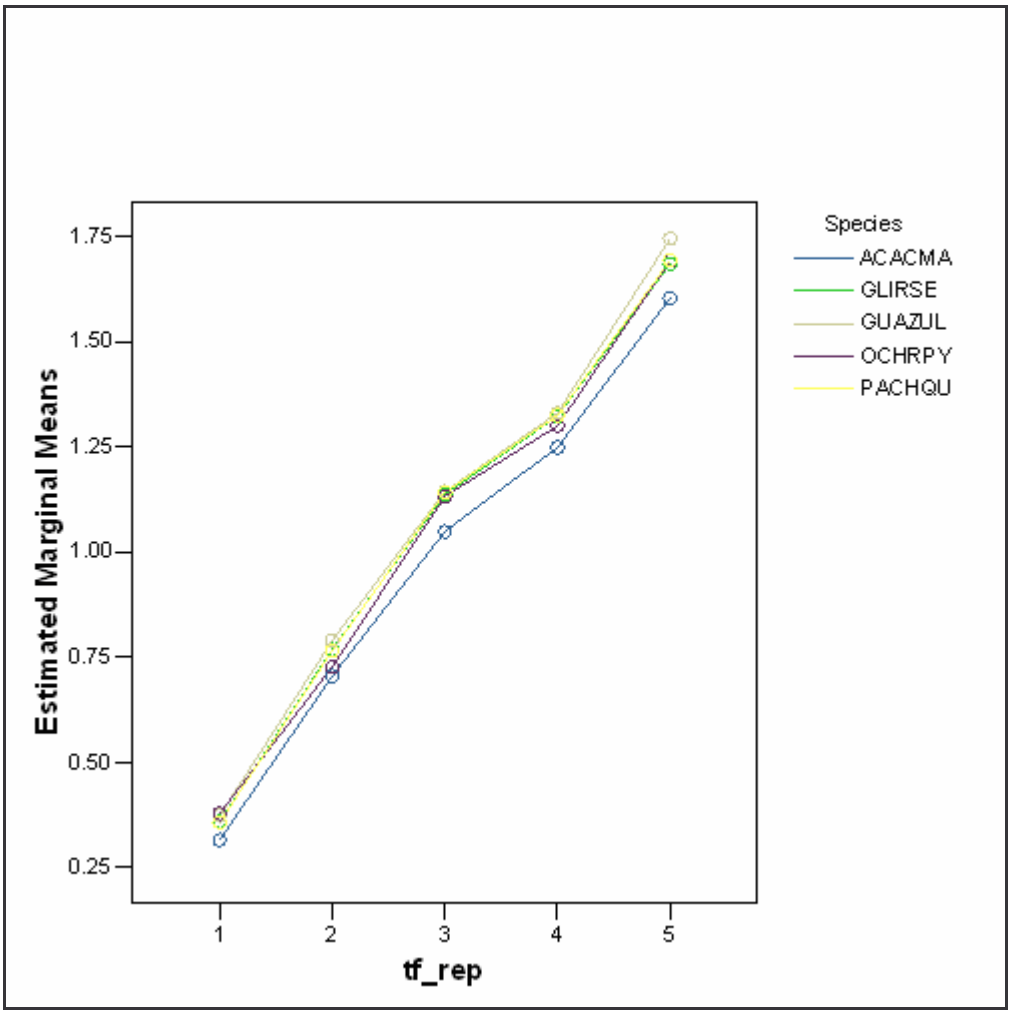

Figure 6: Interaction plot for effects of species from multivariate testing using Wilks' Lambda. The variables for analysis were tf_rep (representing the five rainfall depth classes) versus the estimated marginal means for throughfall (predicted means from the ANOVA model). Species were denoted by the species codes used for analysis (ACACMA-*Acacia mangium*, GLIRSE-*Gliricidia sepium*, GUAZUL-*Guazuma ulmifolia*, OCHRPY-*Ochroma pyramidale*, PACHQU-*Pachira quinata*). Rainfall depth classes were donated by numbers 1 – 5 (1 – <5mm, 2 – 5-10mm, 3 – 10-20mm, 4 – 10-20mm, 5 - >30mm).

3.2 Crown traits

3.2.1 Interspecific differences

Significant interspecific differences ($P \leq 0.05$) were found for overall height, crown length, and LAI, but not for crown openness or crown area (Table 2). *Acacia mangium* (mean height 10.1 m), *O. pyramidale* (mean height 11.5 m) were at least 2.4 m taller than the other three species. *Gliricidia sepium*, *G. ulmifolia* and *P. quinata*, whose mean heights ranged from 5.1 – 7.7 m were also significantly different in height. *Acacia mangium* similarly separated itself from other species by supporting a crown length of 9.2 m versus short-crowned trees (*G. sepium* and *P. quinata*) and those with medium crown lengths (*G. ulmifolia* and *O. pyramidale*). *Acacia mangium* and *P. quinata* supported the highest LAIs (2.51 and 2.38, respectively), while G. sepium and G. ulmifolia had intermediate values (1.86 and 1.75, respectively), and *O. pyramidale* had a low LAI of 1.25.

Table 7: Crown and stem traits for the five subject species with (mean ± standard deviation). Means followed by different letters are significantly different (Least Significant Difference (LSD), $P \leq 0.05$).

Species	Height (m)		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)	2.51	(0.45)a	20.6	(2.83)
G. sepium	7.7	(1.35)b	3.9	(3.09)b	30.3	(6.55)	1.86	(0.32)b	24.9	(2.53)
G. ulmifolia	6.8	(0.75)c	4.8	(1.10)c	18.1	(2.26)	1.75	(0.20)b	26.6	(2.36)
O. pyramidale	11.5	(0.38)a	7.7	(0.50)c	39.7	(18.93)	1.25	(0.61)c	35.3	(12.75)
P. quinata	5.1	(0.25)d	3.5	(1.03)b	21.7	(5.28)	2.38	(0.25)a	27.3	(10.54)

3.2.2 Crown trait effects on throughfall.

All crown traits affected throughfall significantly ($P \leq 0.009$) in the smallest rainfall depth category (Table 7). Crown depth was the only consistent influence on

throughfall, having significant (P<0.001) effects on all rainfall depth categories except for rainfall events with 5 – 10 mm of rain. Leaf area index had a significant effect on the ≤ 5 mm category and the 10 -20 mm category (P<0.009), but no significant effect on rainfall events any larger than 20 mm. Crown openness had the least influence of the three variables, having a significant effect on only the ≤ 5 mm category (P =0.001) and no effect on rainfall events larger than 5 mm. The non-significant effects of all three crown traits for the 5 – 10 mm category may be due to the small sample size for that category (only one rainfall event). This would decrease the statistical power of the result.

Table 8: Results of linear regressions of crown trait effects on percent throughfall, divided into five rainfall depth classes.

Rainfall	Variable	Value	SE	P-value (variable)	R^2	F	P-Value
≤ 5 mm	Intercept	87.322	5.437	< 0.001	0.164	29.02	< 0.001
	LAI (m^2 m^{-2})	-3.858	1.477	0.009		(df= 3, 55)	
	Crown Length (m)	-1.578	0.244	< 0.001			
	Crown openness (%)	0.343	0.105	0.001			
5-10 mm	Intercept	104.98	18.619	< 0.001	0.254	1.246	0.340
	LAI (m^2 m^{-2})	-4.465	5.065	0.397		(df= 3, 11)	
	Crown Length (m)	-1.453	0.837	0.110			
	Crown openness (%)	-0.119	0.358	0.745			
10 – 20 mm	Intercept	95.115	6.232	< 0.001	0.314	22.625	< 0.001
	LAI (m^2 m^{-2})	-4.715	1.705	0.006		(df= 3, 148)	
	Crown Length (m)	-1.716	0.280	< 0.001			
	Crown openness (%)	0.261	0.121	0.032			
20 – 30 mm	Intercept	88.336	8.759	< 0.001	0.353	9.98	< 0.001
	LAI (m^2 m^{-2})	-2.575	2.378	0.477		(df= 3, 55)	
	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	< 0.001
	LAI (m^2 m^{-2})	-3.931	2.265	0.086		(df= 3, 81)	
	Crown Length (m)	-2.206	0.380	< 0.001			
	Crown openness (%)	-0.018	0.162	0.911			

3.2.3 Understory characteristics

Due to missing data, quadrat samples from *G. ulmifolia* were removed from the analysis. Significant interspecific differences were found in percent litter cover and leaf litter biomass, but not in percent bare ground vegetation cover < 30 cm, or vegetation cover > 30 cm (Tables 8 & 9). *Acacia mangium* and *O. pyramidale* shared similar understory characteristics, but were generally different from the remaining species. *Acacia mangium* had significantly more litter cover than *G. sepium* and *P. quinata* ($P \leq 0.040$). *Ochroma pyramidale* also had more litter cover than *P. quinata* ($P = 0.006$). For the leaf litter biomass measurements, *A. mangium* was found to have a greater biomass than *G. sepium*, *G. ulmifolia*, and *P. quinata* ($P \leq 0.005$). Similarly, *O. pyramidale* had more biomass than *G. sepium*, *G. ulmifolia*, and *P. quinata* ($P \leq 0.007$).

Table 9: Average values for selected understory variables. Figures separated by different letters are significantly different (LSD, $P \leq 0.05$).

Species	Litter biomass (g.)	Bare ground (pct)†	Litter cover (pct) †	Litter Depth (cm) †
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	32.6	2.6
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)

† Only one sample collected for G. ulmifolia in these categories.

4. Discussion

4.1 Interspecific differences in throughfall (and stemflow) quantities

It has been shown that tree species pre-selected to have similar canopy cover but different crown traits can display distinct relationships with rainfall. Interspecific differences in throughfall depth were found in this study. In particular, *A. mangium* intercepted 10.9 % to 16.2% more rain than the other four species.

Interspecific differences in rainfall interception have implications for local hydrology. Greater interception means greater evaporation of rainwater stored on leaf surfaces (Germer *et al.* 2005). As a result, less water will reach the forest floor. This will have an impact on the degree of erosion that occurs underneath tree crowns which can be an issue in restoration efforts (Sinun *et al.* 1992).

Asdak *et al.* (1998) and Scatena (1990) have both shown that interception losses are of major importance in influencing the water yield of forested and deforested areas. Deforested areas could potentially be more heavily impacted by the erosivity of rain, due to an understory environment that is relatively underdeveloped in most cases.

In this study, however, *A. mangium* only intercepted approximately 13% more of the total rainfall than the other species. Considering that the research site receives over 2100 mm of rain annually, the implications of 13% less rainfall reaching the soil are unknown. Further research is needed to evaluate the impact of *A. mangium* and other species that share similar crown traits on two areas of plantation hydrology: (1) the

influence of interception on infiltration, soil moisture and water yields at the stand scale, and (2) the potential influence of large areas of plantation on regional atmospheric water balance.

Other authors have found stemflow to be more important than throughfall for nutrient cycling due to a higher nutrient concentration (Olson *et al.* 1981, Sinun *et al.* 1992, Johnson & Lehmann 2006. This is caused by a longer canopy residence time for stemflow than throughfall.

After preliminary analyses, it appeared that the relationship between stemflow and rainfall was not as distinct as that with throughfall. Gomez *et al.* (2002) reported a correlation between increased rainfall intensity and increased stemflow values, which could be in part due to the knowledge that saturation of bark and water transmission along the trunk and branches increases with rainfall intensity. The authors suggested that stemflow is significantly more important than throughfall as a source of local rainfall concentration in olive plantations where the individual tree is the subject of measurement.

Stemflow depth is influenced by many factors which were not examined in this study, including bark texture and branch orientation (Hutchinson & Roberts 1981, Crockford & Richardson 2000). Smooth, easily wetted bark such as that of *O. pyramidale* and *G. ulmifolia* has the potential for high stemflow yields. Conversely, thick absorptive bark such as that of *P. quinata* would result in smaller stemflow values because the bark has to be saturated before stemflow commences (Crockford & Richardson 2000).

The analysis of stemflow for this study was complicated by the overflow of collecting equipment on several occasions. Overflow problems have been reported previously, and may be a common occurrence (Carlyle-Moses, personal communication). Olson *et al.* (1981) reported overflow in 2% of their collections and Sinun *et al.* (1992) were forced to replace 1 l stemflow containers with 4 l buckets. Masukata *et al.* (1990) reported that even 75 l plastic buckets could not prevent overflow during the heaviest storms that they encountered.

4.2 Throughfall distribution beneath the canopy

Spatial heterogeneity was not found in any of the five tree species in this study. This result was accompanied by low statistical power, indicating that spatial heterogeneity may not be adequately sampled with the current number of gauges. This is especially true for large-leaved trees such as *O. pyramidale*.

Spatial heterogeneity involves the concentration of rainfall in some areas of the canopy (primarily the dripline) and thus under-representation of rainfall in other portions of the canopy. Temporal heterogeneity of throughfall distribution beneath individual tree canopies has been observed, especially for smaller rainfall events (Gomez *et al.* 2002). Gomez *et al.* (2002) found a consistent storm to storm pattern in spatial distribution among high rainfall events, and non-consistent patterns among low rainfall events. In our study, three rings of four gauges proved insufficient statistical power to distinguish differences in throughfall between regions of the canopy. Future studies with a similar

research hypothesis regarding spatial heterogeneity should include a greater number of gauges beneath single canopy.

Several authors have found systematic trends in throughfall spatial distribution (Robson *et al.* 1994; Whelan & Anderson 1996) and Loustau *et al.* (1992) reported a random distribution of throughfall. This can be attributed to differences among species, sites and rainfall characteristics. For example, Gomez *et al.* (2001) has quantified rainfall partitioning in olive orchards in relation to leaf area index.

4.3 Canopy trait influences on throughfall quantity

The differences in interception values seen in the analyses were likely to be due to the contrasting crown properties of the five tree species. Crown openness is somewhat important at low rainfall depths/ intensities, but live crown length is the only consistently significant limitation on throughfall depth at higher intensities.

One would expect that increased leaf area index would result in decreased throughfall quantities. Increased LAI is similar to crown depth in that increasing the horizontal overlap of leaves creates more raindrop-leaf surface interactions per unit area. This would be expected to result in less rainfall reaching the ground. Therefore, when choosing trees for reclamation projects where erosion is a potential impediment to success, selecting species with a greater LAI may be beneficial.

According to preliminary findings, however, LAI only influences throughfall in rainfall events less than 20 mm. The influence of LAI over throughfall is therefore likely to come from increased temporary storage due to the multiple leaf layers. Heavy or extremely intense storms would rapidly overwhelm this storage capacity, leading to the observed lack of influence of LAI under large storms.

This study also examined the influence of crown openness on throughfall depth. In this case, one would expect that the more open the canopy is, the greater the amount of rainfall that would reach the forest floor. That is, as crown openness increases, interception losses decrease. Therefore a tree with a more open crown would allow more rain to reach the forest floor uninterrupted than a tree with a lesser crown. Crown closure can then be viewed as having a crucial influence on water balance in the forest. Choosing trees with a greater crown closure would result in less rain (and less intense rain) reaching the soil, which again is an important consideration for restoration of degraded lands. Crown openness was found to influence interception losses in smaller rainfall events only.

The most consistent crown trait influence was crown length. This trait influenced rainfall events of all sizes, unlike the other two variables. *Acacia mangium* had a much greater crown length than other species and subsequently intercepted more rainfall than the remaining four species.

This study has illustrated that the greater the crown length of the tree, the more water the tree is able to store and intercept. Crown length may increase interception as

follows. As crown length increases, so does the number of interactions between rainfall and leaves. This is because crown length describes the number of leaves distributed vertically, rather than horizontally as in leaf area index or crown openness estimations. A greater crown length would result in individual raindrops and streams of coalescing raindrops contacting more leaves on their way to the forest floor than if they followed the same trajectory through a crown of lesser length. With a greater number of rainfall/leaf interactions, more water would be expected to be retained on leaves and later evaporated, rather than fall to the ground. It can be concluded that crown length may be the most important parameter on which to choose plantation species when the goal is to decrease erosion or leaching potential.

These findings suggest that an interaction model may exist between crown traits and rainfall duration/intensity. A certain depth of rainfall must fall before any throughfall will occur, and this depth is determined by the canopy storage capacity of the tree (Nanko *et al.* 2006). This is influenced by the intensity of storms. High intensity storms will saturate the storage capacity more rapidly. These results and the work of other authors shows that species-specific storage responds to differences in leaf size, crown depth and LAI.; and the makeup and texture of leaf and wood surfaces (Crockford & Richardson 2000; Germer *et al.* 2005).

4.4 Understory Characteristics

A. mangium and *O. pyramidale* had greater litter coverage and biomass beneath their crowns. For soil conservation purposes, trees that produce a deeper and more

evenly distributed litter layer would absorb the kinetic energy of raindrops more efficiently. An even covering of litter that leaves a minimum of bare ground exposed would also decrease the amount of soil and water that is lost as overland flow (Sinun *et al.* 1992).

The subject species chosen for this study varied greatly in leaf size, shape, and arrangement. However, the influence of leaf size and shape on throughfall were not directly studied in this research. This type of analysis would require interception study at the sub-canopy scale which would necessitate the examination of individual leaves in the laboratory with rainfall simulators.

5. Conclusions

1. Interspecific differences existed between individual tree species and their modification of incident rainfall (throughfall and stemflow). *A.mangium* was found to intercept on average 13% more rain than any other species, despite changes in rainfall depth/intensity.

2. Spatial heterogeneity of throughfall distribution could not be determined by gauge placement in young plantation grown trees in the Neotropics (Panama). This could be at least partially due to a need for a greater number of gauges beneath a single tree.

3. Crown properties, including leaf area index, crown openness and crown length influence throughfall quantity during smaller rainfall events. Crown length is the most influential crown trait, having an effect irrespective of rainfall depth.

References

ANAM. 2005. Panama. http://www.itto.or.jp/live/Live_Server/1255/Panama.e.pdf Accessed 2007 January 18.

Asdak, C., Jarvis, P.G., van Gardingen, P., & Fraser, A. 1998. Rainfall interception loss in unlogged and logged forest areas of Central Kalimantan, Indonesia. Journal of Hydrology. 206(3-4): 237-244.

Calder, I.R. 1976. The measurement of water losses from a forested area using a 'natural' lysimeter. Journal of Hydrology. 30: 311-325.

Calder, I.R. 2001. Canopy processes: implications for transpiration, interception and splash induced erosion, ultimately for forest management and water resources. Plant Ecology. 153: 203-214.

Chappell, N.A., Bidin, K., & Tych, W. 2001. Modelling rainfall and canopy controls on net-precipitation beneath selectively-logged tropical forest. Plant Ecology. 153: 215-229.

Crichton, N. 2000. Information Point: Wilks' lambda. http://www.blackwellpublishing.com/specialarticles/jcn_9_381.pdf . Accessed 2007 February 23.

Crockford, R. H. & Richardson, D.P. 2000. Partitioning of rainfall into throughfall, stemflow and interception: effect of forest type, ground cover and climate. Hydrological Processes. 14: 2903-2920.

Cusack, D., & Montagnini, F. 2004. The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. Forest Ecology and Management. 188 (1-3): 1-15.

Dunisch, O., M. Erbreich, &Eilers, T. 2003. Water balance and water potentials of a monoculture and an enrichment plantation of Carapa *guianensis* Aubl. in the Central Amazon. Forest Ecology and Management. 172: 355-367.

Evans, J. 1999. Planted forests of the wet and dry tropics: their variety, nature, and significance. New Forests 17: 25-36.

Frazer, G.W., Canham, C.D., & Lertzman, K.P. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and

program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Gash, J.H.C. & Stewart, J.B. 1977. The evaporation from Thetford Forest during 1975. Journal of Hydrology. 35: 385-396.

Germer, S., H. Elsenbeer, & Moraes, J.M. 2005. Throughfall and temporal trends of rainfall redistribution in an open tropical rainforest, south-western Amazonia (Rondônia, Brazil). Hydrology and Earth Systems Science 10: 383-393.

Gomez, J.A., Giraldez, J.V., & Fereres, E. 2001. Rainfall interception by olive trees in relation to leaf area. Agricultural Water Management. 49: 65-76.

Gomez, J.A., Vanderlin, K., Giraldez, J.V., & Fereres, E. 2002. Rainfall concentration under olive trees. Agricultural Water Management. 55: 53-70.

Hairiah, K., H. Sulistyani, D. Suprayogo, Widianto, P. Purnomosidhi, R. H. Widodo, & Noordwijk, M.V. 2006. Litter layer residence time in forest and coffee agroforestry systems in Sumberjaya, West Lampung. Forest Ecology and Management 224 (1-2): 45-57.

Herwitz, S. R. 1985. Interception storage capacities of tropical rain forest trees. Journal of Hydrology 77: 237-252.

I.T.T.O. 2005. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. *ITTO Policy Development Series, No 13.* http://www.itto.or.jp/live/PageDisplay/Handler?pageId=201 . Accessed 2006 October 12.

Johnson, M.S. & Lehmann, J. 2006. Double-funneling of trees: Stemflow and root-induced preferential flow. Ecoscience. 13 (3): 324-333.

Keim, R.F. & Skaugset, A.E. 2004. A linear system model of dynamic throughfall rates beneath forest canopies. Water Resources Research. 40: 1-12.

Kuusipalo, J., Adjers, G., Jafarsidik, Y., Otsama, A., Tuomela, K., & Vuokko, R. 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland – understorey development in forest plantations. Journal of Vegetation Science. 6 (2): 205-210.

Landau, S. & Everitt, B.S. 2004. A Handbook of Statistical Analyses using SPSS. Chapman & Hall/CRC, Library of Congress: Boca Raton, FL.

Lamb, D. 1998. Large-scale ecological restoration of degraded tropical forest lands: The potential role of timber plantations. Restoration Ecology. 6: 271-279.

Levia Jr., D. F. & Herwitz, S.R. 2000. Physical properties of water in relation to stemflow leachate dynamics: implications for nutrient cycling. Canadian Journal of Forest Research. 30: 662–666.

Loustau, D., Berbigier, P., Granier, A., & El Hadj Moussa, F. 1992. Interception loss, throughfall and stemflow in a maritime pine stand. I. Variability of throughfall and stemflow beneath the pine canopy. Journal of Hydrology. 138: 449-467.

Lloyd, C. R. 1990. The temporal distribution of Amazonian rainfall and its implications for forest interception. Quarterly Journal of the Royal Meteorological Society. 116: 1487–1494.

Martinez-Meza, E. & Whitford, W.G. 1996. Stemflow, throughfall, and channelization of stemflow by roots in three Chihuahuan desert shrubs. Journal of Arid Environments. 32 (3): 271-287.

Mohan, S. & Arumugam, N. 1996. Relative importance of meteorological variables in evapotranspiration: factor analysis approach. Water Resources Management. 10(1): 1-20.

Murakami, S. 2006. A proposal for a new forest canopy interception mechanism: Splash droplet evaporation. Journal of Hydrology. 319: 72-82.

Munishi, P.K.T& Shear, T.H. 2005. Rainfall interception and partitioning in afromontane rainforests of the Eastern Arc Mountains, Tanzania: implications for water conservation. Journal of Tropical Forest Science. 17(3): 355-365.

Nanko, K., Hotta, N., & Suzuki, M. 2006. Evaluating the influence of canopy species and meterological factors on throughfall drop size distribution. Journal of Hydrology. 329: 422-431.

Olson, R.K., Reiners, W.A., Cronan, C.S., & Lang, G.E. 1981. The chemistry and flux of throughfall and stemflow in subalpine balsam fir forests. Holarctic Ecology. 4: 291-300.

PRORENA. 2003. PRO-07: Selection trials with 25 native tree species. STRI and Yale University School of Forestry and Environmental Studies, Panama City, Panama.

Pypker, T. G., B. J. Bond, T. E. Link, D. Marks, & Unsworth, M.H. 2005. The importance of canopy structure in controlling the interception loss of rainfall: Examples from a young and an old-growth Douglas-fir forest. Agricultural and Forest Meteorology 130: 113–129.

Robson, A.J., Neal, C., Ryland, G.P., & Harrow, M. 1994. Spatial variations in throughfall chemistry at the small plot scale. Journal of Hydrology. 158: 107-122.

Rowe, L.K., 1983. Rainfall interception by an evergreen beech forest, Nelson, New Zealand. Journal of Hydrology. 66: 143-158.

Scatena, F.N. 1990. Watershed scale rainfall interception on two forested watersheds in the Luquillo mountains of Puerto Rico. J. Hydrol. 113: 89-102.

Schroth, G., L. F. d. Silva, M.-A. Wolf, W. G. Teixeira, & Zech, W. 1999. Distribution of throughfall and stemflow in multi-strata agroforestry, perennial monoculture, fallow and primary forest in central Amazonia, Brazil. Hydrological Processes. 13: 1423 -1436.

Silva, I.C. & Okumura, T. 1996. Rainfall partitioning in a mixed white oak forest with dwarf bamboo undergrowth. Journal of Environmental Hydrology. 4: 1-16.

Sinun, W., Meng, W.W., Douglas, I., & Spencer, T. 1992. Throughfall, stemflow, overland flow and throughfall in the Ulu Segama rain forest, Sabah, Malaysia. Philosophical Transactions: Biological Sciences. 335(1275): 389-395.

Wiersum, K. F. 1985. Effects of various vegetation layers in an Acacia *auriculiformis* forest plantation on surface erosion in Java, Indonesia. Pages 79-89 in S. A. El-Swaify, W. C. Moldenhauer, and A. Lo, (editors). Soil erosion and conservation. Soil Conservation Society of America, Ankeny, Iowa.

Whelan, M.J., & Anderson, J.M. 1996. Modelling spatial patterns of throughfall and interception loss in a Norway spruce (*Picea abies*) plantation at the plot scale. Journal of Hydrology. 186: 335-354.

Xiao, Q., McPherson, G., Ustin, S.L., Grismer, M.E., & Simpson, J.R. 2001. Winter rainfall interception by two mature open-grown trees in Davis, California. Hydrological Processes. 14: 763-784.

Xiao, Q., McPherson, G., Ustin, S.L., Grismer, M.E., & Simpson, J.R. 1997. A new rainfall interception measuring system. Presented at American Geophysical Union (AGU) Meeting, Fall 1997. http://www.fs.fed.us/psw/programs/cufr/products/4/cufr_141.pdf Accessed 2006 January 15.

Yun, X. & Liu, B. 2002. A practical threshold for separating erosive and non-erosive storms. Transactions of the ASAE. www.ars.usda.gov . Accessed 2006 January 30.

Zar, J.H. 1996. Biostatistical Analysis. 3rd ed. Prentice-Hall, Inc.: Upper Saddle River, N.J.

Appendix A

Appendix A, Figure 1: *Pachira quinata* with trial setup of throughfall gauges in June 2006. Throughfall gauges for the trial were constructed with 1.5 l. bottles. This was later changed to the larger capacity Chlorox bottles due to frequent overflow.

Appendix B

Appendix B, Table 1: Summary of all rain events used for statistical analyses, TF: throughfall; SF: stemflow; n_{tf}: number of trees for throughfall analyses; n_sf: number of trees for stemflow analyses.

Rain Event	Date Fell	Date Collected	Total Rain (mm)	Max Int.	Duration (mins)	avg. TF (mm)	TF as pct. RF	n_{tf}	SF (mm)	SF as pct. RF	n_{sf}
33	22/07/2006	23/07/2006	13.6	3.3	230	11.7	86.3	15	0.1041	0.8	14
34	23/07/2006	24/07/2006	9.8	3	125	8.4	85.5	15	0.1625	1.7	12
35	24/07/2006	25/07/2006	1.2	0.3	310	0.7	60.3	15	0.0093	0.8	15
36	25/07/2006	26/07/2006	26.5	5.1	105	23.4	88.4	15	0.0316	0.1	1
39	28/07/2006	29/07/2006	0.6	0.3	85	0.4	65.9	15	0.0010	0.2	15
40	29/07/2006	30/07/2006	2.4	1	26	2.2	91.3	15	0.0334	1.4	14
42	2/8/2006	3/8/2006	30.8	5.6	160	76.8	249.2	15	0.0000	0.0	0
43	3/8/2006	4/8/2006	14.0	4.8	30	12.1	86.7	15	0.2873	2.1	14
44	4/8/2006	5/8/2006	4.1	0.8	160	11.6	282.4	15	0.2465	6.0	10
45	8/8/2006	9/8/2006	16.5	1.8	550	13.1	79.5	15	0.2953	1.8	11
46	9/8/2006	10/8/2006	0.3	0.3	5.0	0.2	77.7	15	0.0005	0.2	11
47	10/8/2006	11/8/2006	14.8	3.8	510	12.6	85.1	15	0.4382	3.0	14
48	11/8/2006	12/8/2006	35.0	7.1	595	31.5	90.0	15	0.6763	1.9	13
50	15/08/2006	16/08/2006	1.8	1	155	1.5	80.7	15	0.0035	0.2	15
51	16/08/2006	17/08/2006	22.7	4.8	260	18.1	79.9	15	0.4958	2.2	9
53	17/08/2006	18/08/2006	0.9	0.3	425	6.3	701.0	10	0.0000	0.0	0
54	20/08/2006	21/08/2006	0.8	0.5	5	0.7	89.8	15	0.0012	0.1	12
55	23/08/2006	24/08/2006	56.6	13.7	155	52.2	92.3	15	0.0000	0.0	0
56	25/08/2006	26/08/2006	4.2	0.8	420	3.3	77.4	15	0.0177	0.4	15
57	26/08/2006	27/08/2006	23.8	2.3	425	18.3	76.7	15	0.1938	0.8	8
58	28/08/2006	29/08/2006	0.8	0.5	125	0.5	66.2	15	0.0007	0.1	13
59	30/08/2006	31/08/2006	3.3	0.3	195	2.1	64.2	15	0.0248	0.8	14
68	7/9/2006	8/9/2006	20.0	5.6	260	17.3	86.3	15	0.3962	2.0	10
69	8/9/2006	10/9/2006	10.2	3	130	11.3	111.1	15	0.1469	1.4	13
70	10/9/2006	11/9/2006	20.1	6.6	360	17.8	88.4	15	0.3745	1.9	11
71	11/9/2006	12/9/2006	12.2	2.3	165	9.7	79.7	15	0.1550	1.3	12
72	14/09/2006	15/09/2006	48.7	7.9	365	40.7	83.6	15	0.5480	1.1	6
77	18/09/2006	19/09/2006	7.2	0.3	55	1.0	14.2	15	0.0127	0.2	13
78	19/09/2006	20/09/2006	13.8	4.6	15	11.8	85.4	15	0.1835	1.3	12