

Water inputs across a tropical montane landscape in Veracruz, Mexico: synergistic effects of land cover, rain and fog seasonality, and interannual precipitation variability

ALEXANDRA G. PONETTE-GONZÁLEZ*, KATHLEEN C. WEATHERS† and LISA M. CURRAN‡

*Yale School of Forestry & Environmental Studies, 195 Prospect Street, New Haven, CT 06511, USA, †Cary Institute of Ecosystem Studies, PO Box AB, Millbrook, NY 12545, USA, ‡Stanford University, 450 Serra Mall Bldg 50, Stanford, CA 94305, USA

Abstract

Land-cover change can alter the spatiotemporal distribution of water inputs to mountain ecosystems, an important control on land-surface and land-atmosphere hydrologic fluxes. In eastern Mexico, we examined the influence of three widespread land-cover types, montane cloud forest, coffee agroforestry, and cleared areas, on total and net water inputs to soil. Stand structural characteristics, as well as rain, fog, stemflow, and throughfall (water that falls through the canopy) water fluxes were measured across 11 sites during wet and dry seasons from 2005 to 2008. Land-cover type had a significant effect on annual and seasonal net throughfall (NTF < 0 = canopy water retention plus canopy evaporation; NTF > 0 = fog water deposition). Forest canopies retained and/or lost to evaporation (i.e. NTF < 0) five- to 11-fold more water than coffee agroforests. Moreover, stemflow was fourfold higher under coffee shade than forest trees. Precipitation seasonality and phenological patterns determined the magnitude of these land-cover differences, as well as their implications for the hydrologic cycle. Significant negative relationships were found between NTF and tree leaf area index ($R^2 = 0.38$, $P < 0.002$), NTF and stand basal area ($R^2 = 0.664$, $P < 0.002$), and stemflow and epiphyte loading ($R^2 = 0.414$, $P < 0.001$). These findings indicate that leaf and epiphyte surface area reductions associated with forest conversion decrease canopy water retention/evaporation, thereby increasing throughfall and stemflow inputs to soil. Interannual precipitation variability also altered patterns of water redistribution across this landscape. Storms and hurricanes resulted in little difference in forest-coffee wet season NTF, while El Niño Southern Oscillation was associated with a twofold increase in dry season rain and fog throughfall water deposition. In montane headwater regions, changes in water delivery to canopies and soils may affect infiltration, runoff, and evapotranspiration, with implications for provisioning (e.g. water supply) and regulating (e.g. flood mitigation) ecosystem services.

Keywords: cloud forest, ENSO, fog, highlands, hydrology, land-use change, shade coffee, stemflow, throughfall, tropical hurricanes

Received 10 March 2009 and accepted 28 April 2009

Introduction

By modifying ecosystem structure and composition, land-cover change contributes to the spatiotemporal redistribution of water to the soil surface. Because water is a limiting resource for a suite of ecological processes, the creation of altered patterns of water availability

has the potential to affect plant population dynamics and species' distributions (Asbjornsen *et al.*, 2004; Condit *et al.*, 2004; Engelbrecht *et al.*, 2007; Nepstad *et al.*, 2007), ecosystem hydrology and biogeochemistry (Baron *et al.*, 1998; Nepstad *et al.*, 2002; Farley *et al.*, 2004), as well as evapotranspiration and runoff (Nobre *et al.*, 1991). Moreover, positive or negative land-atmosphere feedbacks that further modify water fluxes can lead to ecosystem regime shifts (e.g. cloud forest to woodland) (Lawton *et al.*, 2001; Gordon *et al.*, 2008)

Correspondence: A. G. Ponette-González, tel. + (845) 677-7600 ext. 137, fax + (845) 677-5976, e-mail: alexandra.ponette@gmail.com

and affect regional climate (Avisar *et al.*, 2002; DeFries *et al.*, 2002).

Over the past century, various Neotropical montane regions have experienced dramatic and widespread changes in land use/land cover (Thomlinson *et al.*, 1996; Kammerbauer & Ardon, 1999; Sarmiento & Frolich, 2002; Cayuela *et al.*, 2006; Kintz *et al.*, 2006). Some of the most prominent land-cover trajectories include: forest clearing for urban and suburban development (Romero & Ordenes, 2004), surface and subsurface mining (Bury, 2005), and cattle grazing (Sarmiento, 1997); grassland conversion for tree plantation establishment (Farley *et al.*, 2004); replacement of agroforestry systems with pasture, sugar cane, or other crops and/or coffee intensification (Guhl, 2008); forest degradation through fuelwood harvesting and selective logging (Ochoa-Gaona & González-Espinosa, 2000); and agricultural land abandonment and forest succession (Hecht & Saatchi, 2007). Our understanding of how these land-change pathways affect water flows at broad spatial scales is currently constrained by lack of information on the hydrological responses of and interactions among diverse land-cover types (Giambelluca, 2002).

However, research conducted largely in native and planted forests underscores the multiple spatial scales at which vegetation can mediate water transfers to soil: leaf morphology (Cavelier & Goldstein, 1989; Brewer & Smith, 1997; Holder, 2007), tree and stand properties (Carlyle-Moses *et al.*, 2004; Nadkarni & Sumera, 2004; Staelens *et al.*, 2006), and landscape features (Cavelier *et al.*, 1996; Weathers *et al.*, 2000, 2006) have all been shown to govern water inputs to ecosystems. Stemflow, for example, is highly dependent on bark texture and tree architecture (Ford & Deans, 1978). Trees with smooth bark and upward oriented branches have greater stemflow than trees with fissured bark and depressed branches (Carlyle-Moses, 2004). The effects of stem density, tree height, and canopy properties [including leaf area index (LAI), canopy cover, crown volume, and epiphyte loading] on throughfall have yielded conflicting results, in part, because of the differential effects of vegetation on the vertical and horizontal delivery of water (Levia & Frost, 2006). In general, throughfall volumes increase while stemflow amounts decrease as canopy surface area decreases (Stogsdill *et al.*, 1989). However, in coastal and montane forests, where fog water may be a primary component of the dry season or annual water budget, clearing or stand thinning may result in altered canopy fog interception and thus lower, or higher, throughfall water inputs (Lovett & Reiners, 1986; Ataroff & Rada, 2000). Moreover, landscape features (e.g. vegetation type, elevation, aspect, and edges) are conditions that also influence water redis-

tribution (Weathers *et al.*, 2000). The amount of rain and fog deposited to ecosystems can change considerably over short distances in mountainous terrain due to orographic effects on precipitation (Lovett *et al.*, 1997; Weathers *et al.*, 2000, 2006; Holder, 2003). Further, forest-grassland edges and coniferous vegetation have been shown to enhance rain- and fog-water deposition (e.g. Weathers *et al.*, 1995, 2000, 2001, 2006; Ewing *et al.*, 2009). Surprisingly, few empirical studies have examined the influence of land cover on water inputs to tropical mountain regions despite their sensitivity to disturbance and climatic change, and the major implications for downstream water resources.

Many montane species and ecosystems exhibit low resilience to land-use/land-cover changes that affect the quantity, type, and timing of water inputs to canopies and soils. For example, epiphyte species' distributions in Neotropical forests are tightly coupled to moisture conditions (Gentry & Dodson, 1987). In highland Mexico, management activities promoting drier conditions within tree canopies (e.g. oak coppicing and stand thinning for coffee production) have been associated with increased abundance and biomass of drought-tolerant epiphyte species (Hietz, 2005; Wolf, 2005). Seasonally or annually water-limited ecosystems, or those strongly dependent on fog as a water source, are also highly sensitive to canopy changes (Pounds *et al.*, 1999). The documented persistence of fog-dependent rainforest patches at hydrologically marginal sites (i.e. aridity and rainfall variability) in Chile and Australia suggests that reduced fog capture rates following land-cover change could affect tree survival and regeneration patterns, resulting in profound compositional shifts within these ecosystems (Hutley *et al.*, 1997; del-Val *et al.*, 2006; Gutiérrez *et al.*, 2008).

In upland areas, vegetation patterns exert control over hydrologic processes as well, including evapotranspiration, infiltration, soil water storage, and runoff (Bruijnzeel & Proctor, 1995). Although forest conversion often results in lower evapotranspiration rates and higher water yields (Bosch & Hewlett, 1982), land-use change can sometimes have unanticipated consequences. In northern Thailand, findings indicate that sensible heat advection from cultivated sites may contribute to high evapotranspiration rates from adjoining secondary vegetation (Giambelluca *et al.*, 2000). In their grassland afforestation study, Farley *et al.* (2004) demonstrated that loss of soil organic matter under pine plantations can lead to significant reductions in soil water retention capacity. Deforestation in wet montane regions has also been linked with increased frequency of landslide events (Dai & Lee, 2002; Restrepo & Alvar-

ez, 2006), increased surface water runoff (Ziegler *et al.*, 2004; Molina *et al.*, 2007), and downstream flooding (Bradshaw *et al.*, 2007). These studies combined underscore the critical and diverse role of land cover in regulating water fluxes.

Finally, land conversion on tropical mountains may interact with increasing precipitation variability to affect water resources. Vegetation type is likely to modulate the magnitude of climate impacts, including extreme rainfall events or El Niño Southern Oscillation (ENSO) (Dale, 1997). Positive feedbacks between land-cover change and climatic variability could therefore exacerbate the risk of natural hazards and reduce the temporal reliability of water supply for domestic consumption, agricultural production, and industrial activities. Regions dependent on annual or seasonal discharge from headwater areas may be particularly vulnerable to such feedbacks (Viviroli *et al.*, 2003).

The overarching objective of this study was to examine the effects of three land-cover types on water inputs across a moist, but seasonally dry montane landscape affected by fog and characterized by high interannual precipitation variability. Here, we address the following questions: (1) How does land-cover type affect the partitioning of rainfall into throughfall and stemflow fluxes? (2) How does vegetation stand structure affect the amount, type, timing, and spatial distribution of water inputs to soil? and (3) How do tropical storms, hurricanes, and ENSO-related variability in seasonal precipitation affect throughfall fluxes to dominant land-cover types?

Materials and methods

Study region

This study was conducted at mid-elevations in the central highlands of Veracruz State in eastern Mexico (19°20'N, 96°50'W; Fig. 1). Regional climate is tropical with a mean annual temperature of ~17–20 °C (García, 1973). Total annual rainfall ranges from 1000 to 2200 mm, and relative humidity is 70–80% year round (Jáuregui Ostos, 2004). The central highlands are influenced by tropical maritime and continental polar air masses during the wet (May–October) and dry (November–April) seasons, respectively, creating pronounced seasonal differences in rainfall. Approximately 80% of annual rainfall occurs during wet season months, when small-scale convective systems, tropical storms, depressions, and hurricanes regularly develop in the Gulf of Mexico. From November to April, the study region receives only 20% of annual rainfall inputs. Dry season climate is strongly influenced by Northerners that bring cold air and additional moisture in the form of drizzle and fog (Báez *et al.*, 1997). ENSO also modifies seasonal precipitation amount and timing (Cavazos & Hastenrath, 1990). El Niño events are generally associated with higher than mean, while La Niña events with lower than mean, dry season rainfall (Cavazos, 1997; Magaña *et al.*, 2003).

Colonial era and current land-use practices add complexity to the natural environmental heterogeneity of the Sierra Madre Oriental mountain range. Remnant patches of lower montane rain forest (*sensu* Grubb,

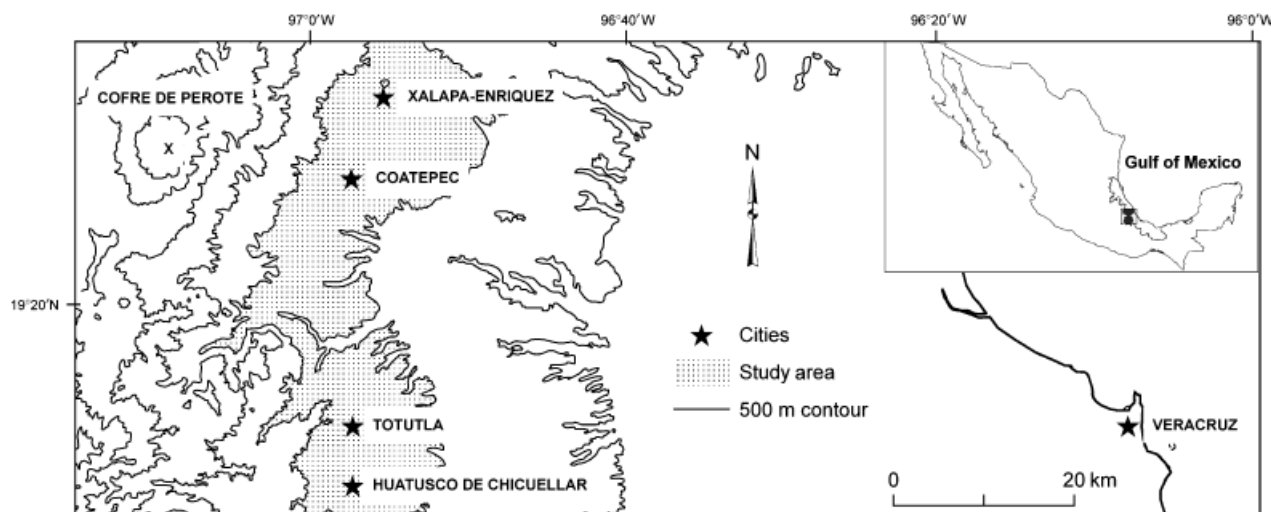


Fig. 1 Location of the study region (stippled area) at mid-elevations in central Veracruz, Mexico. Between 1000 and 1500 m a.s.l., dominant land-cover types are tropical montane cloud forest, cattle pasture, coffee agroforestry, and sugar cane. Towns and cities in close proximity to the study sites are marked with stars. The port city of Veracruz (1 m a.s.l.) and Cofre de Perote Volcano (4282 m) are east and west of Xalapa, respectively.

1977), here used interchangeably with 'cloud' forest (i.e. forests receiving moisture inputs from fog or mist; Stadtmüller, 1987), are nested within a matrix of shade coffee agroforests, sugar cane fields, and cattle pastures. These agroecosystems persist as the most prevalent land-cover types in the study region. Together, they represent 40–60% of the total land area (Muñoz-Villers & López-Blanco, 2008). In addition, urban and peri-urban settlements, including the capital city of Xalapa and the town of Coatepec, are expanding into forested and agricultural lands.

Site selection

An existing contrast in land management was used to examine total and net water inputs within and across three widespread, and structurally distinct, land-cover types: lower montane rain forest (Grubb, 1977) ($n = 6$), shade coffee (commercial polycultures; *sensu* Moguel & Toledo, 1999) ($n = 5$), and cleared areas ($n = 6$). Cleared areas here refer to cattle pastures and grassy areas with low herbaceous cover. Forest fragments adjacent or in close proximity (<3 km) to coffee agroforests and cleared areas were chosen to ensure that the experimental treatment – land-cover type – would not be confounded by the effects of local meteorological conditions. In April 2005, three paired sites were selected in the Xalapa–Coatepec region (Table 1). These sites were located in the upper catchment of the Antigua watershed (1325 km²) between 1300 and 1500 m a.s.l. on east-facing (i.e. windward) slopes of Cofre de Perote Volcano (4282 m). In June and August 2006, three additional paired sites, one in Xalapa–Coatepec and two in Huatusco–Totutla, were included in the study. The Huatusco–Totutla area is ~ 35 km south of Xalapa–Coatepec (Fig. 1). Totutla lies within the lower Antigua watershed (1475 km²) and Huatusco within the Jamapa watershed (1924 km²). Sites were located between 1100 and 1350 m a.s.l. northeast of Pico de Orizaba (5675 m). Site descriptions are summarized in Table 1.

Land-cover types surveyed

Forests in this region are composed of a unique mixture of temperate and tropical tree species (Williams-Linera, 1997). The most common species in the semi-deciduous overstory are *Carpinus caroliniana* Walt., *Clethra mexicana* DC., *Liquidambar styraciflua* L., and *Quercus* spp. In the evergreen broadleaf understory, abundant species include *Cinnamomum effusum* (Meissner) Kostermans, *Hedyosmum mexicanum* Cordem., *Oreopanax xalapensis* (Kunth) Decne. & Planch., and *Turpinia insignis* (Kunth) Tul. Commercial polyculture coffee agroforests are dominated by native, non-native, and exotic species, most of which are evergreen. Preferred shade trees are *Citrus* spp., *Heliocarpus donnell-smithii* Rose, *Inga* spp., *Leucaena leucocephala* (Lam.) de Wit, *Trema micrantha* L. Blume, and increasingly *Macadamia integrifolia* Maiden & Betche.

Precipitation monitoring and historic rainfall data

Two monitoring stations, each consisting of a passive string fog water collector (after Falconer & Falconer, 1980) attached to a tipping bucket rainwater collector and a tipping bucket rainwater collector, were employed in clearings to monitor the temporal distribution of precipitation (defined as fog plus rain). The 25 cm × 50 cm cylinder-shaped fog collectors were made from high-density polypropylene and strung with Teflon (0.5 mm diameter). Each collector was covered with a circular hood (50 cm diameter) to exclude vertical rainwater inputs and attached to a funnel (31 cm diameter). Water collected onto Teflon strands passed through the funnel and into a tipping bucket rain gauge (RainWise Inc., Bar Harbor, ME, USA). A second tipping bucket rain gauge was placed next to the fog collector to measure rain-only deposition. Both fog- and rainwater collectors were connected to a datalogger (Campbell Scientific Inc., Logan, UT, USA). Calculation of fog water deposition (to the artificial collectors) took into account collection area of passive fog samplers

Table 1 Geographic location and duration of sampling at six paired sites in central Veracruz, Mexico

Paired site	Region	Coordinates	Elevation (m a.s.l.)	Land-cover types	Distance (forest to coffee)	Sampling (months)
1	Xalapa–Coatepec	N19°30'W96°58'	1400–1450	Forest-coffee-cleared	Adjacent	34.5
2	Xalapa–Coatepec	N19°27'W96°59'	1300–1350	Forest-coffee-cleared	Adjacent	32.5
3	Xalapa–Coatepec	N19°31'W96°59'	1400–1500	Forest-coffee-cleared	<3 km	32.5
4	Xalapa–Coatepec	N19°28'W97°00'	1550–1600	Forest-cleared	na	22
5	Huatusco–Totutla	N19°12'W96°54'	1050–1150	Forest-coffee-cleared	<1 km	19
6	Huatusco–Totutla	N19°11'W96°59'	1350–1400	Forest-coffee-cleared	<1 km	19

Distance between forest and coffee plots was <3 km. Rainfall measurements were made in clearings adjacent to all forest fragments and coffee agroforests.

(1069 cm²). Monitoring stations were mounted on rooftops in the cities of Xalapa and Coatepec <1–5 km distant from the study sites. Beginning in September 2005, dataloggers were programmed to collect data on fog- and rainwater inputs at 30 min intervals. Datalogger malfunctions occurred during several months of 2005 and 2006, thus some wet and dry season data are not used here to describe rain and fog patterns. However, we also deployed rainfall (open 'bulk' funnels) collectors in clearings adjacent to all sites where throughfall was measured (see 'Throughfall measurements') and used these data to supplement missing tipping bucket rain gauge data. Dry season fog water inputs (to the artificial passive collectors) were calculated per day (127 days per dry season) and then scaled to estimate total dry season (181 days) fog deposition. We also identified the occurrence, timing, duration, frequency, and volume of fog, rain, and mixed rain-fog events. In addition, we compared our data with monthly rainfall 'normals' (i.e. rainfall averaged over a 30-year period) for 1971–2000 from Mexico's Comisión Nacional del Agua (National Water Commission) for the meteorological stations closest to each sampling location.

To assess ENSO effects on dry season rainfall, historic rainfall data for all meteorological stations in central Veracruz > 1000 m were obtained from Mexico's Servicio Meteorológico Nacional (National Weather Service). Eleven stations with overlapping temporal measurements spanning 1965–1999 were included in the analysis (Appendix S1). Monthly rainfall totals were compiled for each station and year. Years with missing data were excluded (e.g. 1966 for Las Ánimas meteorological station). Median monthly station rainfall was computed for November, December, January, February, March, and April of each year. These values were then summed to obtain an estimate of annual dry season rainfall for the central highlands. Monthly Southern Oscillation Index (SOI) values were downloaded from the Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/current/soihtm1.shtml>). Average SOI values were used to classify each dry season as neutral (SOI \geq -2 and SOI \leq 2), El Niño (SOI < -2), or La Niña (SOI > 2) after Caso *et al.* (2007). Differences in dry season rainfall among neutral, El Niño and La Niña events were evaluated.

Throughfall measurements

From April 2005 to March 2008, throughfall, water that falls through plant canopies, was measured in six forest fragments and five shade coffee agroforests. Rainfall was also collected in eight clearings (see 'Precipitation monitoring') (Table 1). Throughfall samplers were con-

structed following the design of Weathers *et al.* (2001, 2006). Twenty centimeter (8 in) diameter funnels, connected to Tygon tubing and maintained upright with PVC, were used to collect throughfall in 6 L containers. A polywool filter was inserted into the funnel neck to prevent debris from inhibiting water flow (Weathers *et al.*, 2001). Using a stratified random sampling design, 167 collectors were installed in the six forest ($n = 90$) and five shade coffee ($n = 77$) plots. Fifteen collectors were established in each forest and 14–16 collectors in each coffee plot. Average plot size was ~ 1300 m². Samplers were mounted 1 m aboveground and spaced at 12 m intervals in fixed rather than roving locations to reduce soil disturbance. The cumulative area over which throughfall was sampled was ca. 1.4 ha. Seventeen rainfall collectors were installed in clearings adjacent to sampling areas.

Water from throughfall and rainfall collectors was collected weekly. As distance between sites prohibited collection on the same days, collection dates were staggered (i.e. Monday, Wednesday, and Friday) such that water at each paired site was collected on the same day each week.

Stemflow sampling

Stemflow was measured within three (of the six) forests and three (of the five) coffee agroforests from May 2006 to April 2007. Vegetation structure and composition data were used to compute relative species dominance and relative species abundance for each site. Species with the highest combined values [i.e. (relative basal area + relative density)/2] were selected for stemflow measurements: *Quercus pinnatifida*, *C. mexicana*, *Alchornea latifolia*, *T. micrantha*, and *Mimosa scabrella*. *T. micrantha* was sampled at two coffee sites. The bark of *Q. pinnatifida* is highly fissured, while *C. mexicana*'s bark is intermediate between fissured and smooth. *A. latifolia* and *T. micrantha* have nearly smooth bark, and *M. scabrella* has very smooth bark. Four trees per site, two small [10–20 cm diameter at breast height (dbh)] and two mid-size (20–40 cm dbh), were randomly selected for collar installation. Stemflow collars, ~ 8 mm thick, were constructed from heavy aluminum foil and polyurethane foam and fitted to trees ($n = 24$) at dbh following Butler & Likens (1995). Tygon tubing drained water into 60 L collection containers located at the base of trees. A polywool filter was inserted into the tubing to prevent debris from interfering with water flow. An additional throughfall collector was installed 1 m from the bole of the same tree to allow for direct comparison between stemflow and throughfall. Stemflow was collected twice and once per week during the

rainy and dry seasons, respectively. Collars were checked monthly for leakage.

Stand structure and composition

At 10 sites, stand structure and composition measurements were conducted on all trees ≥ 5 cm dbh and ≥ 2 m tall within 80 m² circular vegetation plots around each throughfall collector ($n = 152$). Voucher samples for all tree species were collected and identified at the Institute of Ecology, A.C., in Xalapa. Tree height and diameter were measured with a clinometer and dbh tape, and number of stems per tree was counted. Crown projection area was estimated by measuring the length of the tree crown, from the bole of the tree to the edge of the crown, six times. The mean radius length and the formula for the area of a circle were used to calculate crown projection area (m²). Epiphyte loading per tree was evaluated qualitatively by conducting visual observations from underneath the tree. Following Nadkarni *et al.* (2004), each tree was assigned to an abundance category: 1, no epiphytes; 2, scarcely covered; 3, moderately covered; and 4, heavily covered. Wet season (i.e. July 2006) and dry season (i.e. January 2007) LAI was measured with a LI-COR 2000 Plant Canopy Analyzer (Lincoln, NE, USA) at sites in Xalapa-Coatepec.

Statistical analysis

Sample periods beginning in April and ending in March are referred to as 'water years.' Total throughfall per site was measured for each season and sample year, and the net throughfall flux calculated as:

$$TF - BR = NTF, \quad (1)$$

where TF is the throughfall in mm, BR the rainfall in mm, and NTF the net throughfall flux in mm. We considered negative net throughfall (NTF < 0) to indicate canopy water retention plus canopy evaporation. Positive net throughfall (NTF > 0) was considered to be fog water deposition. To quantify fog contribution to total throughfall, weeks with positive NTF were summed to calculate fog water deposition per dry season (181 days). However, positive NTF values still underestimate fog inputs, because canopy evaporation and stemflow are not accounted for in this calculation (Weathers *et al.*, 1992). For each tree under which stemflow was sampled, weekly stemflow was summed over wet and dry seasons. The ratio of stemflow (liters) to throughfall (mm) was then calculated to compare relative species effects on stemflow generation (Schroth *et al.*, 1999).

Throughfall and net throughfall data were averaged to calculate total and net fluxes by land-cover type, the

main unit of statistical analysis. These data are expressed both in volumetric terms and as a percentage of rainfall. Owing to logistical difficulties, rainfall and throughfall were not collected in three forests and three coffee agroforests in Xalapa-Coatepec during September, October, and November 2007. Given spatial variability of precipitation in mountainous terrain (Lovett *et al.*, 1997), we did not model water fluxes to these sites for the periods with missing data. Instead, water flux data for these 3 months were not included in the analyses. Therefore, measurements for water year 2007–2008 are for 9 months only.

Wilcoxon's signed ranks test was employed to examine differences between fog water inputs to passive fog and throughfall collectors. Nonparametric Kruskal–Wallis test and Mann–Whitney *U* pair-wise comparisons were used to detect differences in throughfall among land-cover types and stemflow among species. These tests were also used to compare storm and hurricane weeks with nonevent weeks. Differences among seasons and years were tested with repeated measures ANOVA. Relationships between total and net water inputs and stand variables were analyzed using linear regression. All analyses were performed using SPSS v.14. Significance was set at $P < 0.05$ (two-tailed).

Results

Above-canopy rain and fog inputs

Rainfall in Xalapa-Coatepec ranged from 1464 to 2203 mm during water year April 2005 to March 2006; 1901–2609 mm during water year April 2006 to March 2007; and from 1002 to 1182 mm during water year April 2007 to March 2008. Based on these measurements and 30-year rainfall 'normals' for September–November (441–556 mm), water years 2005–2006 and 2007–2008 had similar rainfall. Maximum rainfall was recorded in water year 2006–2007, when sites experienced wetter than average conditions. Rainfall during water year 2006–2007 was 18–48% greater than mean annual rainfall for the period 1971–2000 (1500–1765 mm) and 18–51% greater than in water year 2005–2006.

Significantly more rainfall was recorded during wet (RMANOVA: $F = 3.9$, $P < 0.05$) and dry (RMANOVA: $F = 10.9$, $P < 0.001$) seasons of water year 2006–2007. A total of 9–47% (158–531 mm) more rainwater fell on Xalapa-Coatepec sites from May to October 2006 than from May to October 2005. Maximum half-hourly rainfall during wet season months was 42 mm. An exceptional spike in rainfall was observed during the ENSO dry season from January to March 2007 (Fig. 2). Rainfall inputs were 70–92% (+ 244–339 mm) greater than during the preceding dry season (November 2005 to April

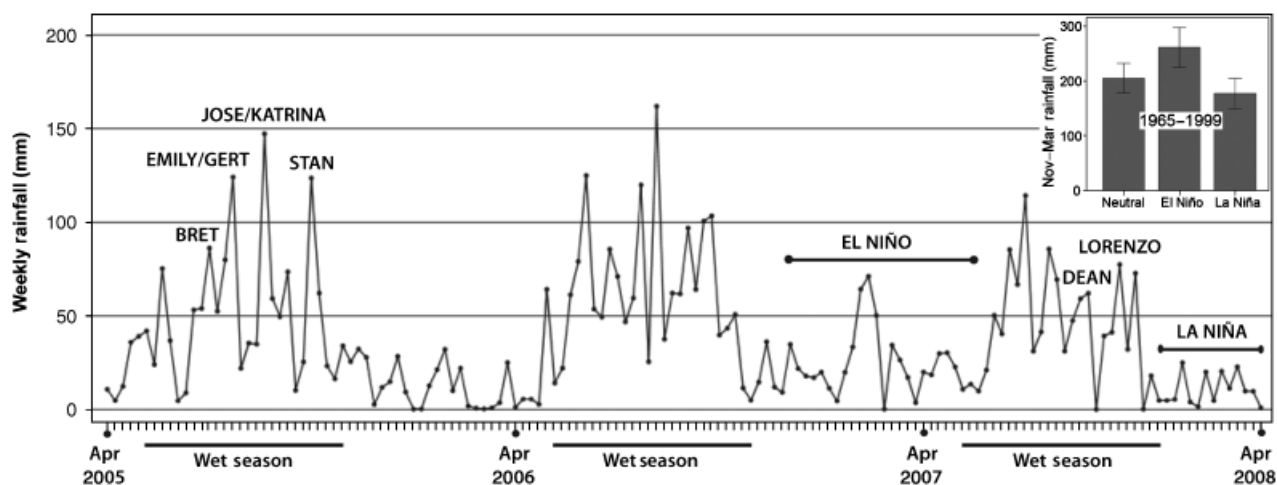


Fig. 2 Rainfall (mm) measured weekly from April 2005 to March 2008 in four clearings in the Xalapa–Coatepec region of central Veracruz, Mexico. Rainfall collections were conducted during the 2005 Atlantic Hurricane season, a mild ENSO warm phase event (peak December 6 to February 7), and moderate to strong La Niña conditions (December 7 to March 8). Inset: Data from 1965–1999 representing 11 stations >1000 m a.s.l. in central Veracruz indicate that ENSO events are associated with a significant increase in dry season (November–March) rainfall. Error bars indicate ± 2 SE.

Table 2 Average and range of rain and fog water inputs (mm day^{-1}) measured in clearings during three consecutive dry seasons

Season	Rainfall (mm)		Fog input (mm day^{-1})		Fog input (mm) Total	Water input (mm) Total (rain + fog)	% Fog	N (weeks)
	Mean	Range	Mean	Range				
DS1	363	324–410	0.37	0.15–0.59	67	430	15	26
DS2	643	575–708	0.65	0.36–0.94	118	761	15	26
DS3	144	104–178	0.33	0.20–0.44	34	178	19	15

Data were collected from 2005 to 2008 in the Xalapa–Coatepec region of central Veracruz, Mexico. Fog water was sampled with two artificial passive fog samplers installed near the cities of Xalapa and Coatepec. Fog inputs were calculated based on the collection area of passive fog samplers.

2006). Although dry season rainfall in Huatusco–Totutla was lower (mean = 439 mm) than in Xalapa–Coatepec (mean = 644 mm), winter rainfall was above average across the entire study area (mean = 598 mm). Fog water inputs were also twofold greater during the 2006–2007 dry season compared with other years' dry seasons (Table 2).

Average daily dry season fog input was 0.45 mm day^{-1} . Fog water represented $\sim 16\%$ (3-year mean) of the total (rainfall plus fog inputs to passive collectors) above-canopy water input. Dry season fog water inputs to passive collectors and rainfall showed a significant positive relationship (fog water deposition = $0.3 + 0.154 \times \text{rainfall}$, $R^2 = 0.531$, $P < 0.001$).

Annual below-canopy throughfall water inputs

On average, $1441 \pm 299 \text{ mm}$ (83%) and $1694 \pm 352 \text{ mm}$ (98%) of annual rainfall measured in cleared areas,

$1732 \pm 350 \text{ mm}$, reached the soils of forests and coffee agroforests, respectively. Mean annual forest canopy throughfall ranged from 80% to 87% of incident rainfall, whereas throughfall measured under coffee canopies was 97–102% of rainfall. Again, all values $>100\%$ indicate fog water deposition. Although throughfall volumes did not differ significantly among land-cover types, significant differences in annual percent throughfall, NTF amount, and percent NTF were detected (Kruskal–Wallis test: $\chi^2 = 7.4$, $P < 0.02$). Depending on the year, forest canopies retained and/or lost to evaporation five- to 11-fold (204–381 mm, 17%) more water (i.e. $\text{NTF} < 0$) than coffee agroforests (34–41 mm, 2%).

Throughfall displayed similar temporal patterns as rainfall, with total volume inputs to forest and coffee sites significantly greater during water year 2006–2007 (RMANOVA: $F = 58.8$, $P < 0.001$). Weekly rainfall sampled in clearings vs. throughfall measured under forest

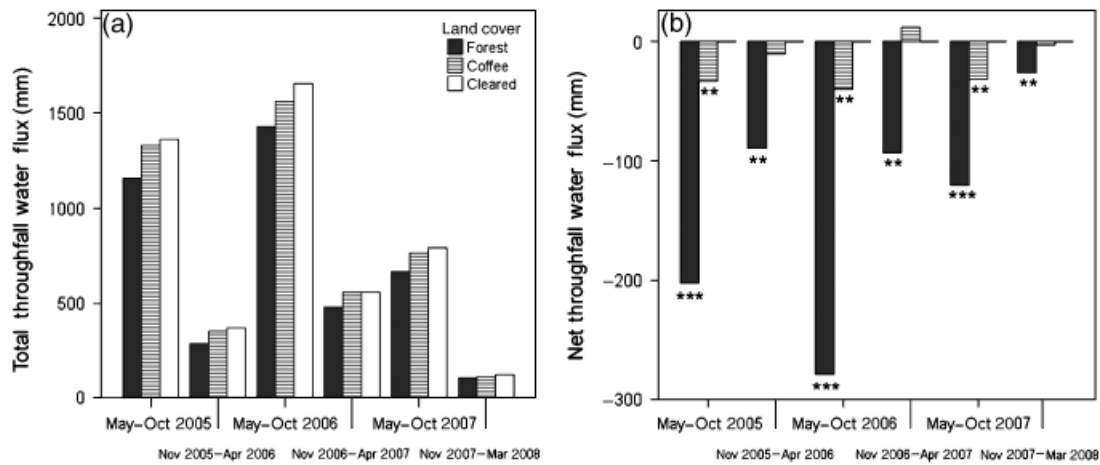


Fig. 3 (a) Total and (b) net throughfall fluxes (mm) by land-cover type, measured during three wet (May–October) and three dry (November–April) seasons from 2005 to 2008, Veracruz, Mexico. Total throughfall volumes were similar among land-cover types. Significant differences between forest fragments and cleared areas and shade coffee agroforests and cleared areas are indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Note: although water year 3 does not include data for September, October, and November 2007, land-cover patterns are consistent during the three sample years.

and coffee canopies explained 97% of the variation in throughfall (throughfall = $-0.095 + 0.959 \times \text{rainfall}$, $R^2 = 0.971$, $P < 0.001$). Significant negative relationships also were found between weekly rainfall and percent net throughfall inputs to forest (NTF = $6.511 - 0.299 \times \text{rainfall}$, $R^2 = 0.257$, $P < 0.000001$) and coffee sites (NTF = $4.740 - 0.278 \times \text{rainfall}$, $R^2 = 0.196$, $P < 0.001$).

Seasonality of water inputs

Compared to 1287 ± 266 mm of rainfall, mean wet season throughfall flux was 1087 ± 220 mm (84%) to forest and 1252 ± 264 mm (97%) to coffee (Fig. 3a). However, there was considerable variation among sites. Between 79% and 91% of rainfall reached forest soils, whereas 97–100% was deposited to shade coffee sites. Wet season NTF to all forest and coffee sites was negative, indicating water retention and/or evaporation from plant canopies (Fig. 3b). Net throughfall flux measured under forest canopies was four- to sevenfold (-120 to -279 mm, 16%) more negative than under shade coffee agroforests (-32 to -40 mm, 3%). Differences in NTF amount and percentage were detected between forests and shade coffee agroforests (Mann–Whitney U -test: $P < 0.002$), forests and cleared areas (Mann–Whitney U -test: $P < 0.001$), and shade coffee agroforests and cleared areas (Mann–Whitney U -test: $P < 0.007$).

Average dry season throughfall water input was approximately one-third of the wet season flux. Relative to 359 ± 127 mm of rainfall, 289 ± 107 mm (81%), and 359 ± 131 mm (100%) were delivered to forests and coffee agroforests, respectively. Between 75% and 98%

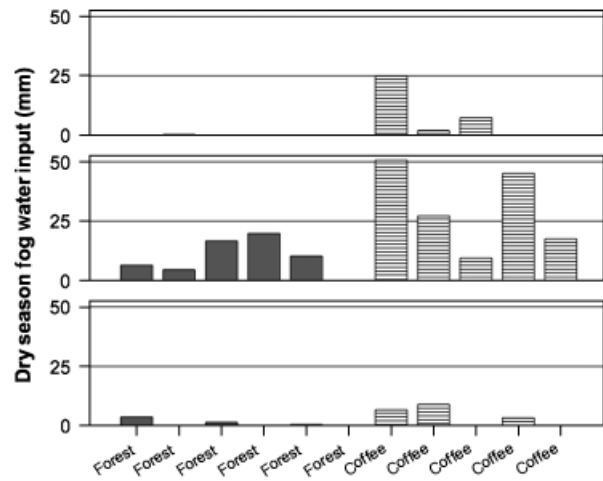


Fig. 4 Fog water throughfall inputs [net throughfall (NTF) > 0] to forests and shade coffee agroforests, Veracruz, Mexico, measured during three consecutive dry seasons. On average, fog water deposition to shade coffee was greater than to forest fragments. In addition, fog inputs were twofold greater during the 2006–2007 El Niño dry season (November 2006 to April 2007).

of rainfall was deposited to forest soils during the dry season, whereas throughfall under coffee agroforests was 96–104% of rainfall. Dry season differences in NTF volume and percentage of rainfall between forests (-69 ± 22 mm, 19%) and shade coffee agroforests (-0.3 ± 7 mm, 2%) (Mann–Whitney U -test: $P < 0.05$) and forests and cleared areas (Mann–Whitney U -test: $P < 0.037$) were also significant, but only percent NTF differed between coffee agroforests and cleared areas (Mann–Whitney U -test: $P < 0.037$). Overall, land-cover differences in NTF amount were more pronounced

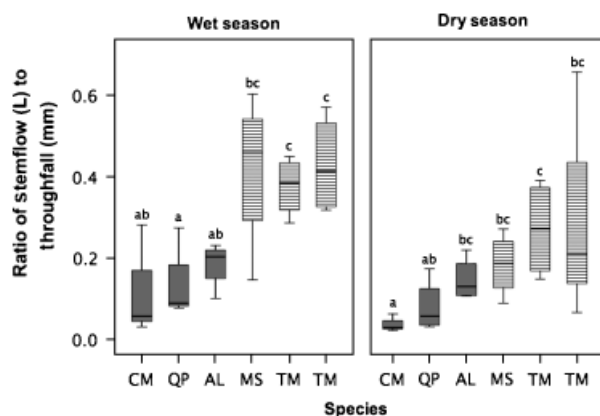


Fig. 5 Ratio of stemflow (L) to throughfall (mm). Stemflow and throughfall were measured under three forest and two coffee shade tree species: *Quercus pinnatovenulosa* (QP), *Clethra mexicana* (CM), *Alchornea latifolia* (AL), *Trema micrantha* (TM, TM2), and *Mimosa scabrella* (MS) in three cloud forest fragments and three shade coffee plantations from May 2006 to April 2007, Veracruz, Mexico. Different letters (a,b,c) denote significant differences between species ($P < 0.05$).

during the wet season, but proportionally, these were greater during the dry season.

During the dry season, fog water deposition in throughfall ranged from 0% to 7% (0–25 mm; dry season 2005–2006); 0–10% (0–51 mm; dry season 2006–2007); and 0–6% (0–9 mm; dry season 2007–2008) of total (rain + fog) dry season throughfall (Fig. 4). Dry season fog inputs to coffee agroforests were significantly higher than inputs to forests during dry seasons 2005–2006 and 2006–2007 (Mann–Whitney U -test: $P < 0.045$), but not in 2007–2008. Mean fog water input to coffee land cover comprised <5% of dry season throughfall. Fog water deposition to passive fog collectors was significantly greater than fog inputs to forest and coffee sites (Wilcoxon's signed ranks test, $P < 0.001$).

Stemflow was measured during the wettest water year (2006–2007) over which we sampled. Individual trees generated 100–1000 L of stemflow during the wet season and 15–400 L during the dry season. Mean rates of stemflow generation ($L\ mm^{-1}$ of throughfall) were higher under coffee shade trees than under forest trees during both seasons (Fig. 5). *C. mexicana* and *Q. pinnatovenulosa* had low stemflow to throughfall ratios (<0.1), while *M. scabrella* (0.4) and *T. micrantha* (0.3) had the highest ratios. Species differences varied seasonally, with dissimilarity among forest and coffee species most pronounced in the wet season.

Tropical storms, hurricanes, and ENSO

During this study, seven tropical storms and hurricanes affected water inputs to the region. In 2005, Tropical

Storm Bret (June 29), Tropical Storm Gert (July 24), Tropical Storm Jose (August 22), and Hurricane Stan (October 4) made landfall on the coast of Veracruz, while Hurricane Emily (July 20) made landfall north of Veracruz in Tamaulipas State. In 2007, Hurricanes Dean (August 22) and Lorenzo (September 28) landed in Veracruz. Although these events varied in duration, maximum wind velocity, and rainfall intensity, their effects on rain and throughfall were clear (Table 3). Mean rainfall during nonstorm event weeks was 36 ± 3 mm, as compared with 109 ± 12 mm during storm and hurricane event weeks. Total throughfall fluxes to forest and coffee soils were also threefold higher during storm and hurricane weeks, reflecting the increase in rainfall.

Response of forest canopies to extreme rainfall was more variable than that of coffee canopies, as evidenced by the net throughfall flux (Table 3). During nonstorm weeks, forest NTF was 0 to –16 mm (mean = -6 ± 1 mm), and coffee NTF was 0 to –7 mm (mean = -1 ± 1 mm). During storm and hurricane weeks, NTF to forests and coffee agroforests ranged from –6 to –29 mm (mean = -14 ± 3 mm) and –1 to –6 mm (mean = -4 ± 1 mm), respectively. With the exception of Jose, storms and hurricanes appeared to lessen differences in percent canopy interception between forest and coffee sites.

Interannual comparisons of dry season rainfall (November–April) for the period 1965–1999 indicate that ENSO events were associated with higher than (313 ± 23 mm) and La Niña events with lower than (236 ± 15 mm) mean dry season rainfall (278 ± 16 mm), but these differences were not significant. Relative to the 1965–1999 data, the 2007–2008 La Niña dry season we monitored ranked 25th in terms of rainfall (1 = driest, 31 = wettest). When defined as November–March, ENSO dry seasons were significantly wetter than neutral dry seasons (Mann–Whitney U -test: $P < 0.05$) (Fig. 2, inset). Rainwater inputs increased by 28%, but there was much inter-ENSO variability (November–April; 203–549 mm). We measured rainfall during one mild ENSO event in 2006–2007. In comparison with 1965–1999 dry season rainfall, this was the rainiest dry season on record (598 mm). We compared our Xalapa site (site 3; Table 1) with Xalapa meteorological station rainfall data for 1920–2000 and found similar results.

Although our ENSO dataset is limited, the 2006–2007 dry season was extreme and had a major impact on below-canopy water fluxes. Throughfall water inputs to all land-cover types were twofold greater from November 2006 to April 2007 than during the previous (November 2005–April 2006) and subsequent (December 2007–March 2008) dry seasons (Fig. 3b). Estimated fog water deposition to forest and coffee

Table 3 Characteristics of tropical storms and hurricanes that made landfall on or near the coast of Veracruz between 2005 and 2007, as well as throughfall and net throughfall inputs to forest (F) and coffee (C) plots

Storm/hurricane event	Landfall date, location	Wind speed (km h ⁻¹)	Duration (h)	Rainfall intensity (mm day ⁻¹)	Rainfall (mm week ⁻¹)	Throughfall (mm week ⁻¹)	Net Throughfall (mm wk ⁻¹)
No event					36 ± 4 36 ± 4	F: 30 ± 3 C: 35 ± 4	F: -6 ± 1(17%) C: -1 ± 1(3%)
Tropical Storm Bret (June 28–29, 2005)	June 29 Tuxpan, Veracruz	65	29	10	89 ± 39 87 ± 39	F: 83 ± 39 C: 85 ± 39	F: -6 ± 2(7%) C: -2 ± 1(2%)
Hurricane Emily (July 10–20, 2005)	July 20 Carboneras, Tamaulipas	205	246	20	117 ± 25 108 ± 30	F: 105 ± 17 C: 104 ± 27	F: -12 ± 11(10%) C: -4 ± 4(4%)
Tropical Storm Gert (July 23–25, 2005)	July 24 Horconcos, Veracruz	75	42	50	121 ± 24 127 ± 20	F: 104 ± 22 C: 122 ± 17	F: -17 ± 8(14%) C: -5 ± 3(4%)
Tropical Storm Jose (August 22–23, 2005)	August 22 N/NE Port of Veracruz, Veracruz	85	32	>50	156 ± 25 153 ± 25	F: 127 ± 23 C: 147 ± 20	F: -29 ± 4(19%) C: -6 ± 7(4%)
Hurricane Stan (October 1–5, 2005)	October 4 San Andres Tuxtla, Veracruz	130	96	>50(58)*	136 ± 19 141 ± 19	F: 118 ± 21 C: 136 ± 17	F: -18 ± 2(13%) C: -5 ± 3(4%)
Hurricane Dean (August 13–23, 2007)	August 22 Tecolutla, Veracruz	155	228	50*(42)*	71 ± 6 68 ± 4	F: 65 ± 8 C: 67 ± 7	F: -6 ± 3(8%) C: -1 ± 4(1%)
Hurricane Lorenzo (September 23–25, 2007)	September 28 Barra de Tecolutla, Veracruz	130	71	>50*(46)*	79 ± 3	F: ND C: ND	F: ND C: ND

*Rainfall intensity data gathered with on-site precipitation monitoring are reported in parentheses for Stan, Dean, and Lorenzo. Data on date and location of landfall, maximum wind speed, duration, and rainfall intensity were obtained from Mexico's National Weather Service (<http://smn.cna.gob.mx/>).

soils was also higher (Fig. 4); a small (12 mm) net water gain was even recorded in coffee agroforests (Fig. 3b). As a result, throughfall measured under coffee slightly exceeded rainfall to adjacent clearings, causing an unexpected throughfall pattern: coffee > cleared > forest.

Stand structure and composition

Importance Value Index (IVI; Curtis & McIntosh, 1951) was calculated for each tree species recorded in forest and coffee plots and used to describe species composition of each land-cover type. Forest species with the highest IVIs ($\geq 5\%$) were *Quercus* spp. (23%), *C. mexicana* (13%),

H. mexicanum (9%), *L. styraciflua* (8%), *C. caroliniana* (5%), *A. latifolia* (5%), and *T. insignis* (5%). In shade coffee agroforests, the most important species were *T. micrantha* (27%), *M. scabrella* (10%), *Quercus* sp. (9%), *Grevillea robusta* (8%), *Inga vera* (8%), *Lippia myriocephala* (6%), and *A. latifolia* (6%). Sites displayed wide variability in the abundance of trees with deciduous habit; these comprised 5–60% of individuals. Thus, $\sim 34\%$ of all trees measured within forests were deciduous, whereas <16% of coffee shade trees were deciduous.

Significant differences in vegetation structural parameters were found among land-cover types. Mean density of individuals (>5 cm dbh ≥ 2 m tall) was threefold greater in forests (936 ± 166 trees ha⁻¹) than in coffee agroforests (299 ± 62 trees ha⁻¹) (Kruskal–

Wallis test: $\chi^2 = 6.036$, $P < 0.014$). Mean minimum tree height was lower in forest (6.6 ± 0.4) than in coffee plots (9.6 ± 1.1) (Kruskal–Wallis test: $\chi^2 = 6.036$, $P < 0.014$). Basal area was almost threefold greater in forest ($31 \pm 3.5 \text{ m}^2 \text{ ha}^{-1}$) than in coffee sites ($13 \pm 2.5 \text{ m}^2 \text{ ha}^{-1}$) (Kruskal–Wallis test: $\chi^2 = 6.036$, $P < 0.014$), while crown projection area, summer and winter LAI were at least twofold greater in forest than in coffee plots (Kruskal–Wallis test: $\chi^2 = 4.321$, $P < 0.038$; $\chi^2 = 4.5$, $P < 0.034$; $\chi^2 = 3.857$, $P < 0.05$). Differences in basal area corresponded with LAI measurements. Mean wet season LAI across forest sites was $4.6 \text{ m}^2 \text{ m}^{-2}$, while LAI across coffee sites was $1.6 \text{ m}^2 \text{ m}^{-2}$. Dry season LAI decreased at two of three measured forest sites, while LAI within coffee agroforests did not vary seasonally. Forty-six percent of forest trees supported epiphytes; 27% were scarcely, 11% were moderately, and 8% were heavily covered. Epiphytes were observed on 22% of coffee shade trees; 13% had few, while 1% was moderately, and 8% were heavily covered.

Stand structure and net throughfall fluxes

Significant negative correlations were detected between NTF and LAI at tree and stand scales. Mean tree LAI (average of wet and dry season LAI values; $n = 72$) alone explained 38% of the variation in median weekly net throughfall under individual trees (NTF = $2.343 - 1.906 \times \text{mean LAI}$, $R^2 = 0.38$, $P < 0.001$) (Fig. 6a). Stand basal area was significantly and positively correlated with LAI ($r = 0.95$, $P < 0.001$), while mean minimum tree height was negatively correlated with NTF.

Basal area accounted for 66% of NTF variation ($R^2 = 0.664$, $P < 0.002$) (Fig. 6b). When mean minimum height was added to the regression, these two variables predicted 78% of the variation in annual net throughfall flux to the sites (NTF = $-318.426 - 7.476 \times \text{basal area} \text{ m}^2 \text{ ha}^{-1} + 37.393 \times \text{mean minimum height}$, $R^2 = 0.781$, $P < 0.005$).

Total annual stemflow per tree was positively correlated with NTF ($r = 0.485$, $P < 0.019$) and negatively correlated with epiphyte load ($r = -0.643$, $P < 0.001$). Together, these variables explained 62% of stemflow variation (stemflow = $1.163\text{E}6 + 519 \times \text{net throughfall} - 3.298\text{E}5 \times \text{epiphyte load}$, $R^2 = 0.622$, $P < 0.0001$), with species type explaining an additional 5% of the variation.

Discussion

Land-cover change and canopy water fluxes

Our findings demonstrate that land-cover change can dramatically alter the amount, type, and spatiotemporal distribution of water delivery to canopies and soils. Throughfall water inputs decreased in the order: cleared areas > shade coffee agroforests > lower montane rain forests. Forest canopy throughfall estimates fell within the range of values reported for lower montane cloud forests, 80–101% (Bruijnzeel, 2002), but throughfall inputs to coffee agroforests were higher than expected compared with measurements conducted in Colombian (42–49%) and Venezuelan (79%) shade coffee plantations (Ataroff, 2002; Jaramillo-Robledo,

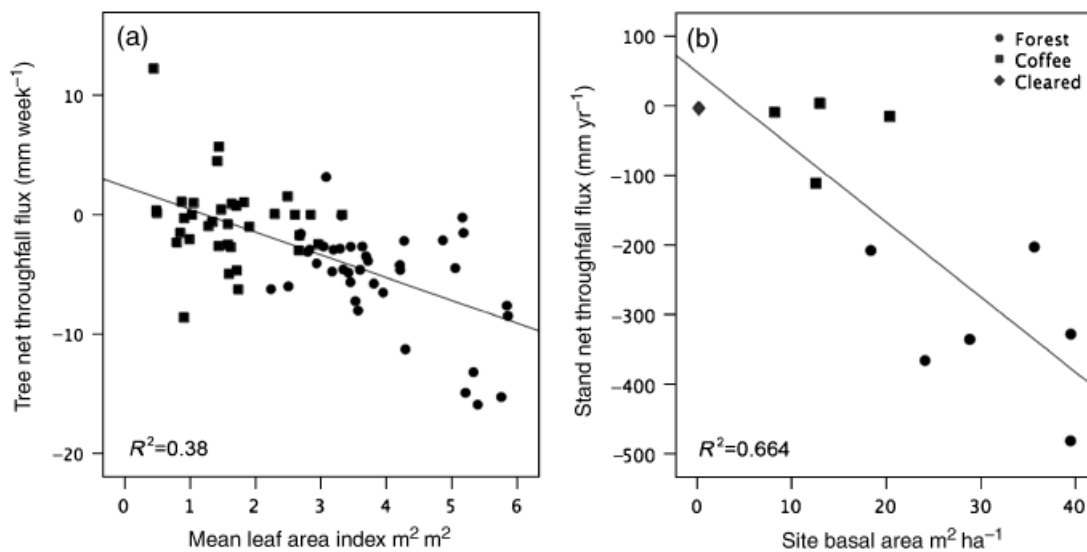


Fig. 6 Linear regressions of (a) mean leaf area index per tree against median weekly net throughfall to forest trees (●) and coffee shade trees (■), and (b) stand basal area $\text{m}^2 \text{ ha}^{-1}$ against net annual throughfall flux (mm) to forest fragments (●), shade coffee plantations (■), and cleared areas (◆), Veracruz, Mexico.

2003). An approximate threefold reduction in LAI associated with forest to coffee conversion resulted in an eightfold decrease in canopy water retention/evaporation and a corresponding 15% increase in throughfall water flux to soils. Replacement of coffee agroforestry with pasture was found to be equivalent to a fourfold decrease in canopy interception and a 2% increase in throughfall.

As we and López-Gómez *et al.* (2008) have shown, forest structural heterogeneity in this region is highly simplified by commercial polyculture coffee production. Tree density, LAI, basal area, epiphyte load, and mean minimum tree height all decrease sharply along a gradient from cloud forest to cleared areas. Of these parameters, basal area (a correlate of LAI) and vertical stratification appear to be the most important vegetation factors governing annual net throughfall inputs to forests and coffee agroforests. In Indonesia, forest management – forest with extraction of small and large diameter trees, and agroforestry – caused a 9–11% increase in throughfall to montane soils, with LAI and tree height explaining 81% of the variation within these forest use types (Dietz *et al.*, 2006). Similarly, in the Luquillo Experimental Watershed in Puerto Rico, throughfall amounts measured under closed (27%), multistrata (48%), and monostrata (66%) canopies, and in riparian areas, recent gaps, and open canopies (80–88%) were best explained by canopy cover, canopy stratification, total branches above throughfall collectors, and stand density (Scatena, 1990). As with our findings, these studies suggest that relative to other land-cover transitions (e.g. agroforestry to pasture), forest conversion may have a disproportionately large impact on water delivery to soils.

The effect of distinct canopy types on stemflow has received less attention, but appears to be equally variable. In this study, coffee shade species *T. micrantha* and *M. scabrella* had higher stemflow than forest species *Q. pinnativenulosa*, *C. mexicana*, and *A. latifolia*. Coffee tree species had smooth bark and supported fewer epiphytes. In turn, epiphyte abundance was negatively correlated with stemflow, suggesting that management practices resulting in diminished water storage in the epiphyte compartment enhance the flow of water down tree stems. However, as epiphyte load and bark roughness often covary in montane cloud forest regions (Hietz & Hietz-Seifert, 1995), it is difficult to ascertain whether changes in epiphyte abundance, tree species, or both combined, affected stemflow.

Epiphytes and epiphyte mats increase the capturing surface area of individual trees (Nadkarni, 1984) and have large canopy water storage capacities (e.g. 7–3300 L ha⁻¹; Richardson *et al.*, 2000). That epiphytes modify stemflow fluxes beneath forest canopies has

now been established (Veneklaas & Vanek, 1990; Hölscher *et al.*, 2004; Fleischbein *et al.*, 2005; Zimmermann *et al.*, 2007). For example, stemflow measured in 10-year old, 40-year old, and old-growth tropical montane forest stands decreased with increasing non-vascular epiphyte coverage (Hölscher *et al.*, 2003). Tree species composition has also been shown to influence stemflow. Schroth *et al.* (1999) compared tree-based land-use systems in Amazonia and found that high stemflow-yielding peach palm trees (*Bactris gasipaes*) generated similar stemflow amounts in peach palm monocultures as in forest fallows despite much higher tree densities in the latter. Epiphyte removal and changes in canopy composition can therefore increase within-stand spatial heterogeneity of water inputs – by concentrating water around tree stems – as well as total stemflow volume.

At fine spatial scales, discerning the effects of specific canopy properties on throughfall water inputs is equally challenging (Loescher *et al.*, 2002; Nadkarni & Sumera, 2004). Problems arise from leaf area sampling techniques – plant canopy analyzers, hemispherical photography, and litterfall traps (Levia & Frost, 2006) – that differ in spatial resolution from throughfall collectors, and, thus, do not accurately capture three-dimensional canopy structure. Despite these limitations, we found a significant negative relationship between tree-scale LAI and tree NTF (Fig. 6a), another correlate of stemflow. Taken together, our data show that major reductions in leaf and epiphyte surface area associated with forest conversion decrease the amount of water retained in plant canopies and available for evaporation, thereby increasing throughfall and local stemflow generation.

Seasonality of water inputs

Interactions among rain and fog seasonality and land-cover attributes had effects on water redistribution that were masked when land-cover types were compared annually. Tree phenology and precipitation characteristics determined the magnitude of land-cover differences in water inputs to canopies and soils, as well as their implications for the hydrologic cycle. In these lower montane rain forests, canopy cover is highest from May to October, when temperate and tropical trees are photosynthetically active (Williams-Linera & Tolome, 1996), and lowest between November and February when some temperate forest trees abscise their leaves. Conversely, commercial coffee agroforests have low LAI, irrespective of season. These phenological dissimilarities heightened (attenuated) the absolute forest-coffee difference in canopy net throughfall during the wet (dry) season. However, as a percentage of rainfall,

land-cover contrast in NTF was more pronounced during the dry season. Partial leaf abscission by forest canopies may have been insufficient to 'wash out' the land cover effect. Alternatively, a seasonal shift in precipitation type and intensity may explain the enhanced dry season disparity between forest and coffee cover types. Fog and 'chipi-chipi' (i.e. drizzling rain; Ruxton, 1848) are more prevalent during dry season months, and these low-intensity precipitation events generally result in higher proportions of canopy interception. Furthermore, the relationship between rainfall intensity and canopy interception was stronger for forest than for coffee sites. In this highly fragmented landscape, another possibility is that a 'vegetation breeze' (i.e. increased rainfall over clearings adjoining forest sites) (Wang *et al.*, 2000) led us to overestimate dry season forest canopy water retention/evaporation. In contrast with our NTF calculations, effects of forest vs. coffee species on stemflow generation were more pronounced during the wet season (Fig. 5). On average, coffee trees generated 654 L of stemflow from 1601 mm of throughfall (TF/SF = 0.4), compared with 151 L per 1512 mm (TF/SF = 0.1) under forest trees.

Decreased wet season canopy water retention/evaporation by coffee agroforests and cleared areas implies that land-use change could potentially alter the ratio of sensible to latent heat fluxes to the atmosphere (Giambelluca *et al.*, 2000). Lower rates of wet-canopy evaporation also increase the amount of water available for surface flow (Bonell, 1998). We have shown that forest to coffee conversion dramatically accelerates the rate of water delivery to soils via throughfall and stemflow, especially when rainfall is heavy and frequent, further suggesting that the shade coffee canopies we studied may have a reduced capacity to buffer soils against the impacts of high-intensity rainfall. While increases in below-canopy water fluxes can increase rainsplash erosion (Herwitz, 1985), reduce opportunities for infiltration (Herwitz, 1986; Harden & Scruggs, 2003), and contribute to surface runoff (Sinun *et al.*, 1992; Harden, 1996), soil properties and underlying geology will clearly influence the magnitude of these effects (Bruijnzeel, 2004). In a study conducted at some of our study sites, Geissert & Ibáñez (2008) found that shade coffee soils had higher bulk density, lower organic matter, and soil porosity than forest soils. In addition, saturated hydraulic conductivity at 0–10 and 10–20 cm depth was 57–82 mm h⁻¹ in forest and 6–15 mm h⁻¹ in coffee sites. Over the course of this study, ~30% of wet season days had hourly rainfall totals >6 mm h⁻¹ and ~20% had hourly totals >15 mm h⁻¹. It is therefore reasonable to expect that altered water partitioning as a result of forest to coffee land-use change, and/or increasing rainfall intensities will enhance runoff from this mountain watershed.

During the dry season, we estimated that fog contributed an additional 16% to total above-canopy water inputs. For the most part, incident fog inputs remained trapped in vegetation canopies, with <5% deposited to forest and coffee soils in throughfall. Recent research indicates that canopy wetting by fog droplets may comprise an important component of stand evaporation in montane cloud forests (Klemm *et al.*, 2006; Giambelluca *et al.*, 2009). Such studies suggest that land-cover change effects on fog deposition rates may also have major consequences for energy partitioning during the dry season (Lawton *et al.*, 2001).

Several possible explanations may account for the low volume of fog drip under plant canopies relative to total incident fog at our sites: overestimation of fog water deposition, evaporation from tree canopies, foliar uptake of fog water, or interception by canopy epiphytes (Weathers *et al.*, 1992; Lovett, 1994; Burgess & Dawson, 2004; Richardson *et al.*, 2000; Nadkarni & Sumera, 2004; Ewing *et al.*, 2009). First, artificial fog collectors may have overestimated fog water deposition to plant canopies, even though fog water inputs fell at the low end of the 0.2–4 mm day⁻¹ range reported for montane cloud forests (Bruijnzeel & Proctor, 1995). A significant positive relationship between rain and fog inputs measured in clearings suggests that passive fog collectors captured wind-driven rain during 'chipi-chipi' (i.e. drizzle) events. In addition, our precipitation monitoring data show that fog events seldom occurred without rain, and when they did, they were generally brief: 89% of all fog events recorded spanned <30 min. That fog water deposition to passive collectors was significantly greater than fog inputs measured in forest and coffee canopy throughfall is not surprising given that passive fog collectors and natural plant surfaces are likely to differ in rates of fog water collection (Lovett, 1994). Second, fog water may have evaporated from plant canopies (Weathers *et al.*, 1992; Klemm *et al.*, 2006). Crown overlap increases the foliage layers through which water must pass (Nadkarni & Sumera, 2004), and, in turn, increases the likelihood that water droplets deposited to leaf surfaces will evaporate (Ford & Deans, 1978). In addition, crown overlap can create a 'shelter' effect, whereby fewer leaves are exposed to fog droplets and thereby fog drip is reduced (Unsworth & Crossley, 1987). Third, although foliar uptake of fog water typically represents a small fraction of plant water use, it is plausible that evergreen cloud forest trees absorb fog water through their leaves during dry periods to rehydrate plant parts (Hutley *et al.*, 1997; Burgess & Dawson, 2004). Finally, canopy epiphytes may intercept fog inputs (Nadkarni, 1984).

Ecologically, these dry season fog inputs may be important for canopy communities and evergreen trees within the forests studied. Epiphytes with high

moisture requirements are likely to benefit from this added water input, while for Neotropical tree species at the latitudinal limit of their distributional range, fog may ameliorate water stress. In the coffee agroforests we studied, fog drip increased the amount of dry season water deposited to soils. Fog water inputs that increase surface soil moisture, stimulate mineralization processes, or are absorbed by plant roots may affect plant vigor (Ewing *et al.*, 2009). Further, fog can act as a significant control on transpirational losses (Ewing *et al.*, 2009). As certain genotypes of *Coffea arabica* are highly sensitive to water stress (DaMatta & Cochicho Ramalho, 2006), fog inputs to coffee soils during water-limited periods coupled with diminished water losses from coffee plants may lower plant water stress, thereby improving coffee production. Therefore, fog capture and deposition may have direct economic benefits for farmers.

Precipitation variability

Over the course of this 3-year study, water fluxes were sampled during one of the most active Atlantic hurricane seasons on record, a mild ENSO event, and during strong La Niña conditions (Fig. 2). This variability provided us with a unique opportunity to examine how tropical storms, hurricanes, and ENSO associated-changes in seasonal precipitation might affect throughfall fluxes to different land-cover types. Our findings show that forest-coffee differences in percent canopy interception were reduced during extreme rainfall events. We did not observe major increases in litterfall inputs following these events, suggesting that increased rainfall intensity rather than leaf area reductions lessened the differences between forest and coffee sites. However, we cannot evaluate the relative importance of canopy characteristics vs. meteorological conditions here, because we did not sample throughfall on an event basis. In addition, rain and fog measurements (Table 2) and historic rainfall data support the observation that dry season rainfall is enhanced during ENSO events (Cavazos, 1997). Because this enhancement coincides with the dry season when water inputs are low, ENSO-associated water pulses may affect forest dynamics, including changes in plant recruitment and biomass production (Holmgren *et al.*, 2001; Weltzin *et al.*, 2003; Lewis *et al.*, 2004). Such marked interannual differences in winter rainfall are of major agricultural importance as well. Central Veracruz is the second largest coffee-producing region in Mexico. Moisture stress is thought to stimulate flowering and bud break in coffee plants (Alvim, 1960), thus excessive dry season rainfall can interfere with coffee development and affect yields.

Implications

Understanding how land-use change and precipitation variability alter water partitioning can help elucidate possible climate change impacts on water resources (Bonell, 1998). Climate scenarios for Central America indicate that rising temperatures may lead to increased precipitation intensity and frequency of extreme rainfall events and dry seasons (Easterling *et al.*, 2000; Bates *et al.*, 2008). Of particular relevance for tropical mountains, rising cloud levels have been suggested as a potential consequence of land-use change and atmospheric warming (Pounds *et al.*, 1999; Still *et al.*, 1999). Climate change effects on ENSO cycles are highly uncertain, but the strength and frequency of these events may also increase (Timmermann *et al.*, 1999).

Our data demonstrate that the fraction of water retained/evaporated from plant canopies decreases with increasing rainfall intensity and that during tropical storms and hurricanes, this decrease is especially pronounced in forests. It is interesting to note that the maximum annual change in throughfall water flux imparted by forest conversion (17%) was greater than the maximum change recorded in forests following tropical storms and hurricanes (10%). On short time-scales, land-cover change may thus have a greater effect on water redistribution than increasing rainfall intensity. Nonetheless, in fragmented human-modified mountain landscapes, an increase in precipitation intensity and in the number of extreme events will likely exacerbate the effects of land-cover change to further promote runoff in these mountain watersheds. In areas where soil hydraulic properties have been substantially altered as a result of intensive land management, high runoff during rainy season months may intensify the risk of natural hazards and/or hinder soil water and groundwater recharge (Bruijnzeel, 2004). These results have regional implications for northern Latin America, where hurricanes are frequent, much terrain is mountainous, and where coffee cultivation and cattle grazing are dominant land uses.

Based on our measurements, forest conversion to pasture could result in a 16% decrease in fog input to plant canopies during the dry season. This decrease is nearly equivalent to the maximum projected rainfall reduction of 20% for the Latin American region by 2080 (IPCC, 2007). In our study region, where dry season ENSO events are associated with wetter than average conditions, it is unclear whether or not an increase in the strength or number of ENSO events might offset these effects. Regardless, synergistic interactions between climatic variability and land-cover change could converge to affect the structure and composition of this transitional mixed temperate deciduous-tropical

evergreen forest, as well as the productivity of coffee agroforests. The extreme sensitivity of montane ecosystems to climatic oscillations (Bush *et al.*, 2004) and documented changes in species distributions and abundances on tropical mountains (Pounds *et al.*, 1999; Parmesan & Yohe, 2003) further suggest that changing hydrologic cycles will have profound effects on these land-use systems (Enquist, 2002).

Acknowledgements

We owe much gratitude to all landowners for their unending support. We thank Milton Díaz Toribio, Carlos Cesar Pérez de San Martín, Raquel Cervantes Alday, Romeo Saldaña Vásquez, Alejandra Tauro, Manuel, Odilón, Eliseo, Alejandro Paz, Matthew Fry, and Alejandro Hernández Sánchez for field assistance, and Amanda E. Elliott for laboratory assistance. We are indebted to Guadalupe Williams-Linera, Robert H. Manson, and the staff at the Functional Ecology Laboratory, Instituto de Ecología, A.C., in Xalapa, Veracruz, for their support. We are extremely grateful to Kenneth R. Young and four anonymous reviewers for their comments and suggestions on this paper. Funding was provided by the NASA Graduate Student Research Fellowship (K. Jon Ranson, technical advisor), the National Science Foundation (DEB-0608184, DBI-0521091), the Ford Foundation, the Institute of International Education, the Compton Foundation, the Tinker Foundation, Yale Institute for Biospheric Studies and the Tropical Resources Institute of Yale University.

References

- Alvim PDT (1960) Moisture stress as a requirement for flowering of coffee. *Science*, **132**, 354.
- Asbjornsen H, Vogt KA, Ashton MS (2004) Synergistic responses of oak, pine and shrub seedlings to edge environments and drought in a fragmented tropical highland oak forest, Oaxaca, Mexico. *Forest Ecology and Management*, **192**, 313–334.
- Ataroff M (2002) Precipitación e intercepción en ecosistemas boscosos de los andes venezolanos. *Ecotropicos*, **15**, 195–202.
- Ataroff V, Rada F (2000) Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. *Ambio*, **29**, 440–444.
- Avisar R, Silva Dias PL, Silva Dias MAF, Nobre C (2002) The Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA): Insights and future research needs. *Journal of Geophysical Research-Atmospheres*, **107**, 8086, doi: 10.1029/2002JD002704.
- Báez AP, Padilla H, Cervantes J, Pereyra D, Belmont R (1997) Rainwater chemistry at the eastern flanks of the Sierra Madre Oriental, Veracruz, Mexico. *Journal of Geophysical Research*, **102**, 23329–23336.
- Baron JS, Hartman MD, Kittel TGF, Band LE, Ojima DS, Lambers RB (1998) Effects of land cover, water redistribution, and temperature on ecosystem processes in the South Platte Basin. *Ecological Applications*, **8**, 1037–1051.
- Bates BC, Kundzewicz ZW, Wu S, Palutikof JP (eds) (2008) *Climate Change and Water*. Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat, Geneva.
- Bonell M (1998) Possible impacts of climate variability and change on tropical forest hydrology. *Climatic Change*, **39**, 215–272.
- Bosch JM, Hewlett JD (1982) A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology*, **55**, 3–23.
- Bradshaw CJA, Sodhi NS, Peh KSH, Brook BW (2007) Global evidence that deforestation amplifies flood risk and severity in the developing world. *Global Change Biology*, **13**, 2379–2395.
- Brewer CA, Smith WK (1997) Patterns of leaf surface wetness for montane and subalpine plants. *Plant, Cell, and Environment*, **20**, 1–11.
- Bruijnzeel LA (2002) Hydrology of tropical montane cloud forests: a reassessment. In: *Proceedings of the Second International Colloquium on Hydrology and Water Management of the Humid Tropics* (ed. Gladwell JS), pp. 353–383. UNESCO, Paris and Cathalac, Panama City.
- Bruijnzeel LA (2004) Hydrological functions of tropical forests: not seeing the soil for the trees? *Agriculture Ecosystems and Environment*, **104**, 185–228.
- Bruijnzeel LA, Proctor J (1995) Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? In: *Tropical Montane Cloud Forests* (eds Churchill SP, Blaslev H, Forero E, Luteyn JL), pp. 38–78. Springer-Verlag, New York.
- Burgess SSO, Dawson TE (2004) The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell, and Environment*, **27**, 1023–1034.
- Bury J (2005) Mining mountains: neoliberalism, land tenure, livelihoods, and the new Peruvian mining industry in Cajamarca. *Environment and Planning A*, **37**, 221–239.
- Bush MB, Silman MR, Urrego DH (2004) 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303**, 827–829.
- Butler TJ, Likens GE (1995) A direct comparison of throughfall plus stemflow to estimates of dry and total deposition for sulfur and nitrogen. *Atmospheric Environment*, **29**, 1253–1265.
- Carlyle-Moses DE (2004) Throughfall, stemflow, and canopy interception loss fluxes in a semi-arid Sierra Madre Oriental matorral community. *Journal of Arid Environments*, **58**, 181–202.
- Carlyle-Moses DE, Flores Laureano JS, Price AG (2004) Throughfall and throughfall spatial variability in Madrean oak forest communities of northeastern Mexico. *Journal of Hydrology*, **297**, 124–135.
- Caso M, González-Abraham C, Ezcurra E (2007) Divergent ecological effects of oceanographic anomalies on terrestrial ecosystems of the Mexican Pacific coast. *Proceedings of the National Academy of Sciences*, **104**, 10530–10535.
- Cavazos T (1997) Downscaling large-scale circulation to local winter rainfall in north-eastern Mexico. *International Journal of Climatology*, **17**, 1069–1082.
- Cavazos T, Hastenrath S (1990) Convection and rainfall over Mexico and their modulation by the Southern Oscillation. *International Journal of Climatology*, **10**, 377–386.
- Cavelier J, Goldstein G (1989) Mist and fog interception in elfin cloud forests in Colombia and Venezuela. *Journal of Tropical Ecology*, **5**, 309–322.
- Cavelier J, Solis D, Jaramillo MA (1996) Fog interception in montane forests across the central cordillera of Panama. *Journal of Tropical Ecology*, **12**, 357–369.

- Cayuela L, Benayas JMR, Echeverría C (2006) Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico (1975–2000). *Forest Ecology and Management*, **226**, 208–218.
- Condit R, Aguilar S, Hernandez A *et al.* (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology*, **20**, 51–72.
- Curtis JT, McIntosh RP (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, **32**, 476–496.
- Dai FC, Lee CF (2002) Landslide characteristics and slope instability modeling using GIS, Lantau Island, Hong Kong. *Geomorphology*, **42**, 213–228.
- Dale VH (1997) The relationship between land-use change and climate change. *Ecological Applications*, **7**, 753–769.
- DaMatta FM, Cochicho Ramalho JD (2006) Impacts of drought and temperature stress on coffee physiology and production: a review. *Brazilian Journal of Plant Physiology*, **18**, 55–81.
- DeFries RS, Bounoua L, Collatz GJ (2002) Human modification of the landscape and surface climate in the next fifty years. *Global Change Biology*, **8**, 438–458.
- del-Val E, Armesto JJ, Barbosa O *et al.* (2006) Rain forest islands in the Chilean semiarid region: fog-dependency, ecosystem persistence and tree regeneration. *Ecosystems*, **9**, 598–608.
- Dietz J, Hölscher D, Leuschner C, Hendrayanto (2006) Rainfall partitioning in relation to forest structure in differently managed montane forest stands in Central Sulawesi, Indonesia. *Forest Ecology and Management*, **237**, 170–178.
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.
- Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.
- Enquist CAF (2002) Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *Journal of Biogeography*, **29**, 519–534.
- Ewing HA, Weathers KC, Templer PH, Dawson TE, Firestone MK, Elliott AE, Boukili VKS (2009) Fog water and ecosystem function: heterogeneity in a California redwood forest. *Ecosystems*, **12**, 417–433.
- Falconer RE, Falconer PD (1980) Determination of cloud water acidity at a mountain observatory in the Adirondack Mountains of New York State. *Journal of Geophysical Research-Oceans and Atmospheres*, **85**, 7465–7470.
- Farley KA, Kelly EF, Hofstede RGM (2004) Soil organic carbon and water retention following conversion of grasslands to pine plantations in the Ecuadorian Andes. *Ecosystems*, **7**, 729–739.
- Fleischbein K, Wilcke W, Goller R, Boy J, Valarezo C, Zech W, Knoblich K (2005) Rainfall interception in a lower montane forest in Ecuador: effects of canopy properties. *Hydrological Processes*, **19**, 1355–1371.
- Ford ED, Deans JD (1978) The effects of canopy structure on stemflow, throughfall, and interception loss in a young Sitka Spruce plantation. *Journal of Applied Ecology*, **15**, 905–917.
- García E (1973) *Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la República Mexicana)*. Universidad Nacional Autónoma de México, Mexico City.
- Geissert D, Ibáñez I (2008) Calidad y ambiente físico-químico de los suelos. In: *Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación* (eds Manson RH, Hernández Ortiz V, Gallina S, Mehlreter K), pp. 213–221. Instituto Nacional de Ecología, México D.F., Mexico.
- Gentry AH, Dodson CH (1987) Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, **74**, 205–233.
- Giambelluca TW (2002) Hydrology of altered tropical forest. *Hydrological Processes*, **16**, 1665–1669.
- Giambelluca TW, Martin RE, Asner GP *et al.* (2009) Evapotranspiration and energy balance of native wet montane cloud forest in Hawai'i. *Agricultural and Forest Meteorology*, **149**, 230–243.
- Giambelluca TW, Nullet MA, Ziegler AD, Tran L (2000) Latent and sensible energy flux over deforested land surfaces in the eastern Amazon and northern Thailand. *Singapore Journal of Tropical Geography*, **21**, 107–130.
- Gordon LJ, Peterson GD, Bennett EM (2008) Agricultural modifications of hydrological flows create ecological surprises. *Trends in Ecology and Evolution*, **23**, 211–219.
- Grubb PJ (1977) Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics*, **8**, 83–107.
- Guhl A (2008) Coffee production intensification and landscape change in Colombia, 1970–2002. In: *Land-Change Science in the Tropics: Changing Agricultural Landscapes* (eds Millington A, Jepson W), pp. 93–116. Springer, New York.
- Gutiérrez AG, Barbosa O, Christie DA *et al.* (2008) Regeneration patterns and persistence of the fog-dependent Fray Jorge forest in semiarid Chile during the past two centuries. *Global Change Biology*, **14**, 161–176.
- Harden CP (1996) Interrelationships between land abandonment and land degradation: a case from the Ecuadorian Andes. *Mountain Research and Development*, **16**, 274–280.
- Harden CP, Scruggs PD (2003) Infiltration on mountain slopes: a comparison of three environments. *Geomorphology*, **55**, 5–24.
- Hecht SB, Saatchi SS (2007) Globalization and forest resurgence: changes in forest cover in El Salvador. *BioScience*, **57**, 663–672.
- Herwitz SR (1985) Interception storage capacities of tropical rainforest canopy trees. *Journal of Hydrology*, **77**, 237–252.
- Herwitz SR (1986) Infiltration-excess caused by stemflow in a cyclone-prone tropical rainforest. *Earth Surface Processes and Landforms*, **11**, 401–412.
- Hietz P (2005) Conservation of vascular epiphyte diversity in Mexican coffee plantations. *Conservation Biology*, **19**, 391–399.
- Hietz P, Hietz-Seifert U (1995) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in Central Veracruz, Mexico. *Journal of Vegetation Science*, **6**, 487–498.
- Holder CD (2003) Fog precipitation in the Sierra de las Minas Biosphere Reserve, Guatemala. *Hydrological Processes*, **17**, 2001–2010.

- Holder CD (2007) Leaf water repellency of species in Guatemala and Colorado (USA) and its significance to forest hydrology studies. *Journal of Hydrology*, **336**, 147–154.
- Holmgren M, Scheffer M, Ezcurra E, Gutiérrez JR, Mohren GMJ (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution*, **16**, 89–94.
- Hölscher D, Bruijnzeel LA, Köhler L, Leuschner C, Kappelle M (2003) Nutrient fluxes in stemflow and throughfall in three successional stages of an upper montane rain forest in Costa Rica. *Journal of Tropical Ecology*, **19**, 557–565.
- Hölscher D, Köhler L, van Dijk A, Bruijnzeel LA (2004) The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology*, **292**, 308–322.
- Hutley LB, Doley D, Yates DJ, Boonsaner A (1997) Water balance of an Australian subtropical rainforest at altitude: the ecological and physiological significance of intercepted cloud and fog. *Australian Journal of Botany*, **45**, 311–329.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge, UK.
- Jaramillo-Robledo A (2003) La lluvia y el transporte de nutrientes dentro de ecosistemas de bosque y cafetales. *Cenicafé*, **54**, 134–144.
- Jáuregui Ostos E (2004) Contrastes bioclimáticos entre el mar y la montaña en la zona central del Estado de Veracruz (México). In: *El Clima entre el Mar y la Montaña* (eds García Codron JC, Diego Liaño C, Fdez. De Arróyabe Hernández P, Garmendia Pedraja C, Rasilla Álvarez D), Asociación Española de Climatología y Universidad de Cantabria, Santander.
- Kammerbauer J, Ardon C (1999) Land use dynamics and landscape change pattern in a typical watershed in the hillside region of central Honduras. *Agriculture, Ecosystems and Environment*, **75**, 93–100.
- Kintz DB, Young KR, Crews-Meyer KA (2006) Implications of land use/land cover change in the buffer zone of a national park in the tropical Andes. *Environmental Management*, **38**, 238–252.
- Klemm O, Chang SC, Hsia YJ (2006) Energy fluxes at a subtropical mountain cloud forest. *Forest Ecology and Management*, **224**, 5–10.
- Lawton RO, Nair US, Pielke RA, Welch RM (2001) Climatic impacts of tropical lowland deforestation on nearby montane cloud forests. *Science*, **294**, 584–587.
- Levia DF, Frost EE (2006) Variability of throughfall volume and solute inputs in wooded ecosystems. *Progress in Physical Geography*, **30**, 605–632.
- Lewis SL, Malhi Y, Phillips OL (2004) Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 437–462.
- Loescher HW, Powers JS, Oberbauer SF (2002) Spatial variation of throughfall volume in an old-growth tropical wet forest, Costa Rica. *Journal of Tropical Ecology*, **18**, 397–407.
- López-Gómez AA, Williams-Linera G, Manson RH (2008) Tree species diversity and vegetation structure in shade coffee farms in Veracruz, Mexico. *Agriculture Ecosystems and Environment*, **124**, 160–172.
- Lovett GM (1994) Atmospheric deposition of nutrients and pollutants in North America: an ecological perspective. *Ecological Applications*, **4**, 629–650.
- Lovett GM, Bowser JJ, Edgerton ES (1997) Atmospheric deposition to watersheds in complex terrain. *Hydrological Processes*, **11**, 645–654.
- Lovett GM, Reiners WA (1986) Canopy structure and cloud water deposition in subalpine coniferous forests. *Tellus*, **38B**, 319–326.
- Magaña VO, Vásquez JL, Pérez JL, Pérez JB (2003) Impact of El Niño on precipitation in Mexico. *Geofísica Internacional*, **42**, 313–330.
- Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology*, **13**, 1–11.
- Molina A, Govers G, Vanacker V, Poesen J, Zeelmaekers E, Cisneros F (2007) Runoff generation in a degraded Andean ecosystem: interaction of vegetation cover and land use. *Catena*, **71**, 357–370.
- Muñoz-Villers LE, López-Blanco J (2008) Land use/cover changes using Landsat TM/ETM images in a tropical and biodiverse mountainous area of central-eastern Mexico. *International Journal of Remote Sensing*, **29**, 71–93.
- Nadkarni NM (1984) Epiphyte biomass and nutrient capital of a Neotropical Elfin forest. *Biotropica*, **16**, 249–256.
- Nadkarni NM, Schaefer D, Matelson TJ, Solano R (2004) Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecology and Management*, **198**, 223–236.
- Nadkarni NM, Sumera MM (2004) Old-growth forest canopy structure and its relationship to throughfall interception. *Forest Science*, **50**, 290–298.
- Nepstad DC, Moutinho P, Dias MB *et al.* (2002) The effects of partial throughfall exclusion on canopy processes, above-ground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research-Atmospheres*, **107**, 8085, doi: 10.1029/2001JD000360.
- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**, 2259–2269.
- Nobre CA, Sellers PJ, Shukla J (1991) Amazonian deforestation and regional climate change. *Journal of Climate*, **4**, 957–988.
- Ochoa-Gaona S, González-Espinosa M (2000) Land use and deforestation in the highlands of Chiapas, Mexico. *Applied Geography*, **20**, 17–42.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **42**, 37–42.
- Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.
- Restrepo C, Alvarez N (2006) Landslides and their contribution to land-cover change in the mountains of Mexico and Central America. *Biotropica*, **38**, 446–457.
- Richardson BA, Richardson MJ, Scatena FN, McDowell WH (2000) Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Tropical Ecology*, **16**, 167–188.

- Romero H, Ordenes F (2004) Emerging urbanization in the southern Andes: environmental impacts of urban sprawl in Santiago de Chile on the Andean piedmont. *Mountain Research and Development*, **24**, 197–201.
- Ruxton GFA (1848) *Adventures in Mexico and the Rocky Mountains*. Harper & Brothers, New York.
- Sarmiento FO (1997) Arrested succession in pastures hinders regeneration of Tropicandean forests and shreds mountain landscapes. *Environmental Conservation*, **24**, 14–23.
- Sarmiento FO, Frolich LM (2002) Andean cloud forest tree lines: naturalness, agriculture and the human dimension. *Mountain Research and Development*, **22**, 278–287.
- Scatena FN (1990) Watershed scale rainfall interception on two forested watersheds in the Luquillo Mountains of Puerto Rico. *Journal of Hydrology*, **113**, 89–102.
- Schroth G, da Silva LF, Wolf MA, Teixeira WG, 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.
- Sinun W, Meng WW, Douglas I, Spencer T (1992) Throughfall, stemflow, overland flow and throughflow in the Ulu Segama rain forest, Sabah, Malaysia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **335**, 389–395.
- Stadtmüller T (1987) *Los bosques nublados en el trópico húmedo. Una revisión bibliográfica*. Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba.
- Staelens J, De Schrijver A, Verheyen K, Verhoest NEC (2006) Spatial variability and temporal stability of throughfall water under a dominant beech (*Fagus sylvatica* L.) tree in relationship to canopy cover. *Journal of Hydrology*, **330**, 651–662.
- Still C, Foster PN, Schneider SH (1999) Simulating the effects of climate change on tropical montane cloud forests. *Nature*, **398**, 608–610.
- Stogsdill WR, Wittwer RF, Hennessey TC, Dougherty PM (1989) Relationship between throughfall and stand density in a *Pinus taeda* plantation. *Forest Ecology and Management*, **29**, 105–113.
- Thomlinson JR, Serrano MI, Lopez MT, Aide TM, Zimmerman JK (1996) Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). *Biotropica*, **28**, 525–536.
- Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694–696.
- Unsworth MH, Crossley A (1987) Capture of wind-driven cloud by vegetation. In: *Pollutant Transport and Fate in Ecosystems* (eds Coughtrey PJ, Martin MH, Unsworth MH), pp. 125–137. Blackwell Scientific Publishing, Oxford.
- Veneklaas EJ, Vanek R (1990) Rainfall interception in two tropical montane rain forests, Colombia. *Hydrological Processes*, **4**, 311–326.
- Viviroli D, Weingartner R, Messerli B (2003) Assessing the hydrological significance of the world's mountains. *Mountain Research and Development*, **23**, 32–40.
- Wang J, Bras RL, Eltahir EAB (2000) The impact of observed deforestation on the mesoscale distribution of rainfall and clouds in Amazonia. *Journal of Hydrometeorology*, **1**, 267.
- Weathers KC, Cadenasso ML, Pickett STA (2001) Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology*, **15**, 1506–1514.
- Weathers KC, Lovett GM, Likens GE (1992) The influence of a forest edge on cloud deposition. In: *Precipitation scavenging and atmosphere-surface exchange: the summers volume* (eds Schwartz SE, Slinn WGN), pp. 1415–1423. Hemisphere Publishing, Washington, DC.
- Weathers KC, Lovett GM, Likens GE (1995) Cloud deposition to a spruce forest edge. *Atmospheric Environment*, **29**, 665–672.
- Weathers KC, Lovett GM, Likens GE, Lathrop R (2000) The effect of landscape features on deposition to Hunter Mountain, Catskill Mountains, New York. *Ecological Applications*, **10**, 528–540.
- Weathers KC, Simkin SM, Lovett GM, Lindberg SE (2006) Empirical modeling of atmospheric deposition in mountainous landscapes. *Ecological Applications*, **16**, 1590–1607.
- Weltzin JF, Loik ME, Schwinning S *et al.* (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience*, **53**, 941–952.
- Williams-Linera G (1997) Phenology of deciduous and broad-leaved-evergreen tree species in a Mexican tropical lower montane forest. *Global Ecology and Biogeography Letters*, **6**, 115–127.
- Williams-Linera G, Tolome J (1996) Litterfall, temperate and tropical dominant trees, and climate in a Mexican lower montane forest. *Biotropica*, **28**, 649–656.
- Wolf JHD (2005) The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *Forest Ecology and Management*, **212**, 376–393.
- Ziegler AD, Giambelluca TW, Tran LT *et al.* (2004) Hydrological consequences of landscape fragmentation in mountainous northern Vietnam: evidence of accelerated overland flow generation. *Journal of Hydrology*, **287**, 124–146.
- Zimmermann A, Wilcke W, Elsenbeer H (2007) Spatial and temporal patterns of throughfall quantity and quality in a tropical montane forest in Ecuador. *Journal of Hydrology*, **343**, 80–96.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Name and location of 11 meteorological stations >1000 m in central Veracruz, Mexico, with overlapping rainfall measurements for 1965–1999 (Servicio Meteorológico Nacional). These data were used to assess the effects of El Niño Southern Oscillation on dry season rainfall in the study region.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.