Plant Ecology **169:** 259–271, 2003.

Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest

Gerardo Segura[1,4], Patricia Balvanera[2,*], Elvira Durán[1] and Alfredo Pérez[3]
*[1]Departamento de Ecología Funcional y Aplicada, Instituto de Ecología, Universidad Nacional Autónoma de México, Mexico; [2]Departamento de Ecología de los Recursos Naturales, Instituto de Ecología, Universidad Nacional Autónoma de México, Xangari, Apdo. Postal 27-3, Morelia, 58089, Michoacán, Mexico; [3]Instituto de Biología, Universidad Nacional Autónoma de México, Mexico; [4]Current address: Secretaría del Medio Ambiente y Recursos Naturales, Mexico; *Author for correspondence (e-mail: pbalvane@ate.oikos.unam.mx)*

Received 22 May 2001; accepted in revised form 25 August 2002

Key words: Dominance/diversity, Elevation gradient, Moisture gradient, Species diversity, Stand structure, Woody debris

Abstract

We document spatial changes in species diversity, composition, community structure, and mortality of trees across a gradient of water availability in a tropical dry forest in western Mexico. This gradient occurs along the main stream of a small watershed of less than 1 km in length. Four 30 × 80 m plots were established systematically to include the driest (ridge top of the watershed) to the wettest sites (watershed bottom) within this watershed. All stems larger than 5 cm were identified, and measured for diameter and height. Dead stems larger than 5 cm were measured and classified as: a) found on live or dead trees, and b) standing (″snags″) or lying (″downlogs″) on the ground. The number of recorded species per plot declined from 73 to 44 species as water availability decreased. A decline in estimated total richness, and in Shannon-Wiener and Simpson diversity indices was also observed in the drier plots. Species composition strongly changed along the gradient, with the two ends of the gradient sharing only 11% of the species. Stem density and percentage of dead stems and trees increased in abundance and basal area from the wetter to the drier sites. Tree and stem size (basal area, height and stem diameter) showed the opposite trend. Nonetheless, total basal area of live trees was largest at the two end gradient locations and oscillated between 12.22 m^2 ha^{-1} and 7.93 m^2 ha^{-1}. Proportion of snags increased towards the driest site (from 46 to 72%), while that of down logs decreased. Overall, our results suggest that small-scale gradients of water availability play a paramount role in the spatial organization of tree communities in seasonal tropical environments.

Introduction

The unique vegetation structure found in tropical dry forest (TDF) communities has evolved under a peculiar habitat, one with two to six months of severe to absolute drought (Mooney et al. 1995). In such a drastic environment, soil water availability appears to be the main limiting resource to plant growth and survival, influencing individual species performance, distribution (Borchert 1994) and phenology (Bullock and Solis-Magallanes 1990; Olivares and Medina 1992; Borchert 1994).

Within a biogeographical context, it has been shown that community attributes of TDF trees, such as species diversity, species dominance, species composition, tree density, biomass, and canopy cover and biomass, vary with climatic, edaphic and topographic variables associated with water availability. Thus, a positive relationship between species diversity and total annual precipitation has been found for TDF in Mexico and other Neotropical regions (Gentry 1995; Trejo 1998). Differences in species composition and dominance/diversity in TDF have been related to climatic, topographic and edaphic (water availability related variables) factors in Kenya, Senegal, Brazil, and

Mexico (Arriaga and León 1989; Arriaga et al. 1993; Coughenour and Ellis 1993; DeWolf 1998; Oliveira-Filho et al. 1998). The abundance of trees increased with the length of the rainy season or annual precipitation in TDF in Mexico (Trejo 1998), and it decreased with soil moisture in Madagascar (Sussman and Rakotozafy 1994). Total density of trees was positively correlated with number of wet months, while density of large trees was positively correlated with total annual precipitation for TDF in Mexico (Trejo 1998). Finally, TDF canopy cover increased with annual precipitation within the Turkana District in Kenya (Coughenour and Ellis 1993).

Differences in water availability are also expected to influence tree mortality, nevertheless little information is available on this topic, especially for TDF habitats. Episodic tree mortality events related to drought have been documented (e.g., Condit et al. (1995) and Villalba and Veblen (1998)) but the spatial context of such mortality processes are waiting to be explored.

At local scales, where the same climatic and geological conditions occur, soil water availability may significantly change with terrain topography, especially in hilly areas, where a complex of micro-topography is found (Lott et al. 1987; Borchert 1994; Oliveira-Filho et al. 1998). Within a hill water drains to lower sites, so that soil water availability is highest at the bottom and lowest at the ridge top, creating gradients of water availability (Lott et al. 1987; Borchert 1994; Galicia et al. 1995; Oliveira-Filho et al. 1998; Daws et al. 2002). Changes in tree species composition, stand structure and canopy structure have been observed at these spatial scales (Lott et al. 1987; Borchert 1994; Martínez-Yrízar et al. 1996; Oliveira-Filho et al. 1998). Yet, comprehensive studies that simultaneously explore changes in community structure, composition and spatial changes in tree mortality are still needed to understand how they are interrelated. To what extent do such small-scale gradients promote spatial changes in community attributes of TDF trees? How are these changes related to differential stem mortality and thus community turnover? What is the role of environmental heterogeneity in the maintenance of species diversity? Such an analysis should be based on stems, rather than individual trees, since re-sprouting or coppicing has been proposed as the primary mechanism of regeneration for TDFs (Murphy and Lugo 1986).

In this study we use a gradient of water availability within a small watershed (< 1 km length) to explore fine-scale spatial patterns of the TDF tree community. We document changes in species diversity, dominance, composition, and structure of the tree community along the watershed main stream. If patterns at local scales are similar to ones at biogeographical scales, we expect that as water availability decreases attributes such as diversity, stem density, and average stem size (diameter and height) will decline. Spatial species turnover along the gradient may imply the existence of species differentiation along a wide range of drought tolerance conditions. On the contrary, low spatial species turnover may imply the existence of generalist species with a wide range of drought tolerance. Additionally, the relative frequency of dead stems and their relation to re-sprouting and gap formation will be explored and related to changes in diversity and structure.

Methods

Study area

The study was conducted in the 13,000 ha Chamela-Cuixmala Biosphere Reserve located in western Mexico, within an area that has only been colonized for the past 30 years (SEMARNAP 1995). This reserve is considered one of the largest and most well preserved areas of tropical dry forests in the world (Murphy and Lugo 1995). The reserve is located in the state of Jalisco, two kilometres from the shoreline of the Pacific Ocean (19°30′ N, 105°3′ W; Figure 1). Mean annual temperature is 24.9 °C, and mean annual precipitation is 714 mm; rainfall is strongly seasonal with 80% falling between July and October (Bullock 1986). Seventy percent of the precipitation is received during tropical cyclonic storms and the rest results from frequent, low intensity, convective storms of local atmospheric origin (García-Oliva et al. 1991, 1995). Total annual precipitation is highly variable ranging from 374 to 897 mm (García-Oliva et al. 1995), with a high frequency of erratic winter storms (García-Oliva et al. 1991).

The TDF at Chamela has been described as one of the most diverse TDF in the world, with the highest reported endemism in species, genus and families of plants (Lott 1993; Gentry 1995). More than 1100 species of vascular plants and 233 species of trees have been identified (Lott 1993). Canopy height at TDF oscillates around 10 m, with high densities of stems within 5 and 10 cm DBH. Most important families are Leguminosae, Euphorbiaceae and Rubiaceae (Lott et

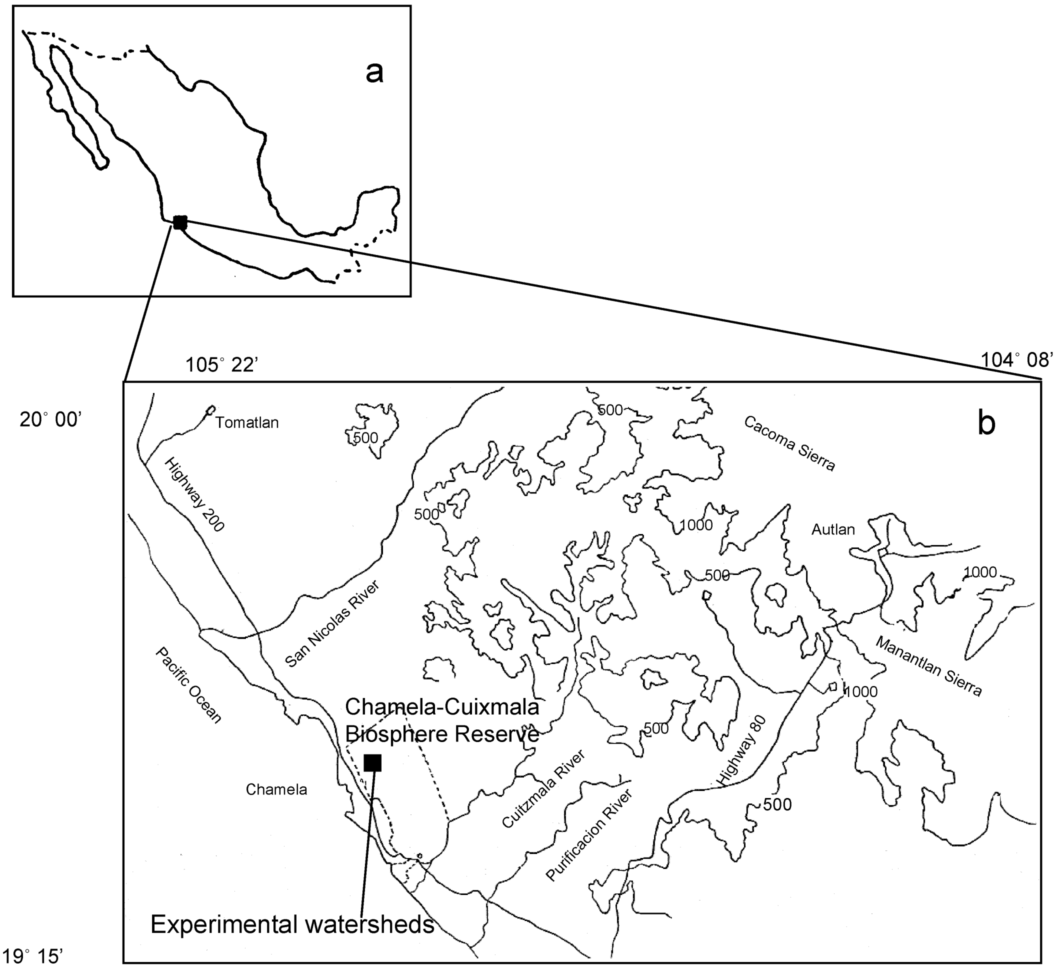


Figure 1. Location of study area. a) Location in Mexico; b) Regional setting and location of the Chamela-Cuixmala Biosphere Reserve, showing elevation contour lines, main rivers and main highways, as well as experimental watershed where the study was conducted.

al. 1987). Most important species include *Plumeria rubra* (Apocynaceae), *Piranhea mexicana* (= *Celaenodendron mexicanum*, Euphorbiaceae) and *Guapira macrocarpa* (Nyctaginaceae).

Although the vegetation of the reserve falls into the category of tropical dry forest (Holdridge 1967), a semi-deciduous tropical forest with distinctive species composition and vegetation structure also occurs along all riparian zones of temporary streams (Lott et al. 1987), covering small strips scattered throughout all the reserve. This semi-deciduous forest is taller (average 18 m) and presents higher frequency of large individuals (> 30 cm DBH). Most important species include *Thouinidium decandrum* (Sapindaceae) and *Trichilia trifolia* (Meliaceae).

Water availability gradient

The area selected for the study encompasses the main stream of a small watershed approximately 1 km length, with a small elevation gradient (Figure 2). This area does not present evidence of selective logging and has been owned by the National University of Mexico since 1940 (SEMARNAP 1995). The watershed is on uniform granite (Maass et al. 1994, Cotler et al. (in press)). Along the main stream of the watershed, soil water availability diminishes as elevation increases (Galicia et al. 1999). During the rainy season, topographic position and soil water holding capacity result in water availability being highest at the watershed bottom, where water drains and soils are deeper. During the dry season, solar radiation interception results in soil water availability being lowest at the ridge top of the watershed, as it drives high evapotranspiration, particularly in the most exposed sites. This water availability gradient is closely associated with a gradient in soil nutrient and organic matter availability, which are highest at the watershed bottom (Solis 1993).

Field methods and data analysis

The study was restricted to trees as they constitute the most important structural component of TDF communities (Lott et al. 1987). To compare changes in species diversity, dominance, composition, structure and turnover of the tree community along the water availability gradient, we laid out four 2,400 m^2 (30 × 80 m) plots perpendicular to both sides of the main stream channel of the watershed at low, middle, high and ridge top locations (Figure 2).

Since water availability is strongly determined by solar radiation interception, differences in water availability are also expected to be associated with differences in aspect. Northern-facing slopes have higher water availability than southern-facing ones, especially at the watershed bottom where slopes steepness and shading from surrounding slopes is highest (Galicia et al. 1999; Balvanera et al. 2002). To control for differences in water availability originated by aspect, we laid half of the plots on north-facing slopes and the other half on south-facing ones.

We recorded and measured all trees with at least one stem larger than 5 cm in diameter at breast height (dbh: 1.37 m above ground) and identified them taxonomically. Nomenclature followed Lott (1993) and voucher specimens are available at the herbarium of the Estación de Biología Chamela. We measured diameter of all dead stems larger than 5 cm in dbh. We distinguished those from dead trees and those from re-sprouting of live trees. We also classified dead stems as those found standing (″snags″) and those found lying down (″down logs″).

For each plot, we obtained species diversity values by calculating species richness, Shannon and Simpson diversity indexes (Magurran 1988). We also used abundance incidence-based richness estimators (Colwell 1994–2000) constructed by dividing plots into 10 × 10 m quadrats. We chose this array of indices to account for biases attributed to differences in number of trees among sites.

We analyzed changes in species dominance by building dominance-diversity curves. The curves were drawn using data on the logarithm of species abundance for each plot and fitting simple lineal and polynomial models to the observed data; the model with the highest determination coefficient was chosen (SAS I.I. 1989–1996). We compared the shape of the fitted graphs to the alternative models of species abundance patterns and community structure proposed by Tokeshi (1993).

To describe changes in species composition, both quantitatively and qualitatively, we calculated Jaccard index of species similarity using presence/absence data for all possible pair-wise comparisons among the four plots (Magurran 1988). To assess the proportion of the similarity attributable only to changes in species richness we calculated a Jaccard's index correction factor (Balvanera et al. 2002).

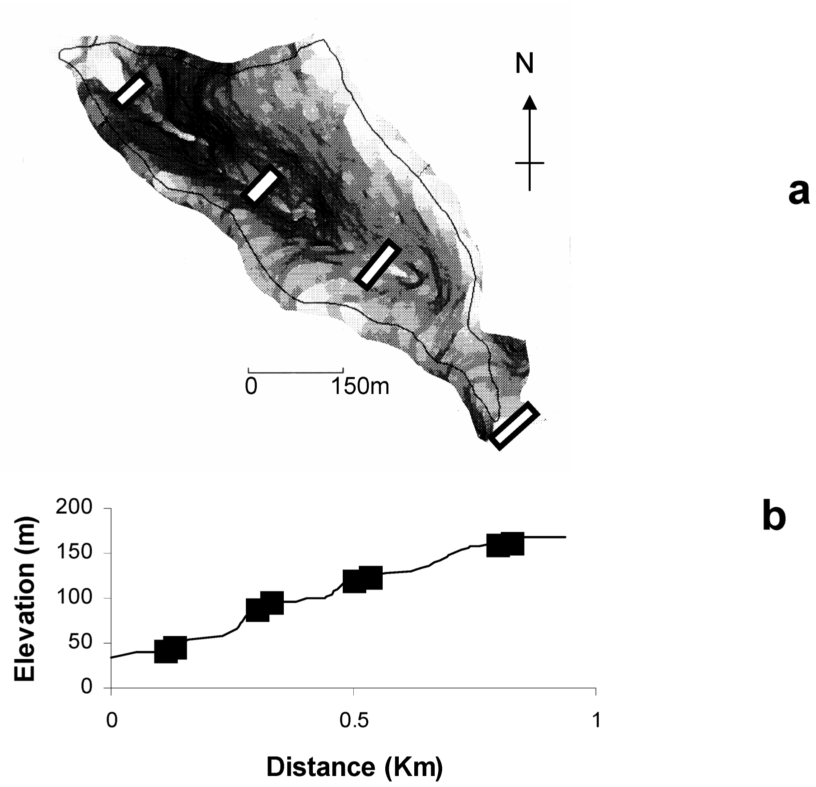
To describe stand structure characteristics for each plot we used stem density, basal area per hectare, average stem diameter, average tree height, tree diameter and height distributions. To test for statistical differences in these variables among gradient locations, we used one-way non-parametric Kruskall-Wallis analysis of variance (SAS I.I. 1989–1996) due to lack of homogeneity in variances among plots.

We assessed changes in stem mortality patterns along the gradient by comparing the proportion of dead stems (density and basal area), their proportion by dbh categories, by origin (dead trees vs resproutings of live trees) and position (snags vs. downlogs). To test for statistical differences in these variables among gradient locations we used analysis of deviance (ANDEVA) with a bivariate Binomial model (Crawley 1993).

Results

Species diversity, dominance and composition

Distinctive patterns of species diversity were detected along the water availability gradient of the watershed studied. Species richness and species diversity declined as water availability decreased (Table 1). Decline in species richness along the gradient was accompanied by changes in species dominance. Dominance-diversity graphs at the low and middle plots tended to be closer to log or log-normal distributions, while the high and ridge top ones were closer to a geometric series (Figure 3). These patterns indicate that dominance tends to be shared by a larger number of species of intermediate abundance towards the lower end of the gradient. At the upper end of the



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Variable	Low	Middle	Top	Ridgetop
Slope (degrees)	16-40	10-16	6-10	3-5
Soil depth (cm)	20-25	10-15	45	76
Sand (%)	22	12	45	
Clay (%)	68	63	57	
Water holding capacity (%)	20-30	15-20	40	
Total annual insolation (MJ ha^{-1} y^{-1})	4-16	10-15	11-14	12-14
Soil water content during rainy season (mm)	7.8-12.5	6.8-6.9	5.3-6.2	
Soil water content at beginning dry season (mm)	15.4-17.3	14.2-17.1	12.4-13.6	
Organic matter (Kg ha^{-1})	101	68	57	10
Assimilable P (Kg ha-1)	60-158	34-36	30-32	10

Figure 2. Description of the water availability gradient. a) Slope map of the studied watershed, where shade intensity denotes slope steepness. Lighter shades correspond to 0 to 4 slope degrees and darkest ones to more than 30 degrees (López-Blanco et al. 1999). The lowest part of the elevation gradient is at the left upper corner. b) Elevation changes along the gradient showing the location of the four plots. c) Synthesis of available information for the gradient; multiple values are given to account for differences among north-facing and south-facing parts of the transects. Information for low, middle and high transects was obtained from the literature (Solis 1993; Martínez-Yrízar et al. 1996; Galicia et al. (1999)). Ridgetop plot information was obtained from Cotler et al. (in press). Insolation values were calculated using methods described in Balvanera et al. (2002).

Table 1. Species diversity, stand structure attributes and tree turnover in four tropical dry forest plots along a water availability gradient. Average values and standard error values are given for stem diameter and tree height. Small letters indicate significant differences among pairs of values, obtained from Tuckey test for diameter and height, and from binomial model for basal area. ACE and ICE = Abundance-based and Incidence-based (respectively) coverage estimators.

	Plot location			
	Low	Middle	High	Ridge top
Species richness	73	64	58	44
Estimated richness (ACE)	122.4 ± 1.2	89.1 ± 0.3	62.8 ± 0.3	51.1 ± 0.3
Estimated richness (ICE)	134.5 ± 1.3	90.4 ± 0.4	62.7 ± 0.3	49.8 ± 0.3
Shannon diversity Index	3.77	3.63	3.57	3.30
Simpson diversity index	27.14	23.57	26.59	19.28
Live stem density (stems ha^{-1})	567	1275	886	2,075
Live stem total basal area (m^2 ha^{-1})	10.74	8.09	7.93	12.22
Stem diameter (cm)	10.47 ± 0.46 ^{a}	8.35 ± 0.19 ^{b}	8.52 ± 0.23 ^{b}	8.14 ± 0.13 ^{b}
Tree height (m)	7.44 ± 0.25	5.52 ± 0.09	5.63 ± 0.08	6.26 ± 0.05
Dead/total density ratio	0.28	0.33	0.36	0.33
Dead/total basal area ratio	0.25 ^{a}	0.33 ^{ab}	0.36 ^{ab}	0.30 ^{b}

gradient, dominance was restricted to a small group of species, with the remaining species tending to be rare.

Species composition changed along the water availability gradient, where the most distinct plot was the lowest one, and the more distant plots were most dissimilar. The low plot shared less than a third of the species with the middle, high and ridge top ones (Jaccard index *Cj* Middle = 0.36, High = 0.25, Ridge Top = 0.16). The three higher plots shared with each other close to half of the species (Jaccard index *Cj* middle-high = 0.55, middle-ridge top = 0.42, high-ridge top = 0.53). When correcting Jaccard's index values to account for differences in species diversity, similarity among plots dropped to as low as 0.11 for low and ridge top sites.

Individual species dominance also changed along the gradient at the four locations sampled (Figure 4). Species such as *Thohuinidium decandrum* (Humb. & Bonpl.) Radlk. (THODEC) were only found in the low plot. Others like *Guapira macrocarpa* Miranda (GUAMAC) and *Plumeria rubra* L. (PLURUB) were found in most locations but changed in relative importance. Others like *Cochlospermum vitifolium* (Willd.) Spreng. (COCVIT) and *Gliricidia sepium* (Jacq.) Kunth ex Steudel (GLISEP) were only dominant in the ridge top plot.

Community structure

Live stem density increased substantially along the water availability gradient. The overall increase from the low to the ridge top plot was threefold (Table 1). Changes were most pronounced between the low and middle plots and the high and ridge top ones. Little difference in density was observed between the middle and high plots.

Total basal area of live stems changed along the water availability gradient, but patterns were different from those found for changes in total density. The total basal area was largest at the ridge top and low plots and smallest at the middle and high ones (Table 1). Mean stem basal area decreased between the low and the ridge top plots from 129.9 to 58.9 cm^2.

Both average and variance of stem diameter of live trees significantly changed among plots. The variance decreased from the low plot to the ridge top (Bartlett test, $\chi^2 = 86.39$, d.f. = 3, $p < 0.0001$). Average stem diameter followed the same pattern (Non-parametric ANOVA, $\chi^2 = 18.34$, d.f. = 3, $p = 0.0004$; Table 1). Similarly, the average (Non-parametric ANOVA, $\chi^2 = 91$, d.f. = 3, $p < 0.0001$) and the variance (Bartlett test, $\chi^2 = 265$, d.f. = 3, $p < 0.0001$) for tree height decreased from the low to the ridge top plot (Table 1).

The shape of the frequency distribution of live stems per dbh classes showed a typical reverse J shape curve in all locations, i.e., there were significantly more small sized stems than large ones (ANDEVA, $\chi^2 = 2305$, d.f. = 3, $p = 0$, $R^2 = 0.97$). We detected a significant interaction between plot position and dbh classes ($\chi^2 = 64$, d.f. = 9, $p < 0.0001$, $R^2 = 0.02$). Proportion of stems within the smallest diameter category (5–10 cm) increased along the gradient, while that of large stems (> 20 cm) decreased

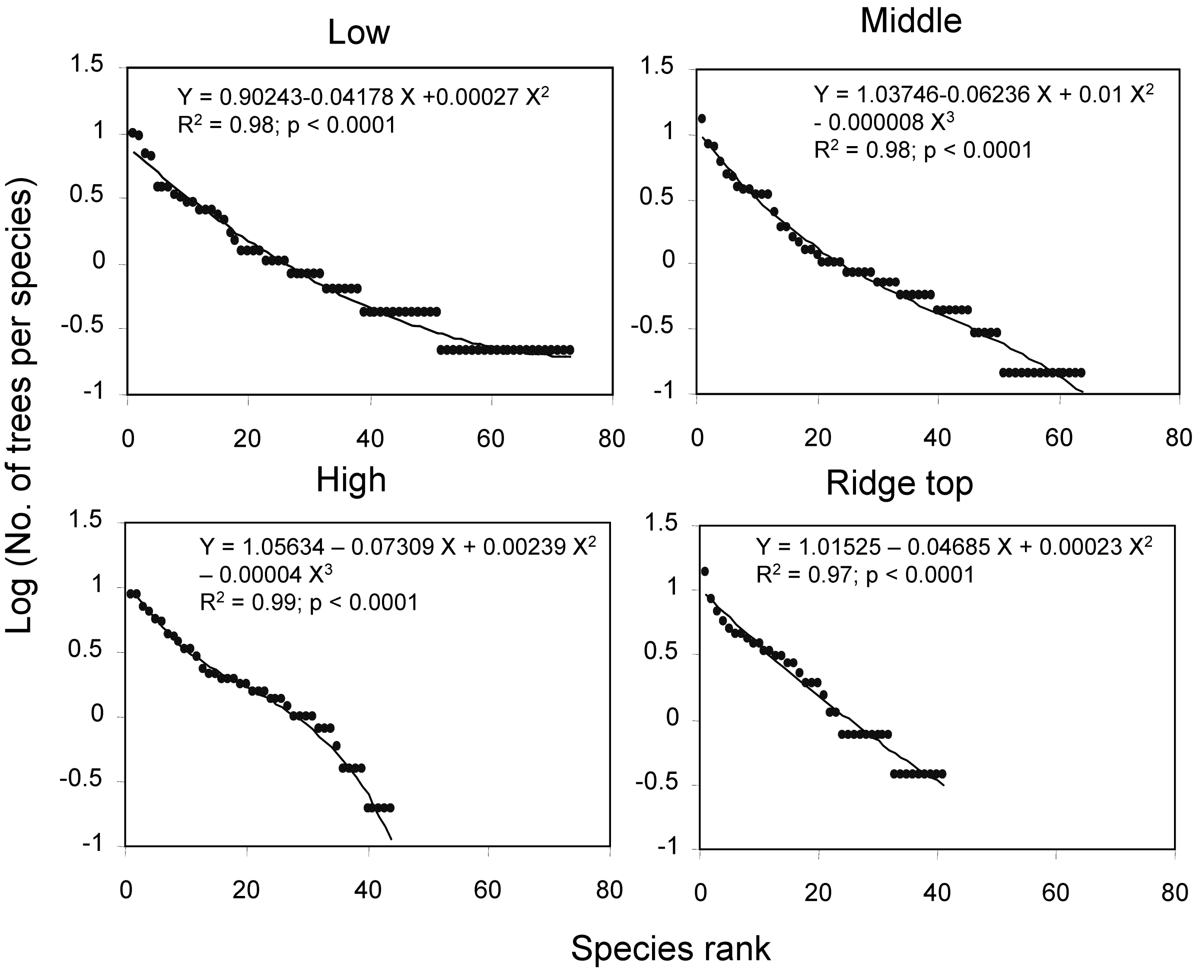

Figure 3. Dominance-diversity curves in four tropical dry forest plots along a small-scale elevation gradient constructed using logarithm values of abundance of each species.

(Figure 5a). Maximum stem diameter declined consistently along the gradient.

The tree height frequency distribution tended to approach a bell shaped curve, skewed to the right at the low and middle plots, and tending to a normal distribution at the high plot and a leptokurtic one at the ridge top plot (Figure 6). Such different distributions were statistically distinct as the interaction between height class and plot position was significant (χ^2 = 586, d.f. = 9, R^2 = 0.23, $p < 0.00001$). Maximum tree height declined from the low to the ridge top plots.

Tree mortality

The proportion of dead stems increased towards the driest sites considering both density and basal area (Table 1); however, only the basal area trend was significant (χ^2 = 16.74, d.f. = 3, $p < 0.001$). Dead stems were not homogenously found for all diameter classes and their proportion changed along the gradient. No difference in average diameter was found between live and dead stems (χ^2 = 0.0046, d.f. = 1, $p > 0.05$). A larger variance in stem diameter was found for live stems than for dead ones (Bartlett test, χ^2 = 25.62, d.f. = 1, $p < 0.0001$). This difference was significant at the low site where more larger stems were found than smaller ones (χ^2 = 21.3, d.f. = 3, $p < 0.0001$, R^2 = 0.68). No significant effect of plot position (χ^2 = 3.7, d.f. = 3, $p > 0.05$) nor significant interaction between plot position and dbh class (χ^2 = 6.2, d.f. = 6, $p > 0.05$) was observed for tree mortality (Figure 5b).

The proportion of dead stems found on live trees increased as water availability decreased relative to

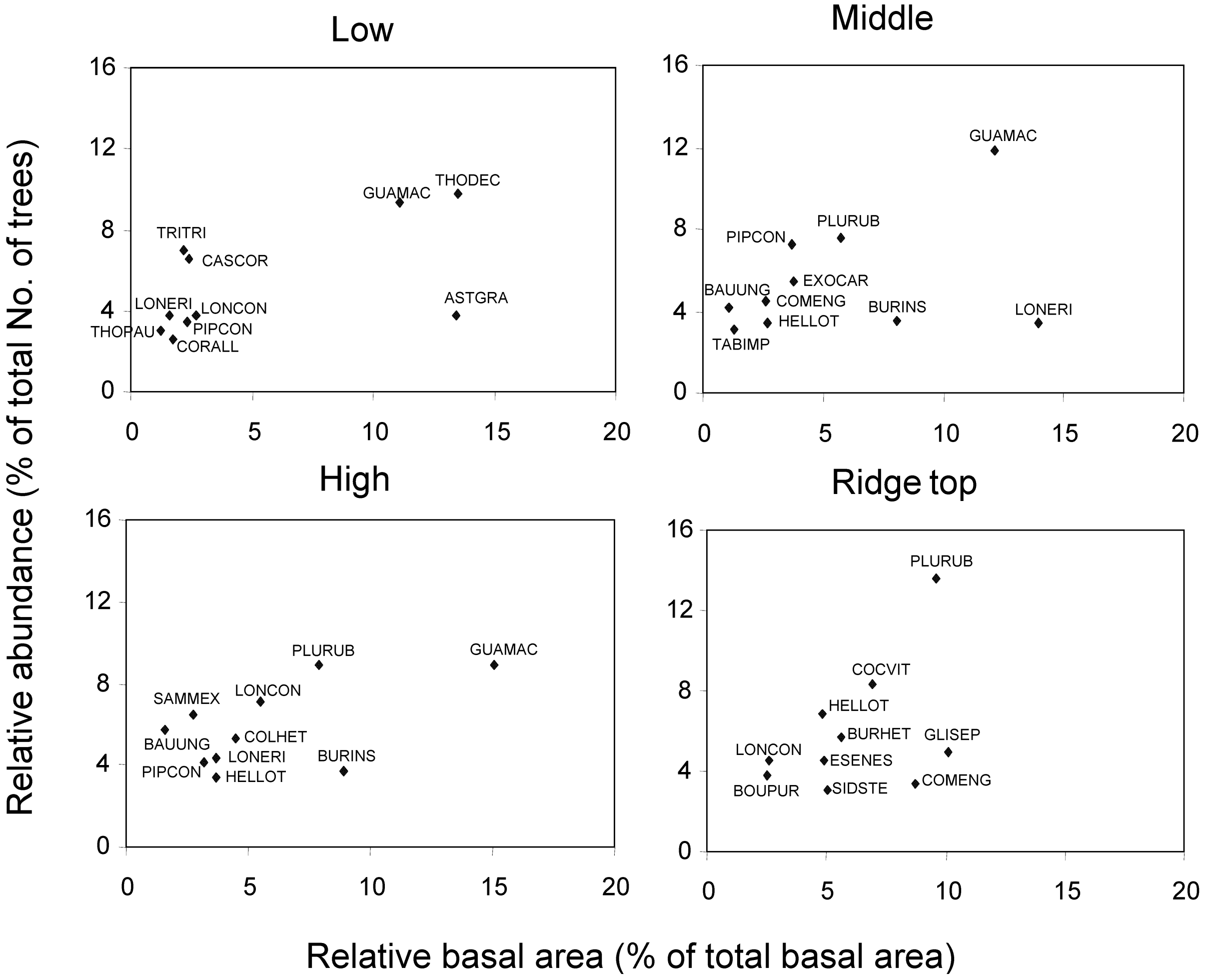

Figure 4. Relative abundance and relative basal area of the most important species (frequent, abundant and/or dominant) in four tropical dry forest plots along a small-scale elevation gradient. Codes for species names are indicated in Appendix 1.

that of dead stems corresponding to dead trees (χ^2 = 8.4, d.f. = 3, p = 0.038; Figure 6). Snags significantly increased from the low to the ridge top plots relative to that of downlogs (χ^2 = 24.5, d.f. = 3, p < 0.001; Figure 7).

Discussion

Species diversity, dominance and composition

Spatial patterns in species diversity, dominance and composition along a small scale water availability gradient were similar to those found at biogeographical and regional scales. Species diversity decreased, dominance increased, and species composition changed as water availability decreased. These patterns can be associated with a decrease in productivity (Rosenzweig 1995) and favorableness (e.g., Brown (1988)) at driest sites. A positive or hump-shaped relationship between species diversity and productivity has been found for most studies with terrestrial vegetation at local scales (Waide et al. 1999). In fact, a decrease in TDF primary productivity with soil water availability has been reported at this site (Martínez-Yrízar et al. 1996).

The reduction in species richness towards the driest sites of the study gradient was not a random loss of some species from a larger pool, but rather involved a clear spatial species turnover, where the two end locations of the gradient had only 11% of species in common. This species turnover could either be due to differential responses of the species to changes in the environmental conditions along the gradient or to

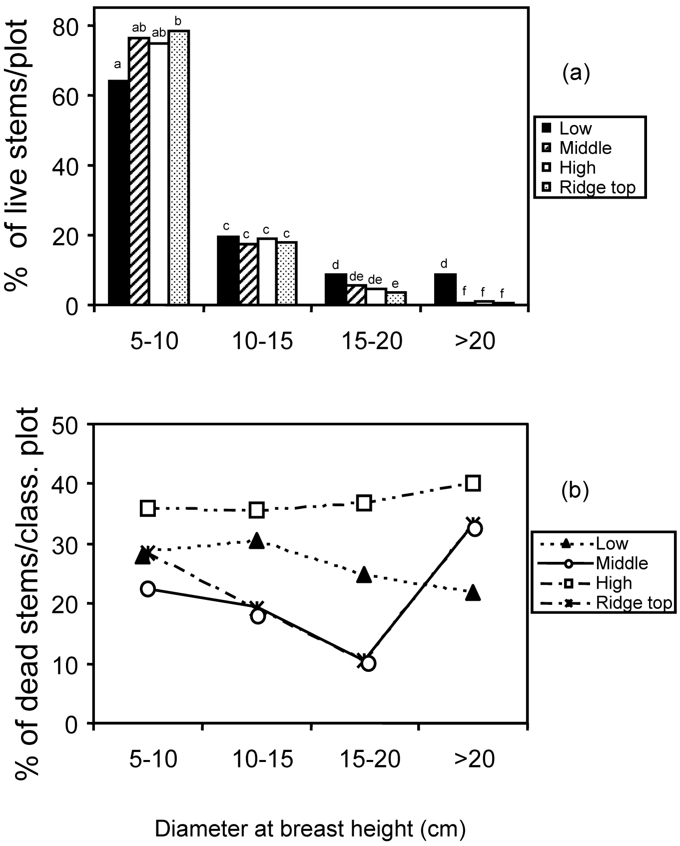

Figure 5. Diameter distributions of live stems and proportion of dead stems in four tropical dry forest plots along a small-scale elevation gradient. a) Distribution of the proportion of stems per plot in each diameter class; b) distribution of the proportion of dead stems per plot per diameter class. Small letters indicate significant differences among frequencies; in the case of live stems differences among plots and among diameter categories can be observed; in the case of dead stems, only differences among plots are shown.

patchy distributions of the species associated with ecological processes such as limited recruitment (i.e., poor seed dispersal or vegetative recruitment). Changes in species composition have previously been associated with variation in water availability (Balvanera et al. 2002). Evidence for highly clumped species distributions are also available at this site (Balvanera (1999), unpublished data). Yet, distances considered within this study (< 1 km) do not suggest distance-dependent limitations as a source of the spatial species turnover.

Community structure

Changes in stem density, height, and basal area of the tree community along the water availability gradient are comparable to those previously found at landscape (Sussman and Rakotozafy 1994) and biogeographical scales (Trejo 1998). At more mesic, nutrient rich and productive conditions (bottom of the watershed), a higher frequency of larger trees, results in a reduction of total stand density but a higher basal area. A more complex structure was found at those mesic sites due to less even-sized trees (in both diameter and height). Similar structural comparisons have been done among tropical dry and wet forests (Murphy and Lugo 1986); however, these studies have not compared such short distances as 1 km within a TDF matrix.

Stem mortality and synthesis

This is the first study to present tree mortality data for TDF. An increase in proportion of dead basal area was found as water availability decreased, where dead stems on live trees and standing dead trees tended to increase. This increased mortality can be attributed to water stress-related mortality, since higher sites

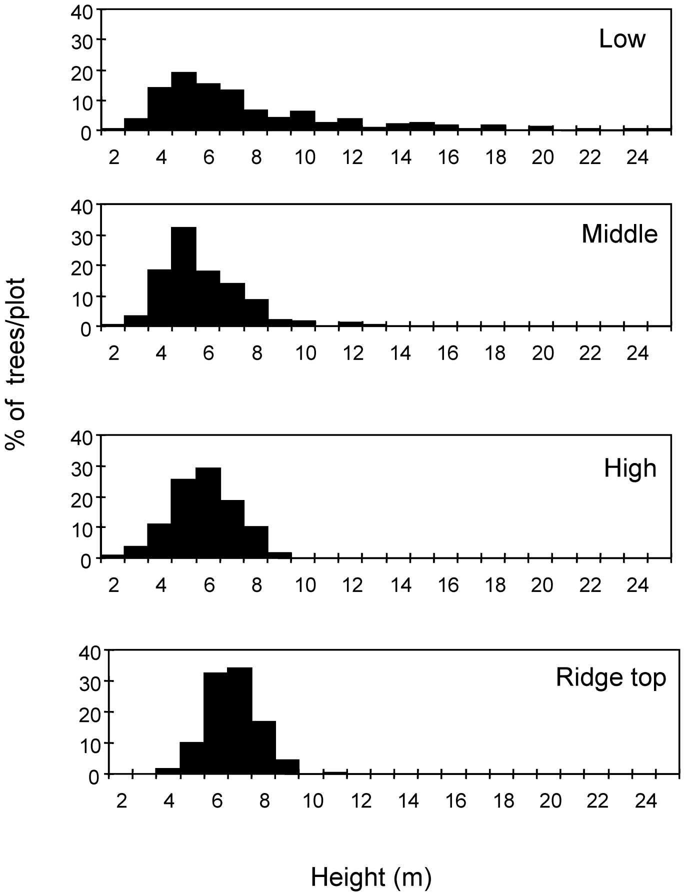

Figure 6. Height distributions of live stems in four tropical dry forest plots along a small-scale elevation gradient the four plots along the elevation gradient.

present more xeric conditions. Drought can be quite severe at Chamela where some years total annual precipitation may be below 380 mm with no winter rains (García-Oliva et al. 1995).

Analyses of diameter and height distributions for live stems show a decreasing variance for both variables as water availability decreases. Even-aged distributions found at higher locations are normally associated with discrete colonization events occurring when large areas of growing space are made available following natural large-scale disturbance events like fire or windthrow (Segura and Snook 1992; Oliver and Larson 1996). In Chamela, such disturbance events are likely to be associated with drought followed by windthrow, due to the proximity of the study site to the Pacific Ocean, and the frequency of severe tropical summer storms (García-Oliva et al. 1991). In this area, large destructive natural fires do not tend to occur (Martijena and Bullock 1994). Effects of wind could be less influential at higher elevations, where more homogeneous and denser forest canopies occur. Nevertheless, these sites are more exposed to wind. Larger individuals that could stand out above the average canopy showed an increased mortality.

At lower elevations, where community structures were more heterogeneous and more mesic conditions prevail, a higher proportion of down logs could indicate that an important natural disturbance factor is likely to be associated to gaps created by the fall of scattered large dominant canopy-emergent individuals. These large trees are generally more susceptible to windthrow, despite their location in more protected riparian valley bottoms and ravines, or to events associated with flooding or erosion, since lower sites present steeper slopes. In contrast, at higher locations drought related mortality leads to even-aged stands

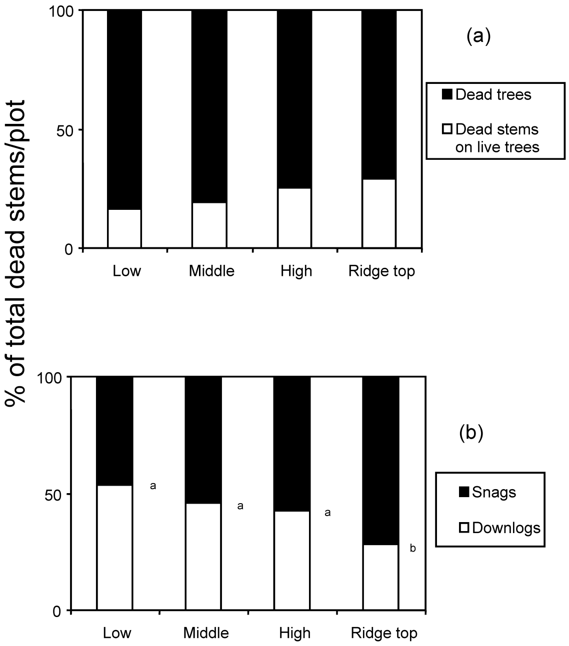

Figure 7. Characteristics of the dead tree component in four tropical dry forest plots along a small-scale elevation gradient. a) Proportion of dead stems relative to the characteristics of the tree where they were found (dead trees, or ramifications or resprouting of live trees); b) proportion of dead stems with respect to their position (snags = standing, downlog = fallen). Small letters indicate significant differences among plots.

and to mortality of standing stems, many of them found re-sprouting on live trees.

The ratio of live trees with dead stems relative to that of dead trees observed is surprisingly low. It has been argued that resprouting is an important regeneration mechanism in TDF (Murphy and Lugo 1995), and yet dead stems on live trees constituted only 16.7% of dead stems at the lower elevation locations, and increased up to 29.2% at the higher extreme of the gradient. The increase in the proportion of live trees with dead stems towards the driest sites seems to be associated with a drought resistance mechanism.

Overall, our results suggest that small-scale environmental gradients in topographically irregular areas promote the occurrence of different habitats where species segregate or where the same species perform differentially. The environmental conditions associated with differences in water and nutrient availability, are also tightly coupled with different biotic conditions. Increasing species diversity and structural complexity is coupled to highest water availability and productivity. Disturbance factors are predominantly associated with the fall of the tallest canopy trees in the wettest sites and to drought and stem mortality in the driest sites. The mosaic of biotic and environmental conditions found within topographically complex tropical dry forests could play a paramount role in the maintenance of the elevated species diversity found in these ecosystems.

Acknowledgements

This study was funded by grants from the Mexico-US Foundation for Science (E-198) and from CONACyT. A. Solís, J. Sarukhán and L. Cervantes helped establish the three lower plots. We thank C. Kelly, E. Aguirre, S. Quijas, A. Castillo, M. Gonzalez, and J. Rodriguez for their valuable field assistance. M. Martinez-Ramos, L. Olsvig-Whittaker, an anonymous reviewer and K. Stoner contributed to strengthen the manuscript.

Appendix

Table A1. List of the most important species (frequent, abundant and/or dominant) in the plots indicating family, and the code used to name them in the figures.

Scientific name	Family	Code
Astronium graveolens Jacq.	Anacardiaceae	ASTGRA
Bauhinia ungulata L.	Leguminosae	BAUUNG
Bourreria purpusii Brandegee	Boraginaceae	BOUPUR
Bursera heterestes Bullock	Burseraceae	BURHET
Bursera instabilis McVaugh & Rzed.	Burseraceae	BURINS
Casearia corymbosa HBK.	Flacourtiaceae	CASCOR
Cochlospermum vitifolium (Willd.) Spreng.	Cochlospermaceae	COCVIT
Colubrina heteroneura (Griseb.) Standl.	Rhamnaceae	

Table A1. Continued

Scientific name	Family	Code
COLHET		
Comocladia engleriana Loes.	Anacardiaceae	COMENG
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	CORALL
Esenbeckia nesiotica Standl.	Rutaceae	ESENES
Exostema caribaeum (Jacq.) Roem. & Schult.	Rubiaceae	EXOCAR
Gliricidia sepium (Jacq.) Kunth ex Steudel	Leguminosae	GLISEP
Guapira macrocarpa Miranda	Nyctaginaceae	GUAMAC
Guettarda elliptica Sw.	Rubiaceae	GUEELL
Helietta lottiae Chiang	Rutaceae	HELLOT
Lonchocarpus constrictus Pitt.	Leguminosae	LONCON
Lonchocarpus eriocarinalis Micheli	Leguminosae	LONERI
Piptadenia constricta (Micheli) Macbr.	Leguminosae	PIPCON
Plumeria rubra L.	Apocynaceae	PLURUB
Psidium sartorianum (Berg.) Ndzu.	Myrtaceae	PSISAR
Samyda mexicana Rose	Flacourtiaceae	SAMMEX
Sideroxylon stenospermum (Standl.) Pennington	Sapotaceae	SIDSTE
Thouinidium decandrum (Humb. & Bonpl.) Radlk.	Sapindaceae	THODEC
Thouinia paucidendata Radlk.	Sapindaceae	THOPAU
Trichilia trifolia L. subsp. *palmeri* (C. DC.) Pennington	Meliaceae	TRITRI

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