Stand Dynamics and Regeneration of Tropical Dry Forests in Nicaragua

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Abstract

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Tropical dry forests are one of the most degraded and threatened forest ecosystems in Central America. The thesis summarises results from four separate studies in the dry forests of Nicaragua with the aim to gain knowledge that will support future restoration endeavours. In the first study, aspects of stand dynamics in dry deciduous and gallery forests were investigated over a 7-year period. The result shows that stem density and basal area decreased by 13% and 8%, respectively for the dry deciduous forest. The changes in stem density and basal area for the gallery forest were negligibly low. The mortality and recruitment rates for the deciduous forest were 4.5 and 2.5 % year^{-1}, respectively, and the corresponding values were 4.2 and 4.0% year^{-1} for the gallery forest. The causes of mortality could be anthropogenic and natural disturbances. In the second study, the natural regeneration of three dry forest species (*Lonchocarpus minimiflorus*, *Tabebuia ochracea* and *Lysiloma divaricatum*) in relation to slope of the terrain and crown exposure to direct sunlight was investigated over three years. The density of recruits varied significantly among species and over time. *L. minimiflorus* and *T. ochracea* had the highest densities compared with *L. divaricatum*, and the net change in population density was slightly positive for *T. ochracea* only. Regeneration was more abundant in the gentle and steep slopes under partial exposure of the crown to sunlight, thus resulting in aggregated pattern of distribution, especially for *L. minimiflorus* and *T. ochracea*. The third study dealt with recovery of woody vegetation after 4, 9 and 14 years of abandonment of agriculture. The floristic, structural and diversity measures increased with age of abandoned fields. In the fourth study, seed germination responses of four dry forest species: *Bombacopsis quinata*, *L. divaricatum*, *Cordia alliodora* and *Tabebuia rosea*, 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 *B. quinata*, *C. alliodora* and *T. rosea* in the field were investigated. The optimal temperature for germination was between 20 and 25°C for all species. The alternating temperature regimes tested in the present study did not bring beneficial effect on germination compared with the constant temperature regimes, although its effect was modulated by light condition for some of the species. Survival of *C. alliodora* seedlings was higher in open and partially-open sites than in the understory. *B. quinata* had the lowest survival, and survival of *T. rosea* was higher on open site. It can be concluded that restoration of degraded forests in the future should involve local people, natural regeneration alone is not sufficient, management plans for secondary forests derived from abandoned fields should be prepared and further screening of candidate framework species should be carried out.

Keyword: Chacocente Wildlife Reserve; gallery forest, mortality; recruitment; spatial pattern, secondary succession, diversity, structure, survival, temperature, light

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To Carla, Sofía Belén and Adrián Marcelo

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Appendix

Papers I–IV

This thesis is based on the following papers, which will be referred to by the corresponding Roman numerals in the text

I. Guillermo Castro Marín, Robert Nygård, Benigno Gonzales Rivas, Per Christer Odén. 2005. Stand dynamics and basal area change in a tropical dry forest reserve in Nicaragua. Forest Ecology and Management. 208: 63-75.

II. Guillermo Castro-Marín, Mulualem Tigabu, Benigno González, Per Christer Odén. 2005. Natural Regeneration Dynamics of three Dry Deciduous Forest Species in Chacocente Wildlife Reserve, Nicaragua (Manuscript).

III. Guillermo Castro-Marín, Mulualem Tigabu, Benigno González, Per Christer Odén. 2005**.** A chronosequence Analysis of Forest Recovery on Abandoned Agricultural Fields in Nicaragua (Submitted).

IV. Guillermo Castro-Marín, Mulualem Tigabu, Benigno González, Per Christer Odén. 2005. Seed germination and seedling establishment of four dry forest species in Nicaragua (Submitted).

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Introduction

Tropical dry forests in Latin America

Over 40% of earth's tropical and subtropical landmass is dominated by open or closed forest, of which 42% is dry forest (Murphy & Lugo, 1986). Tropical dry forest includes vegetation types such as dry deciduous forest, thickets, open woodlands and savannas (Bellefontaine, Gasto & Petruci, 2000). They occur in frost-free areas where mean annual temperature is above 17^{o}C , a potential evapotranspiration to precipitation ratio greater than one, and 250-2000 mm of precipitation a year with 4-6 month of little or no precipitation (Murphy & Lugo, 1995). Tropical dry deciduous forests are closed stands, with no substantial opening in the crown cover (above 80%), there are 1-2 stories which are relatively poor in species, the trees are approximately 15-20 m in height and they lose their leaves, with few exceptions, during part of the year. The understory comprises sparse and scattered evergreen or deciduous shrubs with few grass tufts (Lamprectht, 1990; Bellefontaine, Gasto & Petruci, 2000). Two important characteristics of the dry deciduous forests are increasing trend of species richness when they are farthest from equator (Gentry, 1988) and have high floristic endemism. Gentry (1995) estimated endemism to be as high as 73% in South America.

In Latin America, tropical dry deciduous forests are situated to the north and south of tropical evergreen rainforests in South America, on the Pacific side of Central America, and on islands in the Caribbean Sea (Baskin & Baskin, 1998). Of the total forested area, dry forests account for 50% and 22% in Central and South America, respectively. Dry forests in Central America are located along the Pacific coast, extending from Guatemala to Panama (Sabogal, 1992; Sabogal & Valerio, 1998). Estimates put the size of dry forests in Central America as 3.4 million ha, representing less than 0.1% of its original superficies (Janzen, 1988; Sabogal & Valerio, 1998; Gillespie, 1999). Nicaragua is the largest country in Central America with a land surface of 13 million ha and population of *ca*. 5.5 million inhabitants (Roldan, 2001). Nicaragua has *ca.* 400,000 ha of natural pine forest and 4 million ha of broad- leaved forests of which 100,000 ha are dry forest located mainly in the Pacific coast, where 60% of the human population is concentrated due to favourable climatic conditions and good infrastructure facilities (Alves-Milho, 1996; Faurby & Barahona, 1998; Roldan, 2001).

Similar to other tropical dry forests, Nicaraguan dry forests have been intensively exploited and have traditionally provided firewood, charcoal and timber for the domestic market and for export, for instance, *Swietenia humilis, Cedrela odorata, Bombacopsis quinata, Dalbergia retusa, Guaicum sanctum* (Sabogal, 1992; Roldan, 2001). The deforestation rate (in all forest types in the country) for the period 1983 – 2000 is estimated as *ca*. 120,000 ha per year (Anon., 2004). The main reasons for this deforestation are the conversion of forests to agricultural lands, illegal cutting and fire (Roldan, 2001; Anon., 2004; Castro-Marín *et al*., 2005). Secondary forests developing on abandoned agricultural fields are the main forest resources in the Pacific region (Sabogal, 1992; Alves-Milho, 1996). For instance, *ca*. 88% of the firewood consumption of the Pacific region is taken from dry secondary stands (Sabogal, 1992). The remaining mature forests are located generally in less accessible areas and often conserved due to the fact that the forest areas have been declared as natural reserves as well as of the owners' particular interest (Sabogal & Valerio, 1998). However, these conservation areas often contain extensively degraded forests, which require immediate restoration attention. There are few studies available about the country's dry forest resources and little information on species ecology, biology and silviculture (Sabogal & Valerio, 1998; Gillespie, Grijalva & Farris, 2000).

Dynamics of tropical dry forest

The description of any forest includes attributes such as floristic composition and structure. An understanding of the structure and floristic composition is important to develop guidelines for sustainable management. Floristic composition is related with species richness, absolute and relative abundances of species and species diversity (Louman, Valerio & Jiménez, 2001). Dry forests are less diverse than wet or moist forest, although they are more diverse than some subtropical moist forest types. On average, Neotropical dry forests have around 50-70 species (individual > 2.5 cm dbh) in 0.1 ha (Gentry, 1995; Gillespie, Grijalva & Farris, 2000). Forest structure includes attributes such as abundance and basal area per diameter classes and individual height among the different layers in the forest. Murphy & Lugo (1995) have reported canopy height between 10-40 m, basal area from 17 to 40 m^2 ha^{-1} in dry deciduous forest. According to Gillespie, Grijalva & Farris (2000), the average basal area and abundance of tropical dry forest in Central America are 22.03 m^2 ha^{-1} and 147 individuals per 0.1 ha (trees and shrubs $\geq$ 2.5 cm dbh).

Generally, studies of forest stand dynamics include measurement of recruitment, mortality and growth rates (Loumam, Mejía & Jiménez, 2001). Recruitment is the number of new individuals that come into to the forest during a period of time, and mortality is the number of individuals that have died in a given period of time. Tree growth is a biological phenomenon of increase in size with time. Increment is the quantitative increase in size in a specified time interval due to growth (Valerio, 1997). Studies on forest stand dynamics are carried out in permanent sample plots of different sizes according to the forest type (Manokaran & Kochummen, 1987; Finegan & Camacho, 1999, Elzinga *et al*., 2001; Louman, Valerio & Jiménez, 2001). Recruitment, mortality and growth rates provide useful insights to analyze factors affecting population dynamics.

Natural regeneration of tropical dry forest

Natural regeneration refers to the natural process by which plants replace or re-establish themselves by means of self-sown seed or vegetative recovery (sprouting from stumps, rhizomes or roots) (Bueso, 1997; Petrie, 1999). The natural regeneration dynamics of the dry forest is an extremely complex process that depend on environmental factors such as distribution of rainfall, topographic, edaphic and light conditions (Gerhardt & Hytteborn, 1992; Bekele, 2000; McLaren & McDonal, 2003) and also factors such as seed viability and dormancy, seed predation and herbivory (Khurana & Singh, 2001). Enoki & Abe (2004) point out that topography affects the soil characteristics and plays a critical role in the variation of stand structure and floristic composition of the forests by causing drainage, moisture, and nutrients to vary from ridge top to valley bottom. Light availability is an important factor that influences the development of individuals and their spatial distribution (Khurana & Singh, 2001; Enoki & Abe, 2004). Studies on natural regeneration dynamics and spatial patterns in dry deciduous forest are relevant for rehabilitation and conservation purposes (Teketay, 1996; Bekele, 2000).

Colonization of abandoned fields

Conversion of tropical dry forests to agriculture and pasture has been occurring for years or century, and entails nearly total destruction of forest structure and composition, and disruption of ecosystem functions (Maass, 1995). Much of these lands are in frontier areas where human poverty is high, and soils are not suitable for sustained arable agriculture. In the past few decades, vast forest areas that had been converted to agricultural fields have been abandoned due to shift in the economic interest, industrialization and urbanization processes (Thomlinson *et al.*, 1996). Evidences indicate that abandoned agricultural fields have been rapidly recolonized by plants through secondary succession, depending on the severity of land use intensity prior to abandonment (Guariguata & Ostertag, 2001). Tropical secondary forests are important sources of timber and non-timber forest products (Finegan, 1992; Chazdon & Coe, 1999), and provide environmental services such as protection of soil erosion and sequestration of atmospheric carbon dioxide (Silver, Ostertag & Lugo, 2000). In addition, they are important templates for forest ecosystem restoration and refuge of biodiversity in fragmented landscapes (Lugo, 1992; Lamb *et al.*, 1997). Thus, the study of colonization and vegetation dynamics after abandonment of agriculture plays an important role in shaping our understanding of secondary succession (Peterson & Haines, 2000) and enables us to design successful restoration strategies (Aide *et al.*, 2000). Nonetheless, most of the studies on Neotropical secondary forest succession have been made in wet or humid tropical forests (Brown & Lugo, 1990; Finegan, 1996; Guariguata *et al.*, 1997; Guariguata & Ostergad, 2001; Peñas-Claros, 2003), and little is known about dry forests.

Seed germination and seedling establishment

Seed germination and early seedling establishment are demographically critical phases in the regeneration of plants from seeds. Germination and early establishment of seedlings in dry areas are mainly dependent upon moisture availability (Gerhardt, 1996a, b; McLaren & McDonald, 2003). However, seeds of the majority of dry tropical species mature during the dry season and are dispersed at the beginning of the rainy season when sufficient moisture is available for germination and seedling growth (Singh & Singh, 1992). Seed germination is the emergence of the radicle through the seed coat and occurs when seed dormancy has been broken and conditions favourable to germination are met (Copeland & McDonald, 2001). Provided that sufficient aeration and moisture are available, light and temperature are two important factors affecting seed germination (Pons, 2000). Light is an important environmental factor that breaks dormancy in seeds of some species. Seeds of species with a strict light requirement will remain ungerminated if covered by litter or soil. Thus, germination in darkness can explain the absence of a persistent soil seed bank (Pons, 1991). Germination, survival and seedling growth responses to light intensity vary among tropical dry forest species (Khurana & Singh, 2001). Ray & Brown (1995) reported that most species in a secondary dry forest germinated well in shaded than un-shaded sites. Light availability is important for seedling establishment during the rainy season in dry forest but high insolation during the dry season will lower survival significantly for some species by causing exacerbated desiccation of seedling (Gerhardt, 1996b). Tree seedling showed increased growth rates with increasing light in a Mexican deciduous dry forest (Rincon & Huante, 1993).

Temperature is the most important environmental variable responsible for the synchronization of germination with conditions suitable for seedling establishment (Probert, 2000). It acts to regulate germination in three ways: a) by determining the capacity and rate of germination, b) by removing primary and/or secondary dormancy, and c) by inducing secondary dormancy (Bewley & Black, 1994). Thus, for any non-dormant seed population germination occurs within well defined temperature limits, and three cardinal temperatures can be recognized over the short period: minimum, optimum and maximum. The response to temperature depends on a number of factors, including the species, variety, growing region, quality of the seed, and duration of time from harvest (Copeland & McDonald, 2001). Evidences indicate that germination responses depend on the interactive effect of light and temperature; however, it is not possible to reduce these to a unified picture (Baskin & Baskin, 1998). Kigel (1995) pointed out that interaction between light and temperature may also determine the timing of germination in light-sensitive seeds. Seeds may be light-requiring at one temperature but unaffected by light at other temperatures. Knowledge of germination and seedling establishment requirements is of pivotal importance for understanding such community processes as plant recruitment, succession and for the management of plant populations (Khurana & Singh, 2001).

Objectives

The thesis is based on four separate studies covering aspects of stand dynamics, natural regeneration of selected dry forest species; recovery of woody vegetation on abandoned agricultural fields and seed germination of important tree species in Nicaragua. The general objective was to gain knowledge that support restoration of degraded dry forests in Nicaragua. The specific objectives were the following:
(1) to asses the dynamics and growth of dry forests over a 7-year period (study-I);
(2) to examine the temporal variation in population density of recruits of three dry forest species and analyzing heterogeneity of natural regeneration (study-II);

(3) to describe the floristic composition, structure, diversity and similarity of secondary forests derived from abandoned agricultural fields in a chronosequence (study-III);
(4) to investigate the germination responses of seeds of four species to different regimes of temperature and light conditions in the laboratory and evaluate survival and growth of transplanted seedlings of three species under different canopy cover (study-IV).

Material and Methods

Study sites

The first, second and part of the fourth studies were conducted in Chacocente Wildlife Reserve (11^{o} 36$^{'}$ N - 11^{o}30$^{'}$N and 86^{0}08$^{'}$ – 86^{0}15$^{'}$W) located on the Pacific Coast, in the department of Carazo (fig 1). The total area of the wildlife reserve is *ca*. 4650 ha of which two third is dry deciduous forest type and one tenth is gallery forest type. The remaining area is scrubs, pasture and agriculture land (Anon., 2002). The altitude varies from sea level to *ca*. 300 m.a.s.l (Sabogal, 1992). Soils in the deciduous dry forest type are classified as Vertic and Ferric Luvisol (FAO system) (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 (FAO system). 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 community "La Chipopa- Rio Medina" (11° 42' 30" N and 86°05' 30" W), which located about 7 km south of the city of Nandaime in the province of Granada (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 (black soils) and Alfisols (brown soils), originated of volcanic materials and basic rocks from the Tertiary (Rodríguez, Aguirre & Mendoza, 2003). In the sixties, most of the forests were clear cut and used for production of agricultural crops (beans, maize, and rice) and animal grazing. Recently, agricultural and grazing areas have been abandoned. For the present study, three abandoned patches were located with the assistance of key informants. The three sites were abandoned 4, 9 and 14 years ago and the sizes are 1, 3.7 and 4 hectares respectively (Mario Soza & Carlos Soza, Nandarola; pers. comm.).

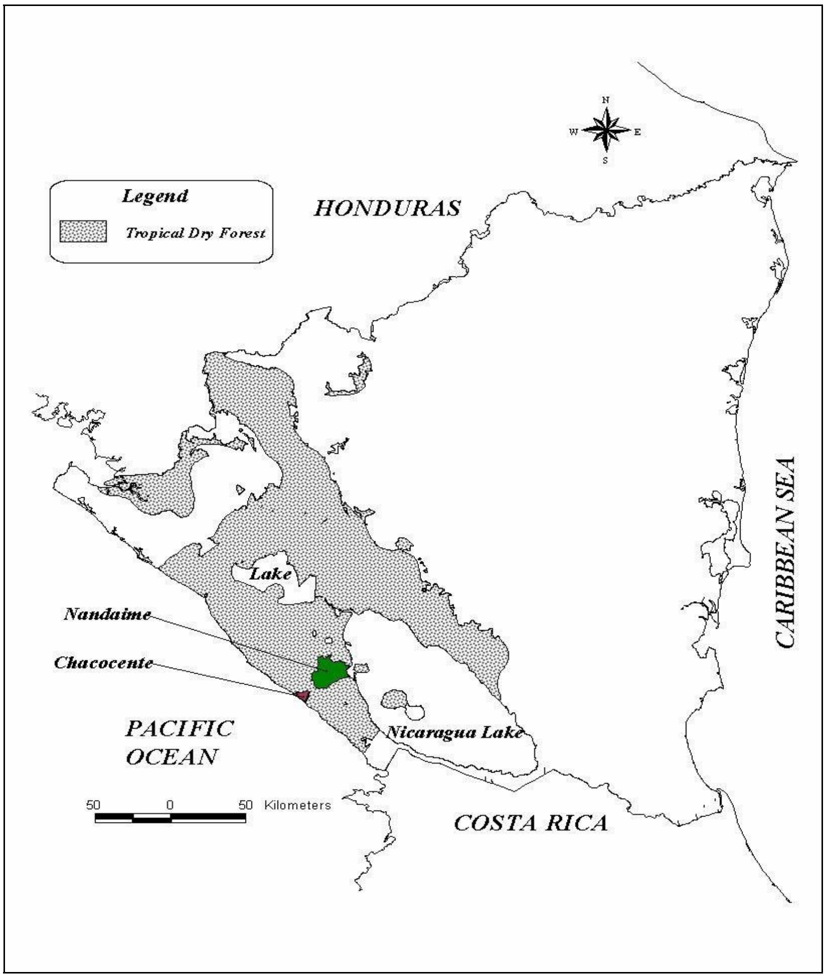

Figure 1. A map showing distribution of the dry forest in Nicaragua and the location of the study areas.

The meteorological station located at Nandaime was used to estimate the climate data of the two experimental sites. This meteorological station is located 10 and 20 km away from the community of La Chipopa- Rio Medina and the Chacocente Wildlife Reserve, respectively. During the period 1984 to 2003, total mean annual rainfall was 1440.52± 370.7 mm and ranged from 1000 to 2300 mm (fig 2). Normally, the rainy season starts in May and ends in November. Mean monthly rainfall exceeded 200 mm in four months of the year during the period from 1984 to 2004 (fig 3). Mean annual temperature was 26.6 ± 0.34°C, and monthly mean temperature fluctuated within a very narrow range of 25.9 to 28.4°C (fig 3).

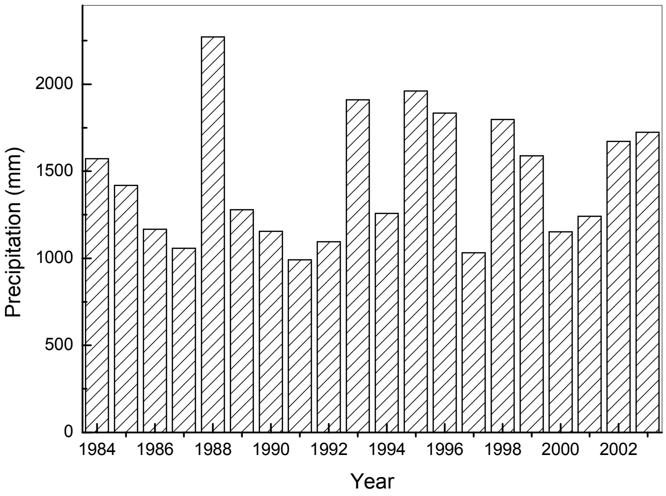

Figure 2. Total annual precipitation for 1984 – 2003 from Nandaime station 20 km to Chacocente Wildlife Reserve and 10 km to the Chipopa-Rio Medina Community (Nandaime).

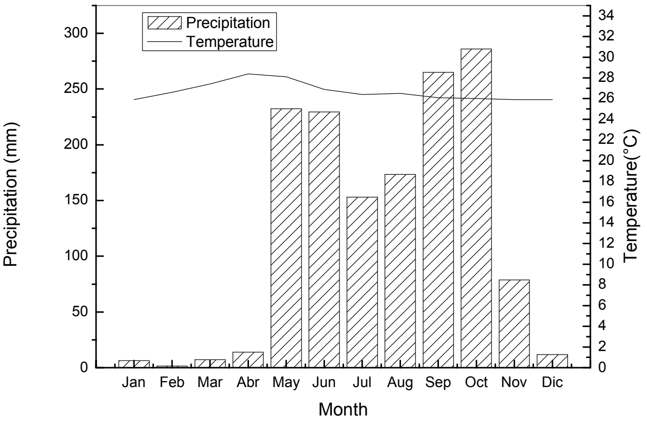

Figure 3. Average total monthly precipitation and monthly temperature from Nandaime station 20 km to Chacocente Wildlife Reserve and 10 km to the Chipopa-Rio Medina Community (Nandaime)

Methods

Study I

In 1993 girths of all trees with at least one stem ≥10 cm dbh were measured, identified by species and tagged on four permanent sample plots, two in the dry deciduous forest and two in the gallery forest. Each plot was 1.0 ha in size and divided into 25 subplots of 20 x 20 m. Girths were measured with a tape and the point of measurement was marked on each tree with paint, as was the code identifying each individual. In year 2000 the girth of all tagged stems was re-measured and all new recruited stems ≥ 10 cm dbh were measured and identified by species.

Stand structure in terms of number of trees per hectare (N ha^{-1}) and basal area (m^2 ha^{-1}) and their distribution in 10 cm diameter classes were quantified for year 1993 and 2000 for the deciduous forest and the gallery forest. The annual rates of mortality (m), recruitment (r), loss (l), gain (g) and ingrowth (i) were estimated using a logarithmic model (Lieberman & Lieberman, 1987; Sheil, Burslem & Alder, 1995; Hoshino, Nishimura & Yamamoto, 2002). A comparison of stem density and basal area during the study period for each of the two forest types was made with a Student's t-test.

All species were classified into four groups according to their main uses based on previous ethno-botanical studies (Morales & Rueda, 1989; Sabogal, 1992; Carrillo, 1993) as
(1) Timber (TW): species used mainly for rural construction, furniture and sawn wood;
(2) Firewood (FW): species used mainly for firewood;
(3) Non-timber forest products (NT): species used mainly for other uses different from timber and firewood (medicine, tannin)
(4) Uses not known locally (UN): species not used by the local population.

Study II

The natural regeneration of three species was investigated in this study: *Lonchocarpus minimiflorus*, *Tabebuia ochracea ssp neochrysantha* and *Lysiloma divaricatum*. The study species were selected based on their economic and ornamental values for the people that live around the forest.

Permanent sample plots were established in 2001 following a systematic design in which 200 plots of 100 m^2 (20 m × 5 m) were located continuously along 4 transects. The length of each transect was 1 km and the distance between two adjacent transects was 800 m. The sample plots covered the variation in environmental gradients, especially topography and incidence of light. All individuals between 10 cm height and 9.9 cm dbh were recorded for three consecutive years from 2001 to 2003. The natural regeneration was classified as seedling (0.1-1.0 m height); sapling (1.0 m height and ≤ 4.9 cm dbh) and pole (5 – 9.9 cm dbh). For each individual, 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 (0-2%); gentle slope (2-13%)

and steep slope (>13%) (FAO, 1977; Faniran & Areola, 1978; Bosworth & Foster, 1982).

The annual rate of population change was estimated using a logarithmic model for each species (Lieberman & Lieberman, 1987; Condit, Hubbell & Foster, 1996). In order to determine the spatial pattern of regeneration of each species, the Standardized Morisita's Index was calculated using the mean density across the census years (Krebs, 1999). Chi-square analysis was performed to examine temporal variation in density of seedlings and saplings. The density of poles was not included in the analysis because it was very low and only one species had individuals in pole size. The chi-square analysis was also employed to examine whether the total density of naturally regenerated individuals vary between the different slope classes and crown exposure to direct sunlight.

Study III

An inventory of secondary forests derived from abandoned fields after 4, 9 and 14 years was carried out. On each site, 70 plots of 100 m^2 (10 m × 10 m) were established following a systematic design. Each plot (10 m × 10 m) was composed of nested quadrats, with smaller quadrats situated within larger ones (Sáenz & Finegan, 2000; Louman, Valerio & Nuñez, 2002). In each 10 × 10 m plot, one 5 × 5 m subplot was established randomly. Within 5 × 5 m plot, one 2 × 2 m subplot was established randomly in one of the corners. In all 10 × 10 m plots, we identified and measured all living woody stems ≥ 10 cm dbh. Within each 5 × 5 m plot all the woody individuals from 1.5 m height to 9.9 cm dbh were recorded. In each 2 × 2 m plots all woody individuals from 0.3 m to 1.5 m height were registered. The woody vegetation was classified according to their size as seedlings (individuals with 0.3-1.5 m height); sapling (1.5 height and ≤4.9 cm dbh); pole (5 – 9.9 cm dbh); trees (10 – 20 cm dbh) and remnant trees (> 20 cm dbh) (Sáenz & Finegan, 2000).

Shannon diversity index and Jaccard's similarity coefficient were calculated in order to estimate the diversity and floristic similarity among the different successional stages (Magurran, 1988). Stand structure in terms of number of trees per hectare (N ha^{-1}) and basal area (m^2 ha^{-1}) and their distribution in 10 cm diameter classes were presented for each successional stage. The species importance value index was calculated for all individuals with dbh ≥1cm (Curtis & McIntosh, 1950).

Study IV

In this study the seed germination responses of four dry forest species, *Bombacopsis quinata*, *Lysiloma divaricatum, Cordia alliodora* and *Tabebuia rosea*, to different constant and alternating temperature regimes under continuous light or darkness in the laboratory, and the effect of canopy cover on survival of *B. quinata*, *C. alliodora* and *T. rosea* seedlings over one year were investigated. *L. divaricatum* was not included in the seedling survival study due to scarcity of seeds during the time of seedling production in the nursery. The study species were selected based on their economic and ornamental values for the people who live around the forest.

Seeds were purchased from a tree seed company in Nicaragua. A 2 × 7 factorial experiment was set-up to investigate the effect of light and temperature on seed germination of the study species. The temperature regime had seven levels; five constant temperature regimes (15, 20, 25, 30 and 35°C) and two alternating temperatures (15-20°C and 15-25°C). Two levels of light condition, exposure to continuous light from fluorescent lamp F40 w/33 RS cool white light (light intensity = 20 $\mu Em^{-2}s^{-1}$) and incubation in the dark, were used for examining the light requirement for germination. For all study species, a total 100 seeds, four replicates of 25 seeds each, was used in each treatment. The germination test was run for 21 day. 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 germination capacity (GC) and mean germination time (MGT) of the seeds were computed for each species and treatments. Germination percentages were arcsine transformed to improve normality and Two-Way ANOVA was used to test significance differences among temperature regimes and light conditions for each species separately. The mean germination time was considered for species and treatments that showed some germination in all the replicates and One-Way ANOVA was used to detect significant difference. Means that showed significant differences were compared using Tukey's test at the 5% level of significance.

Six-month-old seedlings of the study species were transplanted in August 2003 under three different canopy covers, open, partially open and closed canopy, in Chacocente Wildlife Reserve. The 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 (table I, paper IV). A second measurement was carried out in August 2004 to evaluated survival, height and root collar diameter growth. A Chi-square analysis of 3 × 3 contingency table was performed to test the null hypothesis that seedling survival is independent of canopy cover. This was followed by a separate Chi-square goodness-of-fit test to examine whether survival of planted seedlings vary among species as well as canopy cover. The current annual increment (CAI) in root collar diameter was computed for *C. alliodora*, as survival of the other two species was extremely low. One-way ANOVA with unequal number of replication was performed to examine differences in CAI among canopy cover using each individual seedling as replicate. CAI in height was not computed for any of the species, as the majority of individual seedlings were clipped by herbivores, resulting in negative height growth rate.

Results and discussion

Stand dynamics

The dry deciduous forest decreased significantly both in density and basal area over the 7-year period. Stem density was reduced by 13% (from 519 to 450 stems per ha) and basal area by 8% (from 17.00 to 16.62 m^2 ha^{-1}) during the study period. The mortality, recruitment and loss in basal area were 4.5% yr^{-1}, 2.5% yr^{-1} and 4.2 yr^{-1}, respectively. For the gallery forest, the changes in stand density and basal area were not significant during the study period (Paper I). The stand density recorded in year 2000 was 1% less than in 1993 (from 311 to 308 stem per ha). The basal area increased by 2% over the 7-year period (from 22.68 to 23.14 m^2 per ha). The annual mortality, recruitment and loss in basal area were 4.2%, 4.0% and 2.7%, respectively. This high annual mortality rate might be due to anthropogenic influence from villagers surrounding the wildlife reserve in terms of recurrent fires, grazing, collection of firewood and poles as well as harvesting of non-timber products (Gillespie, Grijalva & Farris, 2000; Anon., 2002). The annual mortality rates calculated in this study were considerably higher than those reported in other studies in tropical forest (Lieberman & Lieberman, 1987; Swaine, Lieberman & Hall, 1990). The stem density and basal area estimated in this study were lower than those reported in other studies in Neotropical dry forest (Murphy & Lugo, 1986; Lamprecht, 1990; Gentry, 1995). It is important to point out that in Chacocente selective timber harvesting has been going on since the beginning of the last century until 1983 when the forest was declared as Wildlife Reserve prohibiting legal cutting (Sabogal, 1992). This means that there might be historical reasons for the present low density and basal area.

Both forest types had reversed J-shape diameter distributions and 88% of the stems had less than 30 cm dbh (fig 1, paper I). In the deciduous forest, small stems contributed to more than half of the basal area whereas in the gallery forest large stems (> 70 cm dbh) contributed to almost half the basal area (fig 1, paper I). No clear pattern could be found in mortality linked to diameter classes and the variation was large among the four largest classes due to few stems in these classes (fig 2, paper I). This finding is consistent with the data reported by Lieberman *et al.* (1985) and Finegan & Camacho (1999) who point out that there is no evidence that annual mortality rate is dependent on tree size in most tropical forests.

Among the five most common species in each forest type, only *Tabebuia ochracea* and *Capparis pachaca* had a positive annual balance between recruitment and mortality rate (table 2, paper I). This might be due to the fact that *C. pachaca* is not currently under any use by the local people. For *T. ochracea*, a timber species, 92% of its individuals were found in the smallest diameter class and the people mainly use the wood of this species for constructions with diameter higher than 30 cm. In deciduous forest, three of the five most common species had mortality rates above 9% yr^{-1}, which means more than twice the overall average for the deciduous forest. The estimated median diameter (dbh) increment was 0.14 cm $year^{-1}$ for the deciduous forest and 0.24 cm $year^{-1}$ for the gallery forest. The surviving trees grew 2.2% and 2.4% year^{-1} in basal area in deciduous and gallery forests, respectively over a 7-year period. As a whole, the median diameter increment and basal area growth of surviving stems in gallery forest were higher than in deciduous forest. This may be attributed to better soil and moisture condition (Tercero & Urrutia, 1994; Navarrete & Téllez, 1996) and the history of the disturbance in the forest (Sabogal & Valerio, 1998).

The median of the annual diameter increment recorded in this study was in the same order of magnitude as in other studies of tropical dry forests (Murphy & Lugo, 1986; Swaine, Lieberman & Hall, 1990). Analysis of increments of the most abundance tree species indicated variation among individual species. In deciduous forest, *Caesalpinia exostema* and *Gyrocarpus americanus* had the highest median increments (0.26 cm yr^{-1} and 0.24 cm yr^{-1}) with about twice the average (0.14 cm yr^{-1}) of all species included, and *T. ochracea* and *Lonchocarpus minimiflorus* had the lowest (0.04 cm yr^{-1} and 0.04 cm yr^{-1}). In the gallery forest, *C. pachaca* had the highest (0.28 cm yr^{-1}) whereas *Stemmadenia obovata* and *Trichilia hirta* had the lowest (0.16 cm yr^{-1}) of overall growth rates. The different diameter median increment rates by individual species have important implication for silviculture (Sabogal & Valerio, 1998).

Natural regeneration of selected species

The results show that the density of naturally regenerated individuals varied significantly among species. *Lonchocarpus minimiflorus* and *Tabebuaia ochracea* had the highest mean population densities (averaged over the three census years) compared to *Lysiloma divaricatum* (fig 1, paper II). The low density of naturally regenerated individuals of *L. divaricatum* could be related to seed dispersal limitation and low seed viability. In addition, seeds of *L. minimiflorus and T. ochracea* were not encountered in the soil seed bank assessment (Uasuf, 2004); indicating that seedling bank could possibly be the recruitment strategy of these two species.

The density of naturally regenerated individuals varied significantly across the census period. For, *L. minimiflorus*, the total density and the density of seedlings varied significantly over time while no significant difference was observed in density of saplings across the census period. For *T. ochracea* and *L. divaricatum*, no significant difference was found in total density as well as in the density of each size class over time (fig 1, paper II).

As a whole, over the two-year period, the net annual change in total population density was slightly positive for *T. ochracea* (5%) whereas that of *L. minimiflorus* and *L. divaricatum* were negative (-13 and -14% respectively) (table 1, paper II). Furthermore, the annualized rate of change varied considerably for each size class of the studied species (table 1, paper II). The density of seedlings, saplings and poles of *T. ochracea* increased by 18%, 0.4% and 46%, respectively. The density of *L. minimiflorus* seedlings decreased by 54%, while the density of saplings increased by 2%. For *L. divaricatum*, there was a 69% loss of saplings compared to a slight increase in the density of seedlings (11%). Although the causes of mortality were not investigated in this study, anthropogenic disturbances, such as cattle grazing and mowing are very common in this forest, and possibly contribute to the decline in population density of the study species (Sabogal & Valerio, 1998; Gillespie, Grijalva & Ferris, 200; pers. obs.). Gerhardt (1998) pointed out that young seedlings are vulnerable to several biotic and abiotic factors. Predation, herbivory and pathogens are the major biotic factors that affect seedling survival and seedling population densities (Hubbell, 1979; Terborgh & Wright, 1994; Hanley, Fenner & Edwards, 1995; Thomson *et al.*, 1996; Green, O'Down & Lake, 1997; Sherman, 2002; Packer & Clay, 2003; Hood, Swaine & Mason, 2004). Among the abiotic factors, drought is the main cause of seedling mortality in tropical dry forests as well as aseasonal rain forest experiencing an unusual severe drought (Gerhardt, 1996b; Delissio & Primack, 2003).

The mean population density (averaged over the three census years) of seedlings and saplings of the study species differed significantly in relation to slope of the terrain and crown exposure to sunlight. For all species, the mean total density (seedlings plus saplings) was much lower in the flat than in either the gentle or steep slope (fig 2, paper II). The low regeneration in flat area is probably due to flooding that might create anaerobic condition thereby preventing germination and seedling growth. The annualized rate of population change for *L. minimiflorus* showed a slight increase in the flat (4%), but decreased by 12% and 17% in the gentle and steep slopes, respectively over the census years (table 2, paper II). For *T. ochracea*, there was an increase in population by 17%, 7% and 3% in flat, gentle and steep slopes, respectively. The population of *L. divaricatum* has decreased by 80% and 14% in the gentle and steep slopes over the census years.

Partially exposed individuals of *L. minimiflorus* and *T. ochracea* had the largest density compared with fully exposed and overshadowed individuals (fig 3, paper II). The density of *L. divaricatum* recruits was generally low irrespective of crown exposure to direct sunlight. The fact that partially shaded recruits were relatively abundant compared with fully exposed ones could be one survival strategy to avoid the detrimental effect of damagingly high leaf temperature that can not be ameliorated by cooling through transpiration. Ray & Brown (1995) have shown that medium shade increases survival of Caribbean dry forest species due to its interactive effect with drought tolerance. The annualized rate of population change for *L. minimiflorus* showed a 7% increase for fully exposed recruits, but decreased by 21% and 2% for partially exposed and completely overshadowed, respectively (table 2, paper II). While the population of partially exposed recruits of *T. ochracea* decreased by 1.7%, there was an 11% and 19% increases in population of fully exposed and completely overshadowed recruits, respectively. Although the population of fully exposed recruits of *L. divaricatum* remained unchanged, there was a 9% decrease in the population of partially exposed individuals.

Seedling and sapling populations of *L. minimiflorus* and *T. ochracea* displayed a clumped spatial distribution while both seedling and sapling populations of *L. divaricatum* exhibited a uniform pattern (table 3, paper II). Clumped or aggregated spatial pattern is very common among species in tropical forests (Hubbell, 1979; Condit *et al.*, 2000). Poor dispersal of propagules and recruitment limitations (soil nutrient, light, moisture, etc) may lead to such pattern (Bunyavejchewin *et al.*, 2003; Hardy & Sonké, 2004; Palmiotto *et al.*, 2004). Basnet (1992) and Enoki &

Abe (2004) also pointed out that 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 forest.

Secondary forest succession

Floristic composition

A total of 12, 29 and 22 families and subfamilies represented by 17, 48 and 44 species were registered in 4, 9 and 14 year-old stands, respectively (table 1, paper III). There was a shift in the dominant families and subfamilies through the different successional stages. Fabaceae-papilionoideae was dominant in the 4-year old stand while Fabaceae-caesalpinioideae and Flacourtiaceae were dominant in 9- and 14-year old stands, respectively. The most important species by vegetation size class differed across the different successional stages (tables 3-5, paper III). For the seedling class, *Jacquinia aurantiaca* was the most abundance species in 4-year old stand and *Acacia costaricensis* was in 9- and 14-year-old stands. In the 4-year old stand, *Lonchocarpus acuminatus* was the most important species in the sapling class and *Hippocratea rosea* in the pole class. In the 9-year old stand, *Myrospermum frutescens* was the most important species in the sapling class, *Guazuma ulmifolia* in the pole and tree classes and *Cordia alliodora* in remnant trees class. In the 14-year old stand, the most important species were *Caesaeria corymbosa* in the sapling class, *Muntingia calabura* in the pole class, *Gliricidia sepium* in the tree class, and *Tabebuia rosea* in the remnant tree class. The shift in the dominant species through the different successional stages indicates that species achieve their highest dominance at different time during the succession process. This is in line with the general pattern of floristic and structural recovery following abandonment. During the early stage of colonization, the vegetation is dominated by grasses, forbs and shrubs, which are eventually shaded out by short-lived, light demanding pioneer tree species, such as *H. rosea* and *J. aurantiaca* in the present study. After this period, the canopy is dominated by long-lived, tall-statured, light demanding tree species (*e.g. Diphysa robinioidies* and *Gliricidia sepium* in our study), and finally the canopy of these secondary stands will be replaced by other shade tolerant species (Guariguata & Ostertag, 2001).

Structure

The total stem density increased from 5011 to 9629 individuals per ha as the age of abandonment increased from 4 to 14 years (table 1, paper III). A similar increasing pattern of stem density was observed for seedlings, poles and trees classes (table 2, paper III). In the 4-year old stand, neither tree size individuals nor remnant trees were encountered during the census. Significant difference in stem density was found among stands in a chronosequence for seedling, sapling and pole size classes. Also, the density of tree-size and remnant trees was significantly different between 9- and 14-year old stands. The total basal area of individuals ≥ 1cm dbh also increased with the age of abandonment (table 1, paper III). The consistent increase in density of seedlings with increasing age of abandonment suggests that the advancement of succession created favourable conditions for seed dispersal and seedling establishment and growth, which otherwise are known to be the major barriers for recovery of secondary forests on abandoned fields

(Zimmerman, Pascarella & Aide, 2000; Wijdeven & Kuzee, 2000; Slocum, 2000). The density of saplings significantly declined as the age of abandonment increased. This could be related to canopy closure, which in turn increases the disappearance of light-demanding species due to shading (Finegan, 1996; Whitmore, 1998). It should be noted that the number of individuals occupying the canopy (poles and trees) was higher in the 14-year old stand than the 9-year old stand.

Both 9- and 14-year old stands had a reversed J-shape diameter distribution and more than 55% of the individuals had less than 5cm dbh. In 9-year old stand, small individuals (1 to 5 cm dbh) contributed to more than half of the basal area whereas in 14-year old stand individuals between 5 and 9.9 cm dbh contributed to half the basal area. These results suggest that oldest stands have an uneven-aged structure and natural regeneration is abundant.

Diversity and similarity

The species-abundance patterns of secondary forests derived from abandoned fields displayed an inverse J-distribution or the log series distribution (fig 4, paper III). The majority of the species in all stands in a chronosequence were represented by few individuals while few species were represented by many individuals. This is a characteristic typical of many old-growth forests in the tropics (Huang *et al.*, 2003; Pitman *et al.*, 1999). In general, the species diversity was found to be the greatest in the 9-year-old-stand followed by 14- and 4-year old stands. Several studies have shown that species diversity increases with age of succession (Perkulis, Ramos-Prado & Jiménez-Osornio, 1997; Kennard, 2002; Peña-Claros, 2003; Kalacska *et al.*, 2004). When examining the diversity for each size class, the Shannon-Wiener's diversity index for seedling class was higher in the 9- and 14-year old stands than the 4-year old stand. For saplings and poles, diversity was higher in the 9-year old stand compared with the 14- and 4-year old stands (table 6, paper III). This is because a single species (*L. acuminatus*) represented 46% of the total number of individuals in the 4-year old stand while seven species accounted for 50% of the total number of individuals in the 9- and 14-years old stands.

Pooling all vegetation size together, the Jaccard's similarity coefficient found the greatest similarity (57%) between the 9- and 14-year old stands. The coefficient dropped to 24.5% when comparing the floristic similarity between the 4- and 14-year-old stands and decreased to 22% between 4- and 9- year old stands (table 7, paper III). The low species similarity between 4-year old stand and the other two stands provide further evidence about change in species composition as succession advances.

Seed germination

The species tested in the present study responded differently to temperature regimes and light conditions and their interaction. Seeds of *L. divaricatum* germinated rapidly and to a large extent at all constant temperature regimes (15-35°C) in light or darkness. This species exhibited high degree of thermo-plasticity.

The speed of germination was significantly faster for seeds incubated at 25-30°C, which suggest this range is the optimal temperature for seed germination of this species. This range is similar to the natural habitat of this species (Steven *et al*., 2001; Cordero *et al*., 2004).

The germination capacity of *C. alliodora, B. quinata and T. rosea* seeds declined when they were incubated at 15°C in continuous light as well as in darkness. This could be due to induction of secondary dormancy, as seeds remaining ungerminated were still intact. For *C. alliodora* and *B. quinata* seeds the optimal temperature appeared to be between 20 and 25°C. This range is characteristic for many tropical species (Teketay, 1996, Teketay & Tigabu, 1996; Teketay & Granström, 1997; Tigabu & Odén, 2001; Yirdaw & Leinonen, 2002; Delachiave & De Pinho, 2003; Zida *et al*., 2005). The optimal temperature for *T. rosea* could not be determined due to lack of distinct differences in germination capacity and speed of germination among constant temperature regimes from 20°C to 35°C. This could be attributed to the inherent quality of the seed lot used in the present study. In another study made by Gómez & Rojas (2004), 92% germination was found for *T. rosea* seeds incubated at 30°C in a photoperiod of 12 hr light and 12 hr dark.

The germination capacity declined significantly when the seeds were incubated in alternating temperatures compared to the constant temperature. In this study, germination of *L. divaricatum* and *C. alliodora* seeds decreased with increasing amplitude while *B. quinata* and *T. rosea* seeds did not germinated at all. This suggests that sensitivity to alternating temperature is species-specific, in the one hand, and each species has optimum amplitude for germination, on the other. Teketay (2002) pointed out that higher amplitude may be associated with high evapotranspiration, thereby creating rapid desiccation of the germination substrate.

The species tested in the present study showed differential germination responses to light and dark conditions. *L. divaricatum* and *T. rosea* seeds germinated well both in light and in darkness; suggesting that germination in these species in not light-dependent (neutrally photoblastic). *B. quinata* seeds had higher germination in light than in darkness at constant temperatures. However, *B. quinata* seeds had a considerably higher germination when incubated at 20°C in darkness, suggesting that light is not an absolute requirement for germination of this species, but its effect is temperature-dependent.

Seedling survival and growth

Seedling survival varied significantly among species. *C. alliodora* had the highest survival compared with *T. rosea* and *B. quinata*. Variation in seedling survival among species depends on the size and age of seedlings (Kitajima & Fenner, 2000), and for dry forest species a positive correlation between survival and initial seedling size has been documented (Gerhardt, 1996b). The large size of *C. alliodora* seedlings at the time of transplanting may partly explain their high survival rate compared with the other two species. Seedling survival of the studied species was strongly dependent on the degree of canopy cover. For all species combined, survival was significantly higher for seedlings planted on open site, followed by partially-open site. This finding is consistent with previous studies.

For example, Guariguata (2000) reported a drastic decline in survival of transplanted *C. alliodora* seedlings under the forest canopy after one year, and Piotto *et al*. (2004) reported 73% and 41% survival for *C. alliodora* and *B. quinata*, respectively after three years in pure plantations in Nicaragua. Poor survival under closed canopy is a direct consequence of low light intensity and poor spectral quality (red to far-red ratio). Shading has also been shown to increase seedling mortality indirectly by exacerbating fungal attack through increased humidity or by providing concealment for rodents, molluscs and land crabs that predate on seedlings (Augspurger, 1984; Hanley, Fenner & Edwards, 1995; Sherman, 2002).

Seedlings of *B. quinata* had extremely low survival in open and partially-open sites and did not survive at all under closed canopy while *T. rosea* seedlings did not survive at all in partially-open site and under closed canopy. Consequently, CAI in root collar diameter was reported for *C. alliodora* seedlings only. It was not possible to compute CAI in height due to severe clipping incurred by herbivores. Growth of seedlings was favoured in open than closed canopy, as evidenced from the significantly higher current annual increment in root collar diameter of *C. alliodora* seedlings in the present study. This could be related to reduction in competition for one or more resources in the open or partially-open sites, particularly light and soil moisture (Gerhardt, 1996b; Bullock, 2000). In a study made on other *Cordia* species (*C. africana*), Abebe (2003) has reported a significantly higher collar diameter increment for seedlings grown under full exposure to light than either 50% or 25% of the light intensity in the open area.

Conclusions and Implications

The findings in this thesis have several implications for managing the remaining fragmented dry forests, as well as restoration of dry forests. Depletion of tropical forests and the associated effects on timber production, biodiversity and global environment are well recognized today. Tropical forest area is decreasing at the rate of 13.5 million ha/year, mainly due to clearing for agriculture and shifting cultivation (FAO, 1997; Sandewall *et al*., 2001). The underlying causes for these clearing rates are population increases, inappropriate land utilization and conflicts between forestry and agriculture. It is generally agreed that restoration of degraded forests and abandoned lands is an urgent matter from the view point of compensation or enrichment of ecosystems and sustainable use of degraded areas on regional and global scales (Forestry Agency & ITTO, 1991). Basically there are two approaches to restoration of degraded ecosystems – passive and active. The passive approach entails protection of the degraded forest ecosystem from further disturbance and let nature to take its course while active restoration involves all sorts of facilitation to assist the natural processes; such as direct seeding, enrichment planting, artificial seed dispersal facilities, site manipulations etc (Holl *et al*., 2000).

In the past, establishment of protected areas has been the major approach for protection of tropical forests in many parts of the tropics. Over the past 15 years, raising interest in the protection and conservation of forest has led to proliferation of protected area in Nicaragua, and Chacocente Wildlife Reserve is one of the 76 protected areas in the country (Sabogal, 1992; McCrary *et al.*, 2004). In recent years, several countries, notably in East and South Asia, initiated a major program to restore degraded forest ecosystems, mainly through reforestation. However, restoration success is very minimal in many cases due to failure to negotiate with all concerned stakeholders and to recognize and resolve trade-off between local economic and global environmental benefits (McCrary *et al.*, 2004; Sayer, Chokkalingam & Poulsen, 2004). The result from the present study also provides evidence that establishment of reserves without involving local communities both in management and benefit sharing and strict follow-up fails to curve the continuing deforestation. In Chacocente Wildlife Reserve, the annual mortality rates in deciduous and gallery forests are considerably higher compared with other tropical dry forests. The reason for this high mortality could be attributed mainly to anthropogenic influence, as evidenced from a high mortality rate of economically valuable and useful species.

The problem of passive restoration of degraded forests is further exacerbated by the dynamics of natural regeneration processes. The natural regeneration dynamics of dry forest is an extremely complex process that depends on environmental factors such as distribution of rainfall, topographic, edaphic and light conditions and also factors such as seed viability and dormancy, predation and herbivory (Khurana & Singh, 2001). Equally important is the spatial distribution of the regenerated individuals (Condit *et al.*, 2000), as natural regeneration is often heterogeneous on a landscape due to the effects of biotic and abiotic factors. In one of the studies in this thesis (study-II), the natural regeneration of selected dry forest species; notably *Lysiloma divaricatum* and *Lonchocarpus minimiflorus*, showed a declining trend, which suggest that the process of natural regeneration without intervention is not sufficient to maintain the population of the studied species in Chacocente; and hence accentuates the need for active restoration measures to assist the natural regeneration process, such as enrichment planting, direct seeding, and/or site manipulation to increase the population of threatened species.

Land use conflict, especially between forestry and agriculture, as well as lack of economic incentives (*e.g.* market for wood products) and tenure issues are shown to be the major factors hindering tree planting (Sayer, Chokkalingam & Poulsen, 2004). In this context, abandoned agricultural fields, which gained attention in recent years, provide excellent opportunities to promote forest restoration for environmental and/or production purposes. The finding in this thesis illustrates that the recovery of woody vegetation on abandoned fields is promising in terms of floristics, structure and diversity. At the moment, the management objectives of these stands are not defined, the end use of the secondary forests is not set and no active silvicultural interventions are implemented to put these lands either into production or conservation purposes. Therefore, these issues need to be worked out with the assistance of the concerned governmental and non-governmental organizations actively involved in natural resources management in the country and the private owners. At the same time further research should be carried out to develop restoration techniques including identification of suitable framework species. Investigations made on seed germination behaviour and seedling establishment of selected species in one of the studies in the thesis (study-IV) show that seeds of *Bombacopsis quinata*, *Cordia alliodora*, *Lysiloma divaricatum* and *Tabebuia rosea* germinate rapidly, thus direct seeding of such pioneer species could be made in future restoration of abandoned agricultural fields. Seeds should be sown at a lower depth or should be covered with mulches if sown at the surface to avoid desiccation, as diurnal temperature fluctuates much in open sites than under the forest canopy. Based on the survival and growth study, *C. alliodora* and *T. rosea* could serve as framework species for reforestation of abandoned sites.

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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 Sciences, Umeå, Sweden.

Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., Marcano-Vega, H. 2000. Forest Regeneration in Chronosequence of Tropical Abandoned Pasture: Implications for Restoration Ecology. *Restoration ecology* 8, 328-338.

Alves-Milho, S. 1996. *Dinámica del sector forestal de Nicaragua, 1990-1995*. Universidad Nacional Autónoma / Universidad Nacional Agraria, Nicaragua.

Anon., 2002. *Plan de Manejo Reserva de Vida Silvestre Rio Escalante-Chacocente*. MARENA. Managua, Nicaragua.

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 requirements 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, pp 666.

Basnet, K. 1992. Effect of topography on the pattern of trees in a Tabonuco (*Dacryoides excelsa*) dominated forest of Puerto Rico. *Biotropica* 24, 31-42.

Bekele, T. 2000. Plant Population Dynamics of Dodonea angustifolia and Olea europaea ssp. Cuspidate in Dry Afromontane Forest of Ethiopia. Comprehensive Summaries of Uppsala Dissertations . Faculty of Science and Technology 559.

Bellefontaine, A., Gasto, A. & Petruci, Y. 2000. Management of natural forests of dry tropical zones. FAO, Conservation Guide, 32. Roma.

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

Bosworth, D.A. & Foster, A.B. 1982. *Approved Practices in Soil Conservation*. 5th edition, Danvill, Illinois. The Interstate.

Brown, S. & Lugo, A.E. 1990. Tropical secondary forest. *Journal of tropical ecology* 6, 1 – 32.

Bueso, R. 1997. Establecimiento y manejo de regeneración natural, La Esperanza, Honduras. (EMAPIF).

Bullock, J.M. 2000. Gaps and seedling colonization. In: Fenner M. (Ed.). Seeds: *The Ecology of Regeneration in Plant Communities.* CABI Publishing, Wallingford, pp. 375-395.

Bunyavejchewin S., LaFrankie J.V., Barrer P.J., Kanzaki M., Ashton P.S. & Yamakura T. 2003. Spatial distribution patterns of the dominant Canopy dipterocarp species in seasonal dry evergreen forest in western Thailand. *Forest ecology and management* 175, 87-101.

Carrillo, C. 1993. Uso de los recursos forestales en la zona de Chacocente, Carazo, Nicaragua. Trabajo de diploma Universidad Nacional Agraria, Facultad de Recursos naturales y de Ambiente, Managua.

Castro-Marín G., Nygård R., González B. & Odén, P.C. 2005. Stand dynamics and basal area change in a tropical dry forest reserve in Nicaragua. *Forest ecology and management* 208, 63-75.

Chazdon, R.L., Coe, F.G. 1999. Ethnobotany of woody species in second growth, old-growth, and selectively logged forests of Northeastern Costa Rica. *Conservation biology* 13, 1312-1322.

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

Condit, R., Hubbell, S.P. & Foster, R.B. 1996. Changes in tree species abundance in a Neotropical forest: impact of climatic change. *Journal of tropical ecology* 12, 231-256.

Copeland, L.O. & McDonald, M.B. 2001. *Principles of seed science and technology*. 4th edition. Kluwer Academic Publishers, Boston, pp 467.

Cordero, J., Mesén, F., Montero, M., Stewart, J., Boshier D., Chamberlain, J., Pennington, T., Hands, M., Hughes, C. & Detlefsen, G. 2004. Descripción de especies de árboles natives de América Central. In. Boshier, D. & Cordero, J. (Eds.) *Manual de Arboles de Centroamérica*. Oxford Forestry Institute. Centro Agronómico de Investigación y Enseñanza. Costa Rica, pp. 313-958.

Curtis, J.T. & McIntosh, R.P. 1950. The interrelation of certain analytic and synthetic phytosociological characters. *Ecology* 34, 741-757.

Delachiave, M.E.A. & De Pinho, S.Z. 2003. Scarification, temperature and light in germination of Senna occidentalis seed (Caesalpinaceae). *Seed science and technology* 31, 225-230.

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.

Elzinga, C.L., Salzer, D.W., Willoughby, J.W. & Gibbs, J.P. 2001. *Monitoring Plant and Animal populations*. Blackwell Science. Malden, Massachusetts, pp 360.

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

Faniran, A. & Areola, O. 1978. *Essentials of Soil Study: With special reference to tropical areas*. 1 edition. London. Heinemann.

FAO. 1977. *Guías para la descripción de perfiles de suelo*. Roma, Organización de la Naciones Unidas para la Agricultura y la Alimentación.

FAO. 1997. *State of the World's Forests*. Food and Agricultura Organization of the United Nations. Rome, pp 200

Faurby, O. & Barahona, T. 1998. *Silvicultura de especies maderables nativas del trópico seco de Nicaragua*. Instituto de Investigación y Desarrollo Nitlapán, Universidad Centroamericana, Managua, Nicaragua.

Finegan, B. 1992. The management potential of neotropical secondary lowland rain forest. *Forest ecology and management* 47, 295-321.

Finegan, B. 1996. Pattern and process in neotropical secondary forest: the first 100 years of succession. *Trees structural functional* 11, 119-124

Finegan, B. & Camacho, C. 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988-1996. *Forest ecology and management* 121, 177-189.

Forestry Agency and ITTO (International Tropical Timber Organization). 1991. Beyond the Guidelines- An Action Program for Sustainable Management of Tropical Forest. ITTO Technical Series No. 7. ITTO, Yokohama.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ananals Missoury Botanical Garden* 75, 1-34

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

Gerhardt, K. & Hytteborn, H. 1992. "Natural dynamics and germination methods in tropical dry forest- an introduction." *Journal of vegetation science* 3, 361-364.

Gerhardt, K. 1996a. Germination and development of sown mahogany (Swietenia macrophylla King) in secondary tropical dry forest habitats in Costa Rica. *Journal of Tropical Ecology* 12, 275-289.

Gerhardt, K. 1996b. Effect of root competition and Canopy openness on survival and growth of tree seedlings in a tropical seasonally dry forest. *Forest ecology management* 82, 33-48.

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

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. 1999. Life history characteristics and rarity of wood plants in tropical dry forest fragments of Central America. *Journal of tropical ecology* 15, 637–649.

Green, P.T., O'Down, D. & Lake, S. 1997. Control of seedling recruitment by land crabs in a rain forest on a remote oceanic island. *Ecology* 78, 2474-2486.

Gómez, E.U. & Rojas F.A. 2004. Comportamiento de la germinación, incremento y sobrevivencia de tres especies forestales, con tres tipos de substratos a nivel de vivero y laboratorio en la Universidad Nacional Agraria. Trabajo de diploma. Universidad Nacional Agraria. Facultad de Recursos Naturales y del Ambiente.

Guariguata, M. R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M. & Anderson, L. 1997. Structure and floristic of secondary and old-growth forest stands in lowland Costa Rica. *Plant ecology* 132, 107-120.

Guariguata, M.R. 2000. Seed and seedling ecology of tree species in neotropical secondary forest: Management Implications. *Ecological applications* 10, 145-154.

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

Hanley M.E., Fenner M. & Edwards P.J. 1995. The effect of seedling age on the likelihood of herbivory by the slug Deroceras reticulatum. *Functional ecology* 9, 754-759.

Hawthorne, W. D. 1993. Forest Regeneration after Logging. Findings of a study in the Bia South Game Production Reserve Ghana. ODA, Forestry series No. 3. 41 pp.

Hardy, O.J. & Sonké, B. 2004. Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation. *Forest ecology and management* 197, 191-202.

Hood, L.A., Swaine, M.D. & Mason, P.A. 2004. The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest soil. *Journal of ecology* 92, 816-823.

Hoshino, D., Nishimura, D. & Yamamoto, S. 2002. Dynamics of major conifer and deciduous broad-leaved tree species in an old-growth Chamaecyparis obtusa forest, central Japan. *Forest ecology and management* 159, 133-144.

Holl, K.D., Loik, M.E., Lin, E.H.V., Samuels, I.A. 2000. Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. *Restoration ecology* 8, 339-349.

Huang, W., Pohjonen, V., Johansson, S., Nashanda, M., Katigula, M.I.L. & Luukkanen, O. 2003. Species diversity, forest structure and species composition in Tanzania tropical forests. *Forest ecology and management* 173, 11-34.

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.

Kalacska, M., Sanchez-Azofeifa, 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.

Kennard, D.K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *Journal of tropical ecology* 18, 53-66.

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.

Kigel, J. 1995. Seed germination in arid semiarid regions. In Kigel, J. & Galili, G (Eds). *Seed development and germination*. New York, N.Y, M. Dekkeer, cop. pp. 645-663

Kitajima, K. & Fenner, M. 2000. Ecology of Seedling Regeneration. In: Fenner M. (ed), Seed: *The Ecology of Regeneration of Plant Communities*. CABI Publishing, Wallingford, pp 331-359.

Krebs, C.J. 1999. *Ecology Methodology*. 2nd edition. Addison Wesley Longman, Inc. Menlo Park, California. pp 581.

Lamb, D., Parrota, J., Keenan, R., Tucker, N. 1997. Rejoining habitat remnants: restoring degraded rainforest lands. In: Laurance, W.F., Bierregaard Jr., R.O. (eds), *Tropical Forest Remnants*. University of Chicago Press, Chicago, IL, pp. 366-385

Lamprecht, H. 1990. *Silviculture in the tropic*. GTZ. Eschborn, Germany.

Lieberman, D. & Lieberman, M. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1960-1982). *Journal of tropical ecology* 3, 359-366.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. 1985. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *Journal of ecology* 73, 915,924.

Louman, B., Mejía, A. & Núñez, L. 2002. Inventario en bosques secundarios. In Orozco, L. & Brumér, C. (Eds) *Inventario Forestales para Bosques Latifoliados en América Central*. CATIE, Turrialba, Costa Rica, pp 171 – 216.

Louman, B., Valerio, J. & Jiménez, W. 2001. Bases ecológicas.In Louman, B., Quirós, D. & Nilsson, M. (Eds) *Silvicultura de bosques latifoliados húmedos con énfasis en América Central*. Centro Agronómico de Investigación y Enseñanza, pp 19-78.

Lugo, A.E. 1992. Comparision of tropical tree plantation and with secondary forest of similar age. *Ecological monographs* 62, 1-41

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. UK. pp. 399-422.

Magurran, A.E. 1988. *Ecological Diversity and its Measurements*. University Press. Cambridge. London, pp 179.

Manokaran, N. & Kochummen, K.M. 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *Journal of tropical ecology* 3, 315–330.

McCrary, J.K., Hammett, A.L., Barany, M.E., Machado, H.E., García, D.J. & Barrios, J.I. 2004. Illegal Extraction of Forest products in Laguna de Apoyo Nature Reserve, Nicaragua. *Caribbean journal of science* 40, 169-181.

McLaren, K.P. & MacDonald, 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.

Morales, R. & Rueda de Morales, M. 1989. Etnobotanica de las especies forestales en la comunidades Cantimplora y San jacinto, Departamento de Rivas, IV Región. Trabajo de diploma, Escuela de Ciencias Forestales, Instituto Superior de Ciencias Agropecuarias, Managua.

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. UK, pp. 9-34.

Navarrete, R.M. & Téllez, M.A. 1996. Relación de algunos factores ecológicos en la vegetación arbórea de cuatro parcelas del bosque seco en el Refugio de Vida Silvestre, Escalante- Chacocente. Trabajo de diploma. Escuela de Ciencias Forestales, Instituto Superior de Ciencias Agropecuarias, Managua. Nicaragua.

Packer A. & Clay K. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. *Ecology 84*, 108-119.

Palmiotto P.A., Davies S.J., Vogt K.A., Ashton M.S., Vogt D.J. & Ashton P.S. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *Journal of Ecology* 92, 609-623.

Peña-Claros, M. 2003. Changes in forest structure and species composition during secondary succession in the Bolivian Amazon. *Biotropica* 35, 450-461.

Perkulis, A.M., Ramos-Prado, J.M. & Jiménez-Osornio, J.J. 1997. Composition, structure and management potencial of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan, Mexico. *Forest ecology and management* 94, 79-88.

Peterson, C.J., Haines, B.L. 2000. Early Successional Patterns and Potential Facilitation of Woody Plan Colonization by Rotting Logs in Premontane Costa Rican Pasture. *Restoration ecology*. 8, 361-369.

Petrie, M. 1999. Natural Regeneration: Principles and Practice. Land for Wildlife. Note. No. 8

Piotto, D., Montagnini, F., Kanninen, M., Ugalde, L. & Viquez, E. 2004. Forest plantations in Costa and Nicaragua: Performances of species and preferences of farmers. *Journal of sustainable forestry* 18, 59-67.

Pitman, N.C.A., Terbirgh, J., Silman, M.R. & Nuñez, V.P. 1999. Tree species distribution in a upper Amazonian forest. *Ecology* 80, 2651-2661.

Pons, T.L. 1991. Induction of dark dormancy is seeds: its importance for the seed bank in the soil. *Functional ecology* 5, 669-675.

Pons, T.L. 2000. Seed responses to light. In Fenner, M. (Ed) *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. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CABI Publishing, Wallingford, pp. 261-292.

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

Rincon, E. & Huante, P. 1993. Growth responses of tropical deciduous tree seedlings to contrasting light conditions. Trees Structure and Function 7, 2002-207

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 cambios en el uso de la tierra, republica de Nicaragua. Proyecto información y análisis para el manejo forestal sostenible: integrando esfuerzos nacionales e internacionales en 13 países tropicales en América latina. FAO & EC. Santiago, Chile.

Sáenz, G.P. & Finegan, B. 2000. Monitoreo de la regeneración natural con fines de manejo forestal. Manejo Forestal Tropical No 15. CATIE. Turrialba, Costa Rica.

Sabogal, C. 1992. Regeneration of tropical dry forest in Central America, with example 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. F, Dallmeir, J.A., Comiskey (Eds). *Forest Biodiversity in North Central and South America, and the Caribbean: Research and Monitoring*. Man and the Biosphere Series, Vol.21. UNESCO. New York, USA, pp 187-212.

Sandewall, M., Ohlsson, B. & Sawathvong, S. 2001. Assessment of Historical Land-use Changes for Purposes of Strategis Planning – A Case Study in Laos. *Ambio* 30, 55-61.

Sayer, J., Chokkalingam, U. & Poulsen, J. 2004. The restoration of forest biodiversity and ecological values. *Forest ecology and management* 201, 3-11.

Sheil, D., Burslem, D.F.R.P. & Alder, D. 1995. The interpretations and misinterpretation of mortality rate measures. *Journal ecology* 83, 331-333.

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.

Singh J.S. & Singh V.K. 1992. Phenology of seasonally dry tropical forest. *Current science* 63, 684-689.

Silver, W.L., Ostertag, R., Lugo, A.E., 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration ecology* 8, 394-407.

Slocum, M.G. 2000. Logs and fern patches as recruitment sites in a tropical pasture. *Restoration ecology* 8, 408-413.

Steven, W.D., Ulloa C., Pool, A. & Montiel, O.M. 2001. *Flora de Nicaragua*. 85: II. Missouri Botanical Garden Press.

Swaine, M.D., Lieberman, D. & Hall, J.B. 1990. Structure and dynamics of tropical dry forest in Ghana. *Vegetatio* 88, 31-51.

Teketay, D. 1996. Seed ecology and regeneration in dry Afromontane forests of Ethiopia. PhD Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

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

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

Teketay, D. & Tigabu, M. 1996. The effect of pre-sowing seed treatments, temperature and light on the germination of *Tamarindus indica L.*, a multipurpose tree. *Journal of tropical forestry* 12, 73-79.

Terborgh, J. & Wright, S.J. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 5, 1829-1833.

Tercero, M.G. & Urrutia, G.S. 1994. Caracterización florística y estructural del bosque de galleria en Chacocente, Carazo, Nicaragua. Universidad Nacional Agraria, Facultad de Recursos Naturales y del Ambiente, Escuela de Ciencias Forestales. Managua, Nicaragua.

Thomlinson, J.R., Serran, M.I., del M. López, T., Aide, T.M., Zimmerman, J.K. 1996. Land-use dynamics in a post-agriculture Puerto Rican landscape (1936 – 1988). *Biotropica* 28, 525-536.

Thomson J.D., Weiblen G., Thomson B.A., Alfaro S. & Legendre P. 1996. Untangling multiple factors in spatial distribution: lilies, gophers, and rocks. *Ecology* 77, 1698-1715.

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.

Uasuf A. 2004. Soil seed banks and Regeneration patterns in dry deciduous and gallery forests in Nicaragua – Implications for Restoration. MS.C thesis, Swedish University of Agricultural Sciences, Umeå.

Valerio, J. 1997. Informe de consultoria crecimiento y rendimiento. Documento técnico 51. Proyecto BOLFOR, Santa Cruz, Bolivia.

Withmore, T.C. 1998. A pantropical perspective on the ecology that underpins management of tropical secondary rain forest. In: Guariguata, M.R. & Finegan, B. (Eds). *Ecology and Management of tropical secondary forest: Science, People, and Policy*. Serie técnica, Reuniones Técnicas N^{o} 4. CATIE, Turrialba, Costa Rica, pp 19-34.

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

Yirdaw, E. & Leinonen, 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 and technology* (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.