Tree species Diversity and Regeneration of Tropical Dry Forests in Nicaragua

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Abstract

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The thesis summarises results from four studies in dry forests of Nicaragua aiming to gain knowledge supporting conservation and rehabilitation efforts in these highly threatened forests. In the first study, tree species composition, structure and diversity of dry deciduous and gallery forests was carried out in Chacocente National Wildlife Refuge during 1994 and 2000. A total of 29 families, 49 genera and 59 species were represented in 2 ha permanent plots in dry deciduous forest during 1994 and 2000 assessments. In the gallery forest, the number of families, genera and species recorded in 2000 inventory was 33, 48 and 58, respectively, and slightly higher than the 1994 inventory. The number of stems ≥ 10 cm dbh varied from 451 (1994) to 489 (2000) per ha in the deciduous forest, and from 283 (2000) to 298 (1994) per ha in the gallery forest. The gallery forest was found to be more diverse than the deciduous forest using Fisher's diversity index. In the second study, the temporal and spatial variation in seedling and sapling population densities of *Gyroscarpus americanus*, *Calycophyllum candidissimum*, *Haematoxylon brasiletto* and *Cedrela odorata* were investigated in the dry forest in Chacocente National Wildlife Refuge for three consecutive years. The density of seedlings and saplings varied significantly over time and among species. The overall density of recruits was higher for *G. americanus* and *C. candidissimum* compared with *H. brasiletto* and *C. odorata*. The net change in population density of seedlings and saplings was positive for *C. candidissimum* only, indicating a continuous and advanced regeneration. For the two most abundant species, *G. americanus* and *C. candidissimum,* the population density of recruits varied with respect to slope of the terrain and crown exposure to direct sunlight, thus resulted in clumped pattern of regeneration. The third study dealt with soil seed bank assembly following secondary succession on abandoned agricultural fields in a chronosequence of 4 to 14 years. The species composition of the seed bank and seed density varied significantly with increasing age of abandonment. A total of 3, 5 and 9 species were found on sites abandoned 4, 9 and 14 years ago, respectively. The total number of seeds ranged from 327 in the 4-year old site to 146 in the 14-year old site, and the density of viable seeds ranged from 141 seeds m^{-2} in the 4-year old site to 22 seeds m^{-2} in the 14-year old site. In the fourth study, seed germination responses of *C. candidissimum, C. odorata* and *Guaiacum sanctum,* to different constant and alternating temperature regimes under continuous light or darkness in the laboratory, and the effect of canopy cover on seedling survival of *C. odorata* and *G. sanctum* in the field were investigated. Among the species tested, germination of *C. candidissimum* seeds was positively photoblastic, and for all species the optimal temperature for germination was 20-25ºC. Survival of *G. sanctum* seedlings was higher in all three sites, but the relative growth rate in collar diameter was higher in open sites. Survival was poor for *C. odorata*.

Key words: Chacocente, deciduous forest, gallery forest, germination, Nicaragua, seed bank.

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Dedicated to

My wife Matilde

And

My kids Eduardo and Allan

Contents

Appendix

Paper I – IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

I. González-Rivas, B., Tigabu, M., Gerhardt, K., Castro-Marín, G., Odén, P. C. 2005. Species composition, diversity and local use of tropical dry deciduous and gallery forests in Nicaragua (Submitted).

II. González-Rivas, B., Tigabu, M., Castro-Marín, G., Odén, P. C. 2005. Seedling and sapling population densities and spatial patterns of four dry forest species in Nicaragua (Submitted).

III. González-Rivas, B., Tigabu, M., Castro-Marín, G., Odén, P. C. 2005. Soil seed bank assembly following secondary succession on abandoned agricultural fields in Nicaragua (Manuscript).

IV. González-Rivas, B., Tigabu, M., Castro-Marín, G., Odén, P. C. 2005. Seed germination and seedling establishment of three Neotropical forest species in response to temperature and light conditions (Submitted).

Introduction

General background

Nicaragua has 250,000 ha of tropical dry forest, representing *ca*. 2% of the total forest cover (Harcourt & Sayer, 1996). According to Roldan (2001), 80% of dry forests in Nicaragua have been converted to coffee plantations, agricultural fields and animal husbandry farms. In general, the main problems of the forestry sector in Nicaragua include; illegal cutting, conversion of the forest to agricultural land, fire, and insects attacks (Anon., 2004). According to Holdridge´s criteria, tropical and subtropical dry forest are found in frost-free areas where mean annual temperature is above 17ºC, annual rainfall ranges from 250 to 2000 mm, and the ratio of potential evapotranspiration to precipitation is greater than one, to a maximum value of two. By these criteria, 49% of the vegetation of Central America (an area extending from Guatemala to Panama) and the Caribbean (an area extending from Cuba to Grenada) is considered as dry forest (Murphy & Lugo, 1995). Tropical dry forests experience long dry season (4 – 8 months) and the rainy period is somewhat unreliable. During the dry season, not only moisture stress but also temperature increases and daytime humidity drops and watercourses either dry up or greatly diminish in volume. In response to these environmental changes, most plants cease their vegetative growth and many species shed their leaves while several woody species flower, mature their fruits and disperse seeds. Dry tropical forest stands are smaller in stature, lower in biomass and less complex floristically and structurally than tropical rain forests (Murphy & Lugo, 1986). They are closed stands with no substantial opening in the crown cover (above 80 percent), the trees are approximately 15-20 m high and they lose their leaves, with few exceptions, during part of the year. The understory comprises of sparse and scattered evergreen or deciduous shrubs, with a few grass tufts (Bellefontaine & Petrucci, 2000).

Plant species of this ecosystem have slower growth rates and restricted reproductive episodes compared to a tropical rain forest, making them more susceptible to disturbance (Kalacska *et al*., 2004). The gallery forest within the dry zone occurs as narrow patches along the fringes of semi-permanent watercourses (Lamprecht, 1989). It has a different species composition, structure and stand density than the more common deciduous forest. The vegetation is mostly evergreen, the trees are taller and the majority of the trees have a diameter exceeding 35 cm dbh. In Nicaragua, the tropical dry forest environment has the following characteristics; stable and high temperatures with annual mean temperature between 24 and 30ºC, mean annual precipitation between 800 and 1500 mm, and duration of the dry season from five to eight months (Faurby & Barahona, 1998).

Generally, the tendency of human populations to concentrate in drier climates has hastened the rate of dry forest degradation (Murphy & Lugo, 1995). The dry forest in Nicaragua is located in the Pacific region of the country (Faurby & Barahona, 1998). The majority of Nicaraguan populations (60%) also live around tropical dry forest; thus causing a strong pressure on this forest due to increased consumption of timber, firewood and charcoal (Sabogal & Valerio, 1998; Anon., 2004). Historically, the land use along the pacific coast has been extensive agriculture, animal grazing, and subsistence farming. The dry forests in Nicaragua are of significant socioeconomic importance to many rural communities, providing a variety of timber and non-timber products. Sustainable land use systems are urgently needed for tropical dry forest in general and that of Nicaragua in particular, which should be based on detailed knowledge of forest structure, function, and response to perturbation (Maass, 1995).

Tree species diversity of the Neotropical dry forest

Forests are the most diverse terrestrial ecosystems. Forest biodiversity also has important economic, social and cultural roles in the lives of many indigenous and local communities. It provides livelihoods for hundreds of millions of people worldwide, through production of timber, pulpwood, firewood, fodder, meat, and medicinal plants. Forests also provide a variety of ecological services that are extremely important to the health and integrity of the ecosystem.

According to Murphy and Lugo (1986), 1-3 ha of dry forests commonly contain between 35 and 90 tree species. The most diverse Neotropical dry forests are located in Mexico and South America. For example, dry forests of high diversity are found in Chamela, Mexico and Quiapaca, Bolivia (Kalacska *et al*., 2004). Gordon *et al*. (2004) reported that tropical dry forest in Oaxaca, Mexico is more diverse than Honduras tropical dry forest on family, genus and species levels. The most specious families found in Honduras were Mimosaceae with 16 species, Papilionaceae with 11 species and the most specious families encountered in Oaxaca were Mimosaceae with 25 species and Papilionaceae with 24 species.

Species richness and diversity of tropical forest are frequently lower in mature forests than during regeneration phases (Saldarriaga *et al*., 1988; Brown & Lugo, 1990; Aide *et al*., 1996). According to Horn (1976), this is due to higher species diversity reached at intermediate succession stages, when changing environmental conditions allow simultaneous occurrence of species typical of both early and late succession stages. In addition, tropical forest diversity generally increases with precipitation. The average number of tree species occupying 0.1 ha plots in the Neotropics increased by 50 for each 100 cm increase in average yearly precipitation (Perry, 1994; Berry, 2002). Typically lowland forests have 50-70 species with dbh greater than 2.5 cm in 0.1 ha and moist semi-evergreen forests have 100-150 species. The average species richness for 23 Neotropical dry forests is 65 species per ha compared with the lowland wet and moist forests average of 152 species per ha (Gentry, 1995). Fragments of tropical dry forests in Central America differ significantly in floristic diversity and structure, although Fabaceae is generally dominant based on number of tree and shrub species per family by site (Gillespie, Grijalva & farris, 2000).

Forest diversity is being lost because of rapid deforestation, fragmentation and degradation (Perry, 1994; Kattan, 2002). Degradation and conversion of dry forests are far more advanced than in wet forests; only a small fraction remains intact, and the area explicitly conserved is hardly perceptible. Restoration of severely degraded forest ecosystems is harder (Janzen, 1988) and species reintroduction is not an easy task. This is unfortunate since forests with prolonged annual droughts occupy larger areas than wet forests; are of great importance to humans, and are still poorly known in most areas (Mooney, Bullock & Medina, 1995). Conversion of tropical dry forest to agriculture and pasture still continues with an increasing rate in many parts of the tropics, and entails nearly total destruction of forest structure and composition, and disruption of ecosystem functions (Maass, 1995). Deforestation has been variable in time and space, and over the last 50 years it has shown an increasing trend (FAO, 2001). Due to extensive commercial cutting, some species are more threatened, for example, *Cedrela odorata*, *Bombacopsis quinatum* and *Switenia humilis* in the dry forests of Central America (Tercero & Urrutia, 1994). For all these reasons, plant genetic resources are depleted by genetic erosion and by the extinction of certain species (Bellefontaine & Petrucci, 2000). The forest cover in Nicaragua in 1983 was of 7,666,800 ha. In the year 2000 the forest cover was estimated to be 5,597,700 ha. Based on this information Nicaragua has lost 2,069,100 ha of the forest cover in 17 years period, representing 27% of the total forest cover (Anon., 2004). Plant species richness in the country is 6500 species of vascular plants, distributed over 223 families. No information is available about which and how many species are under extinction threat (Anon., 2004). Consequently, there is a great need for such information in order to develop guidelines for conservation and management of the remaining relict patches.

Natural Regeneration

Natural regeneration refers to the natural process by which plants replace or re-establish themselves, usually from an abundant production of seeds that germinate to assure the development of new forests (Malcolm, 1999). Seedlings represent the final stage in the process of regeneration from seed. The period between seed germination and establishment of an independent juvenile plant is one of the most vulnerable stages in the life cycle of plants (Kitajima & Fenner, 2000). Tree seedling dynamics are affected by various environmental factors such as soil moisture, temperature, micro-scale disturbance, canopy cover (light condition) and deep leaf layers (Gerhardt, 1996; Nagamatsu, Kenji & Akiko, 2002). Biotic factors such as herbivores, fungal infection and inter-species competition have also been reported to affect seedling demography (Nagamatsu, Kenji & Akiko, 2002). The spatial distribution of recruits is also important in the understanding of natural regeneration dynamics (Condit *et al.*, 2000), as natural regeneration is often heterogeneous, depending on seed dispersal, viability, dormancy, predation, herbivory and environmental conditions (Gerhardt & Hytteborn, 1992; Bekele, 2000; Kitajima & Fenner, 2000; Khurana & Singh, 2001; McLaren & McDonald, 2003; Enoki & Abe, 2004). In general, the dynamics of tropical dry forests and the environmental and regeneration requirements of particular tree species are still little known (Gerhardt, 1993). Information on the regenerative strategies of especially less common species is often lacking (Grime & Hillier, 2000). Thus, information about the dynamics of natural regeneration of dry forest species is necessary for developing guidelines for its restoration and sustainable management (Saenz & Finegan, 2000).

Soil seed Bank

All viable seeds present on or in the soil or associated litter constitute the soil seed bank (Simpson, Leck & Parker, 1989). There are two general types of soil seed bank; transient and persistent. Transient seed bank is one in which none of the seeds produced in a given year remain viable in the habitat for more than 1 year, whereas seeds in a persistent seed bank remain viable for 1 or more years (Baskin & Baskin, 1998). Seeds display both horizontal and vertical dispersion, reflecting initial dispersal onto the soil and subsequent movement (Simpson, Leck & Parker, 1989). The presence of different types of seed banks provides a vital clue to the mechanisms which permit species to coexist in perennial plant communities. This diversity in seed bank behaviour not only indicates how variation in form, intensity, and seasonal distribution of habitat disturbance facilitates complementary forms of regeneration, but it also provides a basis for manipulations of species composition by shifting the opportunities for seedling establishment in one direction or another (Grime, 1989). Much of the small and large scale spatial heterogeneity of soil seed banks within tropical vegetation may be related to patterns of seed dispersal, abundance of predators, local edaphic conditions (fertility or drainage), or other factors that have been little studied (Garwood, 1989).

It has been shown that soil seed density and richness increase as secondary forest succession advances in tropical dry forests (Scholz, González & Vilchez, 2004), although the size of tropical seed banks are generally low (Skoglund, 1992). Deeper soil layer density of seeds and species richness also decrease in contrast to upper soil layer (Teketay, 1996; Scholz, González & Vilchez, 2004). Seed bank density and richness have been reported to change along temporal (succession) and spatial (altitude, latitude) gradients (Funes. *et al*., 2003). During secondary succession, the soil seed bank assembles as result of the balance between seed input and seed output at the same time as the plant community assembles (Fenner, 1985; Mengistu *et al*., 2005). Knowledge of the seed bank can help us to predict the regeneration patterns that one can expect from a forest (Dalling, 2002). Thus, information about soil seed bank dynamics of secondary forests in a chronosequence is of paramount importance when deciding whether active or passive restoration approaches should be employed to foster the recovery of secondary forests on abandoned fields. Evidences indicate that initial recovery of secondary forests on abandoned fields is dependent on the availability of seeds (Wijdeven & Kuzee, 2000; Zimmerman, Pascarella & Aide, 2000).

Seed germination and seedling growth

Germination is defined as the emergence of the radicle through the seed coat (Copeland & McDonald, 2001). It begins with water uptake (imbibition) and ends with elongation of the embryonic axis, usually the radicle (Bewley & Black, 1994). Knowledge of seed germination requirements and subsequent seedling establishment and growth is crucial, as they are demographically critical phases in the regeneration of plants from seeds (Gerhardt 1996; Teketay, 1996; Kozlowski, 2002). For non-dormant seed populations, temperature and light conditions play an important role in seed germination provided that enough soil moisture and oxygen are present. Studies on dry forest species have shown large interspecific variation in the optimal temperature requirement for germination (Teketay & Granström, 1997; Khurana & Singh, 2001; Tigabu & Odén, 2001; Teketay, 2002; Zida *et al.*, 2005). Light intensity and its spectral quality also markedly influence germination, and survival and growth of seedlings of tropical tree species with marked interspecific variation (Rincon & Huante, 1993; Ray & Brown, 1995; Teketay & Granström, 1997; Teketay, 2002; Yirdaw & Leinonen, 2002; Abebe, 2003; Dokrak *et al.*, 2004; Godoi & Takaki, 2004). Drought has been shown to be the chief factor limiting seedling survival and growth in dry tropics (Gerhardt 1996). The effect of drought on seedling survival has also been shown to interact with shading (Ray & Brown, 1995). In a country like Nicaragua where information about native tree species is generally lacking, the first step in forest restoration is to carry out extensive background studies, ranging from seed germination to seedling establishment and growth in light of the changing environment on degraded open sites.

Objectives

The general objective was to gain knowledge supporting conservation and management of dry forests in Nicaragua. The specific objectives were to;

1) examine whether forest diversity is amply conserved in protected areas by describing tree species composition and diversity of dry deciduous and gallery forests in Chacocente National Wildlife Refuge over 6 years time, assuming that diversity may decline due to anthropogenic and natural disturbances (Study-I),

2) quantify the density of seedlings and saplings of four dry forest species of high socio-economic importance in relation to topography and light incidence. The underlying hypotheses were that mortality varies between recruits growing in direct sunlight or overshadowed due to dry season drought, and mortality also varies in relation to slope of the terrain through its effect on drainage, moisture and nutrient availability (Study-II),

3) investigate the composition and density of seeds in soils of secondary forests developed on abandoned fields 4, 9 and 14 years after abandonment, focusing on the question whether the soil seed bank assembles simultaneously as the plant communities assemble (Study-III), and

(4) investigate the requirements for seed germination and seedling establishment of selected dry forest species. Therefore, the germination response to different constant and alternating temperature regimes and light conditions, as well as survival of seedlings transplanted under different canopy cover were studied.

Materials and methods

Study sites

The first, second and part of the fourth studies were conducted in Chacocente National Wildlife Refuge (11° 36' N - 11° 30'N and 86° 08' – 86° 15'W), which is located on the Pacific Coast in the department of Carazo, Nicaragua (fig 1). The altitude varies from sea level to *ca.* 300 m a.s.l (Sabogal, 1992).The total area of the wildlife reserve is *ca*. 4650 ha of which two thirds are dry deciduous forest type and one tenth is gallery forest type. The remaining areas are scrubs, pasture and agriculture land (Anon., 2002). Soils in the deciduous dry forest type are classified as Vertic and Ferric Luvisol (Sabogal & Valerio, 1998). The gallery forest type is located along a semi-permanent watercourse – the Río Escalante, and is distinguished from the deciduous forest by a species composition dominated by evergreen or semi-deciduous trees (Tercero & Urrutia, 1994). Soils in the gallery forest are classified as Eutric fluvisol. Currently, the land ownership in the reserve is private, and 50% of the reserve belongs to three large estate owners, and the rest of the lands are distributed among 82 small local owners (Anon., 2002). The local communities make their living from subsistence agriculture, fishing, and gathering wood and non-wood products (Sabogal & Valerio, 1998). In addition, their main source of income is gathering eggs of sea turtles, *Lepydochelis olivacea* (Anon., 2002).

The third study was carried out in Nandarola dry forest in the village of La Chipopa (11° 42' 30" N and 86°05' 30" W) located 7 km south of the city of Nandaime in the province of Granada, Nicaragua (fig 1). The natural vegetation in the area is classified as dry deciduous formation. The altitude varies from 92 to 167 m a.s.l. Soils of this area are mainly Vertisols and Alfisols, originating from volcanic materials and basic rocks from the Tertiary (Rodríguez, Aguirre & Mendoza, 2003). In the 1960's, most of the Nandarola dry forests were clear cut and used for production of agricultural crops (beans, maize, and rice) and animal grazing. The fields were recently abandoned and are being colonized by young secondary forests. For the present study, three patches abandoned 4, 9 and 14 years ago were located with the assistance of key informants. The area of these patches was 1, 3.7 and 4 ha for 4, 9 and 14 years old patches, respectively (Mario Soza & Carlos Soza, Nandarola; pers. comm.).

The annual rainfall in the study areas ranges from 992 to 1962 mm (Table 1). The rainy season normally starts in May and ends in November. Chacocente has a dry period of 7 months with less than 50 mm precipitation per months and during the rainy season (June-October) rainfall is irregular with many sunny days (Anon., 2002). The mean annual precipitation during the last 13 years has been 1,422 mm. During October 1998, hurricane Mitch passed over the area and the precipitation that month was as high as 775 mm. The mean (1990-2003) monthly maximum temperature was 28.3ºC (April) and the mean monthly minimum 26.2ºC (December-January).

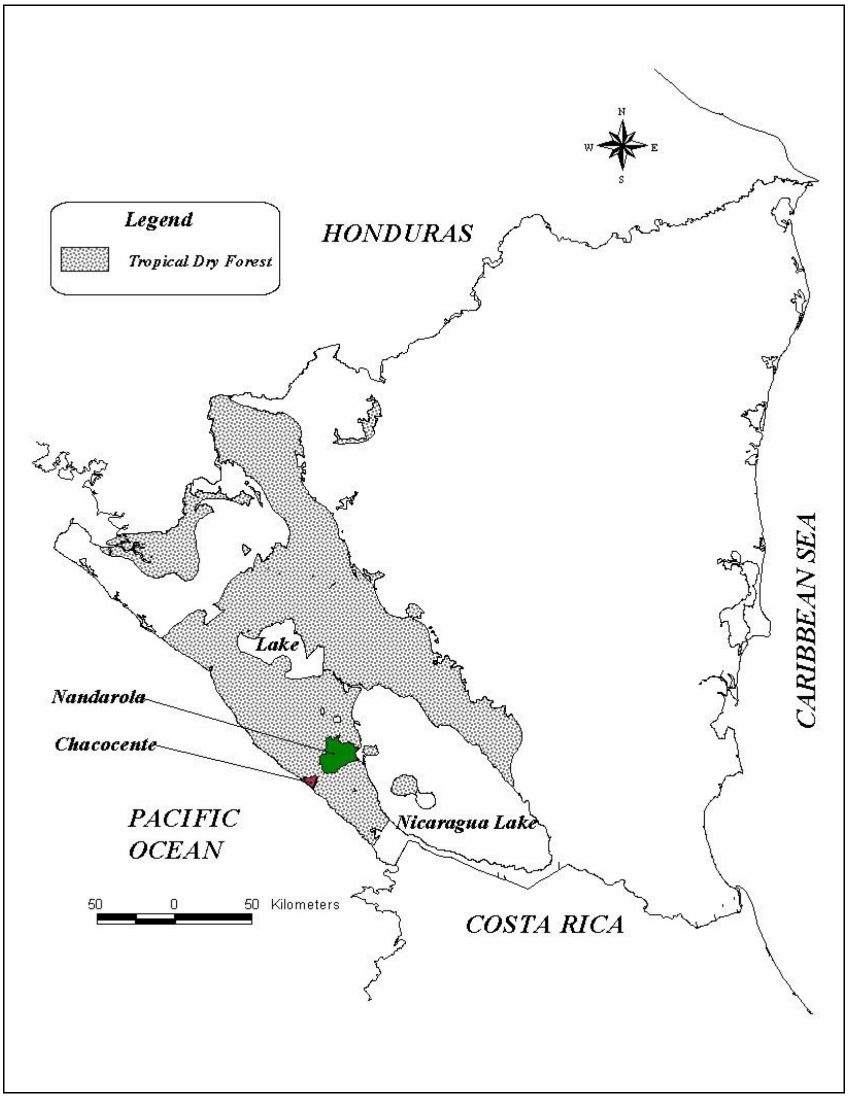

Figure 1. Distribution of tropical dry forests in Nicaragua and location of Chacocente National Wildlife Refuge and Nandarola dry forest.

Table 1. *Annual precipitation, and mean annual temperature from 1990 to 2003 recorded at Nandaime station located 20 km away from Chacocente and 10 km from The Chipopa village. Source: INETER (Instituto Nicaragüense de Estudios Territoriales)*

Year	Precipitation (mm)	Temperature (ºC)
1990	1156	26.5
1991	992	26.7
1992	1095	26.9
1993	1910	26.7
1994	1257	26.8
1995	1962	26.5
1996	1835	26.5
1997	1031	26.9
1998	1796	27.0
1999	1588	26.5
2000	1152	26.4
2001	1242	26.9
2002	1672	27.0
2003	1724	27.1

Methods

Study I

The first study deals with tree species diversity and the local use of dry deciduous and gallery forests in Nicaragua. Two permanent plots in each forest type were established by the Universidad Nacional Agraria, Managua, Nicaragua in 1994 following Alder and Synnot (1992). Each plot was 1 ha and subdivided into 25 subplots of 20 x 20 m. The forest inventories were carried out in 1994 and 2000. Each plot was systematically surveyed by identifying, measuring, and tagging all trees with diameter at breast height (dbh) ≥10 cm. In addition, local names were recorded and information about uses of the tree species was gathered by consulting Nicaraguan forest use specialist (Claudio Calero, personal communication) and the local people. The importance value index (IVI) and family importance value (FIV) were used to describe the species composition of the plots. A variety of diversity indices was calculated in order to permit a more precise comparison of the alpha diversity in each forest community (Magurran, 2004). To compare diversity between forest communities, β-diversity was computed using Jaccard´s coefficient of similarity, and Morisita´s Index of similarity (Krebs, 1999).

Study II

The second study reports the natural regeneration of four dry forest species, *Calycophyllum candidissimum* (Vahl) DC., *Cedrela odorata* L., *Haematoxylon brasiletto* Karst., and *Gyroscarpus americanus* Jacq., for three years in relationship to slope of the terrain and crown exposure to direct sunlight. The study was carried out along four longitudinal transects, 1000 x 5 m (0.5 ha) each. A base line was established with 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 of 20 x 5 m (100 m²). All individuals between 10 cm height and 9.9 cm dbh were recorded for three consecutive years from 2001 to 2003. Recruits were classified according to size as; seedling (10-150 cm height) and saplings (1.5 m height and 4.9 cm dbh) following Teketay (1997) and Saenz & Finegan (2000) with slight modification. For each recruit, the degree of crown exposure to direct sunlight was visually determined as overshadowed, partially exposed and fully exposed (Hawthorne, 1993). The percent slope of each plot was determined, and a slope class was constructed as follows; flat or nearly flat (0-6%), gentle slope (6-25%) and steep slope (>25%) (FAO, 1977; Faniran & Areola, 1978; Bosworth & Foster, 1982).

Study III

The third study deals with soil seed bank assembly following secondary succession on abandoned fields. For this purpose, three sites abandoned 4, 9 and 14 years ago were selected. The three sites had been cultivated since 1965. The area of the study sites was 1, 3.7 and 4 ha for the 4-, 9- and 14-year old, respectively (hereafter referred to as site-4, site-9 and site-14). In early June 2004, a total of 18, 37 and 48 soil samples from site-4, site-9 and site-14, respectively were collected in 15 × 15 cm plots. The number of soil samples taken from each abandoned site was different mainly due to the variation in size of each site and the intent to obtain representative samples. The sample plots at each site were always kept at least 40 m apart. The litter and three successively deeper mineral soil layers, each 3 cm thick, were removed (Teketay & Granström, 1995). Soil samples were sieved using a mesh size of 0.5 mm, and seeds recovered from all sample plots were identified to species level and life forms with the help of a botanist and an agronomist at the National Agrarian University in Managua, Nicaragua, and nomenclature follows Salas (1993). To assess the viability, seeds were germinated at Seed Laboratory of the Swedish University of Agricultural Sciences in Umeå, Sweden. The number of germinants was counted every two days when the radicle reached 2 mm and had a normal appearance. After the germination test was terminated, seeds remaining ungerminated were further assessed for their viability by cutting test. Seeds were considered viable if their content was white and firm while seeds covered with fungi, collapsed when pinched, and having grey, yellow, or brownish contents were considered as dead (Teketay & Granström, 1995; Baskin & Baskin, 1998).

Study IV

The fourth study was comprised of two separate experiments involving seed germination and seedling establishment. In the first experiment, the germination responses of three dry forest species, *Cedrela odorata* L., *Guaiacum sanctum* L. and *Calycophyllum candidissimum* (Vahl) DC., to different constant and alternating temperature regimes and light conditions were examined in the laboratory. The temperature regime had seven levels; five constant temperatures from 15-35°C at an interval of 5°C and two fluctuating temperatures, 20°C/15°C and 25°C/15°C with a thermoperiod of 12 hr. The light condition had two levels; continuous exposure to constant light (20 µE m^{-2} s^{-1}, fluorescent lamp F40 W/33 RS cool white light) for 24 hr and complete darkness. For all studied species, a total of 100 seeds, four replicates of 25 seeds each, were used in each treatment. Seeds were kept moist through out the study period. The germination test was run for 21 days, and the germination process was monitored every day for seeds incubated in continuous light and germinated seeds were counted when the radicle reached 2 mm and had normal appearance. For dark-incubated seeds, the final germination count was made after 21 days. The percentage of germination and mean germination time was calculated for each treatment and replicate. The germination parameters were subjected to analysis of variance.

The second experiment dealt with seedling establishment of *C. odorata* and *G. sanctum* in relation to light conditions. After six months, nursery-grown seedlings of *C. odorata* and *G. sanctum* were in August 2003 transplanted to open site, partially open site and under the canopy of dry deciduous forest in Chacocente National Wildlife Refuge. The density of canopy cover was determined using the spherical densiometer as 0% for open, 50% for partially open and 100% for closed canopy. For each species, a total of 20 seedlings per canopy cover were transplanted at a spacing of 1 × 1 m. Each individual seedling was tagged, and the height and root collar diameter were measured at the time of planting. A second measurement was carried out in August 2004 to evaluated survival and growth of planted seedlings of each species. The relative growth rate (RGR) in root collar diameter was computed for *G. sanctum* only, as survival of *C. odorata* seedlings was too low.

Results and discussion

Tree species diversity and local uses

A total of 29 families, 49 genera and 59 species were found in the dry deciduous forest in the 1994 and 2000 inventory (Table 2). During both inventories, Fabaceae, sub-family Papilionoideae was the most specious family with higher FIV. *Gyroscarpus americanus* was the most abundant species (IVI = 42.4 in 1994 and 29.9 in 2000). The rarest species in both inventories were *Celtis caudata* (IVI = 0.42 in 1994 and 0.40 in 2000) and *Zanthoxylon caribarum* (IVI = 0.37 in 1994 and 0.41 in 2000). In the gallery forest, the number of families, genera and species encountered in the 1994 inventory were 33, 47 and 55, respectively while 48 genera and 58 species were recorded in the 2000 inventory (Table 2). During both inventories, Meliaceae was the most specious family with higher FIV. The most abundant species was *Pithecellobium saman* (IVI = 30.6 in 1994 and 29.2 in 2000) while *Cordia alliodora* was the rarest species (IVI = 0.45). The number of species in the gallery forest slightly increased over the study period. The plausible explanation for the appearance of species in the second inventory could be ascribed to the transition from sapling class in the 1994 inventory to higher class (trees ≥ 10 cm dbh) in the subsequent inventory. As a whole, the number of families, genera and species reported in the present study lies within the range reported earlier in most Neotropical dry forests (Gentry, 1995; Sabogal and Valerio, 1998).

While the stem density decreased in the gallery forest during the study period, the reverse held true for the deciduous forest. There are two possible explanations for this decline; namely, natural phenomenon and anthropogenic disturbance. As the gallery forest has a dense canopy cover, light availability could be one factor hindering advance regeneration. On the other, more people are settled around the gallery forest mainly due to access to the water source, thereby involved in illegal cutting of saplings and poles for firewood and local construction. However, the total basal was much larger for the gallery forest than for the deciduous forest. This could be related to better soil moisture conditions in the latter, as moisture is the major environmental factor limiting tree growth in dry areas. With regard to stem density and basal area, most of our result lies within the range of values reported earlier for other tropical dry forests, but in some cases comparably higher (Rundel & Boonpragob, 1995; Sabogal & Valerio, 1998; Gillespie & Jaffré, 2003; White & Hood, 2004).

Table 2. Summary of floristic composition and structure of trees ≥ 10 cm dbh in dry deciduous and gallery forests inventoried in 1994 and 2000

Forest types-Inventory time	Families	Genera	Species	stem density [a]	Basal area [b]
Deciduous-94	29	49	59	451±25	15.7±1.0
Deciduous-00	29	49	59	489±19	14.5±0.7
Gallery-94	33	47	55	298±17	22.6±1.8
Gallery-00	33	48	58	283±19	24.6±1.8

[a] stem density = No. of individuals ha^{-1}

[b] basal area (m^2 ha^{-1})

The species-abundance patterns of dry deciduous and gallery forests displayed a typical inverse J-distribution or the log series distribution. The majority of the species in both forest communities were represented by few individuals while few species in both forests were represented by many individuals. In the dry deciduous forest, out of the 59 species recorded during both inventories, 37 species were considered as rare, 15 species as intermediate and 7 species as abundant. Of all the species recorded in the gallery forest during both inventories, 43 species was considered as rare, 8 species as intermediate and 4 species as abundant. When comparing the diversity values within each forest community over time, no considerable variation was found (Table 3). Fisher's α diversity measure identified the gallery forest as more diverse than the deciduous forest (based on the 2000 inventory data) while the complement of Simpson's index identified the deciduous forest as more diverse than the gallery forest in both inventories. The complement of Simpson's index attaches more weight to the abundance of the most common species while Fisher's α diversity is based on distribution theory and thus are the most widely recommended measure of diversity (Magurran, 2004). The β-diversity measure also provided further evidence that the two forest communities are less similar (Jaccard's similarity coefficient = 0.27 and Morisita's index = 0.35).

Table 3. Diversity measures for trees ≥ 10 cm dbh in the dry deciduous and gallery forests inventoried in 1994 and 2000 on 2 ha plots.

Diversity Measures	Deciduous 1994	Deciduous 2000	Gallery 1994	Gallery 2000
N[a]	902	979	597	566
S[b]	59	59	55	58
S/N[c]	0.065	0.060	0.092	0.102
D_{Mg}[d]	8.52	8.42	8.45	8.99
J'[e]	1.16	1.15	1.17	1.10
H′[f]	4.71	4.69	4.69	4.48
1/D[g]	17.1	16.9	14.6	14.5
α[h]	14.1	13.8	14.8	16.2

[a] N is the number of individuals enumerated in 2 ha plots

[b] S is the total number of species recorded

[c] S/N refers the rate of species increase per individual enumerated

[d] is Margalef's index of species richness, $D_{Mg} = (S - 1)/\ln N$.

[E] is Shannon's measure of evenness, $J' = H'/\ln S$

[f] is the Shannon-Wiener index, $H' = -\sum pi \log_2 p_i$

[g] is the reciprocal of Simpson's index, $D = \sum(n_i(n_i - 1)/(N_i(N_i - 1))$

[h] is Fisher's index of diversity, $\alpha = N(1 - x)/x$, x is the log series parameter

The local uses of the tree species in both forest communities were identified based on information gathered from the local people, expert consultation and existing literature. It was found that the largest number of species in both forest communities (53% of the total species) was used for firewood, followed by timber extraction (35%), rural construction (27%) and charcoal production (23%). Interestingly, 24% of the species are not currently under any kind of use. The most interesting part of this result is that the abundance of species used for firewood and timber declined from 1994 to 2000 in both forest communities. Although the abundance of the "not used" species in the gallery forest showed an increasing tendency, the reverse held true in the deciduous forest. This indicates an on-going disturbance in the forest reserve and the protection of the forest reserve is loose.

Seedling and sapling population density

Among the four species studied, *G. americanus* had the highest number of individuals in all census years, followed by *C. candidissimum* (Table 4). The density of seedlings and saplings of *H. brasiletto* was much lower while *C. odorata* did not virtually regenerate. The population density *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*. The change in population density of seedlings and saplings was positive for *C. candidissimum*; indicating a continuous and advanced regeneration of this species. Establishment, survival and growth of seedlings is governed by several biotic and abiotic factors (Kitajima & Fenner, 2000). Arrival of viable seeds to the regeneration sites and subsequent germination and establishment of seedlings are vital determinants of the efficacy of natural regeneration (e.g. Felfili, 1997; Howlett & Davidson, 2003). *G. americanus,* a species with abundant regeneration, has also the largest number of mature trees (Table 3), which in turn serve as seed sources. The lack of natural regeneration of *C. odorata* is related to 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 has been subjected to commercial exploitation for many years (Sabogal 1992; Tercero & Urrutia, 1994). Among the abiotic factors, drought is the chief cause of seedling mortality in tropical dry forests (Gerhardt 1996), as well as aseasonal rain forest experiencing an unusual severe drought (Delissio & Primack, 2003). Young seedlings are also succumbed to death due to low-intensity ground fires (Saha & Howe, 2003) and physical damage induced by litterfall (Clark & Clark, 1989 1991; Mack 1998; Scariot 2000; Drake & Pratt, 2001), which in turn varies between species (Gillman, Wright & Ogden, 2003). This is evident in the present study where the density of seedlings declined over time for some of the species (e.g. *G. americanus*).

Table 4. Population density (individuals/2 ha) and rate of population change (%) of seedlings and saplings of four tropical dry forest species in Chacocente, Nicaragua

Species/Size	2001	2002	2003	Rate of change
Gyroscarpus americanus				
Seedling	49	34	29	-26
Sapling	44	59	62	17
Calycophyllum candidissimum				
Seedling	20	16	24	9
Sapling	18	21	20	5
Haematoxylon brasiletto				
Seedling	4	5	3	-14
Sapling	1	1	3	55
Cedrela odorata				
Seedling	1	0	0	nd*
Sapling	0	0	0	nd

* Computation not applicable

The mean population density (averaged over the three census years) of seedlings and saplings of *G. americanus* and *C. candidissimum* differed significantly in relation to crown exposure to sunlight ($\chi^2_{(0.05,\ 2)} = 31.38$ and 48.71 for seedling and sapling populations, respectively and $p < 0.0001$). Seedlings and saplings of *G. americanus* whose crown was partially or fully exposed to direct sunlight were more abundant than overshadowed recruits. On the contrary, the density of seedlings and saplings of *C. candidissimum* was much higher under complete overshadow. The number of seedlings and saplings of *H. brasiletto* found in fully or partially exposed states was relatively higher than completely overshadowed. The shade demand for survival of dry forest species, with marked interspecific variation, is thought to be a mechanism for integrating drought tolerance and light requirement, i.e., allowing seedlings to avoid very high light intensity and very low moisture (Ray & Brown,1995).

The mean population density (averaged over the three census years) of seedlings and saplings of *G. americanus* and *C. candidissimum* also differed significantly in relation to slope of the terrain ($\chi^2_{(0.05,\ 2)} = 21.58$ and 27.56 for seedling and sapling populations, respectively and $p < 0.0001$). Seedlings and saplings of *G.*

americanus were more abundant in the gentle slope than either in the flat or steep slope. For *C. candidissimum*, seedling and sapling densities were much higher in the flat area. Despite low seedling and sapling densities, regeneration of *H. brasiletto* was confined to the gentle slope. Topography, through its effect on drainage, moisture and nutrient variation from ridge top to valley bottom, plays an essential role in spatial distribution of recruits (Enoki, Kawaguhi & Iwatsuba 1997; Enoki & Abe, 2004). As a whole, the spatial analysis revealed that natural regeneration of the studied species is clumped, a very common phenomenon among species in tropical forests (Hubbell, 1979; Condit *et al*., 2000).

Soil seed bank assembly

The total number of species recovered from soil samples varied significantly with age of secondary forests derived from abandoned fields ($\chi^2_{(0.05,\ 2)} = 22.455$; $p < 0.001$). A total of 3, 5 and 9 species were found on sites abandoned 4, 9 and 14 years ago, respectively. Among different life forms, trees were highly represented in the soil seed bank of site-9 (60%) and site-14 (33%) compared to site-4 which was entirely dominated by non-woody flora. The species were distributed among 10 families and the most specious families were Poaceae and Rubiaceae. Generally, two possible pathways for a seed bank assembly process during succession can be distinguished; (1) the seed bank is mainly composed of early successional species that accumulate many persistent seeds in the soil even after the species disappear in the vegetation and (2) the seed bank composition varies as the standing vegetation changes. In the second case, although early successional species disappear from the seed bank as they disappear from the standing vegetation, the seed bank gradually assembles as a result of seed rain from species appearing later during succession and/or from isolated remnant trees, and recent seed dispersal from the nearby vegetation (Beatrijs & Martin, 2004). It is evident from the present study that the number of species, especially the woody flora, in the soil seed bank increased as succession advances. Most likely, the assembly of the soil seed bank observed in the present study followed the second pathway. First, the isolated remnant trees present in site-9 and site-14 and individuals reached tree size (≥ 10 cm dbh) during 14 years of succession might contribute to the build-up of the seed bank through seed rain. Second, both remnant trees and individuals reached tree size possibly attract seed disperser (mainly birds and bats); thereby facilitating recent seed dispersal to the site. Studies have shown that zoochorous dispersal agents do not readily cross or enter open sites due to lack of food resources, perching sites, and visibility to predators (Aide & Cavelier, 1994; Nepstad *et al*., 1996; Wunderle, 1997; Guariguata & Ostertag, 2001).

The total number of seeds recovered from the soil samples and the corresponding seed density significantly varied among abandoned sites in the chronosequence ($\chi^2_{(0.05,\ 2)} = 24.733$, $p < 0.001$ for seed number; and $\chi^2_{(0.05,\ 2)} = 439.841$, $p < 0.001$ for seed density). The total number of seeds was 327, 156 and 146 in site-4, site-9 and site-14, respectively. The corresponding density of viable seed decreased from 141 seeds m^{-2} in site-4 to 76 seeds m^{-2} in site-9 and 22 seeds m^{-2} in site-14. Non-woody species had higher seed density in the 4- year old stands while tree seeds were equally abundant in the soil seed bank of the 9-year old stand (Table 5). The density of buried seeds is a result of the balance between seed input (local seed production and seed dispersal) and seed output, i.e. seed germination, decay and predation (Fenner, 1985). The large quantity of seeds recovered from soil samples collected in site-4 could be related to large quantity of local seed production by herbs and grasses. As secondary succession advances on these abandoned sites, herbs and grasses would be replaced by pioneer, light-demanding species (Finegan, 1996) and hence the seed input started to decline. For example, the density of *Bouteloua alamosana* declined from 106 seeds m^{-2} in site-4 to 2 seeds m^{-2} in site-14. Seed predation is another important determinant of seed bank size. Several studies have shown that predation rates are higher in forest than in open grasslands (Aide & Cavelier, 1994; Kollmann & Pirl, 1995; Hau, 1997), but others still found the opposite trend (Nepstad *et al.*, 1996) or detected no major differences (Holl & Lulow, 1997); suggesting that the effect of predation is site-specific. The soil seed bank could also be depleted by germination due to brief favourable conditions (e.g., temperature, light, moisture condition of the soil) created by secondary forests established on abandoned sites. This, in turn, depends on seed biology of seed bank species, such as recalcitrance, dormancy and longevity of seeds (e.g. Garwood, 1989; Teketay & Granström, 1995, 1997).

Table 5. *Species with seed density ≥ 10 seeds/m^2 in the soil samples collected from three sites abandoned 4, 9 and 14 years ago in Nicaragua*

Abandoned sites	Species	Life form	Seed density
Site-4	*Hybanthus attenuatus*	herb	30
	Bouteloua alamosana	grass	106
Site-9	*Mocuna priurens*	liana	12
	Karwinska calderonii	tree	26
	Guazuma ulmifolia	tree	35

Seed germination and seedling establishment

The germination capacity varied significantly among species, temperature regimes, light conditions, and for the interaction terms ($p < 0.05$). Under continuous exposure to light, seeds of *C. candidissimum* incubated at constant temperatures ranging from 20 to 35°C had the highest germination capacity (fig. 2A). Germination

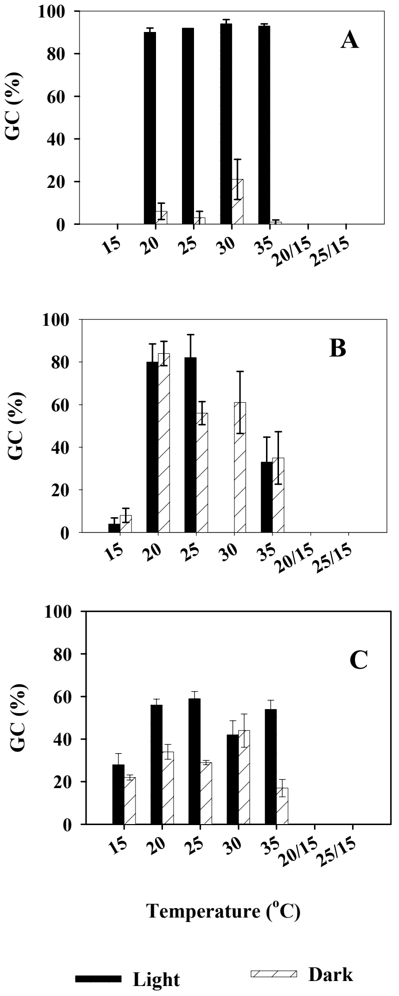

Figure 1. Germination capacity of C. candidissimum (A), G. sanctum (B) and C. odorata (C) seeds in response to different constant and alternating temperature regimes in light or darkness.

was significantly inhibited at 15°C and alternating temperature regimes in light. Germination was also significantly inhibited in darkness at all temperature regimes. *C. candidissimum* is a pioneer species producing a large quantity of small seeds due to highly synchronized flowering with little annual variation (Rivera & Borchert, 2001). Photoblastic germination is a typical characteristic of pioneer species known to have small seeds (Teketay & Granström, 1997; Milberg, Anderson & Thompson, 2000; Yirdaw & Leinonen, 2002; Pearson *et al.,* 2002, 2003; Jensen & Gutekunst, 2003). The ecological significance of photoblastic germination is interpreted as a mechanism for detecting gap formation and/or disturbance on the forest floor, as the ratio of red to far red light has been shown to increase appreciably following such disturbances (Vázguez-Yanes *et al*., 1990; Vázguez-Yanes & Orozco-Segovia, 1992; Pons, 2000; Jensen & Gutekunst, 2003).

Seeds of *G. sanctum* germinated equally well in light and darkness, but the germination capacity was strongly dependent on temperature. Under continuous exposure to light, the germination capacity was significantly higher for seeds incubated at 20 and 25°C (fig 2B). Seeds incubated at 30°C in darkness germinated as high as 61% compared to no germination in light. The overall germination capacity of *C. odorata* was significantly lower than for the other two species (fig 2C). Seeds exposed to continuous light had significantly higher germination capacity than dark incubated seeds; especially at 20, 25 and 35°C.

The optimal germination temperature for *C. odorata* and *G. sanctum* is 20-25°C. The germination of *G. sanctum* seeds was also higher when incubated at 20°C in darkness, and that of *C. odorata* was higher at 30°C in darkness. Although germination of *C. odorata* seeds was relatively higher at 15°C in both continuous light and darkness, germination was markedly depressed at the same temperature for the other two species. This could be related to induction of secondary dormancy, as seeds remaining ungerminated were still intact as determined by the cutting test. For all species, alternating temperature regimes did not bring any beneficial effect on germination. Sensitivity to alternating temperature depends on amplitude (the difference between the maximum and minimum temperature), thermoperiod (time in hours each day above the mean temperature) and number of temperature cycles (Ekstam & Forseby, 1999; Ekstam, Johannesson & Milbert, 1999; Probert, 2000). In some species, germination declines with increasing amplitude of alternating temperature (Teketay & Granström, 1997; Teketay, 2002) while others exhibit a linear increase in germination with amplitude (Thompson & Grime, 1983). As the alternating temperature regimes in the natural habitat are far more complex than those tested in this study, the potential positive effect of alternating temperature on germination of these species, particularly the light-requiring species (*C. candidissimum*) in their natural habitats can not be ruled out.

Survival of transplanted seedlings was strongly dependent on the density of canopy cover ($\chi^2_{(0.05,\ 2)} = 20.843$; $p < 0.0001$) and varied between species. Survival of planted seedlings of *G. sanctum* was higher in open and shaded conditions (70-80%) than *C. odorata* that had 20% survival in open site. Poor survival under closed canopy is a direct consequence of low light intensity, particularly for light-demanding pioneer species like *C. odorata*. Shading has also been shown to increase seedling mortality indirectly by exacerbating fungal attack through increased humidity or by providing concealment for seedling predators (Augspurger, 1984; Hanley, Fenner & Edwards, 1996; Sherman, 2002). Gerhardt (1993, 1998) also suggested that the lower survival rate of *C. odorata* seedlings transplanted in the secondary forests in Guanacaste, Costa Rica is attributed to herbivory combined with drought. We also observed browsing damage on *C. odorata* seedlings during the time of assessment. The relative growth rate in diameter of *G. sanctum* seedlings over one growing season varied among sites. Seedlings on open site had higher relative growth rate than those growing in the shade.

Conclusions

The tree species composition, structural characteristics and diversity of dry forests in Chacocente Wildlife refuge lies within the range reported earlier in most Neotropical dry forests. However, it is very important to point out that there are a considerable number of rare species, which may become locally extinct if the current loose protection of the forest reserve is not strengthened. As the forests are still under continued human pressure, an immediate action should be taken to conserve the remaining flora by involving the local people residing around the forest.

The overall population density of recruits is low and the spatial pattern of regeneration is clumped for all species studied, suggesting that natural regeneration alone may not be sufficient to restore the population of the studied species in Chacocente, especially for *C. odorata* and *H. brasiletto* for which the population densities are extremely low. Therefore, an immediate measure should be taken to assist the natural regeneration process, such as direct seeding, enrichment planting and protection of regenerated individuals from anthropogenic disturbances (e.g. grazing, fire, mowing etc). For some of the species, like *C. candidissimum*, the use of nurse trees in open areas would be useful in future restoration works in order to reduce the impact of damagingly high temperature that aggravates vulnerability to drought.

The species composition of soil seed banks assembles gradually during secondary succession, but the seed density is generally low for natural regeneration of trees to relay upon. To expedite the recovery of secondary forests on such abandoned fields, the seed bank needs to be supplemented by direct seeding, enrichment planting of desired species and installing artificial perches to facilitate seed dispersal. This has to be communicated to the private owners through extension service, as there is a growing interest on the development of secondary forests on abandoned sites among private owners.

Among species tested, light is an absolute requirement for the germination of *C. candidissimum* seeds. This species also exhibits a wider thermo-plasticity. Therefore excessive shading of nursery seed beds, deep sowing and covering with leaf litter during direct seeding in the field or nursery should be avoided. Dark germination of *C. odorata* seeds was comparably lower than germination in light, and germination was higher in narrow temperature range (20-25°C). Medium shading of nursery seed beds and the use of mulches for seeds sown directly in the field will benefit seed germination by lowering the temperature in drier areas like Nicaragua. Temperature is a factor more important than light for the germination of *G. sanctum* seeds. Regulating the temperature using covers both in the nursery and out in the field would be beneficial. Transplanted seedlings of *G. sanctum* have good survival and growth on open and partially-open sites under the prevailing conditions. Thus, this species could be used as framework species for restoration of abandoned fields in drier areas as well as for enrichment planting of disturbed dry forests. Survival of *C. odorata* was low in open and partially-open sites and seedlings failed to survive under the canopy of dry deciduous forest in

Nicaragua, most likely due to its sensitivity to drought. Therefore, this species should preferably be planted in wet and humid areas in the country. As a whole, dry forests in the country deserve top research priority, more precise conservation and management plans, adequate protection, and local people participation. It is still time to conserve and develop the remaining forests.

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References

Abebe, T. 2003. The influence of selective logging on residual stand and regeneration in a tropical rain forest in Southwestern Ethiopia. PhD Dissertation, Swedish University of Agricultural Science, Umeå, Sweden.

Aide, T. M. & Cavalier, J. 1994. Barriers to tropical lowland forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2,219-229.

Aide, T.M., Zimmerman, J.K., Rosario, M.. & Marcano, H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 28, 537-548.

Alder, D. & Synnot, T.J. 1992. Permanent Sampled Plot Techniques for Mixed Tropical Forest. Tropical forestry papers No. 25. Oxford Univesity Press.

Anon., 2002. Plan de manejo del refugio de vida silvestre Río Escalante – Chacocente. Ministerio de Recursos Naturales y del Ambiente. Ramboll/Posaf. Managua, Nicaragua. Pp:89.

Anon., 2004. Estado del Ambiente en Nicaragua 2003. II Informe GEO. Gobierno de Nicaragua. Ministerio del Ambiente y los Recursos Naturales.

Augspurger, C.K. 1984. Light requirement of neotropical tree seedlings a comparative study of growth and survival. *Journal of Ecology* 72, 777-795.

Baskin, C.C. & Baskin, J.M. 1998. Seeds: Ecology, Biogeography, and Evolution of dormancy and germination. Academic press, San Diego. 666 pp.

Beatrijs, B. & Martin, H. 2004. Seed bank assembly follows vegetation succession in dune slacks. *Journal of Vegetation Science* 15, 449-456.

Bekele, T. 2000. Plant Population Dynamics of *Dodonea angustifolia* and *Olea europaea ssp. Cuspidate* in Dry Afromontane Forest of Ethiopia. Ph.D. thesis, Uppsala University, Uppsala.

Bellefontaine, R. & Petrucci, Y. 2000. Management of natural forests of dry tropical zones. FAO Conservation Guide 32.

Berry, P. E. 2002. Diversidad y endemismo en los bosques neotropicales de bajura. In: Guariguata, M. & Kattan, G. (Eds.). Ecología y conservación de bosques neotropicales. Cartago: Ediciones LUR, pp 83-96.

Bewley, J.D. & Black, M. 1994. Seeds: Physiology of Development and Germination. 2nd Edn. Plenum press, New York. 445 pp.

Bosworth, D.A. & Foster, A.B. 1982. Approved Practices in Soil Conservation. Danvill, Illinois.

Brown, S. & Lugo, A.E. 1990. Tropical secondary forest. *Journal of Tropical Ecology* 6, 1-32.

Clark, D.B. & Clark D.A. 1989. The role of physical damage in the seedling mortality of a Neotropical rain forest. *Oikos* 55, 225-230.

Clark, D.B. & Clark, D.A. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* 79, 447-457.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, I.A., Lafrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukuma, R.R. &Yamakura, T. 2000. Spatial pattern in the distribution of tropical tree species. *Science* 288, 1414- 1418.

Copeland, L.O. & McDonald, M.B. 2001. Seed Science and Technology. 4 th Edition. Kluver Acdemic Publishers. Boston/Dordrecht/London.

Dalling, J.W. 2002. Fragmentación: patrones y mecanismos de extinción de especies. In: Guariguata, M & Kattan, G. (Eds.). Ecología y conservación de bosques neotropicales. Cartago: Ediciones LUR, pp 561-590.

Delissio, L.J. & Primack, R.B. 2003. The impact of drought on the population dynamics of canopy-tree seedlings in a seasonal Malaysian rain forest. *Journal of Tropical Ecology* 19, 489-500.

Dokrak, M., Utis, K., Hiroshi, T. & Tohru, N. 2004. Effects of drought and fire on seedling survival and growth under contrasting light conditions in a seasonal tropical forest. *Journal of Vegetation Science* 15, 691-700.

Drake, D.R. & Pratt, L.W. 2001. Seedling mortality in Hawaiian rain forest: The role of small-scale physical disturbance. *Biotropica* 33, 319-323.

Ekstam, B. & Forseby, Å. 1999. Germination response of *Phragmites australis* and *Typha latifolia* to diurnal fluctuations in temperature. *Seed Science Research* 9, 157-163.

Ekstam, B., Johannesson, R. & Milbert, P. 1999. The effect of light and number of diurnal temperature fluctuations on germinations of *Phragmites australis*. *Seed Science Research* 9, 165-170.

Enoki, T. & Abe, A. 2004. Saplings distribution in relation to topography and canopy openness in an evergreen broad-leave forest. *Plant Ecology* 173, 283-291.

Enoki, T., Kawaguhi, H. & Iwatsuba, G. 1997. Nutrient-uptake and nutrient use efficiency of *Pinus thunbergii* Parl. Along a topographical gradient of soil nutrient availability. *Ecological Research* 12, 191-199.

FAO, 1997. Guía para la descripción de perfiles de Suelos. Segunda Edición. – Roma, Italia.

FAO, 2001. Global forest resources assessment 2000. Main report. FAO Forestry Paper 140. Roma, Italia.

Faniran, A. & Areola, O. 1978. Essentials of soil study: with special reference to tropical areas. Heinemann, London.

Faurby, O. & Barahona, T. 1998. Silvicultura de Especies Maderables Nativas del Trópico Seco de Nicaragua. Nitlapán. Universidad Centroamericana (UCA).

Felfili, J.M. 1997. Dynamics of the natural regeneration in the Gama gallery forest in Central Brazil. *Forest Ecology and Management* 91, 235-245.

Fenner, M. 1985. Seed Ecology. Chapman and Hall, London, New York. 151 pp.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Tree* 11, 119-124.

Funes, G., Basconcelo, S., Díaz, S. & Cabido, M. 2003. Seed bank dynamics in tall-tussock grasslands along a latitudinal gradient. *Journal of Vegetation Science* 14, 253-258.

Garwood, N. C. 1989. Tropical soil seed banks: A Review. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (Eds.). Ecology of soil seed bank. Academic Press, London, England. P 149-204.

Gentry, A.H. 1995. Diversity and floristic composition of neotropical dry forest. p.146-190. In: S.H Bullock, H.A Mooney and Medina E (Eds.). Seasonally dry tropical forests. Cambridge University Press, Cambridge, England,

Gerhardt, K. 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *Journal of Vegetation Science* 4, 95 – 102.

Gerhardt, K. 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management* 82, 33-48.

Gerhardt, K. 1998. Leaf defoliation of tropical dry forest tree seedlings implications for survival and growth. *Trees* 13, 88-95.

Gerhardt, K. & Hytteborn, H. 1992. Natural dynamics and regeneration methods in tropical dry forest- an introduction. *Journal of Vegetation Science* 3, 361-364.

Gillespie, T.W., Grijalva, A. & Farris, C.N. 2000. Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology* 147, 37-47.

Gillespie, T.W. & Jaffré, T. 2003. Tropical dry forests in New Caledonia. *Biodiversity and Conservation* 12: 1687-1697.

Gillman, L.N., Wright, S.D. & Ogden, J. 2003. Response of forest tree seedlings to simulated litterfall damage. *Plant Ecology* 169, 53-60.

Godoi, S. & Takaki, M. 2004. Effects of light and temperature on seed germination in Cecropia hololeuca Miq. (Cecropiaceae). *Brazilian Archives of Biology and Technology* 47 (2), 185-191

Gordon, J.E., Hawthorne, W.D., Reyes-Garcia, G.S. & Barrance, A.J. 2004. Assessing landscapes: a case study of tree and shrub diversity in the seasonally dry tropical forests of Oaxaca, Mexico and Southern Honduras. Biological Conservation 117, 429-442.

Grime, J.P. 1989. Seed banks in Ecological perspective. In: Leck, M.A., Parker, V.T and R Simpson, R.L. (Eds.). Ecology of soil seed bank. Academic Press, London, England, pp xv – xxii.

Grime, J. P. & Hillier, S. H. 2000. The contribution of seedling regeneration to the structure and dynamics of plants communities, ecosystems and larger units of the landscape. p. 331-360. In: Fenner, M. (Eds.). Seeds: the ecology of regeneration in plant communities, 2nd edition. CABI Publishing, Wallingford, UK.

Guariguata, M. R. & Ostertag, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148, 185-206.

Hanley, M.E., Fenner, M. & Edwards, P.J. 1996. Molluse grazing and seedling survivorship of four common grassland plant species: the role of gap size, species and season. *Acta Oecologica* 17, 331-341.

Harcourt, C.S. & Sayer, J.A. 1996. The Conservation atlas of tropical forest. The Americas. Simon & Schuster. Pp. 206-211.

Hau, H. H. 1997. Tree seed predation on degraded hillsides in Hong Kong. *Forest Ecology and Management* 99: 215-221.

Hawthorne, W.D. 1993. Forest Regeneration after Logging. Finding of a Study in the Bia south Game Production Reserve Ghana. ODA, Forestry series No. 3. London. 41 pp.

Holl, K.D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* 31, 229-242.

Holl, K.D. & Lulow, M.E. 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. *Biotropica* 29, 459-468.

Horn, H.S. 1976. The ecology of secondary succession. *Annual Review of Ecology Systematics 5*, 24-27.

Howlett, B.E. & Davidson, D.W. 2003. Effects of seed availability, site condition, and herbivory on pioneer recruitments after logging in Sabah, Malaysia. *Forest Ecology and Management* 184, 369-383.

Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203, 1299-1309.

Janzen, D.1988. Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanical Garden* 75, 105-116.

Jensen, K. & Gutekunst, K. 2003. Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic and Applied Ecology* 4, 579-587.

Kalacska, M., Sanchez-Azofeita, G .A., Calvo-Alvarado, J. C., Quesada, M., Rivard, B. & Janzen, D. H. 2004. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. *Forest Ecology and Management* 200, 227-247.

Kattan, G. H. 2002. Fragmentación: patrones y mecanismos de extinción de especies. In: Guariguata, M. & Kattan, G. (Eds.). Ecología y conservación de bosques neotropicales. Cartago: Ediciones LUR, pp. 83-96.

Khurana, E. & Singh, J.S. 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. *Environmental Conservation* 28, 39-52.

Kitajima, K. & Fenner, M. 2000. Ecology of seedling regeneration. In: Fenner, M. (Eds.). Seeds: The ecology of regeneration in plant communities. 2nd edition. CABI Publishing, Wallingford, UK, pp. 331-359.

Krebs, C.J. 1999. Ecology Methodology. 2nd ed. Addison-Wesley Educational Publishers. Inc. 581 pp.

Kollmann, J. & Pirl, M. 1995. Spatial pattern of seed rain of fleshy-fruited plants in a scrubland-grassland transition. *Acta Oecologia* 16, 313-329.

Kozlowski, T.T. 2002. Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. *Forest Ecology and Management* 158,195-221.

Lamprecht, H. 1989. Silviculture in the tropics: Tropical forest ecosystems and their tree species. GTZ, Eschborn.

Maass, J. M. 1995. Conversion of tropical dry forest to pasture and agriculture. In: Bullock, S.H., Mooney, H.A. Medina, E. (Eds.). Seasonally dry tropical forests. Cambridge University Press, Cambridge, England, pp. 399-418.

Mack, A.L. 1998. The potential impact of small-scale physical disturbance on seedlings in a Papuan rainforest. *Biotropica* 30, 547-552.

Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell Publishing, Malden, Oxford and Victoria. 479 pp.

Malcolm, P. 1999. Natural Regeneration: Principles and Practice. Land for Wildlife Note $N_{0.}$ 8.

McLaren, K.P. & McDonald, M.A. 2003. The effects of moisture and shade on seed germination and seedling survival in a tropical dry forest in Jamaica. *Forest Ecology and Management* 183, 61-75.

Mengistu, T., Teketay, D., Hulten, H. & Yemshaw, Y. 2005. The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. *Journal of Arid Environment* 60: 259-281.

Milberg, P., Andersson, L. & Thompson, K. 2000. Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* 10, 99-104.

Mooney, H.A., Bullock, S.H. & Medina, E. 1995. Introduction. In: Bullock, S.H., Mooney, H.A. & Medina, E. (Eds.). Seasonally dry tropical forests. Cambridge University Press, Cambridge, England, pp. 1-8.

Murphy, P. G. & Lugo, A.E. 1986. Ecology of tropical dry forest. *Annual. Review of Ecology and Systematics*. 17, 67-88.

Murphy, P.G. & Lugo, A.E. 1995. Dry forest of Central America and the Caribbean. In: Bullock, S.H., Mooney, H.A. & Medina, E. (Eds.). Seasonally dry tropical forests.Cambridge University Press, Cambridge, England, pp. 9-34.

Nagamatsu, D., Kenji, S. & Akiko, S. 2002. Seedling establishment of deciduous trees in various topographic positions. *Journal of Vegetation Science* 13, 35-44.

Nepstad, D. C., Uhl, C., Pereira, C. A. & Cardoso da Silva, J. M. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76, 25-39.

Pearson, T.R.H., Burslem, D.F.R., Mullins, C.E. & Dalling, J.W. 2002. Germination ecology of Neotropical Pioneers: interacting effects of environmental conditions and seed size. *Ecology* 83, 2798-2807.

Pearson, T.R.H., Burslem, D.F.R., Mullins, C.E. & Dalling, J.W. 2003. Functional significance of photoblastic germination in neotropical pioneer trees: a seed´s aye view. *Functional Ecology* 17, 394-402.

Perry, D. A. 1994. Forest Ecosystems. The Johns Hopkins University Press. Baltimore and London. 649 pp.

Pons, T.L. 2000. Seed responses to ligh*t*. In: Fenner, M. (Eds.). Seeds: Ecology of Regeneration plant communities. CAB International, Wallingford, pp. 237-260.

Probert, R.J. 2000. The role of temperature in the regulation of seed dormancy and germination. In: Fenner, M. (Eds.). Seeds: Ecology of regeneration of plant communities. CABI Publishing, Wallingford, pp. 261-292.

Ray, G.J. & Brown, B.J. 1995. Restoring Caribbean dry forests: evaluation of tree propagation techniques. *Restoration Ecology* 3, 86-94.

Rincon, E. & Huante, P. 1993. Growth response of tropical deciduous tree seedlings to contrasting light conditions. *Trees* 7,202-207

Rivera, G. & Borchert, R. 2001. Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium collections. *Tree Physiology* 21, 201-212.

Rodríguez, I., Aguirre, C. & Mendoza, B. 2003. Actualización del estado del recurso suelo y capacidad de uso de la tierra de los municipios de Santa Teresa y Nandaime. Facultad de Recursos Naturales y del Ambiente, Universidad Nacional Agraria. Proyecto Sur-Oeste de Nicaragua IDR-GTZ.

Roldan, H. 2001. Recursos forestales y cambio en el uso de la tierra, Republica de Nicaragua. Santiago, Chile. pp: 73.

Rundel, P.W. & Boonpragob, K. 1995. Dry forest of Central America and the Caribbean. In: Bullock S.H., Mooney H.A. & Medina E. (Eds). Seasonally dry tropical forests. Cambridge University Press, Cambridge, England, pp. 93-119.

Sabogal, C. 1992. Regeneration of tropical dry forest in Central America with examples from Nicaragua. *Journal of vegetation Science* 3, 407-416.

Sabogal, C. & Valerio, L. 1998. Forest Composition, Structure and Regeneration in a dry forest of the Nicaraguan Pacific Coast. In: Dallmeier, F. & Comiskey, J.A. (Eds.). Forest Biodiversity in North Central and South America, and the Caribbean: Research and Monitoring. Man and The Biosphere Series, Vol. 21, 187-212. – UNESCO, New York.

Saha, S. & Howe, H.F. 2003. Species composition and fire in a dry deciduous forest. *Ecology* 84, 3118-3123.

Saenz, G.P. & Finegan, B. 2000. Monitoreo de la regeneración natural con fines de manejo forestal. Unidad de Manejo de Bosques Naturales, CATIE. Boletin **15**, 8.

Salas, J.B. 1993**.** Arboles de Nicaragua. Instituto Nicaragüense de Recursos Naturales y del Ambiente. Servicio Forestal Nacional. Managua, Nicaragua**.**

Saldarriaga, J.G., West, D.C., Tharp, M.L. & Uhl, C. 1988. Long-term chronosequense of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* 76, 938-958.

Scariot, A. 2000. Seedling mortality by litterfall in Amazonian Forest Fragments. *Biotropica* 32, 662-669.

Scholz, C., González, E. & Vilchez, B. 2004. El banco de semillas del suelo en diferentes estados sucesionales en un bosque seco tropical de Costa Rica. Instituto Tecnológico de Costa Rica. Organización para Estudios Tropicales. Costa Rica.18 pp.

Sherman, P.M. 2002., Effects of land crabs on seedling densities and distributions in a mainland neotropical rainforest. *Journal of Tropical Ecology* 18, 67-89.

Skoglund, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science* 3, 357-360.

Simpson, R. L., Leck, M. A. & Parker, T. 1989. Seed banks: General concepts and methodological issues. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (Eds.). Ecology of soil seed bank. Academic Press, London, England, pp. 3-7.

Teketay, D. 1996. Seed Ecology and Regeneration in Dry Afromontane forests of Ethiopia. PhD Thesis. Swedish University of Agricultural Science, Umeå.

Teketay, D. 1997. Seedling populations and regeneration of woody species in dry Afromontane forest of Ethiopia. *Forest Ecology and Management* 98, 149-165.

Teketay, D. 2002. Germination response of *Discopodium penninervium* Hochst. To temperature and light. *Flora* 197, 76-80.

Teketay, D. & Granström, A. 1995. Soil seed bank in dry Afromontane forests of Ethiopia. *Journal of Vegetation Science* 6, 777-786.

Teketay, D. & Granström, A. 1997. Germination ecology of forest species from the highlands of Ethiopia. *Journal of Tropical Ecology* 13, 805-831.

Tercero, M.G. & Urrutia, G.S. 1994. Caracterización florística y estructural del bosque de galería en Chacocente, Carazo, Nicaragua. Trabajo de diploma. Universidad Nacional Agraria. Managua, Nicaragua.

Tigabu, M. & Odén P.C. 2001. Effect of scarification, gibberellic acid and temperature on seed germination of two multipurpose *Albizia* species from Ethiopia. *Seed Science and Technology* 29: 11-20

Thompson, K. & Grime, J. P. 1983. A Comparative study of germination responses to diurnally-fluctuating temperature. *Journal of Applied Ecology* 20, 141-156.

Vásquez-Yanes, C., Orozco-Segovia. A., Rincón, E., Sánchez-Coronado, M.E., Huante, R., Toledo, J.R. & Barradas, U.L. 1990. Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* 71, 1952-1958.

Vásquez-Yanes, C. & Orozco-Segovia, A. 1992. Effects of litter from a tropical rain forest on tree seed germination and establishment under controlled conditions. *Tree Physiology* 11, 391-400.

White D.A. & Hood C.S. 2004. Vegetation patterns and environmental gradients in tropical dry forests of the northern Yucatán Peninsula. *Journal of Vegetation Science* 15, 151-160.

Wunderle Jr, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99, 223-235.

Wijdeven, S. M. J. & Kuzee, M. 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology* 8, 414-424.

Yirdaw, E. & Leinomen K. 2002. Seed germination responses of four Afromontane tree species to red/far-red ratio and temperature. *Forest Ecology and Management* 168, 53-61.

Zida, D., Tigabu M., Sawadogo L. & Odén P.C. 2005. Germination requirements of seeds of four woody species from the Sudanian savanna in Burkina Faso, West Africa. *Seed Science Technology* 33 (in press)

Zimmerman, J. K., Pascarella, J. B. & Aide, T. M. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8, 350-360.