Regeneration of dry forest species Population dynamics and spatial distribution of seedlings and saplings of four dry forest species in Nicaragua

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Photograph 1.
Good regeneration in the understory with partially open canopy.
Photograph G. Castro-Marin.

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RÉSUMÉ

DYNAMIQUE DES PEUPLEMENTS ET DISTRIBUTION SPATIALE DES SEMIS ET ARBRISSEAUX DE QUATRE ESSENCES DE FORÊT TROPICALE SÈCHE AU NICARAGUA

La variation temporelle des densités de semis et arbrisseaux de quatre essences en forêt tropicale sèche, *Calycophyllum candidissimum, Cedrela odorata*, *Haematoxylon brasiletto* et *Gyroscarpus americanus*, ainsi que l'hétérogénéité dans l'espace de leur régénération selon la pente du terrain et l'exposition des houppiers à l'ensoleillement direct ont été examinées dans le Refuge national de faune de Chacocente, au Nicaragua. Les données relatives à chaque individu de plus de 10 cm de hauteur et de moins de 5 cm de diamètre à hauteur de poitrine ont été enregistrées pendant trois années consécutives, de 2001 à 2003. La densité des semis et arbrisseaux était fortement variable suivant les essences et dans le temps. La densité moyenne des semis au cours des années de recensement s'est établie respectivement à 37, 20 et 4 individus sur 2 ha pour *G. americanus*, *C. candidissimum* et *H. brasiletto*. Aucune régénération n'a été observée pour *C. odorata*. De même, la densité moyenne des arbrisseaux sur une parcelle de 2 ha s'est établie respectivement à 55, 20 et 2 pour *G. americanus*, *C. candidissimum* et *H. brasiletto*. La variation de la densité des peuplements de semis et d'arbrisseaux était positive pour *C. candidissimum*, indiquant une régénération continue et avancée pour cette essence. Pour *G. americanus* et *H. brasiletto*, le peuplement de semis a baissé alors que celui des arbrisseaux a augmenté. Pour *G. americanus* et *C. candidissimum,* les densités de semis et d'arbrisseaux étaient variables selon la pente du terrain et l'exposition des houppiers à l'ensoleillement direct, avec pour conséquence une distribution par paquets de la régénération. Il a été conclu que la régénération naturelle pourrait ne pas suffire au maintien du stock souhaité de ces essences, et qu'il conviendrait de prendre des mesures de restauration immédiates afin de soutenir le processus de régénération naturelle.

Mots-clés : couvert des cimes, régénération, topographie, forêt tropicale sèche.

ABSTRACT

POPULATION DYNAMICS AND SPATIAL DISTRIBUTION OF SEEDLINGS AND SAPLINGS OF FOUR DRY FOREST SPECIES IN NICARAGUA

The temporal variation in seedling and sapling densities of four dry forest species, *Calycophyllum candidissimum*, *Cedrela odorata*, *Haematoxylon brasiletto* and *Gyroscarpus americanus*, and the spatial heterogeneity of regeneration in relationship to terrain slope and crown exposure to direct sunlight were examined in the Chacocente National Wildlife Refuge, Nicaragua. Data on all individuals above 10 cm in height and below 5 cm in diameter at breast height were recorded for three consecutive years from 2001 to 2003. The density of seedlings and saplings varied significantly among species, as well as over time. The mean density of seedlings across the census year was thirty-seven, twenty and four individuals per 2 ha for *G. americanus*, *C. candidissimum* and *H. brasiletto*, respectively. *C. odorata* did not regenerate at all. Similarly, the mean density of saplings in a 2-ha plot was fifty-five, twenty and two for *G. americanus*, *C. candidissimum* and *H. brasiletto*, respectively. The change in population density of seedlings and saplings was positive for *C. candidissimum*, indicating continuous and advanced regeneration of this species. For *G. americanus* and *H. brasiletto* the seedling population declined while the sapling population increased. For *G. americanus* and *C. candidissimum,* seedling and sapling population densities varied with respect to the slope of the terrain and crown exposure to direct sunlight, resulting in a clumped pattern of regeneration. We concluded that natural regeneration alone may not be sufficient to maintain desired stocks of these species, and immediate restoration measures should be taken to assist the natural regeneration process.

Keywords: canopy cover, regeneration, topography, tropical dry forest.

RESUMEN

DINÁMICA DE LOS RODALES Y DISTRIBUCIÓN ESPACIAL DE PLÁNTULAS Y BRINZALES DE CUATRO ESPECIES DEL BOSQUE TROPICAL SECO EN NICARAGUA

En el Refugio de Vida Silvestre de Chacocente, en Nicaragua, se estudió la variación temporal de las densidades de plántulas y brinzales de cuatro especies del bosque tropical seco: *Calycophyllum candidissimum, Cedrela odorata*, *Haematoxylon brasiletto* y *Gyroscarpus americanus*. También se examinó la heterogeneidad espacial de su regeneración según la pendiente del terreno y la exposición de las copas a la insolación directa. Durante tres años consecutivos, de 2001 a 2003, se registraron los datos de cada individuo de más de 10 cm de altura y de menos de 5 cm de diámetro a la altura del pecho. La densidad de plántulas y brinzales era muy variable en el tiempo y según las especies. La densidad media de las plántulas durante los años del conteo fue de 37, 20 y 4 individuos por 2 ha en *G. americanus*, *C. candidissimum* y *H. brasiletto*, respectivamente. No se observo ninguna regeneración en *C. odorata*. Asimismo, la densidad media de brinzales en una parcela de 2 ha fue de 55, 20 y 2 en *G. americanus*, *C. candidissimum* y *H. brasiletto,* respectivamente. La variación de la densidad de rodales de plántulas y brinzales fue positiva en *C. candidissimum*, lo que indica una regeneración continua y avanzada en esta especie. En *G. americanus* y *H. brasiletto*, el rodal de plántulas disminuyó, mientras que el de brinzales aumentó. En *G. americanus* y *C. candidissimum*, las densidades de plántulas y brinzales eran variables según la pendiente del terreno y la exposición de las copas a la insolación directa, lo que provocó una distribución en grupos de la regeneración. Llegamos a la conclusión de que la regeneración natural podría ser insuficiente para mantener la densidad deseada de estas especies y, por tanto, habría que adoptar medidas de restauración inmediatas para contribuir al proceso de regeneración natural.

Palabras clave: cubierta de copas, regeneración, topografía, bosque tropical seco.

Introduction

The future structure and composition of a forest will mainly be a consequence of current recruitment patterns, which are governed by several factors such as specific traits in the life cycle, the physical and biological characteristics of the forest environment, and chance events that change over space and time (Veblen, 1992). Tree seedling dynamics are affected by various environmental factors such as soil moisture, temperature, microscale disturbance, canopy cover (light conditions) and deep leaf layers (Gerhardt, 1996; Nagamatsu *et al.*, 2002). Other biotic factors such as herbivory, fungal infection and interspecies competition have also been reported to affect seedling demography (Nagamatsu *et al.*, 2002). Information about the importance of these different factors on tree regeneration dynamics is critical for the restoration of natural forests in preserved areas, or for timber production based on sustainable silviculture.

The spatial dispersion of trees is mainly a result of their establishment patterns, although factors such as environmental changes, competition and chance events can also determine the distribution of trees. In the case of juveniles, their spatial arrangement results from a combination of seed dispersal modes, distribution of regeneration niches and seedling–sapling survival (Kitajima, Fenner, 2000; Condit *et al.*, 2000; McLaren & McDonald, 2003; Enoki, Abe, 2004). Patterns of forest regeneration following natural or anthropogenic disturbances are also determined by interactions between regimes of disturbance (intensity, frequency, scale) and species biology such as life history and behaviour (Kennard *et al.*, 2002).

Natural regeneration processes (e.g. seed germination, seedling establishment, population change and spatial patterns) in the dry forest species of Central America and elsewhere in the tropics are still poorly documented compared to tropical rain forests (Guariguata, 1998; Khurana, Singh, 2001). Previous studies on natural regeneration and its spatial heterogeneity in dry forest species of Central America have been carried out in Mexico and Costa Rica (e.g. Hubbell, 1979; Gerhardt, 1996; Janzen, 2002), but information is still lacking for many dry forest species in Nicaragua. An understanding of the dynamics of natural regeneration of dry forest species is therefore vital for developing guidelines for restoration and sustainable management plans (Sáenz, Finegan, 2000).

In this study, we examined the dynamics of seedling and sapling populations and the spatial distribution of four dry forest species, *Calycophyllum candidissimum* (Vahl) DC., *Cedrela odorata* L., *Haematoxylon brasiletto* Karst., and *Gyroscarpus americanus* Jacq., over time (2001 – 2003) and in relationship to the slope of the terrain and crown exposure to direct sunlight. The specific objectives were (i) to estimate the population density and rate of annual population change of seedlings and saplings over time, (ii) to estimate the density of seedlings and saplings in relation to the slope of the terrain and crown exposure to sunlight and (iii) to analyze the spatial pattern of natural regeneration. The underlying hypotheses were that the population of recruits fluctuates over time under the influences of biotic and abiotic factors, that mortality varies between recruits fully exposed to direct sunlight and overshadowed due to dry season drought, and in relation to the slope of the terrain through the effect on drainage, moisture and nutrient availability.

Figure 1.
Location of Chacocente Wildlife Refuge where the study was conducted.

Materials and methods

Study area

The study was carried out in the dry forest of the Chacocente National Wildlife Refuge (11°36'-11°30' N and 86°08'-86°15' W), in the province of Carazo, Nicaragua (figure 1). Chacocente has a dry period of 7 months with less than 50 mm precipitation per month; during the rainy season (June-October), rainfall is irregular with many sunny days (Anonymous, 2002). Mean annual precipitation in the last 13 years was 1,422 mm with a maximum in 1995 (1,962 mm) and a minimum in 1991 (991 mm). In October 1998, the area was hit by Hurricane Mitch, and precipitation that month reached 775 mm.

Species description

The species investigated in this study were *H. brasiletto* (Caesalpinioideae), *G. americanus* (Hernandiaceae), *C. odorata* (Meliaceae) and *C. candidissimum* (Rubiaceae). *H. brasiletto*, also commonly known as "*Brasil*", is a small to medium-sized tree [4-25 m in height and up to 60 cm in diameter at breast height (dbh)]. Its natural distribution extends from Southern Florida and Eastern Mexico, along the west coast of Central America to northern South America, at elevations ranging from 10 to 200 m above sea level in Costa Rica and up to 700 m in Nicaragua. It is commonly used for firewood, ornamental planting and for handicrafts and carvings (Salas, 1993). *G. americanus*, commonly known as "*Talalate*", is also a small to medium-sized tree, growing to 18-22 m in height and 40-60 cm in dbh. The natural distribution of the species extends from Mexico to South America. In Nicaragua, it grows naturally in the central and Pacific coast regions. It is a common tree in dry, stony places, usually in clearings and in dry and semi-humid forests. The wood is whitish, soft, light and not durable. It is used for manufacturing toys and boxes (Salas, 1993).

C. odorata, commonly known as "*Cedro*", is a large tree growing to a height of 12-30 m and a dbh of 60-150 cm. The distribution of this species extends from Mexico to South America. In Nicaragua, *Cedro* is found at low elevations with a dry to very humid climate. Isolated *Cedro* trees are also frequently found in grassland and cropland. It is generally found in the whole country, in small groups. *Cedro* is a very important forest tree for its attractive wood properties. The wood is soft, light, easy to work, durable and resistant to termite attacks. It is used to manufacture furniture, closets, doors and cigar boxes, as well as for different construction purposes such as veneers, laminated wood, etc. (Salas, 1993). C. *candidissimum*, commonly known as "*Madroño*", is a tree that grows to 6-30 m and a dbh of 25-60 cm. Its natural distribution extends from southern Mexico to Venezuela and Colombia. In Nicaragua, this species is found in dry and semi-humid areas, mainly along the Pacific coast and in the central region. The species is used for firewood, toothpicks and ornamental purposes. *C. candidissimum* was declared as the National Tree of Nicaragua on 27 August 1971 (Salas, 1993).

Photograph 2.
Poor regeneration in the understory with nearly 100 % canopy cover.
Photograph G. Castro-Marin.

Regeneration survey

The survey on natural regeneration was carried out along four longitudinal transects, each measuring 1000 x 5 m (0.5 ha). A base line was established with an azimuth of 305º, and the four transects were located following an azimuth of 35º. The distance between two adjacent transects was 800 m. Each transect was divided into 50 subplots measuring 20 x 5 m (100 m²). The sample plots covered the variations in environmental gradients, especially terrain slope and crown exposure to direct sunlight. All individuals above 10 cm in height and below 5 cm in dbh were surveyed for three consecutive years from 2001 to 2003. Recruits were classified according to size as seedlings (individuals 10-150 cm in height) and saplings (individuals more than 150 cm in height and below 5 cm in dbh), following Sáenz and Finegan (2000) and Teketay (1997) with slight modifications. For each individual seedling and sapling, the degree of crown exposure to direct sunlight was determined visually, following Hawthorne (1993), as overshadowed, partially exposed or fully exposed. The percentage slope of each plot was determined, and slope classes were defined as flat or nearly flat (0-6 %), gently sloping (6-25 %) and steeply sloping (> 25 %), following Fao (1977) and Bosworth and Foster (1982).

To provide an overview of the density and spatial distribution of mature trees, an inventory was carried out using the distance method (Krebs, 1999). For each species, 30 mature trees were randomly located within the study area, which was extended to include boundary strips, and the distances from each mother tree to its nearest neighbour were measured.

Data analysis

The total number of individuals was calculated for each species, size class and census year (2001, 2002 and 2003). The number of individuals per species was also determined in terms of the degree of crown exposure to direct sunlight and the slope of the terrain. For each species, an annualized rate of population change (r) was calculated, using the standard logarithmic growth model (CONDIT *et al.*, 1996) as follows:

$$r = \left(\frac{1n\ N_{03} - 1n\ N_{01}}{\Delta t}\right)$$

N_{03} and N_{01} are population sizes in the 2003 and 2001 censuses, ln is the natural logarithm and t is the time interval between two assessments.

The chi-square test was employed to examine whether the density of recruits varies with the different classes of crown exposure to direct sunlight and slope. For this analysis, the mean density across the three census years was used. *H. brasiletto* and *C. odorata* were excluded from the analysis since very few individuals were recorded during the inventories, violating the assumption for the chi-square analysis, i.e., that the expected frequency should be 5 or more (ZAR, 1996).

To further account for the spatial pattern of natural regeneration, the standardized Morisita index (I_p) was calculated for each census year. There are a number of spatial indices, but I_p is independent of population density and size (KREBS, 1999). To calculate this index, the Morisita dispersion index (I_d) was calculated first, along with two critical values, the uniform index (M_u) and the clumped index (M_c), as follows:

$$I_d = n\left[\frac{\Sigma x^2 - \Sigma x}{(\Sigma x)^2 - \Sigma x}\right]$$

$$M_u = \frac{X^2_{.925} - n + \Sigma x}{(\Sigma x) - 1}$$

$$M_c = \frac{X^2_{.025} - n + \Sigma x}{(\Sigma x) - 1}$$

where n is the sample size (5 x one-ha plots), x is the number of individuals, $X^2_{.075}$ and $X^2_{.975}$ are the chi-squared values with (n-1) degrees of freedom with 2.5 % or 97.5 % of the area to the right. The standardized Morisita index (I_p) was then calculated using one of the four following formulae:

a) When $I_d \geqslant M_c > 1$,

$$I_p = \left[\frac{I_d - M_c}{n - M_c}\right]$$

b) When $M_c > I_d \geqslant 1$,

$$I_p = 0.5 \text{ x } \left[\frac{I_d - 1}{M_u - 1}\right]$$

c) When $1 > I_d > M_u$,

$$I_p = -0.5 \text{ x } \left[\frac{I_d - 1}{M_u - 1}\right]$$

d) When $1 > M_u > I_d$,

$$I_p = -0.5 + 0.5 \text{ x } \left[\frac{I_d - M_u}{M_u}\right]$$

I_p ranges from -1.0 to +1.0 with 95 % confidence limits at ± 0.5. The distribution of a population was considered random, clumped or uniform if $I_p = 0$, $I_p > 0$ or $I_p < 0$, respectively.

The density and spatial distribution of mature trees were estimated using the following equations:

$$\hat{N}_2 = \frac{n}{\pi \sum (r_i^2)}$$

$$I_E = \left(\frac{s}{\bar{x}}\right)^2 + 1$$

$\hat{N}_2$ = estimate of population density from organism-to-nearest neighbour, n = sample size, r_i = distance from random organism i to nearest neighbour, π = 3.147, I_E = Eberhardt's index of dispersion, s = observed standard deviation of distances and $\bar{x}$ = mean of organism-to-nearest neighbour. *Cedrela odorata* was not included in the analysis because no mature tree was found in the area. The expected value of I_E in a random population is 1.27; values below this suggest a uniform pattern and larger values indicate clumping (KREBS, 1999).

Results

Population density and rate of change

Population density and the annualized rate of population change varied among species (table I). *G. americanus* had the highest number of individuals in all the census years, followed by *C. candidissimum*. While the density of seedlings and saplings of *H. brasiletto* was much lower, no saplings of *C. odorata* were found in any of the census years. The density of *G. americanus* seedlings decreased by 26 % from 2001 to 2003, while the sapling density increased by 17 %. A similar trend was found for *H. brasiletto*. For *C. candidissimum,* both seedling and sapling population densities showed a positive change from 2001 to 2003. For *C. odorata,* the rate of population change could not be calculated as no saplings or seedlings of this species were found during the inventories.

Population density in relation to light incidence and slope

The mean population density (averaged over the three census years) of *G. americanus* and *C. candidissimum* seedlings and saplings differed significantly in terms of crown exposure to sunlight ($\chi^2_{(0.05,\ 2)}$ = 31.38 and 48.71 for seedling and sapling populations, respectively and $p < 0.0001$). *G. americanus* seedlings and saplings that were either partially or fully exposed to direct sunlight were more abundant than overshadowed individuals (figure 2). Although the mean density was generally low, *H. brasiletto* seedlings and saplings found in fully and partially exposed conditions were relatively more numerous than those in full shade. On the other hand, the density of overshadowed *C. candidissimum* seedlings and saplings was much higher than for recruits whose crown was exposed to direct sunlight. Overall, regeneration in the understory is poor under partial shade (photograph 1) compared to regeneration under full shade (photograph 2).

Table I.
Total population density (individuals/2ha) and rate of population change (r %) of seedlings and saplings of four tropical dry forest species in Chacocente, Nicaragua.

Species/size	2001	2002	2003	r
G. americanus				
Seedlings	49	34	29	-26
Saplings	44	59	62	17
C. candidissimum				
Seedlings	20	16	24	9
Saplings	18	21	20	5
H. brasiletto				
Seedlings	4	5	3	-14
Saplings	1	1	3	55
C. odorata				
Seedlings	1	0	0	nd*
Saplings	0	0	0	nd

* Calculation not applicable

The mean population density (averaged over the three census years) of *G. americanus* and *C. candidissimum* seedlings and saplings also differed significantly in terms of the slope of the terrain ($\chi^2_{(0.05,\ 2)}$ = 21.58 and 27.56 respectively for seedling and sapling populations, and $p < 0.0001$). Both seedlings and saplings of *G. americanus* were more abundant on a gentle slope than on flat ground or a steep slope (figure 3). For *C. candidissimum*, seedling and sapling densities were much higher on flat ground. Despite low seedling and sapling densities, regeneration of *H. brasiletto* was confined to the gentle slope (cf. 15 individuals on a gentle slope, 3 on flat ground and none on a steep slope).

Spatial patterns of natural regeneration

The standardized Morisita index was > 0.5 for *C. candidissimum*, *G. americanus* and *H. brasiletto* (table II). Consequently, the spatial distribution of seedling and sapling populations of all the species studied was clumped or aggregated (photograph 3). The spatial pattern did not change during the census years despite changes in the population density of seedlings and saplings of the species studied.

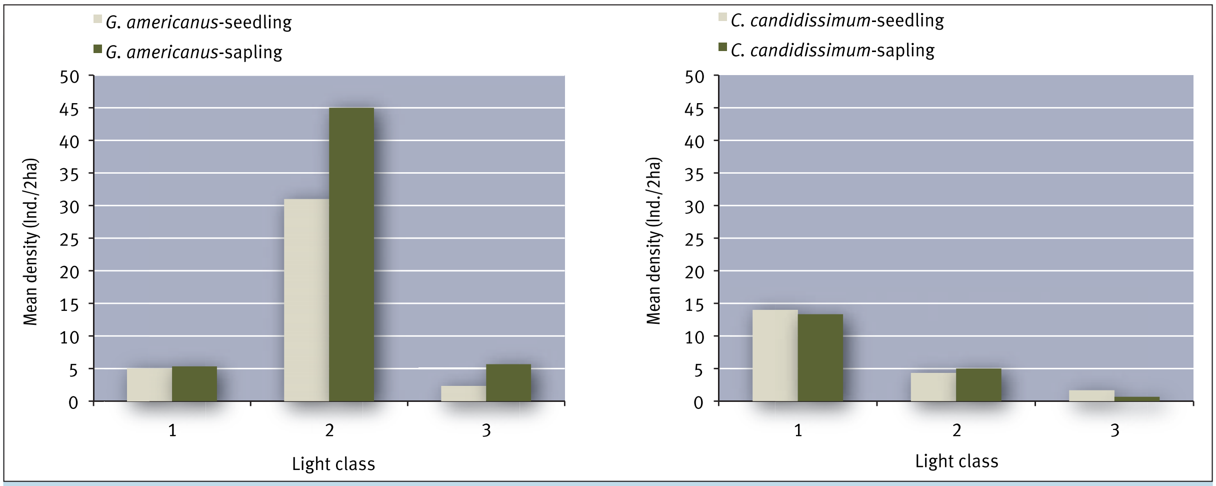

Figure 2.
Mean population density (across the census years) of *C. candidissimum* and *G. americanus* in relation to sunlight exposure classes (1 = fully exposed, 2 = partially exposed and 3 = completely overshadowed). Shaded bars denote seedling density and open bars denote sapling density.

Table II.
Standardized Morisita index and spatial distribution of seedlings and saplings of *C. candidissimum, G. americanus* and *H. brasiletto* in the tropical dry forest of Chacocente, Nicaragua, across the census years.

Species	Year	Standardized Morisita index (I_d)	Spatial patterns
C. candidissimum	2001	0.54	Clumped
	2002	0.52	Clumped
	2003	0.53	Clumped
G. americanus	2001	0.55	Clumped
	2002	0.52	Clumped
	2003	0.53	Clumped
H. brasiletto	2001	0.52	Clumped
	2002	0.51	Clumped
	2003	0.57	Clumped

Density and spatial patterns of mature trees

G. americanus had the largest number of mature trees, followed by *H. brasiletto* and *C. candidissimum* (table III). No mature *C. odorata* trees were found during the inventory.

Eberhardt´s index of dispersion for the three species was above 1.27 (table III), which is the expected value of I_E in a random population. As a result, mature trees of all three species exhibited a clumped or aggregated spatial distribution.

Discussion

Population density

The results show conspicuous differences between the densities of seedlings and saplings of the species studied (table I). In practice, *C. odorata* was not regenerating at all in the Chacocente dry forest. The density of *H. brasiletto* was extremely low compared to the density of *C. candidissimum* and *G. americanus*. The establishment, survival and growth of seedlings is governed by several biotic and abiotic factors (Kitajima, Fenner, 2000). The arrival of viable seeds in regeneration sites and the subsequent germination and establishment of seedlings are vital determinants of the efficacy of natural regeneration (Felfili, 1997; Howlett, Davidson, 2003). *G. americanus*, a species with abundant regeneration, also has the largest number of mature trees (table III), which in turn can serve as seed sources. *G. americanus* is one of the most abundant species in Chacocente (Sabogal, 1992). A soil seed bank study carried out in dry deciduous forest in Chacocente (Uasuf *et al.*, 2009) found no seed for all the species covered in the present study but recorded more than 50 seedlings per ha of *H. brasiletto*,

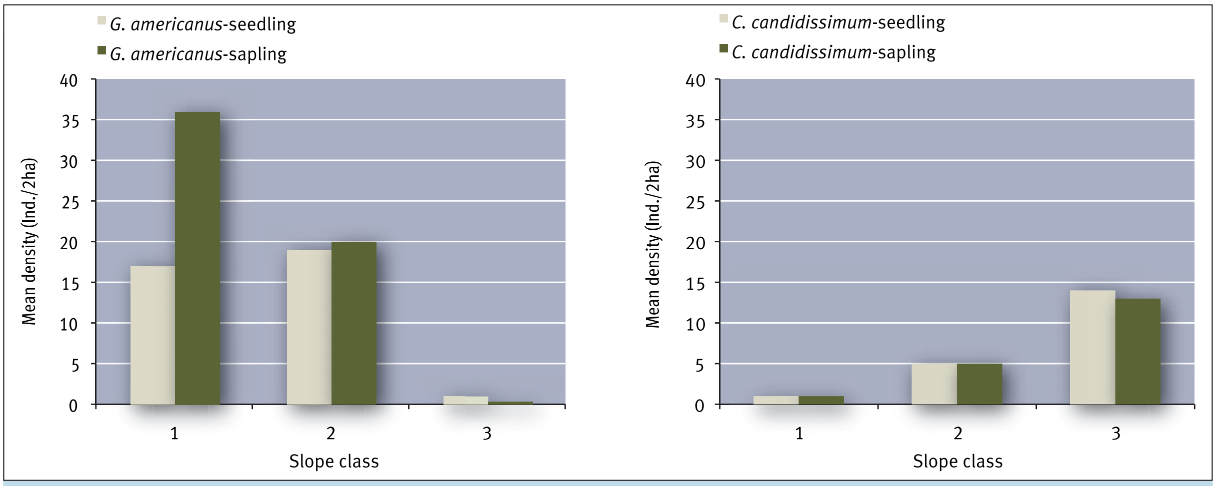

Figure 3.
Mean population density (across the census years) of *C. candidissimum* and *G. americanus* in relation to slope classes (1 = flat, 2 = gentle slope and 3 = steep slope). Shaded bars denote seedling density and open bars denote sapling density.

Photograph 3.
Patchiness in seedling regeneration, resulting in clumped distribution.
Photograph G. Castro-Marin.

Table III.
Density (individuals/ha) and spatial patterns of mature *C. candidissimum, G. americanus* and *H. brasiletto* trees in the dry forest of Chacocente, Nicaragua.

Species	Density	Index of dispersion	Spatial pattern
C. candidissimum	6	1.41	Clumped
G. americanus	16	1.32	Clumped
H. brasiletto	10	1.39	Clumped

C. candidissimum and *G. americanus*. This indicates that a seedling bank could be the recruitment strategy in these species. The lack of natural regeneration of *C. odorata* is related to the paucity of seeds, as evidenced from the complete absence of mature trees in the study area. *C. odorata* is one of the valuable timber species that have been commercially logged for many years (Sabogal, 1992).

Our study found that the overall pattern of natural regeneration of the species studied is consistent with the findings of previous studies made in the dry deciduous forests of Chacocente and Nandarola (25 km away from Chacocente) in Nicaragua (Sabogal, Valerio, 1998; Nuñez, 2002). However, the density of recruits in our study was comparably lower than that reported in Nuñez (2002). This discrepancy could be related to the plots allocated to the study. Unlike those in the previous study, our plots represented large environmental variations, particularly in terms of slope and light conditions. It was also observed that some plots along transects were dominated by bushes and grasses, which might have a negative impact on the density of recruits via competition. The low density of seedlings and saplings of the species studied in the Chacocente dry forest might also be attributed to uncontrolled fires and grazing or browsing, particularly during the dry season (Sabogal, Valerio, 1998).

The annualized rate of change in seedling and sapling densities also varied among species and size classes (table I). For instance, the seedling population of *G. americanus* declined by 26 % from 2001 to 2003, while its sapling population increased by 27 %. A similar trend was observed for *H. brasiletto*, although the estimated rate of population change for saplings is exaggerated due to low density. This indicates that continuous seedling recruitment is lacking while advance regeneration is proceeding satisfactorily. Seedling mortality varies among species, depending on the size and age of seedlings as well as the softness and palatability of tissues (Kitajima, Fenner, 2000). Young seedlings are vulnerable to several biotic and abiotic factors (Gerhardt, 1998). Predation, herbivory and pathogens are the major biotic factors that affect seedling survival and seedling population densities (Terborgh, Wright, 1994; Sherman, 2002; Hood *et al.*, 2004). Among the abiotic factors, drought is the chief cause of seedling mortality in tropical dry forests (Ray, Brown, 1995; Gerhardt, 1996; McLaren, McDonald, 2003), as well as aseasonal rain forest experiencing unusually severe drought (Delissio, Primack, 2003). Young seedlings are also killed by low-intensity ground fires (Saha, Howe, 2003) and physical damage from litter fall (Scariot, 2000), although this is also variable among species (Gillman *et al.*, 2003). Tree fall, mainly due to wind throw (photograph 4), is common in the study area, particularly on sloping ground. *C. candidissimum* had a positive annual population change from 2001 to 2003 in all size classes. This indicates that *C. candidissimum* regenerates successfully and continuously in the Chacocente dry forest.

Photograph 4.
Tree fall liable to cause physical damage to seedlings and saplings.
Photograph G. Castro-Marin.

Spatial pattern

The density of recruits varied considerably in relation to crown exposure to direct sunlight and the slope of the terrain. For instance, the density of *G. americanus* seedlings and saplings that were partially or fully exposed to direct sunlight was much higher than for fully shaded saplings (figure 2). On the other hand, the density of *C. candidissimum* seedlings and saplings was much higher in full shade. Fully or partially exposed *H. brasiletto* seedlings and saplings were found in relatively larger numbers than in full shade, although the overall density was low. The shade requirement for the survival of dry forest species, with marked interspecies variations, is thought to be a mechanism for integrating drought tolerance and light requirement, i.e., to allow seedlings to avoid very high light intensity and very low moisture (Ray, Brown, 1995; McLaren, McDonald, 2003). Similarly, the population density of the species studied varied substantially with respect to the slope of the terrain (figure 3). While *G. americanus* seedlings and saplings were more abundant on a gentle slope, densities of *C. candidissimum* seedlings and saplings were much higher on flat ground. Topography, through its effect on drainage, moisture and nutrient availability, plays an essential role in the spatial distribution of recruits (Enoki *et al.*, 1997; Enoki, Abe, 2004).

Overall, the spatial analysis revealed that natural regeneration of the species studied is clumped. A clumped or aggregated spatial pattern is very common among tropical forest species (Hubbell, 1979; Condit *et al.*, 2000). Poor propagule dispersal and recruitment limitations (soil nutrients, light, moisture, etc) may lead to such patterns (Bunyavejchwin *et al.*, 2003; Hardy, Sonké 2004; Palmiotto *et al.*, 2004). Consequently, resource-based niche differentiation results in habitat specialization, so that different species are best suited to different habitats, where they are competitively dominant and relatively more abundant. The distribution pattern of trees is affected by numerous biotic and abiotic factors and their interaction, but topography is a major physical factor which affects the composition, growth, and distribution of tropical forests (Enoki, Abe, 2004; Castro-Marin *et al.*, 2009). Other studies have also demonstrated topographic habitat association and an association with canopy openness (Martinez, Alvarez, 1995; Enoki, Abe, 2004).

Conclusions

The overall population density of recruits is low, especially for *C. odorata*. For *H. brasiletto, C. candidissimum* and *G. americanus*, recruitment and mortality rates are slightly lower. Regeneration is spatially heterogeneous and clumped for all the species investigated in this study. This suggests that regeneration dynamics are changing due to activities that cause disturbance (e.g. grazing, fire, mowing, etc.) in deciduous forests, and to the impact of high temperatures on seedlings. While climax species like *C. odorata* are disappearing, pioneer light-demanding and drought-resistant species like *H. brasiletto* are becoming established. Consequently, measures like direct seeding, enrichment planting and protection of recruits from anthropogenic disturbance could be taken to assist the natural regeneration process. For some of the species, like *C. candidissimum*, the use of nurse trees in open areas would be useful in future restoration work.

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