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Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall quality in a Mexican tropical deciduous forest ecosystem

J. MANUEL MAASS*[1], ANGELINA MARTÍNEZ-YRÍZAR†, CRISTINA PATIÑO‡ *and* JOSÉ SARUKHÁN‡

**Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 27-3, CP 58089, Morelia, Michoacán, México*
†Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 1354, CP 83000, Hermosillo, Sonora, México
‡Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, CP 04510, México, D.F., México

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ABSTRACT. The amount and annual net accumulation of above-ground dead woody material were quantified in a tropical deciduous forest in western Mexico. Three plots were located within a small watershed (16 ha) and distributed along a 150-m-elevation gradient (Upper, Middle and Lower plot). Total amount of above-ground dead phytomass (fine + coarse) was 27.2 Mg ha^{-1}. Coarse dead category (branches + logs) made up 70.6% (19.2 Mg ha^{-1}) of the total. The rest comprised the fine fraction, which was lying on the forest floor as surface litter. Of the total coarse dead woody mass, 70.8% was standing, hanging or still attached to live trees (13.6 Mg ha^{-1}). Dead wood net accumulation was 6.6 Mg ha^{-1} y^{-1}; 58% of this was coarse woody material and the rest comprised the fine litterfall fraction. The amount of standing, hanging/attached dead branches (2–20 cm circumference) varied significantly among plots, with the highest value in the Upper plot. Dead wood net accumulation was similar between the Upper and Middle plots, and significantly higher than the Lower plot. Compared to the intact canopy, the removal of dead mass (hanging/attached dead branches and standing dead logs) caused a significant decrease in throughfall nutrient concentration and nutrient flux by this pathway.

KEY WORDS: carbon pool, Chamela forest, coarse woody debris, forest canopy, litterfall, nutrient cycling, throughfall quality, watershed

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[1] Corresponding author. Present address: Coweeta Hydrologic Laboratory (USDA-FS), 3160 Coweeta Lab. Road, Otto, NC 28763, USA. Email: maass@oikos.unam.mx

INTRODUCTION

Nearly 65% of the total NPP of the Chamela tropical deciduous forest (TDF) ecosystem in western Mexico flows annually to the decomposer community as litterfall and fine-root litter production (Martínez-Yrízar *et al.* 1996). Most of this material, which includes leaves, twigs, flowers, fruits, seeds and small roots is easily decomposed and recycled in the system each year (Martínez-Yrízar 1980, 1995). The other 35% is mostly accumulated as wood and root increment of living plants, which constitutes a long-term pool of energy and nutrients slowly released to the heterotrophic community. This stored energy is incorporated to the forest floor when branches or complete trees die and fall to the ground. This process, which creates gaps in the canopy, is a common feature in tropical humid forests (Hartshorn 1978), but rare in the TDF. The structure of the vegetation is characterized by a high density of thin and short-statured trees with a profusion of vines and lianas (Gentry 1995) some of which can have relatively large crowns. The presence of a dense liana cover causes many dead branches to remain hanging in the canopy and dead trees to persist standing for a long time. The quantification of the dead compartment and its vertical distribution in the ecosystem has been a relatively neglected aspect of productivity studies, particularly in the tropics. This information is essential to estimate carbon pools and important when predicting how global change will affect carbon cycling in these forests (Chambers *et al.* 2000).

Nutrient transfer from the canopy by rainfall is an important pathway of nutrient input to the soil system (Likens *et al.* 1977, McDowell 1998). In connection to this, three main processes may enhance nutrient input via throughfall to the forest floor in the Chamela TDF: (1) dry deposition of marine aerosols onto the canopy and their subsequent wash-off by rainfall, (2) leaching of highly soluble nutrients, like K^+, from the cells near the leaf surface (Schlesinger 1997), and (3) decomposition and mineralization of the dead material located within the canopy. Studies related to the contribution of these processes to the intrasystem nutrient cycling for TDF are scarce (Campo *et al.* 2000, 2001; Jaramillo & Sanford 1995).

The main objective of the present study is to determine the quantity, spatial distribution and annual net accumulation of above-ground dead phytomass in an undisturbed tropical deciduous forest ecosystem in western Mexico. We also explore the influence of dead woody material in the canopy on throughfall enrichment.

STUDY AREA

This study is part of a long-term ecological research project initiated in 1980 aimed at analysing the structure and functioning of a TDF. The project is conducted at the Estación de Biología Chamela, which is part of the Chamela-Cuixmala Biosphere Reserve. The field station is located at 19° 30′ N, 105° 03′

W in the state of Jalisco, 2 km inland from the Pacific coast of Mexico. The climate is warm (mean annual temperature 24.9 °C) and influenced by tropical cyclones which produce a highly variable and seasonal rainfall regime (García-Oliva *et al.* 1991). The 6–8-mo dry period extends from November to mid-June. Mean annual precipitation is 780 mm (1983–1999, F. García-Oliva *pers. comm.*). August and September are the wettest months. Soils are young, weakly developed Entisols on a substrate of rhyolite and basalts (Solís-Villalpando 1993).

The vegetation is a tropical deciduous forest, a subset of seasonally dry tropical forests, in which a highly seasonal rainfall induces most plant species to drop their leaves as a drought-resistance mechanism. It is a very diverse and dense vegetation type with a well-developed understorey of shrubs (Lott 1993, Lott *et al.* 1987, Pérez-Jiménez *et al.* unpubl. data). The canopy is 4–15 m high. The most conspicuous feature of this vegetation is the markedly seasonal pattern of leaf area index (< 1 m^2 m^{-2} in May, 4.5 m^2 m^{-2} in September, Maass *et al.* 1995) and fine litterfall (wet season = 116 g m^{-2}, dry season = 279 g m^{-2}, Martínez-Yrízar & Sarukhán 1990).

METHODS

Permanent plots

Structural and functional parameters of the Chamela forest have been monitored for 18 y on five contiguous small watersheds (12–28 ha each) with ephemeral streams. The present study was conducted in one of the watersheds, Watershed 1 (Ws-1; 16 ha, 60–160 m elevation, E–W orientation) which was divided in three elevation sections (López-Blanco *et al.* 1999). A permanent plot of about 1/3 ha (80 × 30 m) was located on each section. All three plots were placed perpendicularly to the drainage channel so that one half of each plot is facing north and the other is facing south. Distance between plots was 200–250 m. Site characteristics of each plot, henceforth designated as Upper, Middle and Lower, are listed in Table 1. The most important species on each plot are: in the Upper plot, *Guapira macrocarpa* Miranda, *Plumeria rubra* L., *Lonchocarpus constrictus* Pitt., *Bursera instabilis* McVaugh & Rzed. and *Colubrina heteroneura* (Griseb.) Standl.; in the Middle plot, *Guapira macrocarpa*, *Lonchocarpus eriocarinalis* Micheli, *Plumeria rubra*, *Piptadenia constricta* (Micheli) Macbr. and *Bursera instabilis*; and in the Lower plot, *Thouinidium decandrum* (Humb. & Bompl.) Radlk., *Guapira macrocarpa*, *Astronium graveolens* Jacq., *Trichilia trifolia* L. and *Casearia corymbosa* H.B.K. (A. Pérez-Jiménez, unpubl. data).

Sampling of dead-wood material

In order to reduce plot disturbance by sampling, 5 × 5-m quadrats were set up adjacent to each of the permanent plots for dead-wood measurements during the dry season of 1988 (March to May). The Middle plot was more intensively sampled (32 quadrats) because it was considered to represent the

Table 1. Site characteristics of the permanent plots located in the tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico.

		Sampling plots			
Parameter	Units	Upper	Middle	Lower	Reference
Elevation	m asl	150	130	70	1
Slope interval	degrees	8–16	8–16	16–30	1
Soil depth[1]	cm	40–45	15–25	25–30	1
Soil organic matter (0–10 cm)	%	2.0–2.5	2.5–3.0	3.0–3.5	1
Stem density (dbh > 3.18 cm)	ind ha^{-1}	2790	3221	2104	2
Basal area (dbh > 3.18 cm)	m^2 ha^{-1}	12.7	17.3	19.8	2
Average tree height	m	5.1	4.9	6.2	2
Maximum tree height	m	9.0	14.0	25.0	2
Leaf area index	m^2 m^{-2}	3.3	3.8	5.4	3
Total NPP	Mg ha^{-1} y^{-1}	11.2	11.5	13.5	4

[1] Roots can be found throughout the soil profile although 91% of the below-ground biomass is confined within the upper 40 cm (Castellanos *et al.* 1991).

References: 1. Galicia *et al.* (1999), 2. Pérez-Jiménez *et al.* (unpubl. data), 3. Maass *et al.* (1995), 4. Martínez-Yrízar *et al.* (1996).

most common landscape condition in the area. An analysis of cumulative variance against the increasing sample size indicated that 5–10 quadrats comprised a representative sample. Based on this analysis, fewer quadrats were sampled in the Upper and Lower plots, depending on access to the canopy and time involved (14 and 7 quadrats, respectively). Quadrats were located randomly, except in the Middle plot, where their distribution was systematic.

Dead twigs, branches or stems 2–20 cm in circumference (hereafter designated as 'branches') were collected in each quadrat. This size category also included the attached dead portions of any living branch or stem. Dead wood fragments larger than 20 cm in circumference (> 6.4 cm in diameter, henceforth designated as 'logs') were collected along nine 150-m^2 transects (5 × 30 m) randomly distributed throughout the watershed. Dead logs were separated into two groups: (1) standing, which consisted of all pieces hanging in the canopy, attached to living stems and standing above 30 cm from the forest floor, and (2) downed or fallen, which included all dead segments located within the first 30 cm from the surface soil. The material was weighed in the field and subsamples were taken to the laboratory to determine dry weight (oven-dried at 80 °C to constant weight; about 72 h). To estimate the annual dead wood net accumulation, all quadrats and transects were resampled again 1 y later.

The dead logs and branches included in our sampling comprised the 'coarse' dead fraction of the forest. The values for the 'fine' dead fraction (surface litter and twigs < 2 cm in circumference) were obtained for the same plots and period of our measurements by Patiño (1990). Annual fine litterfall values used to calculate the annual accumulation of fine dead phytomass were obtained from our long-term litter production database (1982–2001). Litterfall was determined by monthly sampling of 24 litter traps (50 cm diameter, 1 m height) located on each plot.

Throughfall measurements

Twelve throughfall collectors (polyvinyl chloride gutters, 0.1 m width × 2 m long) were installed along the watershed elevation gradient. Half of the collectors were located under the intact canopy, and half beneath the canopy where dead woody material was removed for dead phytomass determinations. In addition, six collectors (polyethylene funnels 15 cm in diameter) were installed in open areas for direct rainfall measurements. Each collector drained into a polypropylene reservoir (22.5 litre capacity) via Tygon tubing. Collectors were covered with 1-mm-mesh-size fibreglass. Glass wool was also placed at the mouth of the drainage tubing to prevent contamination from litter debris. The reservoir was attached to a vapour trap and a vapour barrier formed by a loop in the tubing to prevent evaporation and gas exchange with the atmosphere. The reservoir and tubing were shaded from sunlight to avoid algal growth. For 2 y, after every storm 160 ml of rainfall from each collector were preserved by adding 0.5 ml of phenyl mercuric acetate solution (0.1 g in 15 ml dioxane, diluted to 100 ml). Samples were stored in polypropylene containers, analysed for pH and kept refrigerated. The collectors were cleaned after every storm with deionized water. Samples were filtered to remove the suspended material and analysed for cation concentrations. Potassium and sodium were determined by flame emission, and Ca and Mg by atomic absorption, atomising in air-acetylene flame (Perkin-Elmer). One ml of lanthanum (La) solution (29 g La_2O_3 in 250 ml HCl, diluted to 500 ml) was added per 10 ml sample. Concentrations were corrected with deionized water blanks.

Statistical analysis

A two-way analysis of variance (with unequal but proportional subclass number) was performed to test for effects for site (Upper, Middle and Lower plot) and type of material (hanging/attached and fallen) on the amount and accumulation of dead-wood phytomass. Dunnett's test was used for comparisons of means. A Wilcoxon two-sample test was used to test for differences between the amounts of standing and downed dead-wood debris in the transects. Throughfall samples were lumped by treatment across the plots and a t-test was used to compare the means for each time of collection (Sokal & Rohlf 1981).

RESULTS

Dead-wood phytomass

The total above-ground coarse dead phytomass in Ws-1 was 19.2 Mg ha^{-1} (Table 2). About one third of this material was found within the first 30 cm above the forest floor, and the rest either as standing dead trees, or hanging/attached dead branches on living trees. The total fine dead material accumulated on the forest floor, as surface litter or standing crop litter, averaged 8.0 Mg ha^{-1} (Patiño 1990). Thus, the total above-ground dead-wood phytomass in

Table 2. Total above-ground (ABG) dead phytomass (Mg ha^{-1}) in a tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico. Estimates of fine dead material (leaves, twigs and small branches < 2 cm circumference) were taken from Patiño (1990).

Compartment	Standing	Forest floor	Total
Dead coarse woody material			
Branches (2–20 cm in circumference)	8.0	3.7	11.7
Logs (> 20 cm in circumference)	5.6	1.9	7.5
Total coarse (branches + logs)	13.6	5.6	19.2
Total fine (surface litter)	Trace	8.0	8.0
Total ABG dead phytomass	13.6	13.6	27.2

Ws-1 was 27.2 Mg ha^{-1}. There was a significant difference in the quantity of standing dead branches from the Lower to the Upper plot (Table 3); however, the amount of dead branches lying on the forest floor did not vary significantly among plots.

The amount of dead logs (standing + fallen) varied greatly among the transects (range 4–28 Mg ha^{-1}; Figure 1). Except for transect no. 9, the mass of standing dead logs was always higher than the mass of fallen logs.

Dead-wood net accumulation

The annual net accumulation of total above-ground dead phytomass in Ws-1 was 6.6 Mg ha^{-1} y^{-1} (Table 4). The coarse dead woody material (standing + fallen) accounted for 58% of this total, whereas the rest (2.8 Mg ha^{-1} y^{-1}, Martínez-Yrízar *et al.* 1996) comprised the fine fraction. A large proportion (82%) of the coarse dead-wood accumulation (branches + logs) did not reach the forest floor (Table 4).

The annual net accumulation of dead branches varied significantly among plots. The lowest values were recorded in the quadrats sampled adjacent to the Lower permanent plot (Table 5).

Throughfall quantity and quality

The change in rainfall interception as a result of the removal of the canopy dead phytomass was not statistically significant ($P > 0.05$; Table 6). However, the removal of hanging/attached dead wood mass caused a significant decrease

Table 3. Dead-wood phytomass (Mg ha^{-1}) as branches (2–20 cm in circumference) in tropical deciduous forest plots along an elevation gradient in Watershed 1 in Chamela, Jalisco, Mexico. Standard deviations and sample sizes are given in parentheses. Means with the same letter are not significantly different among plots ($P < 0.05$).

Plot	Standing		Forest floor	
Upper	12.21	(3.33, 14) a	4.30	(1.58, 14) c
Middle	7.26	(3.49, 32) b	3.42	(1.30, 32) c
Lower	4.68	(3.29, 7) c	3.54	(0.96, 7) c
Mean	8.05		3.75	

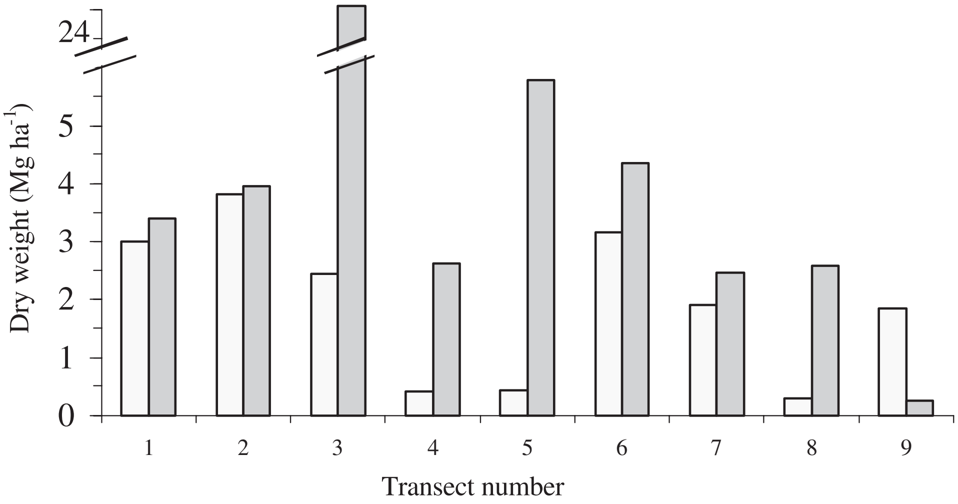

Figure 1. Standing (dark bars) and fallen (light bars) dead phytomass (logs > 20 cm in circumference) in nine 150-m^2 transects (5 × 30 m) in a tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico, as sampled in May 1988. Transects were distributed randomly throughout the watershed.

Table 4. Net accumulation of total above–ground (ABG) dead phytomass (Mg ha^{-1} y^{-1}) in a tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico between May 1988 and May 1989. Fine dead phytomass (leaves, twigs and small branches < 2 cm circumference) for the study period were taken from our long-term litterfall measurements.

Compartment	Standing	Forest floor	Total
Dead coarse material			
Branches (2–20 cm in circumference)	2.3	0.6	2.9
Logs (> 20 cm in circumference)	0.8	0.1	0.9
Total coarse (branches + logs)	3.1	0.7	3.8
Total fine (litterfall)	Trace	2.8	2.8
Total ABG dead-phytomass production	3.1	3.5	6.6

Table 5. Dead-wood phytomass net accumulation (Mg ha^{-1} y^{-1}) as branches (2–20 cm in circumference) between May 1988 and May 1989 in tropical deciduous forest plots along an elevation gradient in Watershed 1 in Chamela, Jalisco, Mexico. Standard deviations and sample sizes are given in parentheses. Means with the same letter are not significantly different among plots ($P < 0.05$).

Plot	Standing		Forest floor	
Upper	2.26	(0.70, 14) a	0.64	(0.21, 14) c
Middle	3.26	(2.16, 32) b	0.63	(0.44, 32) c
Lower	1.30	(0.50, 7) c	0.56	(0.24, 7) c
Mean	2.27		0.61	

in throughfall nutrient concentrations (Figure 2). For example, during the first rain event (8 July) at the start of the study period, the average throughfall K$^+$ concentration below intact forest canopy was 35 times higher than in the direct rainfall (13.75 vs. 0.39 mg l^{-1}). When the dead woody debris in the canopy was

Table 6. Per cent reduction in total flux of cations via throughfall the first 2 y after the dead material was removed from the canopy, in a tropical deciduous forest of Chamela, Mexico. In parentheses are the standard deviation and the sample size.

		First year	Second year
Throughfall (mm)			
	intact canopy	289.5 (20.6, 6)	486.4 (17.3, 6)
	dead material removed	274.5 (19.6, 6)	492.7 (12.6, 6)
	% reduction	5.2 P = 0.077	−1.3 P = 0.267
Na^+ Flow (kg ha^{-1})			
	intact canopy	5.18 (1.34, 6)	6.15 (1.6, 6)
	dead material removed	3.87 (0.69, 6)	4.47 (1.3, 6)
	% reduction	25.4 P = 0.071	27.4 P = 0.051
K^+ Flow (kg ha^{-1})			
	intact canopy	8.61 (2.55, 6)	15.68 (5.01, 6)
	dead material removed	6.42 (3.78, 6)	9.83 (5.18, 6)
	% reduction	25.4 P = 0.201	37.3 P = 0.020
Ca^{2+} Flow (kg ha^{-1})			
	intact canopy	4.56 (1.06, 6)	4.00 (1.51, 6)
	dead material removed	2.62 (1.15, 6)	3.06 (0.74, 6)
	% reduction	42.6 P = 0.038	23.5 P = 0.131
Mg^{2+} Flow (kg ha^{-1})			
	intact canopy	1.97 (0.54, 6)	2.38 (0.57, 6)
	dead material removed	1.64 (0.49, 6)	1.90 (0.73, 6)
	% reduction	16.9 P = 0.193	20.3 P = 0.142

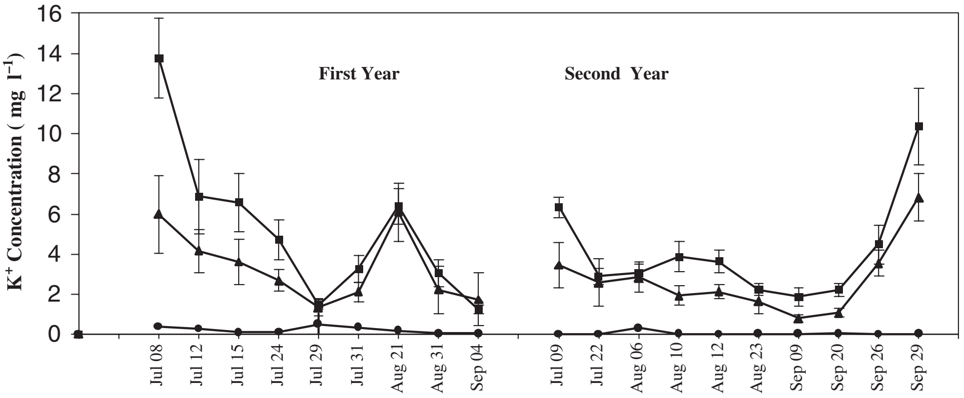

Figure 2. Temporal variability of K^+ concentration (mg l^{-1}) in incident rainfall (●), throughfall collected under intact canopy (live + dead canopy; ■) and throughfall under canopy without dead woody material (live canopy; ▲) in a tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico. Values are means (n = 6) and bars represent one standard error of the mean.

removed, the K^+ concentration in the throughfall was 44% lower than under the intact canopy. This difference in throughfall K^+ concentrations between control and manipulated canopies decreased with time, as the rainfall season proceeded. A similar pattern was observed for the rest of the cations (not shown).

Cation enrichment ratios (i.e. throughfall concentrations under intact canopy divided by the concentrations beneath canopies where dead woody mass was removed) were in general > 1.0 at the beginning of the first year of study, slowly decreasing as the wet season proceeded (Figure 3). During the second year, enrichment ratios were consistently > 1.0, showing that this effect persisted for more than a single rainy season. In fact, monthly variation was less pronounced than in the first year, particularly for Ca^{2+}. Throughfall concentrations under intact canopies were always higher than beneath canopies where the dead woody debris was removed.

Although not always significant, there was a consistent reduction in nutrient flux via throughfall after all dead-wood material was removed from the canopy. As much as 42.6% of the Ca^{2+} flux (first year) and 37.3% of the K^+ flux (second year) were reduced after this manipulation (Table 6).

DISCUSSION

Dead-wood mass distribution

Branches (2–20 cm in circumference) are the most important component (43%) of the forest total above-ground dead phytomass. Structurally, tropical deciduous forests have abundant small stems which branch profusely near to the ground. In the Chamela forest about 41% of the woody plants are multi-stemmed individuals with most of their branches (76%) smaller than 20 cm in circumference (Martínez-Yrízar *et al.* 1992). Also, about 50% of all single-stemmed trees belong to this size class. Therefore, a low contribution of logs to the total dead-wood pool was expected.

The total amount of dead woody material significantly differed among plots, showing an increase along the watershed elevation gradient. Whereas the middle and lower sections of the watershed are better protected from irradiance and winds, the upper part is more exposed to the harmful effects of the summer monsoon-like storms and to the prolonged annual droughts (Galicia *et al.* 1999, García-Oliva *et al.* 1995). These natural disturbance events constitute important agents of mortality in forest ecosystems (Harmon *et al.* 1986, Swaine *et al.* 1990).

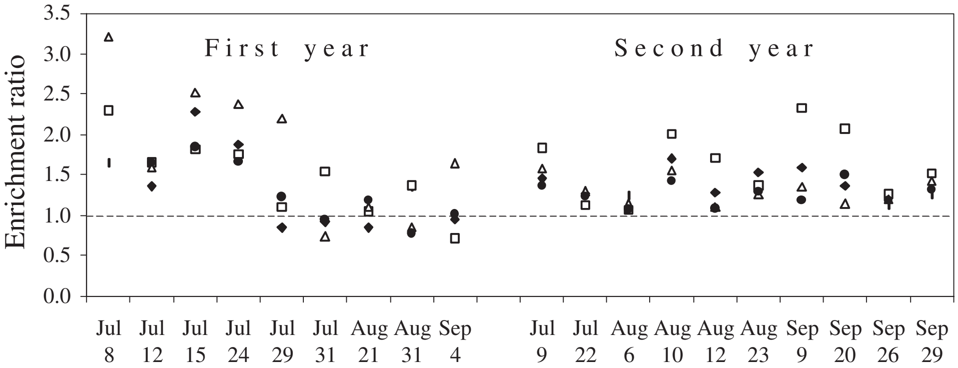

Figure 3. Temporal variability of enrichment ratios (i.e. throughfall concentrations under intact canopies divided by the concentrations beneath canopies where dead-wood mass was removed) of major cations in a tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico (◆ Na^+, □ K^+, △ Ca^{2+}, ● Mg^{2+}).

As in many forest ecosystems, most of the dead-wood phytomass in the Chamela forest was standing (hanging/attached and standing). This is explained in part by the existence of a time lag between the death of a tree or branch and its subsequent fall. This lapse depends on the rate of fragmentation, influenced in turn by such factors as the causes of mortality, size of the dead wood, plant species, microclimate and the nature of the canopy decomposer community (Harmon *et al.* 1986). Also, lianas may entangle many pieces of dead wood in the canopy and delay their fall to the ground. Woody vines in Chamela are abundant and constitute an important structural component of the forest (Bullock 1990, Lott *et al.* 1987). However, strong winds or hurricanes will enhance the sudden transfer of fine and coarse woody debris to the forest floor (Harmon *et al.* 1995, Whigham *et al.* 1991).

The existence of this large pool of dead woody debris in the Chamela TDF highlights the importance of considering the significance of this structural feature in the carbon pool and decomposition process of the forest. Usually, the decomposition of leaf-litter and woody material is considered to be primarily a forest-floor process, because of the higher decomposition rates that result from the increased contact between the plant debris and the soil, and the suitable micro-environmental conditions at the soil–atmosphere interface (Harmon *et al.* 1986). In the upper canopy, higher irradiance and windy conditions create a drier environment, limiting the type and amount of decomposers and, therefore, the decay rates. Decay rates of dead wood in the canopy have not been investigated in the Chamela TDF, but leaching and fragmentation during the rainy season may be important causes of weight loss. Swift *et al.* (1976) reported that decay in the canopy accounted for a weight loss of 40% in a mixed deciduous woodland, largely due to fungi and bark-beetle activity.

The presence of all major termite groups in Chamela, including wood-dwelling and carton-nest-building species (Nickle & Collins 1988), and the occurrence of termite galleries in almost every standing dead stem, suggest that these insects may be an important decomposition agent at the canopy level. In the subtropical dry forests of Mona Island, Puerto Rico, Jones *et al.* (1995) also found that about three-quarters of the available pieces of dead wood had signs of termite attack.

Dead-wood net accumulation

The net accumulation of dead branches was significantly lower in the lowest elevation plot of the watershed. Here, soil variables such as the amount of organic matter (cf. Table 1) and soil moisture were higher than in the other landscape positions (Galicia *et al.* 1999). Although these conditions may reduce the rate of transfer from the living to the dead-wood component (mortality), a detailed evaluation of the relationship between the rate of mortality and the abiotic factors is still needed.

Annual coarse dead-wood accumulation in Ws-1 was, on average, higher than the annual fine litterfall value (3.8 and 2.8 Mg ha^{-1} y^{-1}, respectively). This finding reveals the magnitude of the annual transfer of organic matter to the soil compartment in this ecosystem. However, to improve our estimate, it is important to extend the measurements beyond a single year since causes of wood mortality (i.e. drought, storms and hurricanes) may vary greatly from year to year.

In a previous study we found the above-ground living-wood increment at our study site was one of the most important components of the forest total NPP (Martínez-Yrízar *et al.* 1996). The mean living increment value of 2.4 Mg ha^{-1} y^{-1} for Ws-1 was lower than the dead-wood accumulation estimate (3.8 Mg ha^{-1} y^{-1}). Wood increments were estimated on all living trees > 3.18 cm dbh (> 10 cm in circumference), thus some smaller stems that were part of the dead-wood production measurements were excluded from this growth estimate.

The ratio between the annual rate of dead-coarse-wood accumulation (3.8 Mg ha^{-1} y^{-1}) and the size of the dead-coarse-wood pool (19.2 Mg ha^{-1}) was used as an estimate of the dead-wood turnover rate for the Chamela forest. The resulting estimate of 0.20 y fell within the range of values (0.18 – 0.22 y) reported for the tropical very-dry life-zone in northern Venezuela (Delaney *et al.* 1998), an area with annual precipitation and elevation (800 mm and 130 m elevation) remarkably similar to Chamela (724 mm and 0–150 m elevation). This turnover rate for Chamela should be considered as approximate since it is based only on a single year's data.

Effects on throughfall quality

The strong seasonal character of the TDF may explain why throughfall nutrient concentration was higher at the beginning of the rainy season. Aerosol deposition accumulated during the prolonged dry season is washed down during the first summer rains. Also, photodegradation of dead material (Moorhead & Reynolds 1989) may take place during the hot and dry months previous to the rainy period, enriching throughfall leaching early in the wet season. Another source of leaching material during the first rains may result from the heavy insect herbivory that takes place early in the growing season, as reported by Filip *et al.* (1995) for the Chamela TDF. Higher monthly variation in the first year could be the result of canopy disturbance during manipulation (i.e. breakage of small live branches which may leach nutrients).

Litterfall is considered the main intrasystem pathway of nutrient transfer to the soil (Schlesinger 1997). However, for some nutrients the fluxes from canopy leaching can be as high as these in litterfall. This is the case for potassium in the Chamela forest in which 2.1 g m^{-2} y^{-1} were transferred to soil via throughfall compared with the 2.3 g m^{-2} y^{-1} via litterfall (Campo *et al.* 2000).

Comparison with other TDFs

Measurements of the amount and production of dead-wood phytomass have been mainly restricted to temperate forest ecosystems (Harmon *et al.* 1986, Kirby *et al.* 1998). Information for the tropical region of the world is scant with only a few estimates for tropical dry forests (Delaney *et al.* 1998, Harmon *et al.* 1995, Jones *et al.* 1995, Murphy & Lugo 1986). Our results show that the quantity of above-ground dead-wood mass (19.2 Mg ha^{-1}; not including surface litter) in Chamela was higher than the mean value for the tropical very-dry-forest life-zone in northern Venezuela (4.9 Mg ha^{-1}; Delaney *et al.* 1998). This difference may partly be accounted for by our inclusion of a dead-wood size class (0.64 cm in diameter) lower than the lowest Venezuelan limit (0.64 and 2.5 cm in diameter, respectively). In the undisturbed tropical deciduous forests of the Mexican Yucatan Peninsula, a wide range of total dead-wood phytomass (17.7–42.7 Mg ha^{-1}) was reported by Harmon *et al.* (1995). This limited data set suggests that there is a large variation in the quantity and distribution of woody dead mass in tropical dry forests. The degree of spatial heterogeneity among sites depends on factors such as differences in floristic composition, productivity, tree mortality rates, substrate quality and decomposers (Harmon *et al.* 1986, 1995). Geographical location, forest successional status, frequency and intensity of natural catastrophic events, and history of human perturbations are also determinants of the size of the forest dead-wood pool (Harmon *et al.* 1995, Kirby *et al.* 1998).

The Chamela forest has a living above-ground phytomass of 85 Mg ha^{-1} (Martínez-Yrízar *et al.* 1992). Our value of 27.2 Mg ha^{-1} for the standing and fallen dead phytomass gives a total above-ground (dead + live) value of 112.2 Mg ha^{-1}, and a dead/live ratio of 0.32. These values differ from those reported by Murphy & Lugo (1986) for the Guanica TDF in Puerto Rico: 44.9 Mg ha^{-1}, 23.3 Mg ha^{-1} and 0.52, for the living above-ground phytomass, dead phytomass and living/dead ratio, respectively. Again, differences between these sites can be explained in terms of the variation in forest structure, related in turn to the particular climate and disturbance regime at each site. Whereas the Chamela TDF represents an undisturbed mature forest with no evidence of natural or anthropogenic fires or destruction by clearings, the Guanica forest reflects 50 y of recovery from cutting and grazing (Murphy & Lugo 1986).

The paucity of dead-wood production estimates in tropical forests allows only limited comparisons. In Ghana, Swaine *et al.* (1990) reported that dead branch fall (> 5 cm in diameter) in a tropical dry forest was 1.6 Mg ha^{-1} y^{-1}, while woody litter production (> 1 cm) in a tropical broad-leaved semi-deciduous forest was 3.5 Mg ha^{-1} y^{-1} (Vogt *et al.* 1986), a value closer to our dead-wood accumulation estimate. Rates of mortality differ greatly among forests depending on several factors. These include stand characteristics, climate and agents of disturbance, which need to be analysed in detail for a better understanding of the large differences observed among these forests.

Finally, other aspects of the ecosystem dead-phytomass dynamics need to be considered in parallel. Wood, being a slow-decomposing, recalcitrant fraction of litter, is less amenable to analysis than the other litter components. It is difficult to assign the dead-wood segments to different decay-state categories, but sorting them into undecayed, intermediate and rotten, will provide a better knowledge of the dynamics of the dead-wood compartment. Also, the analysis of the causes of wood mortality (biological agents such as insect attack and diseases, abiotic factors such as droughts, winds, storms and availability of soil nutrients) will help to explain the differences in dead-wood production found along the positions within the watershed.

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