Tropical Dry Forest Recovery

processes and causes of change

Herstel van Tropisch Droog Bos

processen en oorzaken van verandering

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Para los que me dan vida:

amigos y familia,

y para todos los que se interesan en la ciencia.

For those who give me life:

Friends and family,

And for all those who are interested in science.

CONTENTS

CHAPTER 1

General Introduction

Succession is defined as the directional change in species composition and vegetation structure over time. When this occurs in areas where natural or human disturbances have disrupted forest continuity, and hence opened a space for plant colonization and vegetation regrowth, it is called secondary succession (Corlett 1994, Barbour et al. 1998). Despite these relatively simple definitions, succession is a complex process whose three major causes, availability of space, differential species availability, and differential species performance, are influenced by several factors acting at different spatial, temporal and organizational scales (West et al. 1981, Pickett et al. 1987). For these reasons, the development of ecology has been largely influenced by succession, though not without strong discrepancies and heated debate on the explanation of successional causes and mechanisms, and on finding a unified theory (McIntosh 1981, Finegan 1984, Barbour et al. 1998). This latter problem partially derives from attempts to extract generalizations from a limited number of forest types and circumstances that may strongly influence succession (e.g. land-use history; Ewel 1980, Horn 1981, McIntosh 1981, Finegan 1984).

In the case of tropical forests, from the beginning of the twentieth century (e.g. McLean 1919, Kenoyer 1929) a large number of studies in the moist and wet forest types (hereafter referred to only as wet tropical forests) have advanced our understanding of their secondary succession significantly. Such studies have allowed a comprehensive assessment of development trends in community composition, structure and, to a lesser extent, ecosystem functioning (Brown and Lugo 1990, Finegan 1996, Guariguata and Ostertag 2001), of species traits at different successional stages (Bazzaz and Pickett 1980, Popma et al. 1992, Chazdon et al. 2003, Poorter et al. 2005), and, relatively more recently, of successional dynamics (Swaine and Hall 1983, Breugel et al. 2007, Chazdon et al. 2007). The accumulated body of evidence has allowed developing models of species replacement based on species life cycles and life-history strategies (dispersal, germination, growth rates, shade tolerance and longevity), and on competition (Gómez-Pompa and Vázquez-Yanes 1981, Finegan 1996). The developed principles have been effectively used for sound forest restoration and management practices (Finegan 1992, Parrotta et al. 1997, Meli 2003). Unfortunately, the picture for tropical dry forests (TDF) lags far behind in detail in comparison to that of wet tropical forests, and it is doubtful whether the theory developed from tropical wet forests can be applied to TDF.

Tropical dry forests have lower rainfall levels (400-1800 mm) and, most importantly, higher rainfall seasonality (3-8 months of dry season) and ratio of precipitation to potential evapo-transpiration (PET/P > 1) than wet forests (Murphy and Lugo 1986, Gerhardt and Hytteborn 1992). This lower water availability of TDF results in a clearly distinct species composition, structure, and system functioning. In general, TDF have lower species richness, stature, basal area, leaf area index, fewer canopy strata, and a larger ground cover and root/shoot biomass ratio than wet forests (Murphy and Lugo 1986, Holbrook et al. 1995). Similarly, processes such as reproduction, growth, primary productivity, litter production, organic matter turnover, and nutrient cycling, are largely related to seasonality and exhibit lower values compared to wetter forests (Murphy and Lugo 1986, Bullock 1995, Holbrook et al. 1995, Martínez-Yrízar 1995). Because of these differences between wet and dry tropical forests, they may also be expected to differ in their rates, pathways, patterns, and mechanisms of succession (Gerhardt and Hytteborn 1992, Guariguata and Ostertag 2001).

STUDYING SUCCESSION

The time scales at which secondary forest succession takes place (decades to hundreds of years) poses a problem for its study. Most successional knowledge is derived from chronosequences, in which long-term vegetation changes are inferred from surveying sites with different ages since disturbance (Chazdon et al. 2007). This approach can be useful to define basic patterns and formulate hypothesis of succession as long as the selected sites share a (relatively) similar landscape structure, landform, substrate conditions, and disturbance history and regime (Foster and Tilman 2000). Chronosequences, however, cannot directly inform on rates or on causal processes of succession. Surveys over time (longitudinal studies) are therefore needed for these purposes (Bakker et al., 1996). Furthermore, as chronosequence requirements cannot always be met and assumptions are thus made (e.g. same propagule availability), longitudinal studies are very useful for the validation of chronosequence studies (Bakker et al. 1996, Foster and Tilman 2000). To our knowledge, up to now all the information on secondary succession in TDF comes from chronosequence studies.

PATTERNS AND RATES OF SUCCESSION

Unless cleared areas have been seriously degraded, secondary succession in the humid tropics involves four phases characterized by shifts in dominance from herbs and shrubs, to short-lived pioneers, longed-lived pioneers and, finally, shade tolerant species typical of mature forests. In general, several decades elapse (>10) before this latter stage is reached (Finegan 1996, Richards et al. 1996). At the same time, the forest recovers in diversity and species richness, and in structural features such as height, basal area, foliage cover, and stem density (Brown and Lugo 1990, Guariguata and Ostertag 2001, Sheil 2001).

It has been suggested that secondary succession of TDF is less variable, floristically simpler and that it has fewer seral stages compared to wet forest (Ewel 1980, Murphy and Lugo 1986). These characteristics, in combination with the high occurrence of sprouts and the relative lower floristic and structural complexity of mature dry forests, led Ewel (1980) to hypothesize that TDF have the potential to recover faster, and therefore to be more resilient, than wet forests. This statement was toned down later in a conceptual model of resilience that gave greater weight to the negative effects of environmental harshness on absolute rates of forest recovery (Ewel 1983). Without further support by empirical data, the original hypothesis nonetheless rooted in later secondary succession theory (Murphy and Lugo 1986, Kennard 2002, Vieira and Scariot 2006, Chazdon 2008, but see Lugo et al. 2002).

Large differences in structure and environmental constraints between tropical forests may lead to other differences in patterns of secondary succession. For instance, growth and recruitment are slow in TDF because of the intermittent and variable growing seasons, the loss of biomass gains during the dry season (Ewel 1980, Bullock 1986, Whigham et al. 1990), and the high seedling mortality during the dry season following their emergence (Lieberman and Li 1992, Sampaio 1995, McLaren and McDonald 2003a). This may lead to low rates of density and biomass increase, and consequently affect the rates of competitive displacement, and density and diversity patterns (Huston 1979).

Successional patterns in species diversity are more difficult to predict but could also differ substantially. On the one hand, rapid recovery could be expected due to high frequency of sprouting in TDF and a high frequency of wind dispersed species (Murphy and Lugo 1986, Bullock 1995); on the other, slow recovery would be expected based on low rates of seedling establishment due to drought stress (Gerhardt and Hytteborn 1992, Swaine 1992, Roth 1999).

COMMUNITY DYNAMICS AND SUCCESSIONAL MECHANISMS

The explanation of species replacement and community development during succession has originated from two traditionally opposing views: the holistic one, in which succession is an integrated community-controlled process (e.g. due to modification of the physical environment), and the individual centered approach, in which chance and species life histories are the major determinants of succession. Only recently it has been recognized that the successional mechanisms proposed by these views may function side by side, and even more importantly, that integrating these seemingly opposite views would favor a better understanding of forest succession (McIntosh 1981, Finegan 1984).

The most recent body of theory in tropical wet forest succession has nonetheless mainly used an individualistic approach, in which changes in light availability has been central to explain successional change and propose successional mechanisms and processes (Gómez-Pompa and Vázquez-Yanes 1981, Bazzaz 1991, Whitmore 1998). Temporal and spatial heterogeneity in light, caused by canopy gaps formation and closure, has been identified as a major source of evolution and diversification of successional strategies. Species partitioning of the (successional) light gradient (i.e. species shade-tolerance), have formed the basis for the distinction of different successional functional groups (Denslow 1980, Hartshorn 1980, Swaine and Whitmore 1988, Clark and Clark 1992, Poorter et al. 2005). Successional dynamics of species in the wet tropics is therefore the result from the opening-up of a space for colonization, its occupation by individuals eventually present or capable of reaching it, and the differential establishment, growth rate, maturation, and death, with subsequent new space openings, of groups of individuals which differ in their light requirements and life-span (Finegan 1996, Richards et al. 1996, Whitmore 1998). Competition is an essential mechanism and shade-tolerance an essential cause of succession in this model. Pioneer species profit from an increase in resource availability (i.e. light) and escape through fast growth the asymmetric competition due to high densities of individuals. In this way they reach maturity and reproduce before they are suppressed and replaced by slow-growing, shade-tolerant species that are able to grow and survive in low light levels. Changes in the microenvironment are thought to be the result rather than the cause of successional change. Such environmental changes are therefore thought to be neutral or inhibitory, but not facilitators of species replacement (Kellman 1980, Finegan 1984, Richards et al. 1996, Whitmore 1998).

It has been suggested that gap dynamics and light availability could play a less important role in TDF (Gerhardt and Hytteborn 1992). Rates and extent of canopy-gap disturbance are much reduced in TDF (Dickinson et al. 2001), where more trees die standing compared to wetter forests (Durán et al. 2002). In addition, while light availability in the understory of wet tropical forests are typically only 1-2% of that above the canopy (Richards et al. 1996), it might be expected that light levels in the understory of TDF are much higher because of their shorter stature, lower leaf area index, and less stratified canopy. We found only one study reporting light availability in the TDF understory and the data indicate that levels of understory light in TDF can be even higher (McLaren and McDonald 2003a) than those of small gaps (< 400m^2) in wet forests (Chazdon and Fetcher 1984).

Light seems to play a different role in TDF compared to wet forests. Germination and survival of both “light demanding” and “shade tolerant” species is reported to be lower under exposed conditions compared to shaded conditions, because of the low humidity in the air and soil (Lieberman and Li 1992, Ray and Brown 1995, Gerhardt 1996, McLaren and McDonald 2003a). This suggests that amelioration of the microenvironment can markedly enhance the performance of TDF species, even though they have adaptations to cope with strong seasonal drought, such as large root/shoot ratios, sclerophylly, drought-deciduousness, and deep roots (cf. Borchert 1994, Holbrook et al. 1995, Eamus and Prior 2001).

As for tropical wet forests, secondary succession in TDF is expected to lower radiation and daily maximum temperature near the ground, as well as to increase atmospheric relative humidity and the carbon, moisture, nutrient content and cation exchange capacity of the top soil (Aweto 1981, Gómez-Pompa and Vázquez-Yanes 1981, Brown and Lugo 1990, Richards et al. 1996). Several studies suggest that with increasing dryness, plant-induced changes in the microclimate improve the water relations for individuals growing below their canopy. As a result, facilitation might be a more important driver of succession than competition, as long as the advantages from moisture increase compensate the disadvantages from reduced light and enhanced root interference (Callaway and Walker 1997, Holmgren et al. 1997). To date, no studies have evaluated so far how the environment changes during TDF succession, and how it affects the successional replacement of species.

RESEARCH OBJECTIVES AND QUESTIONS

This work aims at unraveling processes and pathways of tropical dry forest (TDF) secondary succession occurring after traditional shifting-cultivation practices. It focuses on the study of community dynamics, the development of forest structure, and changes in floristic composition, to understand what makes a group of species to be present, dominant, and eventually disappear, at a certain space and time. To answer this, the following questions are addressed:

1) How does TDF change in structure and species composition during secondary succession?

2) How is this development explained by the dynamics (i.e. mortality, recruitment and growth), of functional groups of species with similar life history characteristics?

3) What are the abiotic characteristics of the regeneration environment of TDF? How does this regeneration environment change with the structural development of the community during succession?

4) Is community assembly driven by environmental filtering and, hence, is succession driven by the environmental changes that take place during succession?

THESIS OUTLINE

This work combines the classical chronosequence approach with the direct study of successional changes in time (longitudinal approach). In chapter 2 we present the results of a dendrochronological study as a tool to better determine fallows' ages. The presence of annual rings in pioneer and mature-forest species is demonstrated and used to cross-check fallow ages obtained from interviewing land-owners. We further analyze the use of dendrochronology as a complementary technique to study tropical secondary succession.

Starting from the basics, chronosequence patterns of change in forest diversity, structure, and species composition are presented in chapter 3. We examine changes in composition and structure and estimate forest recovery rates and resilience. Results are used to test the hypothesis of a higher resilience of dry compared to wet tropical forests, and to identify particularities and generalities of TDF secondary succession. Hypotheses about the causes of contrasting findings are formulated.

Successional phases and functional groups are distinguished from the results of chapter 3 and used in the analyses of chapter 4. The results of the dendrochronological study are also used in this chapter for fallow age adjustment. The four-year successional trajectories of individual-fallows are presented and compared with the successional trends that we predict using the chronosequence approach. Recruitment, mortality and growth rates of two contrasting functional groups are related to community structural development. Results are used to infer successional mechanisms which are contrasted to generalized mechanisms and concepts of secondary succession. We also asses how predictable is succession and how reliable are the results obtained with the chronosequence approach.

Chapter 5 presents the change in understory environmental conditions as a function of community development and seasonality. This includes successional changes in light, air temperature, vapor pressure deficit, relative humidity, and soil temperature and water potential. The within-fallow spatial heterogeneity of the environment is additionally characterized using the coefficient of variation. The implications of the results for species performance are discussed.

In chapter 6 we test the hypothesis that community-driven changes in the environment determine community assembly by filtering species according to their functional traits. By means of a path analysis and multivariate analysis we establish the relationship between forest structure, environmental conditions, and the functional trait composition of the fallow’s regeneration strata.

Chapter 7 presents the general discussion and summary. In it, I make a synthesis of secondary succession in TDF by linking the main findings of the dissertation, and evaluate whether the results obtained for TDF succession fit the predictions made by two widely accepted models of tropical succession. Discrepancies are discussed and suggestions to improve the wider validity of these models are made.

STUDY SITE

This study was conducted in the surroundings of Nizanda (16° 39′ 30′′ N, 95° 00′ 40′′ W), a village located on the Pacific slope of the Tehuantepec Isthmus, Oaxaca State, S Mexico (Fig. I). The landscape is dominated by hills composed of Mesozoic phyllites and limestone from the early Cretaceous whose elevations vary around 250 m a.s.l. The soils of the area are predominantly Lithosols but Haplic Phaeozems and Eutric Regosols also occur. Mean annual temperature is ca. 26°C and mean annual precipitation is ca. 900 mm; rainfall is very seasonal, with more than 90% of the total concentrated between late May and mid October. These characteristics correspond to an intermediate position within the typical climatic range of tropical dry forests (Murphy and Lugo 1986). In the Holdridge (1979) classification this corresponds to the transition from tropical very dry forest to tropical dry forest. The predominant vegetation is tropical dry deciduous forest, but the region's complex vegetational mosaic also includes communities as diverse as savanna, xeric scrub, thorn scrub, tropical sub-deciduous forest and tropical semi-evergreen forest (Pérez-García et al. 2001). The mature deciduous forest of this area is characterized by a low canopy stature, ca. 7 m tall, with a few prominent trees of the genera *Bursera* and *Lonchocarpus* attaining 15 m. The relatively good conservation state of the area offers the possibility to asses forest recovery having as reference mature forest stands that have never been cleared, to the knowledge of current inhabitants, and have the structure and composition of intact or 'well conserved' Mexican TDF (Trejo and Dirzo 2002; Gordon et al. 2004; Gallardo-Cruz et al. 2005). Several areas of secondary forests of different ages, derived from abandoned low intensity use (slash and burn) agricultural fields, can be found surrounding the village. Cropping areas in the hills of this region are small, rarely exceeding 0.5 ha. Fields are normally used for one year only, which involves cropping twice (mostly maize) during the rainy season, i.e. at the beginning and at the end.

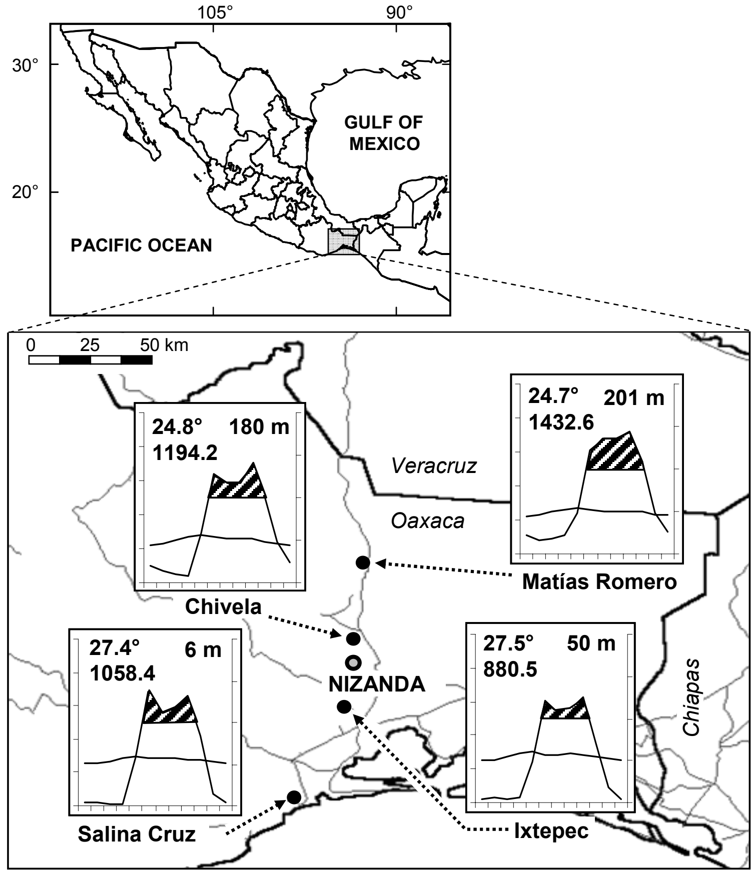

FIGURE I. Location of the study area in the Pacific watershed of the Isthmus of Tehuantepec, S Mexico. Available climatic diagrams of four nearby localities are provided to show precipitation patterns in the region.

CHAPTER 2

The Potential of Tree Rings for the Study of Forest Succession in Southern Mexico

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ABSTRACT

Studies of tropical secondary forest succession face strong limitations due to the slow pace of succession and the time-consuming task of monitoring processes. The occurrence of tree rings in secondary forest trees may help expand our knowledge on succession in these systems and may be useful for fallow dating in chronosequence studies. We examine here the potential of tree rings to study forest succession by sampling 70 species along chronosequences of dry and wet forests in southern Mexico. Based on wood anatomical features, we estimated that about 37 percent of the species presented distinct growth rings useful for ring studies. Overall, maximum number of rings matched well the interview-based fallow ages but, at some sites, trees had consistently higher numbers of rings, probably due to errors in fallow ages derived from interviews. Best fallow age estimations were obtained by examining rings in both pioneer and non-pioneer species. Reconstruction of species' establishment dates revealed that pioneer and non-pioneer species establish early during succession, and that species of both groups continue to recruit after many years. Our study clearly shows that tree ring analysis is a promising tool for studies on secondary forest succession in the tropics.

INTRODUCTION

The extent of tropical secondary forest is increasing rapidly (Wright 2005, Wright and Muller-Landau 2006) and, in many regions, secondary forest is now the main forest type (FAO 2006). Understanding the structure and dynamics of successional forests is of paramount importance, as they are important for global carbon cycles (Archard et al. 2002) and may have a large conservation value (Wright 2005). Tropical forest succession is usually a slow process that may take a century (e.g., Saldarriaga et al. 1988, Worbes et al. 1992, Sheil 2001) or longer (Gemerden et al. 2003). Real-time monitoring from earliest to the latest succession stages is therefore hardly feasible. For this reason, chronosequences are frequently used (e.g., Saldarriaga et al. 1988, Aide et al. 2000, Chazdon et al. 2007) as they make succession studies over long time intervals (e.g., decades) possible, assuming a space-for-time substitution (Pickett 1989). This approach requires data on the abandonment ages of the selected secondary forest stands, which may be difficult to gather. Presently, fallow ages may be inferred from personal accounts of local landowners and/or by use of aerial photographs or remote sensing. Both methods have their limitations as information from local people cannot always be obtained and aerial photographs or remote sensing may only work where such material is available at frequent and short intervals (cf. Aide et al. 2000, Ruiz et al. 2005).

The occurrence of tree rings in secondary forest trees represents an alternative or complementary dating possibility as it may accurately reveal ages of forest stands (Henry and Swan 1974, Glitzenstein et al. 1986, Abrams et al. 1995). Particularly, ages of pioneer species that are expected to establish immediately after abandonment may be good indicators of stand ages. Besides, tree rings can be used to explore successional patterns of species replacement, as the rings contain retrospective information on historical growth rates and give the exact recruitment dates (Henry and Swan 1974). In temperate regions, tree ring analysis has improved our understanding of forest succession without the time-consuming task of long-term monitoring succession (Henry and Swan 1974, Foster et al. 1996). Even the presence of annual rings in a few species may allow us to gain insight on population and community mechanisms leading towards succession. For example, we can examine whether species establish differentially along succession according to their life history attributes (cf. Clements 1916), or alternatively whether species from different functional groups colonize open spaces synchronously (cf. Initial Floristic Composition hypothesis, IFC; Egler, 1954).

To date, relatively few studies in the tropics have used tree rings to determine stand age or study historical growth patterns (Worbes et al. 2003, Baker et al. 2005, Brienen and Zuidema 2006), and none have used tree rings in the context of secondary forests (but see Worbes et al. 1992 for applications in primary succession of flood plains). This is largely due to the widely held assumption among tropical ecologists that most tropical trees do not form annual rings (Lieberman et al. 1985, Chambers et al. 1998, Martínez-Ramos and Alvarez-Buylla 1998, Whitmore 1998). However, this assumption may not be further supported, as the body of evidence on the presence of rings in tropical species is growing rapidly (Worbes 2002 and references therein). Annual formation of tree rings in the tropics has now been demonstrated in all continents (Ogden 1981; Worbes et al. 2003; Schöngart et al. 2004, 2006; Baker et al. 2005; Brienen and Zuidema 2005; Heinrich and Banks 2005), for a wide variety of species, and under a wide range of rainfall regimes, namely from 370 mm (Maingi 2006) to 4000 mm of annual rainfall (Fichtler et al. 2003; for a complete overview see Worbes 2002). The most common trigger behind ring formation in the tropics is the occurrence of a dry season (Worbes 1995). Water limitation during the annual dry season causes reduced cambial growth or cambial dormancy (Borchert, 1999), often combined with leaf-abscission, and results in the formation of a distinct growth layer in the wood (Worbes, 1995).

In this pilot study, we examine the potential of tree rings in studies of tropical secondary forest succession. We analyze discs and increment core samples of 70 tree species obtained from two chronosequences of secondary forests of varying ages (up to 60 yr) in a dry (Lebrija-Trejos et al. 2008) and a wet area (Breugel et al. 2007) in southern Mexico. Specific objectives were to: (1) examine the occurrence of tree rings in dry and wet tropical secondary forests and to identify promising species with annual ring formation; and (2) explore potential applications of tree rings in studies on secondary forest succession. To our knowledge, this is the first study to assess the potential of tree rings for studies of tropical secondary forest succession.

METHODS

STUDY AREA

This study was conducted in two lowland tropical areas in southern Mexico; a wet area near the Guatemala border and a dry area on the Pacific watershed of the Isthmus of Tehuantepec. The wet site is located in the Marqués de Comillas region (Chiapas State), nearby the community Loma Bonita (16º04′ N, 90º45′ W). The region's mean annual temperature is 23°C and total annual rainfall is 2800 mm. Rainfall is not evenly distributed throughout the year and a dry season is distinguished from January to April with < 100 mm monthly. The original vegetation was lowland tropical rain and semi-deciduous forests (Ibarra-Manríquez and Martínez-Ramos 2002) and nowadays is a mosaic of agriculture, pastures, young secondary forests and remnants of old-growth forests. Our research sites are secondary forests derived from abandoned corn fields (Breugel 2007).

The dry site is located in Oaxaca State, in the Isthmus of Tehuantepec, nearby the village of Nizanda (16°39′ N, 95°00′ W). Mean annual temperature is 26°C and total annual rainfall is 930 mm. Rainfall is very seasonal with 6 mo having < 20 mm each, and a short rainy period (May–Oct) accounting for 90 percent of the total annual precipitation. The prevailing natural vegetation is deciduous tropical forest (Pérez-García et al. 2001) and our research sites comprise secondary stands derived from abandoned agricultural corn fields (Lebrija-Trejos et al. 2008).

In the dry area, nearly all (95%) studied species are strictly deciduous and in the wet area 35 percent of the studied species are deciduous (see Table S1; E. Pérez-García, J. Meave and M. Martínez-Ramos, pers. obs.).

SAMPLE COLLECTION AND TREATMENT

Between November 2006 and March 2007 we collected entire stem discs (*N* = 350) or increment cores (*N* = 115) of 70 species, 21 from the dry and 51 from the wet area. Discs were mostly collected from secondary forests that were recently (< 2 mo) cleared for crop cultivation, but in a few cases we felled individual trees. Increment cores were taken with 5- and 12-mm increment borers in one or two directions. Samples were taken as low as possible above ground level (80% < 75 cm), and always < 1.30 m.

In the wet locality (Chiapas), we collected samples from nine different fallows 4–24 yr old. Stand ages were obtained through semi-structured informal interviews with local landowners or relatives (Breugel et al. 2006). For every new species encountered in recently felled stands we collected one disc (objective 1), and for species that seemed promising for ring studies after first inspection, we collected various discs. In these cases, we tried to include the biggest tree of the stand, but also included smaller individuals to capture as far as possible existing size differences (objective 2).

In the dry locality (Oaxaca), we collected discs from a variety of species from recently felled forest stands of known and unknown ages (objective 1). For one common pioneer, *Mimosa acantholoba,* and a few others, we took discs (N = 51) and increment cores (N = 42) along a chronosequence of 14 fallows 4–60 yr old. Ages were obtained by repeated semi-structured interviews (Lebrija-Trejos et al. 2008).

All samples were air or oven dried and grained mechanically with sandpaper of a progressively finer grain (up to grid 600), until wood structure was clearly visible.

GROWTH ZONES AND POTENTIAL FOR RING STUDIES

Wood anatomy and ring structure was studied by naked eye and by using a stereomicroscope (up to 40×). We classified growth boundaries according to Worbes (1995) into four different types: (1) density variations (DV); (2) terminal parenchyma bands (TP); (3) a repeated pattern of alternating fiber and parenchyma bands (AP); and (4) variation in vessel distribution and/or vessel size (VD, VS, VSD). Growth boundaries were often a combination of different types. Having at least one disc for each species allowed us to evaluate carefully the distinctiveness of growth zones over the entire stem surface and to detect irregularities across the stem, such as intra-annual density fluctuations (ID), poorly defined or vague rings (VR) and wedging rings (WR). All relevant features and ring anomalies were recorded, following terminology of the Multilingual Glossary of Dendrochronology (Kaennel and Schweingruber 1995).

For each species, we assessed the potential for ring studies and accurate age determinations. These assessments were carefully based on the following criteria according to whether: (1) growth zones were unambiguously distinguishable and present in all examined samples by naked eye or stereomicroscope; (2) rings were circuit uniform; and (3) ring irregularities did not prevent reliable age determinations using complete discs.

For *Mimosa acantholoba*, we had enough samples to perform crossdatings among several individuals as a means to confirm the annual nature of the growth rings. Crossdating is a procedure that matches variations in ring width patterns among trees (Fritts 1976). Good matching of wide and narrow growth bands between trees and correlations of these patterns to external controlling factors such as rainfall provides strong evidence on the rings' annual nature (Stahle 1999). We measured ring widths to the nearest 0.001 mm using a computer-compatible tree ring measuring system (Velmex Inc. Bloomfield, NY, U.S.A.) and a 40× stereomicroscope. We calculated inter-tree correlation as the mean Pearson correlation coefficient for all pairwise combinations of trees using unstandardized ring widths (i.e., raw data). Mean ring widths were correlated to annual rainfall for the period 1980–2003. Rainfall data were obtained from the Servicio Meteorológico Nacional (SMN) of the Comisión Nacional del Agua (CONAGUA, Mexico) for the nearest weather station of Ciudad Ixtepec, 14 km from the study site. Unfortunately, we could not perform the same analysis for other species due to low sample size and short length of the time series.

RING COUNTS, FALLOW AGE AND SPECIES ESTABLISHMENT PATTERNS

For species with clear growth rings that met our criteria for accurate age determinations (see above), we compared ring counts and fallow ages. Sample sizes of trees and number of stands for which we could make such comparison varied per species. For some common species like *Schizolobium parahyba, Zanthoxylum caribaeum, Zanthoxylum kellermanii,* and *Cordia alliodora* in the wet locality, and *Mimosa acantholoba* in the dry locality, we were able to compare rings and fallow ages for several samples from different stands, whereas for many species we had only one single sample.

When rings were lacking in the tree center (i.e., hollow trees or missed pith in cores), we estimated the pith distance and the average number of rings of other samples of that species to estimate the missing number of rings.

If there were strong reasons to question fallow age estimates of the local landowners, e.g., if multiple tree samples were giving the same amount of rings exceeding that of fallow ages, we re-visited the landowners and double checked the abandonment year (without disclosing the ring-ages to landowners). If these second age estimates matched ring counts, we concluded that the landowners' initial age estimations were probably inaccurate.

For a small set of species from the wet locality, we assessed the extent to which tree rings could reveal historical establishment patterns. To this end, we estimated time between site abandonment and tree establishment in the fallow by subtracting the number of rings from the best estimate of fallow age, i.e. corrected for suspected dating errors (see Table 1). We classified species into pioneers (short-lived, fast growing species only establishing in open spaces) and non-pioneers (including relatively fast-growing, intermediate species and late successional species; Swaine and Whitmore, 1988), using data and observations from long-term studies in the same region (M. Martínez-Ramos, unpubl. data). We tested for differences in median time of establishment after abandonment using the non-parametric Kruskal-Wallis tests and Dunn's tests for group and species' contrasts.

TABLE 1. Number of rings encountered in trees in secondary forest study sites in a wet locality (Chajul, Chiapas) and a dry locality (Nizanda, Oaxaca) in southern Mexico.

Fallow age from interview	Max. no. rings		Best estimate of fallow age (yr)	Observations
	Pioneers	Others		
Wet locality (Chiapas)				
4	–	6	6	Fallow probably 2 yr older
7	8	–	8	Fallow probably 1 yr older
8	9	8	8	
11	10	11	11	
10	7	10	10	
15	10	14	15	
17	19	23	19	Fallow probably 2 yr older; *Lonchocarpus cruentus* and *Pterocarpus rohrii* probably survived last clearing/burning, *L. cruentus* with firemark at 3rd ring (i.e., 19 yr ago)
21	21	–	21	
24	22	19	24	
Dry locality (Oaxaca)				
4	4	–	4	
6	4	–	6	
8	9	7	9	Fallow probably 1 yr older
10	10	–	10	
13	12	–	13	
17	11	–	17	
21	21	–	21	
25	18	–	18	Unreliable fallow age (communal property).
27	12	–	13	Second interview revealed age 13 yr
30	20	25	30	
35	22	32	32	
39	40	39	–	
43	20	–	–	
≈53	-	57	57	Fallow age probably *ca* 57
64	34	30	–	

RESULTS

DISTINCTIVENESS AND STRUCTURE OF GROWTH ZONES

All four types of growth zones (cf. Worbes 1995) were encountered and species often showed a combination of several types (Table S1). Density variations (DV), caused by variation in fiber wall thickness or size (Worbes 1995), were the most commonly observed growth boundary (66% of species). These growth boundaries were best detected by the naked eye and consisted of darker colored wood towards the end of the ring often forming a sharp edge with the lighter wood of each new ring (Fig. 1A,C). About 27 percent of the species showed alternating parenchyma bands (AP; Fig. 1B), which are marked by differences in spacing of parenchyma bands between the beginning and end of a ring. Depending on spacing between growth zones, these structures were also best detected by the naked eye. Terminal parenchyma bands (TP) often concurred with alternating parenchyma bands (Fig. 1B), and were found in 29 percent of the species. Differences in vessel density and/or vessel size (VD/VS) were found in 23 percent of the species, but in only one species were these features alone clear enough to distinguish (annual) growth zones (i.e., *Mimosa acantholoba*; Fig. 1D).

The degree of growth zone's distinctiveness varied from complete absence of growth zones to poorly distinguishable zones in some species (Fig. 1G), and clear rings in others (cf. Fig. 1A–D,H). A considerable portion of species (57%) showed clear to very clear growth zones (Table S1), but several of these species presented irregularities that restrict using its rings for accurate age-estimations. Observed irregularities include intra-annual density fluctuations (ID), varying ring distinctiveness between and/or within samples, and wedging rings (WR) (cf. terminology in Kaennel and Schweingruber 1995). Intra-annual density fluctuations are growth zones that can be distinguished morphologically from true annual rings by their discontinuous character (i.e., circuit non-uniform growth zones; Fig. 1F) or by a less defined, diffuse structure (Fig. 1E). They often occurred in wider growth zones and were the most common problem encountered.

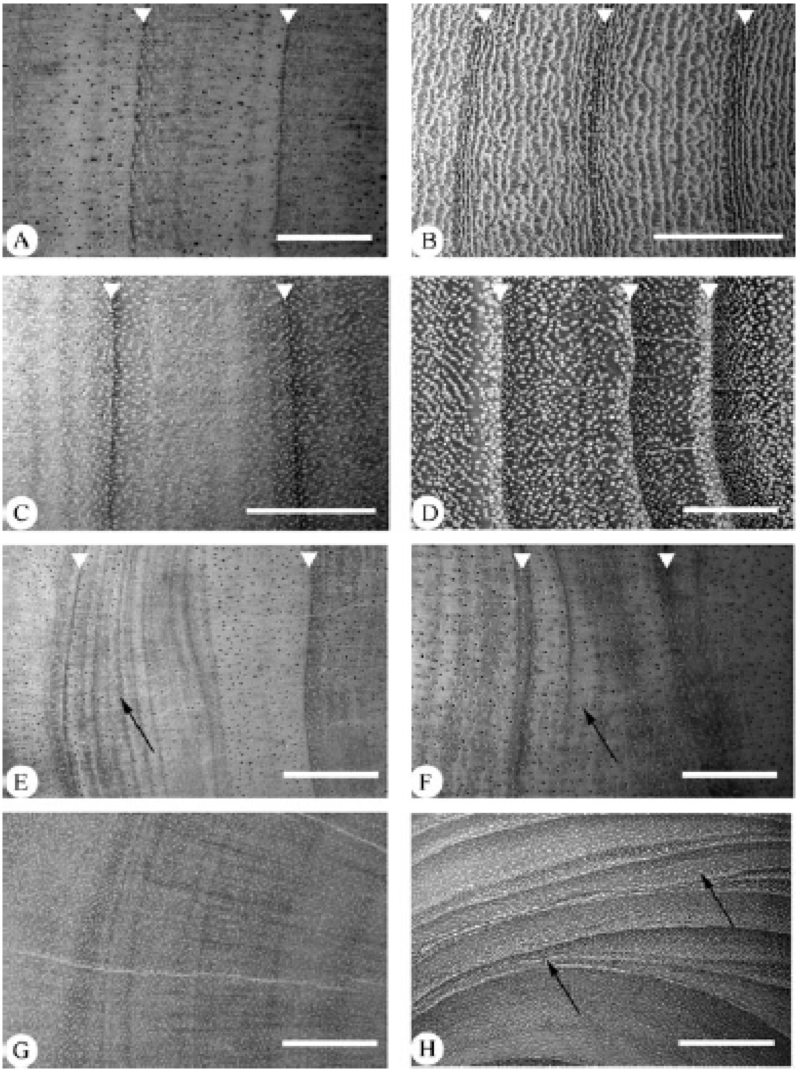

FIGURE 1. General anatomical aspects of growth zones in some of the studied tropical tree species. (A) *Schizolobium parahyba* density variation, (B) *Zanthoxylum kellermanii* alternating parenchyma bands and terminal parenchyma bands, (C) *Zanthoxylum caribaeum* density variation, (D) *Mimosa acantholoba* variation in vessel density and size, (E) *Alchornea latifolia*, multiple intra-annual density fluctuations, (F) *Cecropia peltata*, discontinuous, intra-annual rings, (G)Vague, indistinct growth boundaries in *Bursera simaruba*, (H) *Cordia alliodora*, wedging rings. Scale bars = 1 cm, excepting D and G where bars = 0.5 cm. Growth direction is from right to left (a–f) and from bottom to top (h).

Another common problem was that growth zones might have varying distinctiveness. This occurred within a single sample with, for example, clear rings in the outer part of stems, but vague rings (VR) in the centre, or, in asymmetric stems, among different growth directions of the stem (i.e., circuit non-uniform rings that become vague or disappear completely in one or more directions). Varying distinctiveness between samples occurred in various species, and it was found that rings were well-defined in some samples, but absent in others. Wedging rings (Fig. 1H; synonyms '"discontinuous, partial or incomplete rings"; Kaennel and Schweingruber 1995) constituted another kind of irregularity. These rings gradually join others and become completely absent in one or more directions, due to cambial failure. By examining entire stem surfaces, wedging rings could be detected very well and be accounted for in age determinations.

POTENTIAL SPECIES FOR RING ANALYSIS

Based on the distinctiveness of growth zones, their circuit uniformity, and the occurrence of irregularities, we estimated that 26 of the 70 studied species (37%) had good potential for use in tree ring studies (Table S1). As expected, this fraction was higher in the dry locality than in the wet area (48% vs. 33%). Promising pioneer species in the wet locality that showed good potential for ring studies are *Schizolobium parahyba* (Fig. 1B), *Zanthoxylum kellermani* (Fig. 1B), *Z. caribaeum* (Fig. 1C), and two *Miconia* species. Some common, non-pioneer species with clear rings are *Cordia alliodora* (Fig. 1H), *Lonchocarpus cruentus*, *Pterocarpus rohrii* and *Ficus maxima* (See Table S1 for full list). Several pioneers that are dominant across the secondary forests of the Chiapas region (Breugel 2007) such as *Cecropia peltata, Trema micrantha* and *Trichospermum mexicanum*, proved not useful for ring analyses due to various problems. *Ochroma pyramidale* did show some potential, as we observed distinct growth boundaries in some samples, but not in all of them.

Common and promising species in the dry locality are *Mimosa acantholoba* (Fig. 1D) *Lonchocarpus emarginatus, Lonchocarpus torresiorum*, *Acacia cochliacantha, Ceiba parvifolia* and *Euphorbia schlechtendalii* (Full list in Table S1).

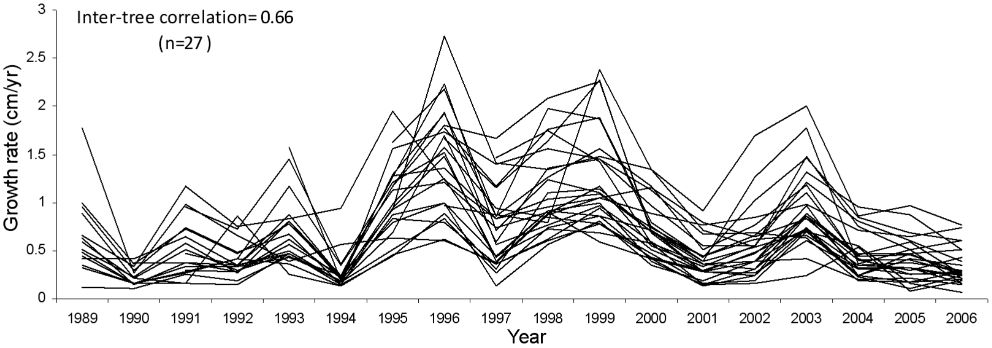

FIGURE 2. Inter-annual ringwidth patterns for 27 *Mimosa acantholoba* trees from Oaxaca for the period 1989–2006. Mean inter-tree correlation is calculated as the mean Pearson correlation coefficient for all pairwise combinations of the 27 trees.

Crossdating of ring width between trees of *Mimosa acantholoba* revealed a highly similar pattern of small and wide rings between different years (Fig. 2) and a high inter-tree correlation of 0.66. Average ring width of these 27 trees correlated strongly to total annual rainfall (Pearson-r = 0.83, $P < 0.001$) for the period 1980–2003.

FALLOW AGES VS. RING COUNTS

The maximum number of rings found per site in the wet locality matched fallow ages closely (Table 1; Fig. 3A,B). At most sites at least one individual had numbers of rings close to the fallow age, although at each site there were species and trees showing lower numbers of rings than the corresponding age. The relation between the maximum number of rings and fallow age was stronger for pioneers than for non-pioneer species (cf. Fig. 3A, B). At one site only, the absolute maximum number of rings differed more than two years from fallow age (Chiapas-17; Table 1); in this stand, two pioneer species showed two rings more than the supposed age, while two non-pioneers species (*L. cruentus* and *P. rohrii,* Table 1) had five and six rings more. One of these non-pioneer trees had a fire mark in the third ring (19 yr ago) and these are probably remnant trees that survived previous clearing and burning. For three other sites (Chiapas-4,7,8), we found 1–2 rings more than the fallow ages. Two of these fallows (4,7) were probably older as multiple samples showed exactly the same (higher) number of rings.

In the dry locality, the (maximum) number of rings matched less well the fallow ages, and especially in some of the older fallows, we observed much lower numbers of rings in *Mimosa acantholoba* than expected for such a pioneer species (Table 1; Fig. 3C). The largest difference between fallow age and rings was observed in the oldest stand (60 yr) in which we only counted 34 rings for the largest, living *Mimosa*. At three sites we found an exact match between fallow age and number of rings, at two other sites we observed a higher number of rings (1 and 4 yr difference), but more often (8 times) the number of rings was lower.

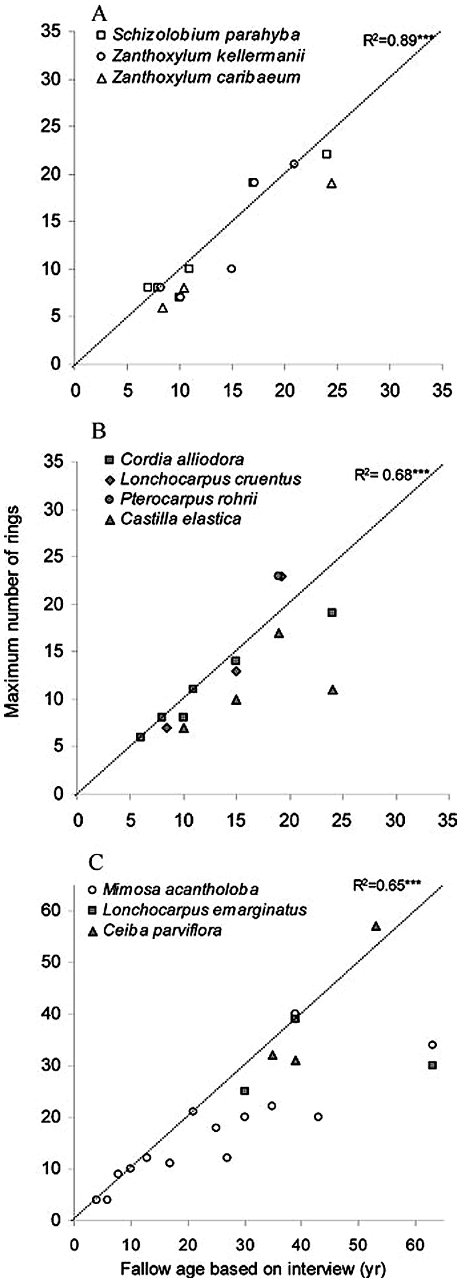

FIGURE 3. Relationship between fallow ages based on interviews and maximum number of rings in different species for the studied wet (A = pioneer species, B = non-pioneer species) and dry site (C). Open symbols are pioneer species (*sensu* Swaine and Whitmore, 1988) and filled symbols non-pioneer species. The diagonals indicate Y = X, where ages match exactly.

For two intermediate-aged fallows (estimated to have 27 and 25 yr) where we found consistently less rings, we have strong evidence that the initial interview-based ages were wrong. In one of these sites (27 yr) ownership changed since field abandonment and the former landowner (who cleared the site for cultivation) confirmed that the ages initially provided by the current landowner were wrong. The new age indications of 13 yr of the former landowner corresponded closely to the numbers of rings found (12 rings). At another site (25 yr) that was not privately but communally owned, fallow age proved inaccurate as different people provided different age-estimations.

By careful evaluation of the differences between rings and fallow ages, and considering the reliability of the interviews with the landowners, we suspected that six of the 24 investigated fallows had initial dating errors, of which two were relatively large errors (7 and 14 yr difference; details in Table 1).

ESTABLISHMENT OF SPECIES AFTER ABANDONMENT

By using tree rings, we could determine for several species of the wet locality, the time elapsed between field abandonment and tree establishment (Fig. 4). This showed that at least one tree of each species appeared in one of the sites immediately after abandonment, except for *Zanthoxylum caribeum*, which first appeared two years after abandonment. We did not find significant differences in median times of establishment between pioneer and non-pioneer species ($P = 0.48$). Among species, we found only significant differences between *Schizolobium parahyba* and *Zanthoxylum caribeum* ($P < 0.05$).

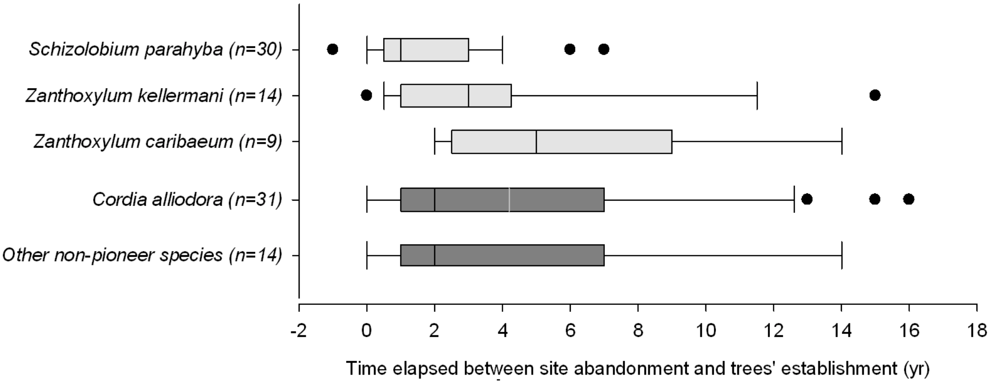

FIGURE 4. Time elapsed between field abandonment and species' establishment, calculated as the difference between fallow age and number of rings of each tree. Bars indicate 90%, 75%, median, 25% and 10% percentiles, separate points are outliers. Light grey bars are pioneer species (*sensu* Swaine and Whitmore, 1988) and dark grey bars are non-pioneer species. The group of 'Other non-pioneer species' include *Lonchocarpus cruentus* (3), *Pterocarpus rohrii* (6), *Dalbergia brownei* (1), *Dialium guianense* (1), *Rollinia jimenezii* (1), and *Casearia sylvestris* (2). Note that the two trees of *L. cruentus* and *P. rohrii* which exceeded fallow age (cf. Table 1, site 17) were omitted from this analysis.

DISCUSSION

RING FORMATION IN TROPICAL SECONDARY FORESTS

We identified a substantial number of species (26) with clear and circuit uniform growth boundaries that may be used for tree ring analysis. For *Mimosa acantholoba* we could confirm the true annual nature of rings (Stahle 1999) by crossdating inter-annual ring width patterns and relating these to an external controlling factor, rainfall. Unfortunately, we could not perform such crossdatings for other species, but we think that rings in all potential species are annual. In the dry locality, there is little doubt concerning the annual nature of rings given the prolonged dry season of six months and the strict deciduous phenology of nearly all ring-forming species. Leaf abscission usually induces cambial dormancy, which is resumed soon after leaf flushing (Borchert 1999). It is this cambial rhythm what determines the formation of an anatomically distinct growth layer in the tree's xylem (Borchert 1999, Worbes 2002). Also for those species in the wet locality that exhibit a strictly deciduous leaf habit once a year, such as *Schizolobium parahyba* and *Zanthoxylum kellermani*, the rings' annual nature is beyond reasonable doubt. Yet, short dry spells during the rainy season may induce intra-annual, false rings (Priya and Bhat 1998, Borchert et al. 2002). In the wet locality, we did observe false, intra-annual bands in various species, but when such bands were frequent and difficult to distinguish from truly annual bands, species were disregarded for analysis. For the 26 species identified as promising for ring analysis, we are confident that we discriminated successfully between false and truly annual rings. In the wet locality, this assertion is further supported by the good match between ages of *Cordia alliodora*, a species with proven annual ring formation (Devall et al. 1995) that establishes early in succession (Breugel 2007; Fig. 4B), and the number of rings of other species in the same stands.

The use of entire discs may hold the key to success in studies on tropical tree rings as it facilitates the visual detection of ring boundaries, allows discrimination between true and (intra-annual) false rings, and to account for wedging rings (Worbes 2002, Brienen and Zuidema 2005). Ideally, one should use increment cores as this method is considerably less destructive and may also be applied in existing plots, but only few species included in this study (e.g., *Schizolobium parahyba* *Lonchocarpus cruentus* and *Mimosa acantholoba*) presented growth zones that were clear enough to distinguish annual rings unambiguously on cores.

The observed proportions of species with tree rings (37%) in our secondary plots match those observed in the Yucatan Peninsula, Mexico (Roig et al. 2005; 40%) and the Amazon basin in Brazil (Alves and Angyalossy-Alfonse 2000, Roig 2000, Worbes 2002; 25–50%). Hence, more species than often thought are useful for ring analysis, including some well-known pioneers such as *Schizolobium parahyba* and *Zanthoxylum kellermani*. Unfortunately, *Cecropia*, the most typical neotropical pioneer taxon, presented too many problems to be easily used in ring studies, even though annual rings in *Cecropia* have been observed in more seasonal climates in the Bolivian Amazon (R.J.W. Brienen, pers. obs.), and in floodplain forests (*várzea*) in Brazil (Worbes 2002). More advanced techniques such as image analysis (Worbes 2004), X-ray densitometry (Polge 1978), synchrotron X-Ray fluorescence (Poussart et al. 2006), and high resolution isotope analysis (Evans and Schrag 2004, Poussart et al. 2004, Verheyden et al. 2004) may be promising to distinguish annual ring boundaries in species with poorly defined and ambiguous rings. Although these techniques are laborious and expensive for use in large scale ecological studies, their applications may yield clues as to how to discriminate between annual and intra-annual, anomalous growth zones using simple wood anatomical features.

DATING FALLOW AGES USING TREE RINGS

The potential of tree rings as a reliable proxy for fallow ages varied among species and sites. No single species revealed fallow ages precisely, but by examining simultaneously pioneer and non-pioneer species, we could often precisely determine fallow ages. This was true at least for stands in the wet locality, where succession starts with a multitude of pioneer and non-pioneer species (Breugel 2007). However, in the dry locality older fallows (> 20 yr), tree rings were often not a good indication of fallow ages and even the oldest *Mimosa* trees were much younger than fallow ages. This was surprising as this species establishes nearly immediately at the beginning of succession (Lebrija-Trejos et al. 2008), and as maximum tree ages in the younger sites (< 20 yr) did match well with fallow ages. The unexpected discrepancy may be attributed to the early death of older trees that established since the beginning of succession, which would imply that the sampled *Mimosa* trees are relatively recent newcomers. This concurs with observations that many *Mimosa* trees showed clear signs of senescence after 20 yr and that this species may establish successfully several years after the onset of succession (E. Lebrija-Trejos, pers. comm.). An important implication of these findings is that tree rings' potential to accurately determine fallow ages depends on the species' longevity and on successional mechanisms. In the wet area, where long-lived pioneers are common from the moment of field abandonment, tree rings may be used successfully to date fallows. In the dry area, however, the long-lived pioneer phase is lacking, and succession proceeds through replacements of species' groups so that early stages are dominated by short-lived pioneers and establishment of longer-lived species occurs only at later stages (Ewel 1980, Lebrija-Trejos et al. 2008). In the absence of long-lived pioneers in dry forests, focusing on resprouts of long-lived non-pioneer species may be a good alternative in determining fallow ages, as resprouting is a very common regeneration method in dry forests and resprouts develop mostly soon after abandonment (Swaine and Hall 1983, Kennard et al. 2002, Vieira and Scariot 2006). Ages of resprouts of *Lonchocarpus emarginatus* and *Ceiba parvifolia* included in this study closely matched older fallows' ages (39 and 57 yr; Table 1).

The occurrence of annual rings allowed us to verify interview-based estimates of fallow ages, something not done before. Overall, interview-based age estimations were accurate or contained only smaller errors of 1–2 yr. In two cases, however, the ages indicated in the first interviews had errors of 7 and 14 yr. These large errors had specific (social) causes: in one case sites' ownership changed after its abandonment, whereas in the other the area was not privately but communally owned and people were unable to assert the exact age. In such specific cases tree rings may be especially useful as they allow detecting and correcting dating errors.

This study shows that tree rings are in general a good tool to independently verify fallow ages and that this may be best achieved by using multiple species instead of seeking an ideal species. Nonetheless, our results also show that relying on tree rings as the sole source of fallow age information can be unsafe in the absence of some knowledge of site-specific successional mechanisms and on individual species' longevities. Successional mechanisms may differ largely between areas (Lebrija-Trejos et al. 2008) and longevity varies widely among species (Lieberman et al. 1985, Finegan 1996, Martínez-Ramos and Alvarez-Buylla 1998, Brienen and Zuidema 2006), affecting the potential and accuracy of rings to determine fallow ages. Therefore, relying uniquely on tree rings may lead to dating errors as much as relying blindly on interviews. The combined application of both methods results in a more accurate dating of secondary forest stands, and we suggest that this approach should be used whenever possible.

USING TREE RINGS TO STUDY SECONDARY FOREST SUCCESSION

How can tree rings further understanding of secondary forest succession in the tropics? Tree rings have successfully been used in temperate forests to reconstruct stand histories (Henry and Swan 1974, Glitzenstein et al. 1986, Abrams et al. 1995), but species diversity in these systems is typically much lower and nearly all species present annual rings (Cook and Kairiukstis 1990). In our study, reconstruction of species' establishment patterns was limited to the wet locality, to the few species that had annual rings, and to a few individuals. This was partly due to the sampling method (i.e., we did not know beforehand which species would have reliable rings), and partly to low species' abundances in these diverse systems (Breugel 2007).

Notwithstanding, our reconstruction of establishment dates for the few species that were included revealed some interesting patterns. Firstly, all species but one recruited very early during succession. They were present immediately after abandonment with at least one individual in one site and this did not vary between regeneration groups. Even non-pioneer species recruited at the beginning of succession, in some stands even before the pioneers included in our comparison. Secondly, pioneers' recruitment appeared not to be limited to the first successional years, but may continue during many years (15–16) after succession has started. These results, crucial for the evaluation of successional theories on the invasion, recruitment and replacement of species (Egler 1954, Finegan 1996), match those obtained by permanent plot studies in the study area (Breugel et al. 2007).

Our pilot study provides an idea of the potential of tree rings to accurately reconstruct historical colonization patterns. We may gather retrospective insight on historical establishment dates of specific species, without the need to perform long-term monitoring of species' recruitment patterns. Such information can obviously not be gathered from static observations of plots along different points of chronosequences, as such static data do not necessarily reflect real time processes (Bakker et al. 1996, Chazdon et al. 2007, Johnson and Miyanishi 2008). Tree rings, however, only provide information on surviving trees and, in older stands, we risk missing the first successional phases, typically dominated by short-lived pioneers that do not live longer than 10–30 yr (Finegan 1996, Martínez-Ramos and Alvarez-Buylla 1998). In our study, we clearly missed the earliest establishment data of the short-lived pioneer species in the dry area's oldest fallows.

We envision other promising applications of tree rings. For example, it is possible to assess the influence of soil variables and land-use history (e.g., Ruffner and Abrams 1998) on the long-term growth of tree species, and to estimate rates of tree biomass gains (e.g., Bascietto et al. 2004) in tropical secondary forests. Also, tree rings may be used to estimate the influence of climate on secondary succession. Our crossdating of *Mimosa* trees showed that tree responses to annual variation in climate may be highly similar among trees and that variation in climate may be very important to tree growth, even significantly influencing successional stands. Finally, the occurrence of annual rings in common neotropical pioneer species, such as *Schizolobium parahyba* may be used to determine ages of natural gaps in primary forests and estimate gap rate formation. Thus, tree rings cannot replace real-time observations of permanent monitoring (Bakker et al. 1996, Finegan 1996, Breugel et al. 2007, Johnson and Miyanishi 2008), but they will certainly prove a valuable addition to existing techniques of studies on tropical forest succession and should be included in the portfolio of methods applied in these systems.

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SUPPORTING INFORMATION

TABLE S1. Species with their types and distinctiveness of growth zones, encountered problems and potential for tree ring studies ('good potential species' in bold).

Family Species	Wet or Dry	Type of growth zone	Distinctiveness	Potential of ring analysis	Problems	Phenology
Anacardiaceae						
Astronium graveolens Jacq.	W	VD	+–	+	VR, WR	D
Spondias mombin L.	W	VD, WD	+– to –	+ to –	VR, ID	D
Spondias radllkoferi Donn.Sm.	W	VD, WD	+– to –	+ to –	VR, ID	D
Annonaceae						
***Rollinia jimenezii* Saff.**	W	WD	++	+++	–	E
Apocynaceae						
Tabernaemontana alba Mill.	W	WD	–	–	VR	E
***Thevetia ahouai* (L.) A.DC.**	W	WD	++	+++	Rings only distinct on wet wood	E
Bignoniaceae						
Amphitecna latifolia (Mill.) A.H.Gentry	W	AP	+–	+	VR	E
***Tabebuia heterophylla* DC. Britton**	D	TP, VD	+	++	–	D/E
***Tabebuia impetiginosa* (Mart. ex DC.) Standl.**	D	TP	+	++	**VR**	**D**
Boraginaceae						
***Cordia alliodora* (Ruiz & Pavón) Oken**	W, D	WD, VD	+ and ++	+++	WR	D
Cordia diversifolia Pavón ex A.Dc.	W	VD, WD	+	+	WR, not circuit uniform	D
Cordia elaeagnoides A.DC.	D	TP	–	–	WR, Difficult patterns	D
Cordia truncatifolia Bartlett	D	VD, TP	+	+–	VR	D
Burseraceae						
Bursera simaruba (L.) Sarg.	W, D	WD	–	–	VR	D
Capparidaceae						
Capparis incana Kunth	D	TP, WD	+	–	Not sure whether annual	D
Chrysobalanaceae						
Licania hypoleuca Benth.	W	AP	+–	+–	VR	E
Clusiaceae						
***Vismia camparaguey* Sprague & Riley**	W	WD, AP	++	++	None	E
Euphorbiaceae						

Family Species	Wet or Dry	Type of growth zone	Distinctiveness	Potential of ring analysis	Problems	Phenology
Acalypha diversifolia Jacq.	W	WD	+	+	VR in outer part	E
Alchornea latifolia Sw.	W	WD	+	+ to –	ID	D
Croton schiedeanus Schltdl.	W	WD	+ to –	+	VR some samples	E
***Euphorbia schlechtendalii* Boiss.**	D	WD	+	++	VR some parts	D
Fabaceae – Caesalpinioideae						
Caesalpinia platyloba S.Wats.	D	WD	+ to –	+	VR some parts	D
***Dialium guianense* (Aublet) Sandw.**	W	AP	+	++	VR	D
***Senna atomaria* (L.) H.S.Irwin & Barneby**	D	WD	++	+++	None	D
***Schizolobium parahyba* (Vell.) Blake**	W	TP (WD, VD)	+	+++	ID, but TP reliable end of annual ring	D
Fabaceae– Papilionoideae						
Apoplanesia paniculata C.Presl	D	TP, VD	+	+	Dark heartwood	D
***Dalbergia brownei* (Jacq.) Urban**	W	WD, VS, AP	+	+++	Dark heartwood	D
***Lonchocarpus cruentus* Lundell**	W	AP, TP	++	++	VR some parts	E
***Lonchocarpus emarginatus* Pittier**	D	AP, TP	+	++	VR some parts	D
***Lonchocarpus torresiorum* M. Sousa**	D	AP, TP	++	++	none	D
***Pterocarpus rohrii* Vahl**	W	AP, TP	++ to –	++ to –	VR some samples	D/E
Fabaceae– Mimosoideae						
***Acacia cochliacantha* Humb. & Bonpl. ex Willd.**	D	TP	+	++	Some double TP–bands	D
Acacia mayana Lundell	W	AP	–	–	VR	E
***Acacia uzumacintla* Lundell**	W	TP, WD	+	+++	Some double TP–bands	D
Albizia leucocalyx (Britton & Rose) L.Rico	W	–	no	–	No growth zones	D
Havardia campylacantha (L.Rico & M.Sousa) Barneby et J.W.Grimes	D	AP,TP	+	++	VR, WR	D
Inga pavoniana G.Don	W	WD, VSD	–	–	ID, VR	E
Inga puntata Willd.	W	WD, VSD	+–	+ to –	ID	E
Inga vera Willd.	W	WD	–	–	ID, VR	E
Lysiloma divaricatum (Jacq.) J.F.Macbr.	D	TP, VD	+	+	WR, ID	D
***Mimosa acantholoba* (Willd.) Poir.**	D	VD, WD	++	+++	Intra–annual parenchyma bands	D

Family Species	Wet or Dry	Type of growth zone	Distinctiveness	Potential of ring analysis	Problems	Phenology
Mimosa tenuiflora (Willd.) Poir.	D	TP, VD	+–	+	VR	D
Flacourtiaceae						
Casearia sylvestris Sw.	W	WD	+ to –	++ to –	Indistinct in some samples	E
Malvaceae						
Ceiba petandra (L.) Gaertn.	W	TP, VD	+	–	False TP–bands	D
***Ceiba parvifolia* Rose**	D	TP	++	++	–	D
***Guazuma ulmifolia* Lam.**	W	WD	+	++	Weak within ring density variations	E
Heliocarpus appendiculatus Turcz.	W	WD	+–	+	VR	D
Luehea speciosa Willd.	W	WD	+ to –	+ to –	VR some samples	E
Ochroma pyramidale (Cav. ex Lam.) Urb.	W	WD	+ to –	+ to –	VR some samples	E
Trichospermum mexicanum (DC.) K. Schum.	W	WD	–	–	VR, ID	E
Melastomataceae						
Bellucia axinanthera Triana	W	WD	+ to –	+ to –	VR some samples	E
Miconia argentea (Sw.) DC.	W	WD	no	–	No visible growth boundaries	E
***Miconia glaberrima* (Schltdl.) Naudin**	W	AP, WD	++	++	VR outer part	E
***Miconia trinervia* (Sw.) D.Don ex Loud.**	W	WD	++	+++	VR cente, WR	E
Meliaceae						
Guarea glabra Vahl	W	WD, AP	+–	+	WR	E
Monimiaceae						
Siparuna andina (Tul.) A.DC.	W	WD	+–	–	VR	E
Moraceae						
Castilla elastica Sessé ex Cerv.	W	AP	+	++	None	D
***Ficus maxima* Mill.**	W	AP	+ to –	++	VR in centre	E
Piperaceae						
Piper hispidum Sw.	W	–	no	–	No growth zones	E
Polygonaceae						
Coccoloba liebmanii Lindau.	D	VD, WD	+ to –	+	VR	D
Rutaceae						
***Zanthoxylum caribaeum* Lam.**	W	WD	+	++	WR	D
***Zanthoxylum kellermanii* P.Wilson**	W	AP, TP	+	++	Vague ID	D
Sapindaceae						

Family Species	Wet or Dry	Type of growth zone	Distinc-tiveness	Potential of ring analysis	Problems	Phe-nology
Cupania dentata DC.	W	WD	+–	+	VR some parts	E
Cupania glabra Swartz	W	WD	+–	–	probably not annual	E
Thouinia villosa DC.A.	D	WD	+–	–	Not sure whether annual	D
Sapotaceae						
Pouteria durlandii (Standley) Baehni	W	AP	–	–	VR	E
Ulmaceae						
Trema micrantha (L.) Blume	W	WD	–	–	VR, ID	E
Urticaceae						
Cecropia peltata L.	W	TP, WD	+–	–	ID, VR, WR	E
Verbenaceae						
Aegiphila monstrosa Moldenke	W	AP, WD	+–	–	VR	E
Vochysiaceae						
Vochysia guatemalensis Donn. Sm.	W	AP	+– to –	–	VR some samples	E

Notes: **Wet or Dry**: D = Dry, Oaxaca, W = Wet, Chiapas, **Types of growth zones**, following Worbes (1995); WD = Variation in wood density (type 1), AP = Alternating parenchyma bands (type 2), TP = Terminal Parenchyma (type 3), VD = Variation in vessel density, VS = Vessel size or a combination (VSD, type 4), **Distinctiveness of growth zone**; ++ very clear, + clear, +– weakly distinguishable, – very weak, no = growth zone absent, **Potential for ring analysis**; +++ very good/precise, ++ good, + possible with difficulties, – impossible. Varying distinctiveness or potential between samples is indicated by a combination of different signs (e.g. '+ to –'), **Problems;** VR = Vague or indistinct growth boundaries, ID = (Intra-annual) density variations, WR = Wedging rings, **Leaf phenology;** D = Deciduous, E = Evergreen, D/E = Facultative deciduous. Leaf phenology is based on the personal observations of E. Pérez-García, J. Meave and M. Martínez-Ramos.

CHAPTER 3

Successional Change and Resilience of a Very Dry Tropical Deciduous Forest Following Shifting Agriculture

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ABSTRACT

We analyzed successional patterns in a very dry tropical deciduous forest by using 15 plots differing in age after abandonment and contrasted them to secondary successions elsewhere in the tropics. We used multivariate ordination and non-linear models to examine changes in composition and structure and to estimate forest recovery rates and resilience. A shrub phase characterized early succession (0−3 yr); afterwards, the tree *Mimosa acantholoba* became dominant. Below its canopy, sprouts and seed-regenerated individuals of mature forest species slowly accumulated. Canopy height, plant density and crown cover stabilized in less than 15 years, whereas species richness, diversity, and basal area continued to increase. The pioneer species group has very low diversity and the long-lived pioneer phase typical of humid forests is absent; species composition may therefore recover soon as suggested by convergence towards mature forest species composition. The time trend of plant density also differed from humid forests for it lacked its characteristic density decline, presumably because of differences in regeneration mechanisms between very dry and other less water-stressed forest types. As opposed to the prevailing hypothesis, resilience was not higher than in moister forests, and thus factors other than structure relative simplicity must be accounted for when assessing resilience.

INTRODUCTION

Tropical dry forests (TDF) covered large areas in Mexico, Central and South America, Africa, India, Southeast Asia and Australia (Gerhardt and Hytteborn 1992), but their current distribution represents only a fraction of their original cover, mostly due to conversion to agriculture or other land uses (Janzen 1988, Maas 1995, FAO 2007). For example, in Mexico less than 27 percent remains undamaged (Trejo and Dirzo 2000) and in other areas it is even less (Venezuela 10% of potential cover, Fajardo et al. 2005; Central America 2%, Janzen 1988; New Caledonia 2%, Guillespie and Jaffré 2003). After field abandonment in many TDF rural areas, secondary forests develop naturally (Swaine 1992, Lugo et al. 2002). Understanding secondary vegetation development is fundamental to achieve restoration and management goals for such successional areas (e.g. Aide et al. 2000).

While research in tropical rain forests (TRF) has produced reasonable insight in their secondary succession (e.g. Finegan 1996, Guariguata and Ostertag 2001, Chazdon in press), research in TDF lags far behind (Sánchez-Azofeifa et al. 2005, Vieira and Scariot, 2006), despite the increased attention recently received (e.g. Kennard 2002, Pereira et al. 2003, McLaren et al. 2005, Ruiz et al. 2005, Molina Colón and Lugo 2006). TDF are very heterogeneous in community and ecosystem properties (Murphy and Lugo 1986, Gerhardt and Hytteborn 1992; Mooney et al. 1995; Vieira and Scariot 2006) and we expect TDF succession to be equally heterogeneous.

Successional TDF pathways may differ substantially from those in TRF, rendering knowledge extrapolations from TRF to TDF inappropriate (Ewel 1980, Sánchez-Azofeifa et al. 2005, Viera and Scariot 2006), particularly to TDF at the dry end of their range, where processes operating in less water-stressed forests may encounter greater difficulties. Several characteristics affecting succession account for the differences. TDF host a greater proportion of wind dispersed species (Bullock 1995), seedling survival is typically unsuccessful (Gerhardt and Hytteborn 1992, Swaine 1992), while coppicing contributes greatly to regeneration (Murphy and Lugo 1986, Perera 2001, Vesk and Westoby 2004). The processes and mechanisms determining late colonists invasion in TRF gap dynamics (Finegan 1996, Guariguata and Ostertag 2001) may not be as relevant in dry forests, for in mature TDF most dead trees remain standing (Durán et al. 2002), gap formation rates and sizes are low (Dickinson et al. 2001), and light conditions are not overriding for seedling establishment (Lieberman and Li 1992, Gerhardt 1996). For example, Poorter and coworkers (Poorter et al. 2006, Markesteijn et al. 2007, Poorter and Kitajima 2007) found that seedling and sapling traits usually related to light requirement gradients deviate from expectations in short stature, dry forests.

Mature TDF have lower species richness (but see Janzen 1988; Trejo and Dirzo 2002), smaller stature, lower basal area, fewer canopy strata, lower leaf area index and more frequent vegetative reproduction than their TRF counterpart (Murphy and Lugo 1986, Swaine 1992, Holbrook et al. 1995). In line with these differences, and from height growth comparisons between the two forest types, Ewel (1977, 1980) stated that TDF succession is floristically simpler, comprises fewer seral stages and, as recovery to pre-disturbed forest height was faster, that TDF are more resilient than TRF. Later, this difference was nuanced in a resilience model (Ewel 1983), but the idea of TDF being more resilient rooted in later secondary succession theory (Murphy and Lugo 1986; Kennard 2002; Fajardo et al. 2005; Vieira and Scariot 2006; Chazdon, 2008; but see Lugo et al. 2002). Evaluating resilience as the speed of return to pre-existing mature forest conditions after perturbation, is a relative task that depends on how fast the same phenomenon occurs in other forests, and that involves the particular community attribute discussed (e.g. Molina Colon and Lugo 2006), the quality of the reference mature forest (lower quality, faster recovery; e.g. Kennard 2002), the land use history of the disturbed sites (higher use intensity, slower recovery; e.g. Uhl et al. 1988), the sampling criteria used, especially when analyzing species diversity and composition (recovery speed increases with decreasing size-class sampled; e.g. Peña Claros 2003), and the degree of isolation of the successional patch and the related propagule availability (Wijdeven and Kuzee 2000). Considering the large heterogeneity of TDF systems, the scarcity of studies, and the dependence of speed of relative recovery on several factors, the assertion of higher resilience of TDF is insufficiently supported and needs further evaluation.

As part of a long-term project, we study forest development in permanent fallow plots in a TDF of southern Mexico whose climatic regime corresponds to the driest end of TDF distribution. Here we analyze development patterns and compare them to other dry and rain forest examples to further understand the variability and particularities of TDF succession. We also model and analyze the degree and velocity of recovery (resilience) in this TDF.

METHODS

STUDY AREA

The study was conducted near Nizanda (16°39′30″ N, 95°00′40″ W), a village on the Pacific slope of the Isthmus of Tehuantepec (Oaxaca), southern Mexico. Mean annual temperature is ~26°C and mean total annual precipitation is ~900 mm (T/P [× 100] = 2.89), with 90 percent falling between late May and mid October (García 2004, Pérez-García et al. 2005; Fig. 1). These features correspond to a transition from subtropical very dry forest to subtropical dry forest sensu Holdridge (1979).

The landscape is hilly, with elevations around 250 m a.s.l., and is dominated by phyllite of Mesozoic age. Lithosols (shallow soils dominated by rock fragments) predominate in the region but medium textured Haplic Phaeozems (porous dark soils, rich in organic matter, with a mollic A horizon) also occur on gentle hillslopes (Pérez-García et al. 2001). The mature TDF has a low canopy stature, ca. 7−8 m, with few prominent trees of *Bursera* and *Lonchocarpus* attaining 15 m. It has neither a clear vertical stratification nor a distinct dominance of any species; in fact, many are rare (Pérez-García et al. 2001, Gallardo et al. 2005). Although the region still has large areas of well-preserved mature forest (some officially under protection), patches of secondary forest derived from abandoned agricultural fields (mostly maize) occur on many hills around the village.

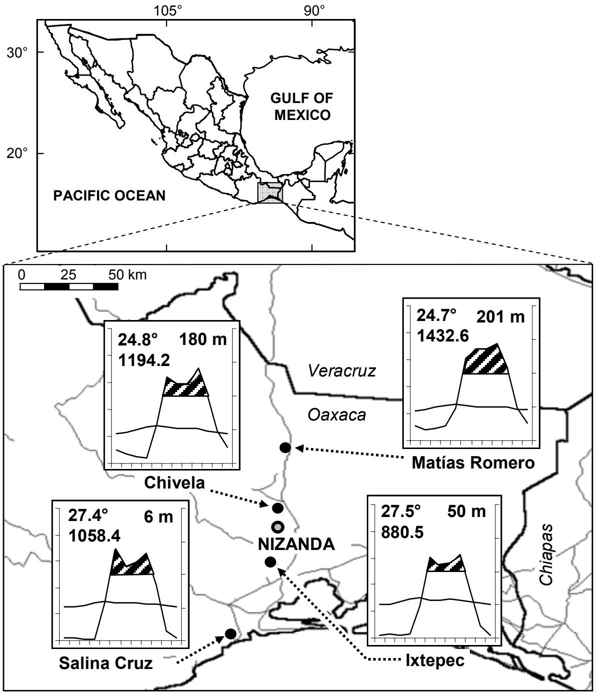

FIGURE 1. Location of the study area in the Pacific watershed of the Isthmus of Tehuantepec, S Mexico. Available climatic diagrams of four nearby localities are provided to show precipitation patterns in the region.

Agricultural fields are small, rarely exceeding 0.5 ha but mostly smaller, and they are normally sown for one or two years only. Heavy machinery is never used in the region's hills. Fallow periods vary but the minimum span is 5−7 yr, coinciding with recovery times of soil nutrients (L. Galicia, unpublished).

SITE SELECTION AND PLOT ESTABLISHMENT

Chronosequence approaches have limitations due to unrealistic assumptions regarding similarities in environmental conditions, site history, and seed availability across sites. Nevertheless, when these variables are carefully addressed, results of studies following changes in time mirror those from chronosequences in important aspects such as density, richness, diversity, life form composition and rate of change (Capers et al. 2005). We carefully selected 15 sites after detailed interviews with local landowners: one recently abandoned field, fallows of 1, 3, 5, 7, 10, 12, 14, 18, 22, 27, 32, 37, and 40 yr, and a mature forest site. Selection was based on homogeneity of the site's land use history (i.e. few years of cultivation without pasture use before abandonment), geological substrate, and topographic position, giving preference to mid-slope hillsides or piedmonts.

For the comparisons, our mature forest plot was supplemented with nine 100-m2 mature forest plots studied by Pérez-García and Meave (2004). These plots were mainly used to set the mature forest confidence intervals. By mature forests we mean sites that have never been cleared, to the knowledge of current inhabitants, and have the structure and composition of intact or under "good conservation" status Mexican TDF (Trejo and Dirzo 2002; Gordon et al. 2004; Gallardo et al. 2005); i.e. over 100 trees/0.1 ha, 7−12 m in height and 20−40 cm DBH, characteristic species such as *Amphipterygium adstringens*, *Apoplanesia paniculata*, *Bursera* spp., *Ceiba parvifolia*, *Euphorbia schlechtendalii*, *Lysiloma divaricatum*, and *Krugiodendron ferreum*, among others, and a continuous layer of native treelets and shrubs.

DATA COLLECTION

At each site, 30 × 30 m plots were fenced. Within each enclosure, four 20 × 5 m transects, separated by 2 m corridors, were marked. Each transect was divided into four 5 × 5 m quadrats (Fig. 2). All woody and succulent plants were sampled using a size-based criterion. For each transect, sampling in one quadrat included individuals ≥ 1 cm DBH, in a second one, individuals ≥ 2.5 cm DBH, and in the remaining two, individuals ≥ 5 cm DBH. The sampling criterion of each 25-m^2 quadrat was assigned randomly. Smaller individuals (DBH < 1 cm, height ≥ 30 cm) were sampled in eight 2 × 2 m squares systematically placed in the plot (Fig. 2).

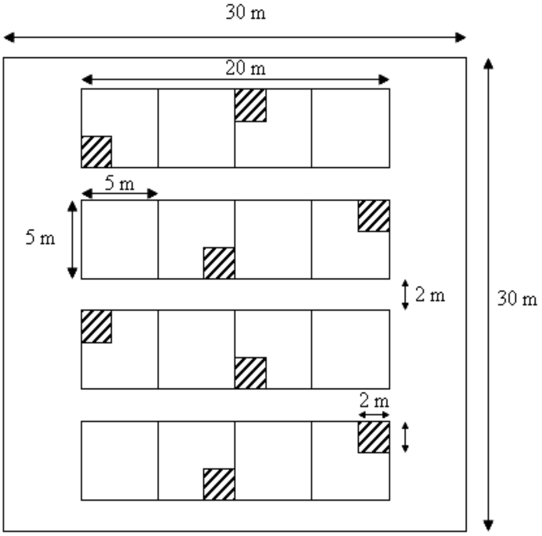

FIGURE 2. Outline of a 900 m^2 enclosure where four 20 × 5 m plots were established to study secondary succession in a 40 yr-old dry forest chronosequence. In each 100 m^2 plot, a different sampling criterion was randomly assigned to the 25 m^2 subdivisions (see methods for details). In total, individuals $\geq$ 5 cm DBH where sampled in all 16 sub-quadrats (400 m^2), those with DBH $\geq$ 2.5 cm in 8 (200 m^2), and those with DBH $\geq$1 cm in 4 (100 m^2). Hatched squares are quadrats where plants < 1 cm DBH and $\geq$ 30 cm tall were sampled (32 m^2 total).

For individuals $\geq$ 1 cm DBH we recorded species name, life form, height, DBH and two perpendicular cover diameters. For the smaller individuals only the first three variables were measured. Suckers from the same individual were considered one individual (for density calculations) but the DBH of all suckers fulfilling the sampling criterion were measured (for species and plot basal area calculations). When species identities were unknown, specimens were collected and identified using a regional reference collection of ca. 900 species, kept at the Faculty of Sciences, National Autonomous University of Mexico. Sampling was conducted in the wet season (August-October 2003).

DATA ANALYSIS

Diversity was described by (1) species density (S); (2) species richness, rarefied to the lowest (80; S_{80}) and to ca. half of the maximum (175; S_{175}) number of individuals recorded in the plots (using Ecosim, Gotelli and Entsminger 2006); (3) Shannon diversity index (H′); and (4) Shannon evenness index (E). H′ and E were chosen due to their widespread use and the comparative goal of the analysis. For a suitable comparison with the mature plots of Pérez-García and Meave (2004), we (re)calculated H′ and E using data only from the four 25-m2 quadrats per fallow; hence, quadrat size and sampling criteria were the same as theirs. We used EstimateS (Colwell 2005) to construct sample-based rarefaction curves, computed without replacement (to include all fallows) and scaled to individuals, to compare joint species richness (Mao Tau function) of fallows with mature forests.

Structural analyses included canopy height, density of individuals, basal area, and total crown cover (calculated for individuals ≥ 1 cm DBH, except for canopy height, as the two youngest plots lacked individuals ≥ 1 cm DBH and hence calculations included only smaller individuals). Canopy height was calculated by averaging the heights of two individuals from each 100-m^2 transect within a plot ($N = 8$). To avoid biases resulting from spots with particularly tall trees, we selected the tallest individuals within the first and second half of each transect, respectively; thus, the sample consisted of tall individuals distributed over the entire plot but not necessarily of the eight tallest within a plot. Absolute crown cover per plot was the sum of the crown areas of individuals rooted inside a plot. Density, basal area and total crown cover were expressed on a per hectare basis for comparison with the mature forest plots.

Successional trends were described fitting a set of non-linear models, as proposed by Huisman, Olff and Fresco (1993; HOF models henceforth), which allow exploring temporal variations within ecologically realistic bounds and without restricting the analysis to a single response type. Model I fits non-significant trends in time; Model II fits increasing or decreasing trends where the maximum reaches an upper bound; Model III resembles model II but the maximum remains below an upper bound; Model IV describes a symmetrical increase and decrease; and Model V depicts an increase and decrease at different rates. We used SPSS non-linear regression module (SPSS 2003) for model fitting. The model upper bound was set to the mature forest mean upper limit (mean + 1.96 SE), or to 1.2 times the highest value found in the dataset, to account for possible higher values not contained in it (Bongers et al. 1999), when data from Pérez-García and Meave (2004) were not available or suitable for calculating comparable confidence intervals (i.e. species density, H′ and E). Selection of the best model was based on a significant improvement of the fit by using the least squares F-statistic (Huisman et al. 1993).

To assess forest recovery we used the HOF model selected for each community attribute to estimate the attributes' value along the chronosequence span. Resilience was measured as the percent recovery of the mature forest mean value (± 1.96 SE) represented by each calculated quantity. These percentages were then compared to those reported or calculated by us for other tropical secondary successions. Compared studies were from forests growing in areas that experienced low to moderate land use intensities, and had reference mature or old-growth forests that were structurally indistinguishable from undisturbed forests, i.e. > 80 yr old, according to Brown and Lugo's (1990) criterion. This included 11 TRF and 7 TDF studies, some comprising sites located in more than one region; all TDF were less dry than ours (T/P ratios from 1.76−2.78). If the recovery of the focal attribute remained below 100 percent along the studied period, we used for the comparison the value at the oldest available stand or age class that was equivalent to ours; if recovery reached a 100 percent within 40 yr (our studied period), then we used the stand or age class at which this maximum level of recovery was reached.

Floristic relationships between stands were examined using non-metric multidimensional scaling ordination (NMDS; Quinn and Keough 2002). Two NMDS were performed, (1) including all individuals, to analyze overall differences between fallows (n = 15), and (2) only considering trees and columnar cacti divided into a lower (ind. < 1 cm DBH and between 0.3–2 m height) and upper (ind. ≥1 cm DBH and > 2 m tall) strata, to analyze successional trends in species composition assuming that trees and cacti occurring in the lower strata will eventually dominate the upper strata (n = 28; the two youngest plots lacked upper strata individuals). A similarity matrix using the abundance-based Jaccard index adjusted for unseen species (Chao et al. 2005), calculated with EstimateS (Colwell 2005), was employed as the input matrix of analyses. We used the SPSS multidimensional scaling module (SPSS 2003) selecting the Simplex method as starting configuration; dimensions were fixed at two, as Kruskal's measures of stress reached levels adequately representing actual dissimilarities between samples (0.132 and 0.152 for analyses 1 and 2, respectively; Quinn and Keough 2002). The first axis of the first ordination was regressed on stand age to evaluate its relationship with the main compositional variation. Species' relative density, crown cover and basal area were calculated for detailed analysis of changes in species composition and species' relative contributions to community structure.

RESULTS

NUMBER OF SPECIES, STAND STRUCTURE AND ABANDONMENT TIME

In total, 141 species (including 21 morphospecies), belonging to 46 families, were found. Among them, 54 were shrubs, 62 trees, 21 lianas and 4 succulents. Most occurred in one (35%) or two (18%) stands only. All community attributes were related to fallow age ($P \leq 0.01$ – < 0.001), which explained 60−91 percent of data variation (Figs. 3, 4). According to the fitted models, all attributes but height would sooner or later reach their characteristic mature forest or maximum value.

Species density was one of the most variable attributes (range: 15−58 species), but showed a gradually increasing pattern along the chronosequence (Fig. 3a). S_{80} and S_{175} paralleled such increments in time albeit with a lower rate and variability, as expected from the relationship between density of individuals and number of species (R^2 = 0.69, linear regression). The sample-based rarefaction curves of mature and fallow plots (Fig. 3c) revealed that joint fallow richness is much lower than the area's mature forest richness (61±8 species vs. 112±15 at 496 individuals). H′ also reflected the patterns in species richness with a gradual increase along the chronosequence (1.36−3.34). Contrastingly, E increased initially fast but varied little after 3 yr (Fig. 3b).

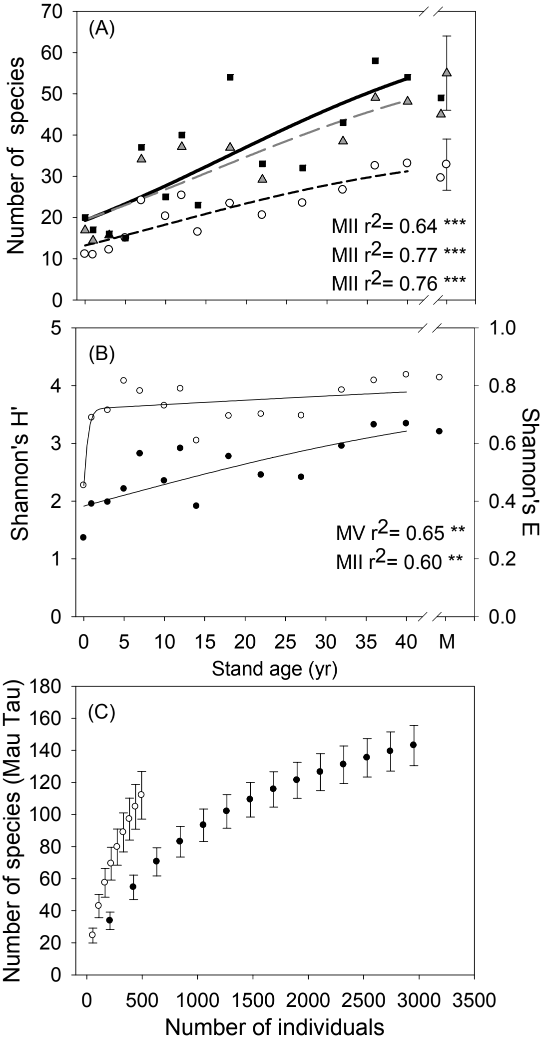

FIGURE 3. Diversity attributes for fallows ranging from recently abandoned field to 40 yr-old. Symbols represent actual stand values. Lines are time trends described by the best fit HOF model (M I–V; ** *P* ≤ 0.01, *** *P* < 0.001). (A) Species density (closed squares, continuous line) and species richness rarefied to 175 individuals (closed triangles, medium dash line) and 80 individuals (open circles, short-dash line). (B) Shannon indices of diversity H′ (closed circles) and evenness E (open circles). (C) Species richness estimates (Mau Tau function; Colwell 2005) with 95% CI of mature (open circles) and secondary (closed circles) forests.

All structural attributes significantly increased with fallow age but differed in their relationship to time. Basal area was the only attribute that gradually increased throughout the chronosequence (0−25 m^2/ha) and remained below the mean 95% CI of the region's mature forests (31.96 ± 6.31 m^2/ha; Fig. 4c). Canopy height, density of individuals and total crown cover (range = 1.0–7.2 m, 0–7475 individuals/ha and 0–44,110 m^2/ha, respectively) had steep increments within the first fifteen years of succession (Figs. 4a, b, d), but hardly changed thereafter.

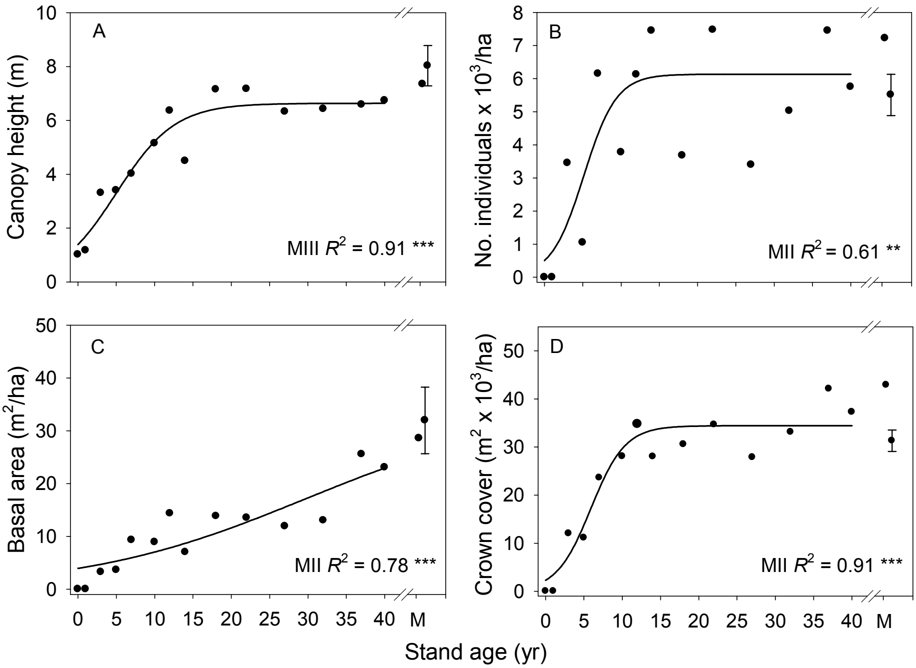

FIGURE 4. Structural attributes for fallows ranging from recently abandoned field to 40 yr-old. Symbols represent actual stand values. Lines are time trends described by the best fit HOF model (M I–V; ** $P \leq 0.01$, *** $P < 0.001$). Canopy height (A), density of individuals (B), basal area (C) and total crown cover (D). Mature forest values (M; chronosequence stand and mean with 95% CI) are depicted for reference but were not included in the regressions.

CHANGES IN LIFE FORMS AND SPECIES COMPOSITION

Life form spectrum drastically changed with abandonment time: the proportion of shrubs changed from > 80 percent of all individuals for the two youngest sites to a maximum of 59 percent in older fallows. From two years after abandonment, life form distribution changed little. Shrubs showed the widest range of values with 18−59 percent of individuals (mean = 34.9, SD = 12); trees between 31−69 percent (mean = 57, SD = 12); and lianas between 2−11 percent (mean = 7, SD = 3). Succulents appeared only after 18 yr and persisted with 1−8 percent of the individuals (mean = 3, SD = 3).

In the two youngest fallows, the shrubs *Waltheria indica*, *Chamaecrista nictitans* var. *jaliscensis* and *Melochia tomentosa* accounted for 68−82 percent of all woody individuals. The two pioneer trees *Mimosa tenuiflora* and *M. acantholoba* var. *eurycarpa* took over dominance from the 3 yr-old stand onwards, either in terms of density of individuals, crown cover, or basal area. *Waltheria indica* and *Chamaecrista nictitans* var. *jaliscensis* were seldom found thereafter. In 3 and 5 yr-old stands, *M. tenuiflora* accounted for up to 95 percent of total basal area, and in 7 yr-old stands and older *M. acantholoba* was dominant. In the two oldest stands, several stems of the dominant *Mimosa* species were uprooted, snapped, or senescent. Species such as *Acacia farnesiana* and *A. cochliacantha*, recognized by locals as early successional, had low relative abundances, and others like *Crescentia alata*, *Guazuma ulmifolia*, *Heliocarpus pallidus* and *Piptadenia flava*, referred elsewhere to as early successional (Sabogal 1992, Rincón and Huante 1993, Bullock 1995, Miller and Kauffman 1998), occurred only sporadically.

Below the canopy of the *Mimosa* species, mature forest species increased gradually in abundance to become conspicuous only at later stages, i.e. from the 32 yr-old stand onwards (e.g. *Amphipterygium adstringens*, *Apoplanesia paniculata*, *Euphorbia schlechtendalii*, *Lysiloma divaricatum*, *Senna atomaria*). The two *Mimosa* species had no young recruits.

Successional changes in species composition are well depicted by the NMDS analyses. Fallow scores on the first axis of the ordination for all individuals had a strong logistic relationship with fallow age (Fig 5a; R^2 = 0.72). When the longer-lived and physiognomically dominant forest components (i.e. trees and cacti) were stratified and analyzed (Fig. 5b), trends of change towards a mature forest composition became clearer. The dissimilarity between the upper and lower strata of any successional plot was larger than that between the upper and lower strata of the mature forest. Moreover, all but one sample within the immediate neighborhood of the mature forest samples were lower stratum samples. For most plots lower strata samples were closer to the mature forest samples than their corresponding upper strata.

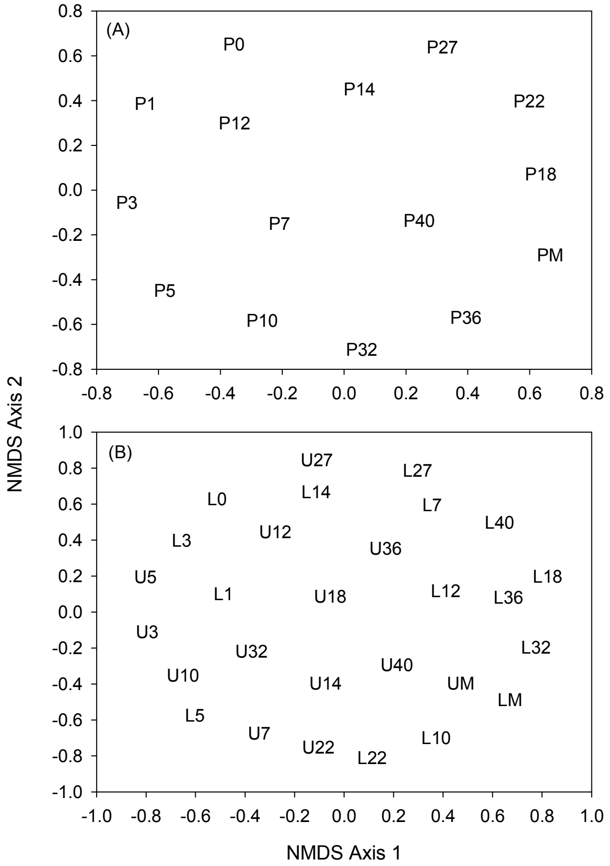

FIGURE 5. NMDS ordination for fallows ranging from recently abandoned field to 40 yr-old and a mature forest stand using the abundance-based Jaccard index adjusted for unseen species of Chao et al. (2005) as input matrix. (A) Including all species sampled; fallows are symbolized by their age in years preceded by the letter P. (B) Only considering trees and columnar cacti divided into a lower (L; ind. < 1 cm DBH and between 0.3 – 2 m tall) and upper (U; ind ≥1 cm DBH and > 2 m tall) strata; the number following the letter is the age of the fallow to which each strata belong.

FOREST RECOVERY AND RESILIENCE

Estimated speed of recovery varied between attributes. Density of individuals, crown cover and height had the fastest recoveries (Fig 6a, b, d); the first two recovered fully (5,511 ± 625 individuals/ha, and 31,283 ± 2 227 m^2/ha, respectively) within 8−13 yr. Canopy height recovered 75% of the mean mature forest height in 13 yr, but remained below full recovery (8.03 ± 0.75 m) within the modeled period. Basal area had the slowest recovery (Fig. 6c); after 40 yr, the secondary forest recovered 60−89 percent of mature forest basal area (31.9 ± 7.2 m^2/ha). Diversity attributes had intermediate recovery rates; S_{175} was the only one to attain at least the lower bound of full recovery (49 ± 7 species) within the 40 yr period (Fig. 6e). In 40 yr, species density, H′ and E reached between 80−96, 86−90, and 78−85 percent of mature forest values (24.6 ± 2.2 species/100 m², 0.91 ± 0.021 and 2.9 ± 0.12), respectively (Fig. 6f, g, h).

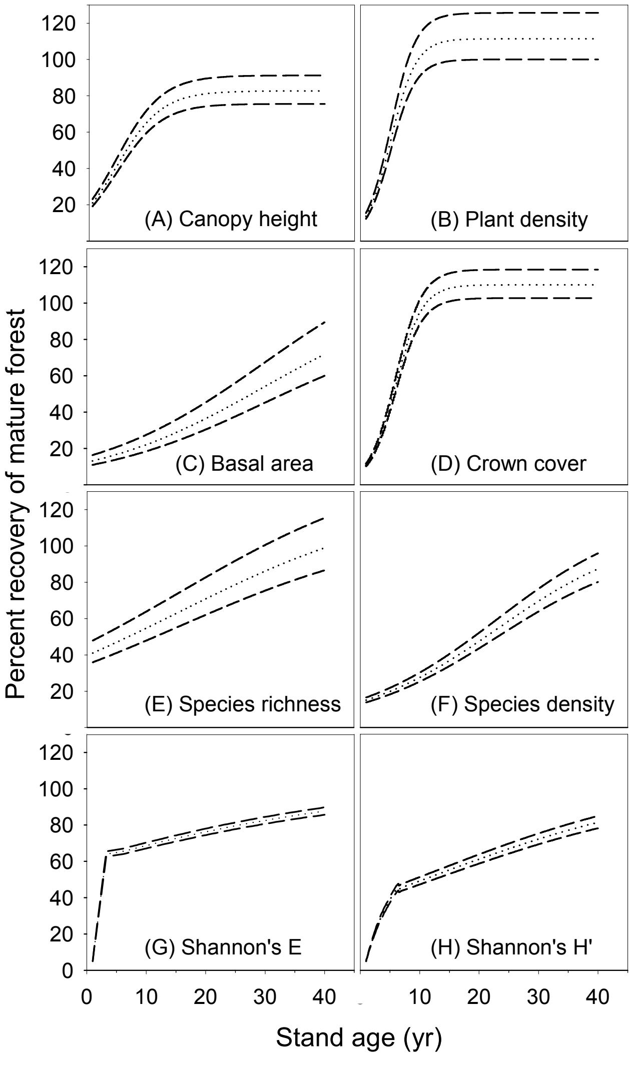

FIGURE 6. Level of secondary forest recovery (%) of mean (dotted line) mature forest canopy height (A), density of individuals (B), basal area (C), crown cover (D), species richness (E), species density (F), Shannon’s evenness (G) and Shannon’s diversity (H). Dashed lines represent the 95% mean CI.

DISCUSSION

Development of species composition, richness and diversity matches patterns of steady recruitment in small-sized, low-intensity disturbed areas like ours, where propagule availability of mature forest species is not limited (Finegan 1996, Wijdeven and Kuzee 2000, Capers et al. 2005). The higher values of species richness, H′ and E in our oldest plots relative to our mature forest match in turn the expectations of a diversity peak according to the intermediate disturbance hypothesis (Connell 1978, Huston 1979), although a sound confirmation requires the analysis of older stands. Shifts in dominance from herbs and shrubs, through pioneer trees, to mature forest tree species can be explained from differences in growth rates, life histories and longevities of new-incoming species as compared to early successional ones; these traits cause species turnover in tropical secondary succession (Gómez-Pompa and Vázquez-Yanes 1981, Finegan 1996, Capers et al. 2005). Fast increments in height and crown cover compared to basal area agree with processes of early allocation to resource acquisition followed by a later shift towards structural materials (Brown and Lugo 1990, Guariguata and Ostertag 2001). Likewise, factors affecting secondary succession such as temporal and spatial variations in propagule, water, and soil nutrient availability (Lieberman and Li 1992, Bullock 1995, Guariguata and Ostertag 2001, Marod et al. 2002), and pre-disturbance differences in composition and structure between stands, may explain the variation not accounted by time only.

Three major aspects in our forest differ from other studies and the main reason is probably site water availability. First, density of individuals rose at early stages but did not decrease as typically observed in TRF (see reviews of Brown and Lugo 1990, Guariguata and Ostertag 2001, and recent studies by DeWalt et al. 2003, Breugel et al. 2006). Studies conducted in TDF that agree with the TRF pattern (e.g. Aweto 1981, Kennard 2002, Ruiz et al. 2005) come from areas with higher water availability (lower T/P rations and shorter drier seasons; 1.75−2.1, and 4−5 months, respectively), while others with behaviors similar to ours are from drier sites (González-Iturbe et al. 2002 and Pereira et al. 2003; T/P from 2.8 – 4.00, and 5−6 months dry season). Read and Lawrence (2003) provide a good regional scale example in this respect: reductions in density were smaller in increasingly dry sites (T/P ratios of 1.76, 2.18 and 2.80, respectively).

The second difference is the pattern of species dominance and replacement, and the recognized successional phases. We found no group of species equivalent to the long-lived pioneers typical of TRF. Our forest succession starts with a short phase dominated by herbs and shrubs, followed by a pioneer tree phase. In TRF, this second phase of pioneer trees is replaced, within 10−30 yr, by a group of long-lived pioneers that dominate the forest during 75−150 yr before mature forest species do so (Finegan 1996, Guariguata and Ostertag 2001). In our forest, the two *Mimosa* tree species that represent the second phase of succession dominated up to the 40 yr-old stand, and they will be replaced by the typical mature forest species that are growing below their dying canopy.

Thirdly, our group of pioneer trees consists of a few legume species only (*Mimosa* and *Acacia* spp.). This is surprising as our study region (Mexico's Pacific tropical watershed) hosts one of the highest floristic diversities of its kind (over 5600 species for TDF, J. L. Villaseñor, unpublished data), and only in Nizanda over 900 plant species have been recorded (Pérez-García et al. 2005). This also contrasts with the pioneer species richness generally found in secondary TRF within a region (e.g. Peña-Claros 2003, Breugel et al. 2006). Dominance by a few species, without implying arrested succession, has been observed in other deciduous forests at the dry end of their range (e.g. Rico-Gray and García-Franco 1992, Nansen et al. 2001, Pereira et al. 2003), and it may be an ecological feature proper of these forests. The dominant pioneer species in our fallows are virtually absent from the natural regeneration dynamics of the mature forest. This is in contrast with secondary succession in TRF where species that colonize fallows are the same ones involved in their gap dynamics.

Observed differences in patterns can be related to general differences between TDF and TRF. Low pioneer species diversity may derive from a pool containing only a few species adapted to the water-stressed early successional conditions (Ewel 1977) and lacking mature forest species specialized to large gaps. Alternatively, it may result from a synergism between recurring disturbance (i.e. repetitive felling) and resprouting (e.g. Rico-Gray and García-Franco 1992), a trait commonly found among TDF species (Brown and Lugo 1986, Miller and Kauffman 1998, Vesk and Westoby 2004). In turn, competition leading to the patterns of density decline (Niklas et al. 2003) may be prevented in TDF by its characteristic regeneration mechanisms. On the one hand, drought-related poor seedling establishment prevents a dense packing of individuals (Ewel 1980, Liebermann and Li 1992, Gerhardt 1996); on the other, a high sprouting incidence produces low individual density and slowed individual and species turnover (Kruger and Midgley 2001; Lebrija-Trejos 2004). Moreover, competition not only decreases with low recruitment (Schwinning and Weiner 1998, Niklas et al. 2003) but also with increasing environmental stress (e.g. drought; Menge and Sutherland 1987; Bunker and Carson 2005). It is also likely that the characteristic high rainfall variability of TDF (Murphy and Lugo 1986) together with the consequent variability in recruitment and survival rates (e.g. Swaine et al. 1990, Ceccon et al. 2004), simply result in an indefinite, highly variable pattern of plant abundance.

FOREST RESILIENCE

Considering that the study site is at the dry end of the TDF range, recovery of some mature forest attributes seems fast (in no more than 13 yr for density of individuals and crown cover), but not of others: H', E, and basal area failed to reach mature forest values within the studied period. How resilient is then our forest compared to others?

Crown cover (sometimes compared with leaf biomass) was the only attribute for which no forest was more resilient than ours, whether TRF (Saldarriaga et al. 1988, Brown and Lugo 1990) or TDF (Kennard 2002, Molina Colon and Lugo 2006). Regarding height, the attribute used by Ewel (1977) to assert that TDF were more resilient than TRF, 11 out of 17 compared forests were indeed less resilient than ours. Three TDF and two TRF were equally resilient (Read and Laurence 2003, Moran et al. 2000, Ruiz et al. 2005, Molina Colon and Lugo 2006), and only one TRF growing on a nutrient rich soil had higher resilience (Moran et al. 2000). The situation is different regarding the slowest recovering attributes. In all studies that evaluated H′ and E, resilience was higher than in ours (Saldarriaga et al. 1988, Peña Claros 2003, Ruiz et al. 2005, Toledo and Salick 2006). This was also true for species density in almost all sites (6 TRF and 4 TDF; with remarkable recoveries up to 55−92% of old-growth forest values only 8 yr after use as pasture; Uhl et al. 1988). Only in one TDF (Molina Colon and Lugo 2006), stands growing in the previously most disturbed sites recovered at a slower (house sites) or similar (farm sites) speed than ours. As to species richness, recovery in our forest was, at best, similar to both TRF and TDF (Guariguata et al. 1997; Ruiz et al. 2005). Regarding basal area, resilience was also higher in most forests (10 TRF and 4 TDF) than in ours. Read and Lawrence (2003) exemplified again the relevance of water availability, even within TDF, as while all of their study sites recovered faster than ours, the difference in speed decreased with increasing T/P ratios (1.76−2.8). Finally, density of individuals showed the highest similarity in resilience with respect to other forests; five TRF and two TDF showed comparable recovery speeds; two of each forest types were more resilient and only the most disturbed sites of Molina Colon and Lugo (2006) were less resilient. As found by Lugo et al. (2002) when comparing between Puerto Rican forests, high relative resilience of our TDF as an absolute statement cannot be sustained; the assumption that a lower structural complexity would lead to a shorter time to reach maturity does not hold for most attributes.

Our results on species convergence indicate that species composition could have a faster recovery to maturity in our TDF, as expected by Ewel (1980) and Murphy and Lugo (1986) from a lower floristic complexity (of the pioneer's group) and the resulting reduction in seral stages. A small pool of pioneer species without long life-spans leaves less room for compositional variation and thus may lead to earlier convergence between secondary and mature forests. Such convergence would not take place before 40 yr of regrowth but is likely to occur earlier than the 75−150 yr estimated for TRF (Finegan 1996, Guariguata and Ostertag 2001).

CONCLUDING REMARKS

Despite chronosequence's limitations, we are confident of its usefulness (given the high R^2 values in regressions on time) to overcome the lag in knowledge of TDF secondary succession, and as a way of generating new hypotheses that are site specific (as long as assumptions are carefully addressed). Indeed, valuable information on major secondary succession patterns and trends can be extracted in short time periods. We stress that a series of studies encompassing the entire range of conditions in which TDF occur, especially in very dry ones in which the early successional floras differ completely from those of TRF, are needed to fully establish and understand patterns and particularities of TDF secondary succession; differences with respect to TRF should not be neglected. Focus on factors related to water availability is essential.

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CHAPTER 4

Community Dynamics of a Secondary Tropical Dry Forest: successional pathways and variability

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ABSTRACT

Pathways and mechanisms of succession are system and site specific, but most models of tropical forest succession are based on wet tropics and on temperate forest succession. To understand the general bases of succession more varied systems need to be studied. We analyzed patterns of community and species functional group dynamics over time in 17 plots covering more than 65 years of successional time after agricultural abandonment in dry tropical forest in Oaxaca, Mexico.

We predicted that dry forest successional pathways would show clear transitions between groups of species, coincide with established chronosequence-based predictions, and deviate from established wet-forest-based successional models.

Dry forest succession showed two tree-dominated phases, one of pioneers and a second-one of mature-forest species. Individual-plot vegetation development followed predicted pathways: basal area, crown cover and species diversity increased with time after abandonment. Tree density, however, did not. Pioneers peaked in basal area at ca. 20 yrs; mature-forest species took over dominance 20 years later. Pioneer recruitment stopped after 10 years and mortality continued, while mature forest species recruited continuously and mortality increased gradually in time. Pioneers did not wither because of increasing dominance of mature-forest species but because pioneers facilitated their own replacement: they aged and declined well before mature-forest plants dominated or even reached maximum development rates. Secondary successional development in our dry forest is less complex than in most wet forests: it consists of less seral stages, probably because long-lived pioneer species do not occur in our dry forest. We conclude that upon fairly homogeneous historical and environmental conditions, an orderly series of delimited changes takes place during secondary succession and that a common set of deterministic underlying forces are strong drivers of this development.

INTRODUCTION

"Deterministic, autogenic, and facilitation components are stronger than perhaps we sometimes consider" A.D. Bradshaw (1983, p.14), on the reconstruction of ecosystems.

Succession is a complex, and therefore difficult to understand, process of vegetation change. It is influenced by multiple interacting factors both intrinsic (autogenic) and extrinsic (allogenic) to plants. These relate to the historical and actual characteristics of the colonization site environment, including its disturbance regime, the characteristics of the landscape surrounding it, and the characteristics of the regional species pool, including the life history attributes of its component species (Pickett et al. 1987, Jentsch 2007). This complexity implies that while successional causes and mechanisms can be generalized, their relative importance in determining the rate and direction of changes cannot. Successional changes are therefore strongly system dependent and, as a consequence, observed pathways and specific causes of change are far more diverse than previously thought and accounted for in most successional models (MacMahon 1981, McCook 1994).

The time scales at which secondary succession takes place (decades to hundreds of years) additionally hinders its understanding. Most successional knowledge derives from surveying sites with different ages since disturbance (chronosequences). Chronosequences allow defining basic patterns and formulating explanatory hypothesis of succession (e.g. Foster and Tilman 2000, Capers et al. 2005) while circumventing the problem of the relatively short time available for studying succession. Chronosequences, however, cannot directly inform on rates or on causal processes of succession, for which surveys over time (longitudinal studies) are needed (Bakker et al. 1996). Furthermore, for chronosequence studies to be valid, the selected sites need to share a (relatively) similar landscape structure, landform, substrate conditions, and disturbance history and regime (Foster and Tilman 2000). These are requirements that many successional studies have not covered sufficiently.

The multiplicity of successional pathways on different systems has been revealed by thousands of studies (see Rejmaneck and Van Katwyk, 2005; http://botanika.bf.jcu.cz/suspa/oldfield.php). Alongside, the number of longitudinal studies testing chronosequence predictions, and their working hypotheses, has increased (e.g. Debussche et al. 1996, Sheil et al. 2000, Breugel et al. 2007). Models of secondary succession have hence been refined or adapted for particular biomes (e.g. Pickett et al. 1987, Denslow and Guzman 2000) and early ideas of succession have moved from considering it a deterministic and therefore highly directional and predictable process, to one that is largely contingent, idiosyncratic, and therefore more stochastic (Finegan 1984, Vandermeer et al. 2004, Chazdon 2008). Recently, the practical though fallible chronosequence method has been seriously questioned (Johnson and Miyanishi 2008).

System and site specific assessment of the pathways and mechanisms of succession is hence currently considered fundamental to understand the general bases of succession (Pickett et al. 1987, McCook 1994, Chazdon et al. 2007). Studies dealing with extrinsic causes of vegetation dynamics (disturbance and landscape processes), which strongly affect successional pathways, indicate that equilibria and stability (or variability) are relative system properties that must be evaluated and studied in the context of specified system conditions and well defined time and space scales (Williamson 1988, Hobbs and Norton 2004, Fraterrigo and Rusak 2008).

Most of our knowledge and ideas on secondary succession are largely biased towards temperate forests and grasslands, and tropical humid forests (MacMahon 1981, Chazdon 2008, Cramer et al. 2008). There is little information on secondary succession of tropical dry forests (TDF) and most, if not all of it, has been obtained from chronosequence studies (Chazdon et al. 2007), so concrete mechanistic explanations are lacking. TDF compose 40-42% of tropical forests worldwide (Murphy and Lugo 1986, Mayaux et al. 2005) and are characterized by their marked dry season and low water availability. They span from 500-2000 mm of rain, have a ratio of potential evapotranspiration to precipitation >1 and < 4, and experience typically 3-8 months of drought (Holdridge 1979, Murphy and Lugo 1986). TDF differ from other tropical forests in many aspects causing and explaining successional change (Bullock et al. 1995, Vieira and Scariot 2006). Most notably, they have a less diverse secondary and mature forest flora with specific adaptations for coping with drought and irradiance stress gradients (Gentry 1982, Medina 1995, Lebrija-Trejos et al. 2008, Poorter and Markesteijn 2008); a lower productivity and more simple physiognomic structure, both shaping distinct disturbance regimes and responses (Dickinson et al. 2001, Durán et al. 2002); and a drought and temperature stressing environment where facilitation is most likely to play a key role (Brooker et al. 2008, Lüttge 2008).

Here we present a combined chronosequence and longitudinal study that covers from very early to advanced stages of succession (<1 - ca. 65 years plus a mature forest stand). To our knowledge this is one of the few studies in the tropics to cover, with such approach, the successional dynamics of a wide range of successional stages and the first one to study empirically TDF successional dynamics. This allows us to study causal process of TDF succession by evaluating (1) how do community structure and species diversity and composition vary over time? How are they shaped by the development of pioneer and mature species? (2) how is the successional dynamics, i.e. recruitment, growth, and mortality, of pioneer and mature-forest species? How are they related to community development and species replacement? Because of the combined approach we can further evaluate how predictable is successional development: do longitudinal trends parallel chronosequence trends? Focusing at the community level and based on available chronosequence studies, we expect TDF succession to show clear transitions between groups of species, as a result of their low floristic complexity and reduced number of seral stages, and of contrasting differences in their life history strategies and alleged facilitative effects of one group over another (Ewel 1977, Álvarez-Yépiz et al. 2008). As landscape fragmentation and degradation in the study area are low, and as study sites have similar land use histories and substrate conditions, we also expect succession in our system to be largely predictable and directional. Reliable chronosequence results are thus also expected.

METHODS

The study was conducted on the hilly landscape surrounding the village of Nizanda (16°39′30″ N, 95°00′40″ W) on the Isthmus of Tehuantepec, Oaxaca, Mexico. The area is characterized by a distinct dry season lasting 6-7 mo (Nov-May), in which less than ten percent of the ca. 900 mm of mean total annual rain occurs. Mean annual temperature is ca. 26°C. Changes in rock substrates such as phyllite and limestone, and variations in soils from shallow and poor hilltop-soils to dark valley-soils rich in organic matter and nutrients, combine with the climatic conditions to create a heterogeneous mosaic of vegetation types. These include savannas, xerophytic scrubs, and riparian semi-evergreen forests occurring in a continuous matrix of a low canopy (i.e. 7-8 m) and deciduous tropical dry to very dry forest (Pérez-García and Meave 2006). Such matrix is composed of a series of inter-dispersed secondary stands and old-growth forests of different ages.

Fourteen secondary forest patches with abandonment times ranging from < 1 yr to ca. 40 yr, plus a mature forest, were selected from field surveys conducted in 2003. Fenced permanent plots of 30 × 30 m were established in 17 patches (two more patches with ages between 50-60 yr were added in 2005). Plot ages were defined by combining information obtained from interviewing land-owners and from chronological analyses of tree rings (Brienen et al. 2009). Selected patches had a similar geological substrate (phyllite), topographic position (mid-slope hillside or piedmont), and originated from traditional shifting cultivation practices extended throughout the tropics (Warner 1991). This specifically meant that patches were <0.5 ha but mostly smaller, burned before the onset of the cropping season, cultivated for one or two years only, and not used as pasture before abandonment (though occasional grazing could have occurred).

Plot sampling followed a size-stratified design and included woody and succulent plants ≥ 1 cm diameter at breast height (dbh, 1.3 m) censused yearly, between August and October, from 2003 to 2007. Four 20 × 5 m transects subdivided in four quadrats (5 × 5 m) were laid per plot and marked with stakes. Within each transect, individuals with 1-2.5 cm dbh were measured in one quadrat, those with dbh > 2.5 and < 5 cm were measure in two quadrats, and individuals ≥ 5 cm dbh were measured in all quadrats. The sampling criterion per quadrat was assigned randomly. All individuals were labeled with metal tags with a unique identification number, mapped, and identified to species. Specimens of unknown species were collected and identified using a regional reference collection of ca. 900 species, kept at the Faculty of Sciences, National Autonomous University of Mexico. Stem dbh was measured with fiber diameter tapes to the nearest 1 mm and the exact measurement point marked with spray paint for subsequent measurements. Two orthogonal crown diameters per individual were measured for crown area (CA) calculations (done only in 2003, 2005, and 2007). Recruits (new individuals with 1 cm dbh) and dead individuals were recorded each year following the first census.

Vegetation changes in forest diversity and structure were analyzed in terms of Shannon diversity index (H'), Smith and Wilson's evenness index (E_{var}, Smith and Wilson, 1996), species richness (rarefied to 100 individuals using Ecosim; Gotelli and Entsminger 2006), individual density, basal area (BA) and CA. Using GraphPad Prism v. 5.00 for Windows, classical chronosequence trends for these attributes were obtained by fitting, to the initial census data of 2003, a series of non-linear models characterized by having distinct maxima, minima and inflections points. This included rational, sigmoidal and exponential association (growth) models commonly used to describe biological responses in time (Huisman et al. 1993, Rossiter 2005). Using the Akaike's information criteria corrected for small sample sizes (Motulsky and Christopoulos 2004), the model that best fitted the data with a minimum number of parameters was selected. To analyze the variation in successional trends, the 95% confidence bands of the selected model were used to contrast the actual individual plot trajectories with the chronosequence prediction models.

Annual community mortality, recruitment, and BA growth (of surviving individuals), were calculated as proportions based on the previous year abundance (for mortality and recruitment) and the previous year basal area (for growth; for simplicity we will refer to these relative rates just as mortality, recruitment and growth). The successional patterns of mortality, recruitment and growth were modeled with non-linear functions as with the structural variables but using the plots' annual rate averages. The relationships between the plot's demographic rates and structural characteristics, all of them averaged per year over the study period, were analyzed with Pearson's product-moment correlations. Variables were $\log_{10}$ or square-root transformed when needed.

As community change patterns are the combined outcome of responses of populations with similar life history attributes (Noble and Slatyer 1980, Rees et al. 2001), we additionally assessed the changes in terms of ecological guilds. A simple pioneer- mature-guild dichotomy was used. The classification was based on: (1) identification by the local inhabitants of initially colonizing and dominant species; (2) functional trait-based multivariate classifications of the most abundant species, which have matched the *a priory* classifications based on local knowledge (Chapter 6, Peters 2006); and (3) studies of species abundance patterns in secondary and mature TDF of the area and elsewhere (Gordon et al. 2004, Álvarez-Yépiz et al. 2008, Lebrija-Trejos et al. 2008). The pioneer and mature guilds comprised 5 and 88 species, respectively (Table S1; fifteen undefined or unknown species included in the entire community analyses were left out from the groupings).

The trajectories of change in species composition through the years were assessed with a non-metric multidimensional scaling ordination (MDS), performed using the Proxscal algorithm of SPSS 15. The abundance-based Sorensen index of similarity, adjusted for unseen species (Chao et al. 2005), was calculated with EstimateS (Colwell 2005) and used as input matrix for the MDS ordination. The chronosequence models of compositional change, with their 95% confidence bands, were obtained for each MDS axis as with the structural variables. Finally, the output Euclidean distance matrix of the resulting MDS (2 dimensional solution, Kruskal's Stress-I = 0.16, dispersion accounted for = 97%) was further used to obtain a measure of compositional change over time by dividing the distance between the plot's first and last census by the years elapsed between measurements. This measure was then related to the plots' age using Pearson's correlation, and to forest structure and demographic rates using multiple linear regression analysis.

RESULTS

CHRONOSEQUENCE TRENDS

All forest diversity and structural attributes but species evenness had directional chronosequence trends with time (Figs. 1, 2a-c). The models for the entire community were similar in shape and indicated a rapid, almost linear development during the first ca. 10 years of succession. Thereafter, development slowed-down strongly but continued gradually, except for density, which stayed constant.

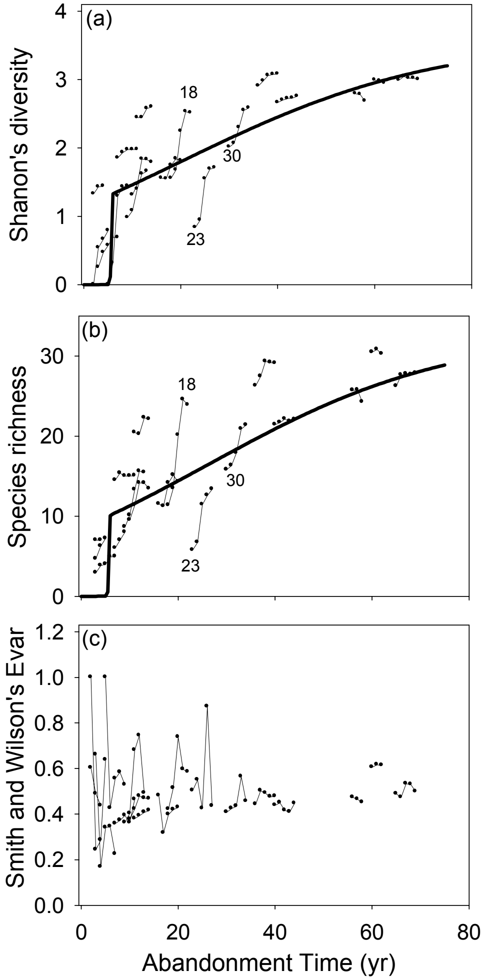

FIGURE 1. Trends of diversity development of sixteen secondary TDF plots ranging from 0 to > 60 yr of abandonment in 2003, plus a mature forest plot. Dots (plot censuses) linked by hairlines represent individual - plot development trajectories from 2003 to 2007. Solid thick lines are chronosequence models fitted to the diversity data of the fourteen secondary plots initially measured in 2003 (≤ 40 yr-old). Numbers inside the graphs mark plots, with their initial age, that showed both large deviations from the expected community trend and high guild-dynamics (see Figure 2 and text for details). Species richness was rarefied to 100 individuals.

The pioneer-guild trends where characterized by strongly right-skewed bell-shaped curves with development maxima that occurred first for density (after 10 yr), then for CA (after 16 yr), and last for BA (after 21 yr; Fig. 2d-f). Mature-guild trends were characterized in turn by s-shaped curves depicting steady developments throughout the modeled period (Fig. 2g-i); their maximum rates of increase (curve inflection points) occurred also at different times: density at 33, CA at 40 and BA at 46 years (Fig. 2g-i). The chronological order was the same as for the pioneer guild. When mature-guild maximum rates of increase occurred, the pioneer-guild was in sharp decline: shifts in dominance from pioneers to mature plants thus occurred, first for density (at ca. 26 yr; range: 17-39 yr, according to the model's 95% confidence bands), then for CA (at ca. 36 yr; range: 31-43 yr), and shortly after for BA (at ca. 38 yr; range: 34-43 yr). Both guilds coexisted anyhow almost throughout the whole studied period.

INDIVIDUAL-PLOT TRAJECTORIES AND DEVIANCES

For the whole community, consistency of individual-plot trajectories with chronosequence trends, based on the 2003 data, varied with the attribute considered and the successional development stage. Consistency was higher at early (< 10 yr) or late (> 40 yr) stages than at intermediate stages (Figs. 1, 2a-c). Diversity attributes were the most variable; their chronosequence trends captured the general direction of change (increase) but several plots differed in the magnitude of change (Fig. 1). For structural development, the chronosequence models nicely described the successional patterns: over 80% of all sample points fell within the 95% confidence intervals of the model. Individual-plot trajectories of BA were mostly parallel to and had the same direction as the chronosequence trend, while, in increasing order, CA and density showed more variability (Fig. 2a-c). Plots that changed at different rates, and sometimes with different directions, than modeled had strong structural changes in either of their guilds (e.g. plots 16, 18, 23 and 30 for density and diversity measures, and plots 23, 36, 40 and 56 for CA; Figs. 1a,b and 2 upper and mid panels).

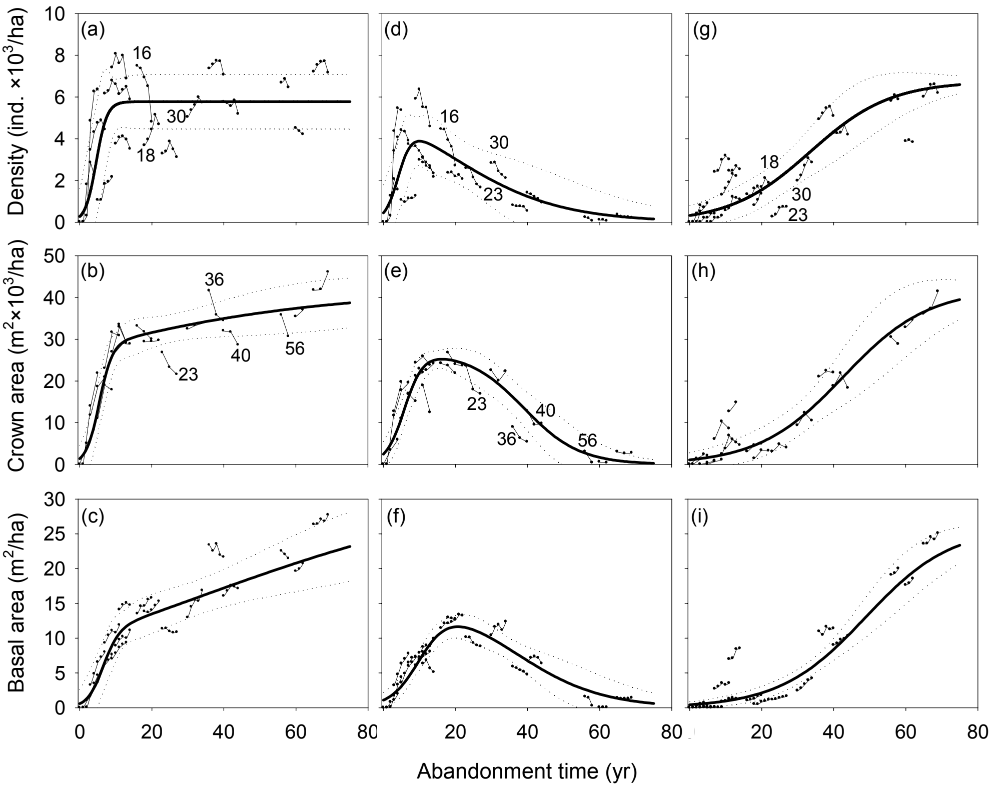

FIGURE 2. Structural development trends of sixteen secondary TDF plots ranging from 0 to > 60 yr of abandonment in 2003, plus a mature forest plot. Dots (plot censuses) linked by hairlines represent individual-plot development trajectories from 2003 to 2007. Solid thick lines are chronosequence models fitted to the structural data of the fourteen secondary plots initially measured in 2003 (≤ 40 yr-old). Dotted lines are the 95% confidence bands of the models. Numbers inside the graphs mark plots, with their initial age, that showed both large deviations from the expected community trend and high guild-dynamics (see text for details). Left panels (a-c) represent the entire plant community; mid-panels represent the pioneer-guild (d-f) and right panels the mature-guild (g-i).

The chronosequence and individual-plot trends for separate guilds were more consistent than for the entire community. Model confidence intervals were narrower and contained more sample points (85%), and most trajectories were largely parallel to the chronosequence trends. From the 102 individual-plot trajectory combinations (attributes × guild), only five had a direction that differed from expected: one of the pioneer's guild CA, two of their BA, and two of the mature's guild CA (Figs. 1e,f,g). Two of these deviations corresponded to the same plot (p10), where numerous large pioneer trees died synchronously after the first census (probably because of a disease), and burned three dry seasons later.

DYNAMICS' TRENDS

During early succession (ca. first 10 yr), growth and recruitment were high (but rapidly decreasing), in contrast to mortality, which was low and slowly increasing (Fig. 3a-c). During the next 30 years, growth decreased slowly. Mortality slightly surpassed recruitment after ca. 15 years, remaining above until advanced succession, when mortality equaled recruitment: in 7 out of 9 plots between 11 to 42 years in average, mortality > recruitment; in the three oldest plots they were close to equal (Fig. 3d).

The steep decline in recruitment and growth was also found for the pioneer guild separately (Fig. 4a,e). Even so, pioneer recruitment extended through the first 10 yr of succession. Recruitment of mature guild species occurred uninterrupted since early succession and increased slightly at mid-successional stages. Their relative growth, although particularly high in the youngest plot, had no significant trend in time (Fig. 4b,f). Mortality of the pioneer-guild was similar to the overall community trend, while mature-guild mortality gradually increased with time (Fig. 4c,d).

CORRELATIONS BETWEEN STRUCTURE AND DYNAMICS

Whole-community mortality was not correlated to any of the community-structure variables. Recruitment and growth decreased with all of them, but most strongly with CA (R=-0.82, $P < 0.001$) and BA (R=-0.87, $P < 0.001$), respectively. Mortality of the pioneer-guild increased with its own guild structure, most strongly with CA (R=0.72, P <0.001). Mature-guild mortality decreased with pioneer-guild's density

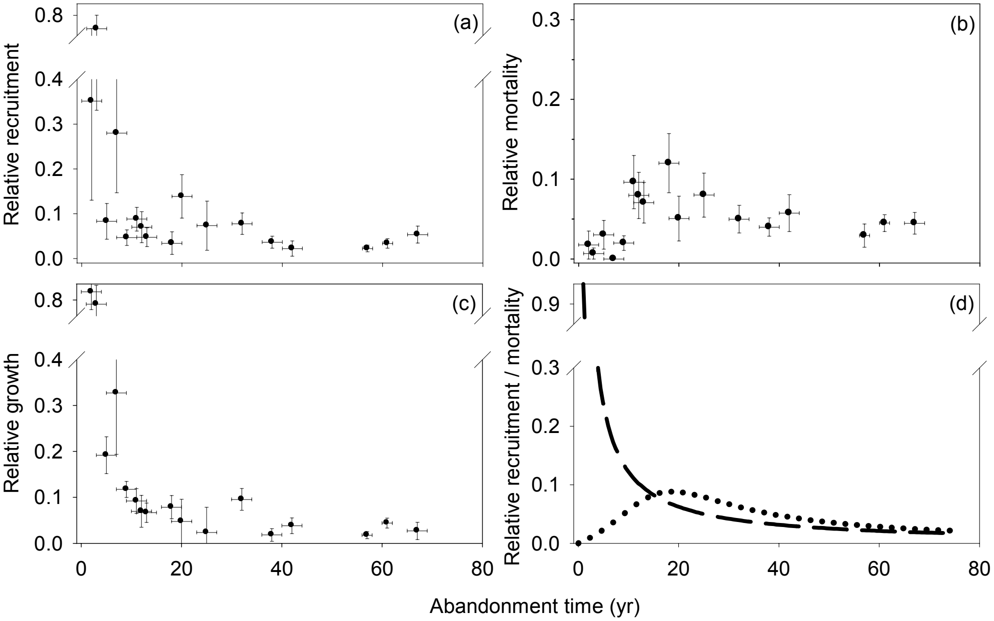

FIGURE 3. Community recruitment (a), mortality (b), and growth (c) of sixteen secondary TDF plots plus a mature forest measured yearly from 2003-2007. Dots represent the average relative dynamics ± SE (vertical error bars) and the range of the plots' abandonment ages for the averaged period (horizontal error bars). For each year, the plot's relative dynamics were calculated as proportions based on the previous year abundance (for mortality and recruitment) and the previous year basal area (for growth). In d, the modeled balance between recruitment (dashed line) and mortality (dotted line) through succession is shown. Models were fitted to the averaged values.

(R = -0.5, P < 0.05) and, as with the pioneer-guild, increased with its own guild structure, most strongly with BA (R = 0.84, P < 0.001). Pioneer-guild recruitment decreased with structural variables of both guilds but strongest with its own guild BA (R = -0.83, P = 0.001), while mature-guild recruitment did not correlate with any of the community-structure variables. Growth of the pioneer-guild increased with its own density (R = 0.68, P < 0.01) and CA (R = 0.57, P < 0.05), but not with its BA, and decreased with the development of mature-guild structure, especially BA (R=-0.82, P<0.001). Mature-guild growth only increased with its own guild structure (more strongly with BA, R = 0.86, P < 0.001).

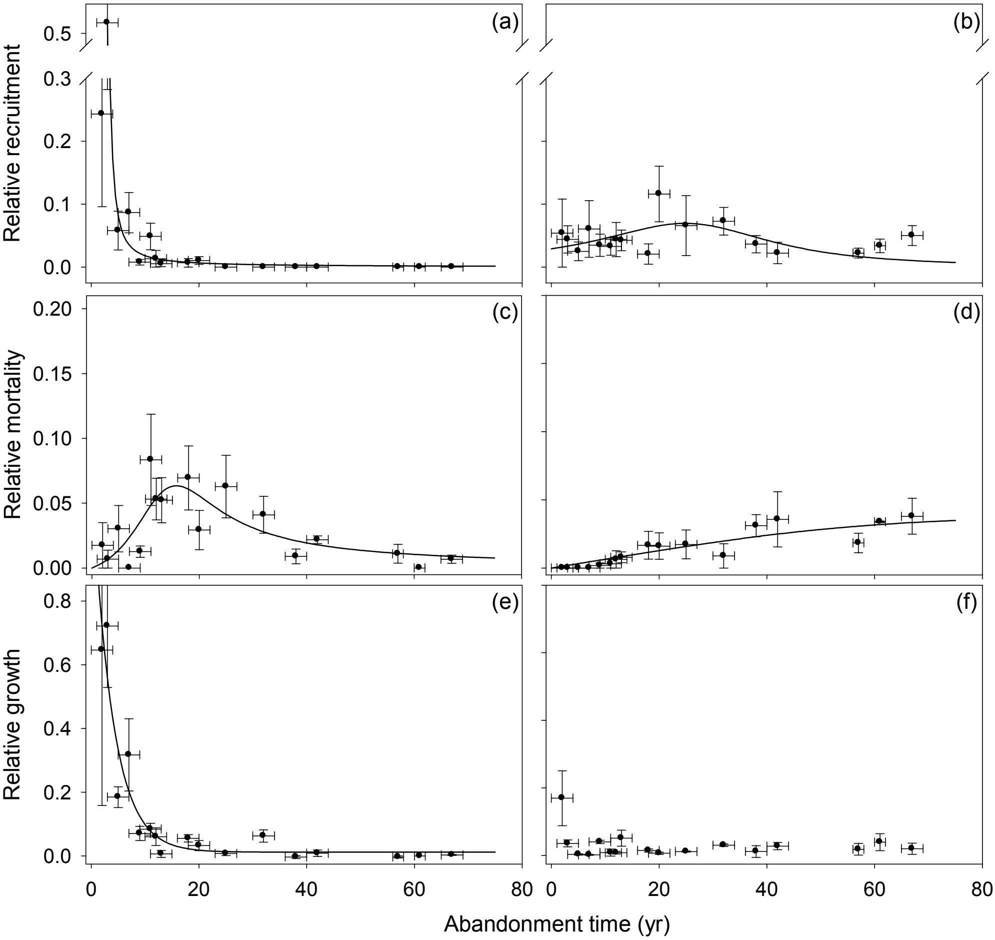

FIGURE 4. Pioneer- (left panels) and mature-guild (right panels) relative recruitment (a,b), mortality (c,d) and growth (e,f) in sixteen secondary TDF plots plus a mature forest measured yearly from 2003-2007. Dots represent the averaged relative dynamics ± SE (vertical error bars) and the range of the plots' abandonment ages for the averaged period (horizontal error bars). Per year, the guild's relative dynamics were calculated as proportions based on the previous year abundance (for mortality and recruitment) and the previous year basal area (for growth) of the entire community. Lines depict successional models fitted to the averaged values.

CHANGES IN SPECIES COMPOSITION

The plots' trajectories of species composition changes showed clear convergent and predictable trends towards old-growth forest in the two MDS axes (Fig. 5). The magnitude of compositional change reduced with age (R = -0.59, P <0.05). Among the structural variables, CA alone could explain the magnitude of changes (R^2 = 0.49, P < 0.01). Increasing crown area led to decreasing change. Among the demographic rates, recruitment alone could explain the magnitude of the changes (R^2= 0.48, P < 0.01): higher recruitment led to higher change.

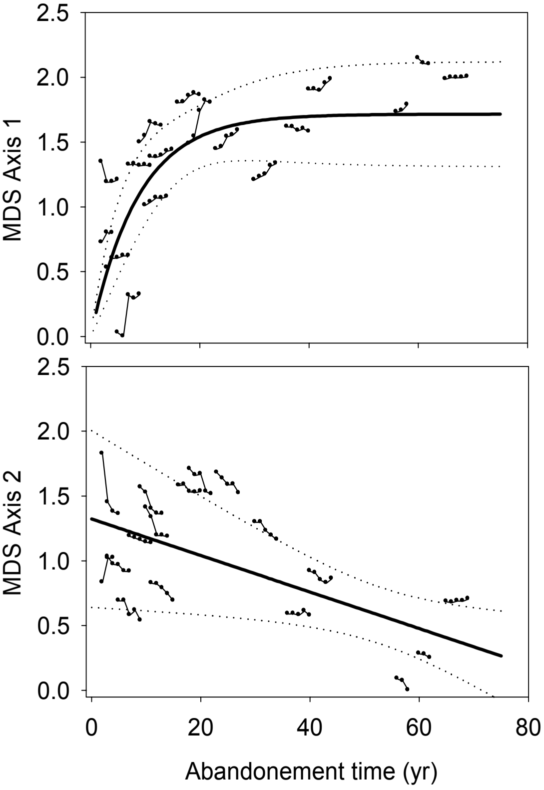

FIGURE 5. Successional change in species composition of sixteen secondary TDF plots plus a mature forest. The individual - plot trajectories from 2003 to 2007 are graphed for each of the two dimensions of a non-metric multi-dimensional ordination performed on the plots' abundance-based Sorensen similarity matrix (see methods for details). Solid thick lines are chronosequence models fitted to the axes scores of the 2003 data points (plots ≤ 40 yr-old). Dotted lines are the 95% confidence bands of the models.

DISCUSSION

Overall, the overlapping time series of individual-plot development indicated clear long-term directional patterns of change in structure and species composition. This implies, as expected, that upon fairly homogeneous historical and environmental (including landscape) conditions, an orderly series of delimited changes takes place during secondary succession and, most significantly, that a common set of deterministic underlying forces are strong drivers of this development.

DEVELOPMENT OF COMMUNITY STRUCTURE AND DIVERSITY

Patterns of community structural development were characterized by a fast phase followed by a slower but steady one that continued through the whole period analyzed. Results show that such community patterns are determined, partly, by the life history characteristics of species belonging to mainly two distinct guilds. Fast structural buildup reflected the high colonization and growth rates of pioneers. After reaching their maximum size, pioneers declined completely but community crown and basal area continued their gradual development with the staggered recruitment and the slow but constant growth of larger-sized mature-forest species.

The contrast in colonization rates, growth rates, and size at maturity between pioneer and mature species is typical to guild-equivalent species in temperate and tropical forests (Bazzaz 1979, Swaine and Whitmore 1988, Turner 2001). Differences in the patterns of biomass change between systems nevertheless arise from differences in tree replacement dynamics (discussed below). In our dry forest, the overlap between the pioneers decline and the growth of mature-forest species into the canopy ensures a continuous increase in CA and BA. In more productive temperate and tropical forests, regeneration suppression early in stand development produces a moderate to long replacement time-lag between the dominants' cohort mortality and the canopy regeneration, so biomass peaks at early-mid succession (Peet 1981, Denslow and Guzman 2000, Guariguata and Ostertag 2001).

A similar but less regular process occurs for tree density. Density was predicted to remain constant after peaking. Nonetheless, average mortality slightly exceeded recruitment in most mid-successional plots (10-30 yr). Individual-plot patterns of density decline were not reflected in the model partly because maximum densities at early and late succession were similar, but mainly because total density reductions were not dramatic (except for the plot with catastrophic death). Net density declines were in fact largely caused by high mortality across all plots during the last (dry) year interval (Fig. 2a-c). The long-term gradual decline in pioneers' density was largely compensated by the continuous increase in individuals of mature-forest species. A similar phenomenon occurs in temperate forests with gradual recruitment and reduced stocking during early succession (Peet and Christensen 1987). By contrast, clear patterns of density decline occur in highly productive systems where stem density in young to mid-aged forests is not only much higher than in old-growth forests but it is also strongly reduced by resource competition (Swaine and Hall 1983, Peet and Christensen 1987, Chazdon et al. 2005, Breugel et al. 2006).

As in other old-field successions, diversity change patterns were not a simple function of time. Variations in diversity measures were clearly coupled to demographic change: large variations followed large changes in the density of pioneer and mature-forest individuals. Although diversity and population dynamics are commonly coupled (Huston and Smith 1987), high population dynamics do not necessarily translate into marked changes in species richness (Chazdon et al. 2007). Successful recruitment by new species, and hence species dispersal, is a crucial component of the large and steep diversity increments occurring with high stem turnover rates (Breugel et al. 2006). The stochastic nature of dispersal may then underscore the large variability of diversity measures. Notwithstanding this variability, Shannon's diversity and species richness had an overall increasing trend. Such trend does not match the humped-back diversity curve that is expected at mid-succession from a prolonged coexistence of pioneer and mature-forest species (Huston and Smith 1987, Sheil 2001). The systems low pioneer diversity combined with a high dominance by a few of them (Lebrija-Trejos et al. 2008) implies that their gradual demise is not as significant to diversity as is the gradual accumulation of mature-forest species.

SUCCESSIONAL DYNAMICS, COMMUNITY DEVELOPMENT AND SPECIES REPLACEMENT

With community development, and as expected from site and resource pre-emption (Pickett et al. 1987), overall tree recruitment and growth decreased, while mortality increased and decreased with a maximum that mainly reflected the pioneers' mortality. Recruitment, mortality and growth patterns were actually very different between guilds. While both pioneer and mature-forest species were present both from seeds and coppice at the onset of succession, only the pioneers recruited abundantly and grew fast at this stage (Figs. 2d, 4a). In terms of the environment, the pioneers early success in this strongly seasonal system is linked to a set of traits that allow them to maximize biomass gain and carbon storage in an environment where vapor pressure deficit and temperature stress are high (e.g. compound leaves, small leaf size, high leaf density, nodulation; Chapter 6).

Pioneer mortality increased and their recruitment was inhibited in parallel with their maximum crown and basal area development. This indicates that competition and self-thinning among pioneers rises with their growth (Fig. 2 mid-panels, 4a, Oliver and Larson 1996, Breugel et al. 2006). The overlap between competition- and senescence-driven (i.e. large trees) density decline supports the idea that successional competition between early colonizers becomes critical later and to a lesser degree in severe than in favorable environments (Walker and Chapin 1987). In tropical humid forests for example, initial stem density can be so high (ca. 8-16 thousand stems/ha) that self-thinning occurs as soon as one year after field abandonment (Breugel et al. 2006, stems ≥ 1 cm dbh), and it may continue for up to 20 years after abandonment (Denslow and Guzman 2000, Chazdon et al. 2005).

Pioneer intra-guild competition and early suppression of recruitment indicate that the pioneers themselves make conditions unacceptable for their persistence. Indeed, the reduction in light availability, temperature and vapor pressure deficit that occurs with crown and basal area increase, constitute more favorable conditions for mature-forest- than pioneer species regeneration (Chapter 6). Accordingly, while the pioneers started their gradual decline after canopy closure, there was a continuous long-term invasion by mature-forest species and individuals as the forest developed (cf. Egler 1954).

In drought stressed environments like ours, plant induced changes in the microclimate ameliorate water relations for individuals that grow below their canopy; facilitation occurs nonetheless as long as the benefits from moisture increase compensate the loss from shoot and root interference, i.e. competition (Callaway and Walker 1997, Holmgren et al. 1997, Valiente-Banuet and Verdú 2008). Mature-forest plant recruitment and growth were not related to the pioneers' structural development. In contrast, their survival was higher when the pioneers were most abundant (before their full development). The abundant mature-forest species in our area are characterized by simple, large leaves with long petioles that are advantageous for reducing self-shading and enhancing light interception per leaf area, but disadvantageous for reducing temperature and evapotranspirational water losses under heating and desiccating conditions (Parkhurst and Loucks 1972, Givnish 1987, Falster and Westoby 2003). Several studies in TDF have shown that establishment of mature-forest species seedlings is largely unsuccessful because of drought stress (Gerhardt and Hytteborn 1992, Swaine 1992, Roth 1999) and that their seedlings survive better in shaded than in open sites (e.g. Lieberman and Li 1992, Hammond 1995, McLaren and McDonald 2003a).

Dispersal enhancement by the pioneers (i.e. indirect facilitation, McDonnell and Stiles 1983, Guevara et al. 1986, Toh et al. 1999) may also be occurring in this forest as with the early development of the canopy structure there is an increase in the number of bird species and guilds that visit the successional stands (Heredia-Morales et al., unpublished data).

Altogether, this is strong evidence that pioneers not only set the conditions for their replacement but actually facilitate it. Even their demise is not attributable to shading by overtopping large-sized mature species, as is common in many temperate forests (McCook 1994, Oliver and Larson 1996). Pioneers aged and decline well before mature-forest plants dominate or even reach maximum development rates. The constancy in the relative growth of mature-forest plants through succession also indicates that their recruitment into the canopy is not dependent on creation of gaps by pioneers as in deeply shaded temperate and tropical forests where they are largely suppressed (Lang and Knight 1983, Saldarriaga et al. 1988, Oliver and Larson 1996, Mesquita et al. 2001, but see Chazdon et al. 2005).

Some degree of inhibition by resource competition between the guilds may occur with the full development of pioneer trees. This is suggested by the slight but significant increase in mature-forest plant recruitment that occurred a few years after large pioneer trees started to decline (indicated by their crown and basal area reduction). The release of resources seems to be nonetheless short, as mature-forest plants recruitment fell again within a few years. The steady increase in mature-forest plant mortality shows in turn that competition within the mature-guild undoubtedly strengthens and takes a predominant role at late successional stages.

Within the span of successional development covered, our results further show that plant interactions as mechanisms of successional replacement are indeed more varied and dynamic (Finegan 1984, McCook 1994) than previously hypothesized (e.g. Connell and Slatyer 1977, Huston and Smith 1987). Interactions occur within and between the guilds with different intensities, durations, and timings, and their shifts result from variations in environmental conditions and the developmental stages and functional relatedness of coexisting plants (Holmgren et al. 1997, Brooker and Kikividze 2008, Valiente-Banuet and Verdú 2008).

We have found important contrasts in processes and mechanisms of community development between forests. In temperate forests, shade-tolerance, competition, and suppression are mayor components of old-field successional change and its models (Huston and Smith 1987, Peet and Christensen 1987, Oliver and Larson 1996). These same ideas have been predominantly applied in models of tropical forest succession (Gómez-Pompa and Vázquez-Yanes 1981, Finegan 1996, Denslow and Guzman 2000). For strongly drought stressed tropical forests, shade actually seems to be more a need than a limitation for survival of mature-forest species. Suppression due to low light levels seems to play a minor role and direct facilitation must be added to competition as an important mechanism in their succession. Less restrictive models of old-field succession need to be developed, at least for tropical forests.

PREDICTABILITY OF SUCCESSION AND THE CHRONOSEQUENCE APPROACH

The individual-plot trajectories of change towards the species composition of the dominant mature or old-growth forest, with rates of change that were highly correlated to community development, is perhaps the most remarkable result given the predominant contemporary view of succession as a largely contingent, idiosyncratic, and therefore stochastic process (Finegan 1984, Vandermeer et al. 2004, Chazdon 2008). It shows that even species composition can follow a directional pathway if the regional pool of species is largely maintained, species dispersal is not hampered, and disturbances create a similar context for vegetation development. This strengthens that succession is not essentially random and that basic and deterministic processes intrinsic to plants and its interactions constitute the successional backbone (McCook 1994, Rees et al. 2001, Cramer et al. 2008).

That succession can have multiple endpoints and be highly variable (in part due to stochastic causes like propagule availability) is nonetheless undeniable. Causes for convergence or divergence in vegetation change are subject to extensive discussion (Gunderson and Pritchard 2002, Chazdon 2003, Temperton et al. 2004). Noteworthy, many of the multiple allogenic factors that influence succession and whose effects have largely motivated the stochastic viewpoints, e.g. landscape and disturbance processes, have as well explicable and predictable outcomes (e.g. Cook et al. 2002, Suding et al. 2004, Fraterrigo and Rusak 2008). Multiple pathways and endpoints are not necessarily synonyms of stochasticity (e.g. Huston and Smith 1987). As Picket et al. (2001) stressed from comparing chronosequence results with > 30 years of longitudinal data of temperate old-field succession: "Explicable local uniqueness rather than random variation is the main point of difference between the patterns…"

Tropical dry forests may be in any case less susceptible to variations produced by allogenic and stochastic factors than more humid and/or productive forests. For instance, TDF have a relatively high percentage of seeds with dormancy and wind dispersion (Khurana and Singh 2001, Vieira and Scariot 2006), species with vegetative reproduction (Murphy and Lugo 1986), and a highly synchronous reproductive phenology to assure germination during the favorable period (Bullock 1995). Combined, these factors diminish the variability introduced by dispersal limitation and the interaction between timing of disturbance and propagule availability. Turnover-rates and the effects of disturbance on community dynamics reduce with decreasing system productivity and resource supply (White and Jentsch 2004, Garnier et al. 2007). Divergence probability reduces together with the species pool size (MacMahon 1981, Chase 2003), while convergence in community composition is promoted by environmental filtering on highly stressed environments (Weiher and Keddy 1995, Holdaway and Sparrow 2006, Chase 2007, Kraft et al. 2008). The length of compositional progression and the window for occurrence of interferences is reduced by the existence of few seral stages and/or lack of pioneers with long life spans (e.g. Janzen 1988, Álvarez-Yépiz et al. 2008, Lebrija-Trejos et al. 2008). The number of alternative stable states in a system decrease together with system complexity and productivity (Gunderson and Pritchard 2002, Chase 2003). Whether these characteristics make succession in TDF, or similarly stressed systems, more predictable or not is a challenging question for future research.

The heterogeneity in the variation within and between community development patterns along succession confirm that organization levels, scales and metrics (i.e. community attributes) must be specifically considered when assessing successional directionality. For instance, Chazdon et al. (2007) pointed out that density trends are highly inconsistent within and between successional studies. By analyzing successional trends at organizational levels lower than the community, i.e. species functional groups, we obtained very discernable patterns (as they hypothesized). Most likely, our analysis of patterns per guild also produced less variable trends than if patterns per species would have been analyzed as species variations are averaged now. In the same line of reasoning, a clear trend in successional species replacement and compositional converge does not imply nor requires a strict sequence of extinctions and arrivals of individual species but of ecologically equivalent species.

As the causal factors of succession, including chance, vary in relative importance with succession (Connell and Slatyer 1977, Walker and Chapin 1987, Chazdon 2008) it is not surprising that pathway variability differed with successional stage. It carries nonetheless another important implication: the time window in which succession is studied strongly affects analysis outputs and interpretations (e.g. Sheil 1999, Woods 2007). Longitudinal data spanning a time frame relevant to the successional progression from early to old-growth forests are hence critical for an adequate appraisal of pathway variability in tropical forest succession. By looking in detail to only a fragment of a long-term phenomenon, the relevance of directional processes could be misjudged.

It is clear from our results that the chronosequence approach is not flawed *per se*. It certainly requires critical evaluation of its assumptions, especially in sites experiencing high landscape and disturbance dynamics. Providing that this is done, chronosequences can be a valuable practical method for system specific evaluation of pathways, formulation of causal hypothesis, and even evaluation of the effects of allogenic factors in successional pathways (e.g. Jacquemyn et al. 2001, Mesquita et al. 2001, Molina-Colón and Lugo 2006). For sound results, a comprehensive chronosequence time-span is as important as fulfillment of its requirements and in combination with longitudinal data, chronosequences provide a powerful tool for vegetation change studies.

FINAL REMARKS

Ideas stressed by defendants of traditionally opposing views of succession were combined to explain succession in this system (see Finegan 1984, for a historical account). Deterministic patterns of species colonization and replacement resulted, to a large extent, from the interplay between species life history traits, community driven changes in the environment, and a non-exclusive set of plant interactions that varied among successional stages, including facilitation. This is not an exclusive expression or explanation of succession but an adequate one to the system under study that may apply to similarly drought-stressed and well connected systems. In understanding succession, the evaluation of the applicability of components of available theories and models proves to be more fruitful than their validation or rejection as a whole. Similarly, succession is not to be seen *per se* as either divergent or convergent, predictable or stochastic but complex. In this respect, the challenge is to understand, at different spatial, temporal and organizational scales, how allogenic factors alter the balance between the stochastic and deterministic (autogenic) forces that drive succession, and what makes some systems more sensitive than others to such alterations.

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SUPPORTING INFORMATION

TABLE S1. List of species, classified as pioneer or mature, occurring in secondary and old-growth forest stands in the tropical dry forest region surrounding the village of Nizanda (16°39′30″ N, 95°00′40″ W), on the Pacific slope of the Isthmus of Tehuantepec, Oaxaca, Mexico.

Pionner-guild
Mimosa acantholoba (Humb. et Bonpl. ex Willd.) Poir. var. *eurycarpa* B.L.Rob., *Acacia cochliacantha* Humb. et Bonpl. ex Willd., *A. farnesiana* (L.) Willd., *Mimosa tenuiflora* (Willd.) Poir., *Piptadenia flava* (Spreng. ex DC.) Benth.
Mature-guild
Acacia picachensis Brandegee, *Adenocalymma inundatum* C.Mart. ex DC., *Aeschynomene compacta* Rose, *Amphipterygium simplicifolium* (Standl.) X.Cuevas-Figueroa, *Apoplanesia paniculata* C.Presl, *Arrabidaea floribunda* (Kunth) Loes. *A. costaricensis* (Kränzl.) A.H. Gentry, *Bourreria purpusii* Brandegee, *Bursera excelsa* (Kunth) Engl., *Bursera simaruba* (L.) Sarg., *Caesalpinia coriaria* (Jacq.) Willd., *C. exostemma* DC., *C. platyloba* S.Watson, *C. sclerocarpa* Standl., *Cayaponia racemosa* (Mill.) Cogn., *Capparis incana* Kunth, *Capparis indica* (L.) Druce, *Casearia tremula* (Griseb.) Griseb. ex C.Wright, *Castela retusa* Liebm., *Ceiba parvifolia* Rose, *Chloroleucon mangense* (Jacq.) Britton et Rose, *Cissus verticillata* (L.) Nicolson et C.E.Jarvis, *Cnidoscolus megacanthus* Breckon, *Coccoloba liebmannii* Lindau, *Combretum farinosum* Kunth, *Cordia curassavica* (Jacq.) Roem. et Schult., *Cordia dentata* Poir., *Cordia truncatifolia* Bartlett, *Croton fragilis* Kunth, *Croton niveus* Jacq., *Croton pseudoniveus* Lundell, *Enterolobium cyclocarpum* (Jacq.) Griseb., *Esenbeckia collina* Brandegee, *Eugenia* aff. *salamensis* Donn.Sm., *Euphorbia schlechtendalii* Boiss., *Exostema caribaeum* (Jacq.) Roem. et Schult., *Forchhammeria pallida* Liebm., *Gliricidia sepium* (Jacq.) Steud, *Grajalesia fasciculata* (Standl.), Miranda,

Mature-guild (continuation).

Gyrocarpus mocinnoi Espejo, *Havardia campylacantha* (L.Rico et M.Sousa) Barneby et J.W.Grimes, *Hemiangium excelsum* (Kunth) A.C.Sm., *Heteropterys cotinifolia* A.Juss., *Hintonia latiflora* (Sessé et Moc. ex DC.) Bullock, *Ibervillea* aff. *hypoleuca* (Standl.) C.Jeffrey, *Iresine* aff. *interrupta* Benth., *Jacaratia mexicana* A.DC., *Jacquemontia mexicana* (Loes.) Standl. et Steyerm., *Jacquinia macrocarpa* Cav., *Jatropha alamanii* Müll.Arg., *Karwinskia humboldtiana* (Roem. et Schult.) Zucc., *Krugiodendron ferreum* (Vahl) Urb., *Lasiocarpus salicifolius* Liebm., *Lonchocarpus emarginatus* Pittier, *Lonchocarpus lanceolatus* Benth., *Lonchocarpus torresorum* M.Sousa (sp. nov. ined.), *Lysiloma divaricatum* (Jacq.) J.F.Macbr., *Malpighia emarginata* Sessé et Moc., *Malpighia mexicana* A.Juss., *Manihot oaxacana* D.J. Rogers et Appan, *Marsdenia coulteri* Hemsl., *Marsdenia gallardoae* Lozada-Pérez, *Mimosa goldmanii* B.L.Rob., *Myrospermum frutescens* Jacq., *Nissolia microptera* Poir., *Nopalea karwinskiana* (Salm-Dyck) K.Schum., *Pachycereus pecten-aboriginum* (A.Berger) Britton et Rose, *Physalis arborescens* L., *Pilosocereus collinsii* (Britton et Rose) Byles et G.D.Rowley, *Piptadenia obliqua* (Pers.) J.F.Macbr., *Randia thurberi* S.Watson, *Ruprechtia pallida* Standl., *Schoepfia mexicana* A.DC., *Senna atomaria* (L.) H.S.Irwin et Barneby, *Serjania triquetra* Radlk., *Sideroxylon obtusifolium* (Roem. et Schult.) T.D.Penn. subsp. *buxifolium* (Roem. et Schult.) T.D.Penn., *Solanum glaucescens* Zucc., *Solanum hazenii* Britton, *Stemmadenia obovata* (Hook. et Arn.) K.Schum., *Tabebuia chrysantha* (Jacq.) G.Nicholson, *Tabebuia impetiginosa* (Mart. ex DC.) Standl., *Tecoma stans* (L.) Kunth, *Cascabela ovata* (Cav.) Lippold, *Thouinia villosa* DC., *Thouinidium decandrum* (Bonpl.) Radlk., *Zanthoxylum* aff. *caribaeum* Lam., *Zanthoxylum fagara* (L.) Sarg., *Ziziphus amole* (Sessé et Moc.) M.C.Johnst.

CHAPTER 5

Successional and Seasonal Changes in the Abiotic Environment of a Tropical Dry Forest

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ABSTRACT

During secondary forest succession the vegetation develops along predictable lines from low open vegetation with mainly pioneer species to denser vegetation with mainly shade tolerant mature species. Environmental conditions in the forest understory are thus thought to develop along predictable lines as well. We predicted that during tropical dry forest secondary succession the understory environment would change from high light, high air and soil temperature, high vapor pressure deficit and low soil water availability early in succession to low light, low air and soil temperatures, and high relative humidity and soil water availability later in succession. We further predicted that spatial heterogeneity and seasonal differences would increase with successional time. We used 17 forest plots covering a chronosequence of >65 years after agricultural abandonment to test these predictions. Light availability, air and soil temperature indeed decreased with time after abandonment, while relative humidity increased. Change in soil water availability was not linear; it increased with early-successional development up to canopy closure and decrease with further vegetation development. Vegetation development (we used basal area) was the driving factor of all these changes. As dry forests have a simple vertical structure light reduction was not very strong while other variables changed only very gradually. Season affected all parameters, with dry season values being harsher than wet season values: more light, higher air and soil temperatures, lower relative humidity. Interactions showed that seasonal differences change along succession: strong successional gradients are created with leaf development during the wet season and fade during the dry season. Environmental heterogeneity was higher in the wet than in the dry season, and larger for resources (i.e. water and light) than for conditions (air and soil temperatures, relative humidity and vapor pressure deficit). Such heterogeneity implies differential microhabitats for growth during the wet season. We conclude that during TDF succession the wet season is most important for plant establishment and growth, while the dry season is crucial for their survival. Temperature, relative humidity and vapor pressure deficit show to be more important than light availability during dry forest succession.

INTRODUCTION

During secondary succession community structure and complexity increase markedly with profound consequences for environmental conditions. Forest density, canopy openness and architecture, and vertical stratification of the forest drive the light environment in temperate and tropical forests (Brown and Parker 1994, Kabakoff and Chazdon 1996). Community composition additionally determines light extinction coefficients of forest canopies (Canham et al. 1994). Concurrently, temperature and vapor pressure deficit conditions change (Brown 1993, Heithecker and Halpern 2007). Soil water contents within a forest depend on the total foliage density in a site, its vertical distribution, and the presence or absence of soil cover (e.g. litter, Camargo and Kapos 1995, Marthews et al. 2008).

Environmental conditions, in turn, co-determine which, where, and when species can regenerate. They affect plant growth and survival, population dynamics, biotic interactions, and thus community dynamics (e.g. Holmgren et al. 1997, Davies 2001, Loik and Holl 2001). They also affect soil biota (De Deyn et al. 2004) and ecosystem functioning by influencing nutrient decomposition and cycling (e.g. Descheemaeker et al. 2006, Mayer 2008). Spatial heterogeneity in environmental conditions (e.g. variability in habitat patches) is an important component of environmental variability and may have large consequences as well (Levins 1968). It is related, for example, to variation in population genotypes and to differential emergence, survivorship, and growth of individuals and species within the same habitat (Jones 1992, Bazzaz 1996). It can also be an opportunity for species with different resource requirements to coexist (Ricklefs 1977, Questad and Foster 2008) or, inversely, a cause of low species diversity if the environmental variation represents conditions outside the species' tolerance ranges (Loucks 1970).

Temporal environmental variability (i.e. seasonality) also strongly affects plant growth and development (Larcher 2003). It can increase or decrease environmental heterogeneity (Hennenberg et al. 2008), and interact with it to affect species performance and distribution: e.g. conditions at a site can be favorable during one season but detrimental in another (Young and Mitchell 1994, Warren 2008).

Successional changes in environmental conditions are expected to encompass changes in averages, spatial and temporal heterogeneity. Such changes are likely to differ strongly between dry and wet tropical forests; dry forest are strongly seasonal, have a more simple tridimensional architecture of the plant cover, a different species composition and diversity structure, and many are largely leafless for several months in a year (Murphy and Lugo 1986, Mooney et al. 1995). As such, environmental changes during succession are expected to be less marked in dry compared to wet tropical forests and to differ strongly between seasons, especially in dry forests. However, only few studies have recorded environmental conditions for tropical dry forests (e.g. McLaren and McDonald 2003b) and we are aware of only one study (i.e., Pinker 1980) that specifically addresses tropical dry forest microclimate, though in an evergreen dry forest and only under contrasting open- vs. closed-canopy sites.

Here we present environmental data for tropical dry forests (TDF) covering a very large successional gradient (0- 65 yr) and including a mature forest. We determine the range of environmental conditions available to seeds and seedlings in TDF and establish the relationships between microclimate variation, community structure and climate seasonality. We specifically ask: How do average environmental conditions and spatial variation therein change as a function of seasonality and fallow age? To what extent are they explained by forest structure? The results are discussed in terms of their implication to plants and vegetation development.

METHODS

The study was conducted on the hilly landscape surrounding the village of Nizanda (16°39′30″ N, 95°00′40″ W) on the Isthmus of Tehuantepec, Oaxaca, Mexico. The area is characterized by a distinct dry season lasting 6-7 mo (Nov-May), in which less than ten percent of the ca. 900 mm of mean total annual rain occurs. Mean annual temperature is ca. 26°C. The main forest type formation is a low-statured (ca. 7−8 m) tropical dry to very dry deciduous forest (> 75% of the species are deciduous), with few prominent trees attaining 15 m. It has neither a clear vertical stratification nor a distinct dominance of any species; in fact, many are rare (Pérez-García et al. 2001).

Although the region still has large areas of well-preserved mature forest, patches of secondary forest derived from abandoned agricultural fields (mostly maize) occur on many hills around the village. After their abandonment, community structure and species composition change markedly with successional development (Lebrija-Trejos et al. 2008). The environmental change associated to this development was assessed by measuring photosynthetically active radiation (PAR), temperature (T) of the air, relative humidity (RH), soil T, and soil water potential (SWP) in the understory of seventeen fallows with abandonment times ranging from < 1 yr to ca. 65 yr, plus a mature forest. Fenced plots of 30 × 30 m have been established in these sites for monitoring vegetation development; this includes144 2 x 2 m quadrates placed regularly in the plots (8 quadrates/plot) for measuring regeneration (see Chapter 4 for details on plot selection, layout and characterization). In or near these quadrates the environmental measurements were taken. Plot ages were defined by combining information obtained from interviewing land-owners and from chronological analyses of tree rings (Brienen et al. 2009). The reliability of the chronosequence has been proved by the consistency between chronosequence-derived successional trends and the individual-plot's trajectories of development (Chapter 4).

Environmental measurements were taken during the rainy season (late May–November), when foliage peaks, and during the largely leafless dry season (December-May). PAR was measured with Licor quantum sensors (Li-190, LI-COR, Lincoln, Nebraska, USA) set at 50 cm above soil level in seven randomly-chosen quadrates per plot. Another sensor was raised above the canopy to calculate light availability as the percentage PAR reaching the understory (%PAR). PAR measurements during one full day have been shown to provide good estimates of long-term light conditions of differing understory microsites (Engelbrecht and Herz 2001). We used two full days per plot. Sensors were placed simultaneously in two plots to record 10 minutes averages with a 5 seconds sampling interval. After recording a faultless two-day period, sensors were moved to two other plots until all plots were characterized.

Daylight Air T and RH were logged also at 50 cm above soil level every hour during ca. 1.5 mo per season (the approximate length of the PAR measurements period). We randomly placed three HOBO Pro Temp/RH dataloggers (Onset, Bourne, Massachusetts, USA) in ten plots and two/three HOBO Pro Temp dataloggers in six/two plots. Simultaneous records of temperature and RH were used to calculate air vapor pressure deficit (VPD; $VPD = VP_{saturated\ air} - VP_{air}$; $VP_{air} = VP_{saturated\ air} \times RH/100$).

Soil T was measured using waterproof digital thermometers with 12.7 cm-long probes. Thermometers were placed in the same quadrates where soil samples were taken for SWP measurements. Temperature was registered every 3 h from 07:00 to 22:00 h during the second day of PAR recordings. For each recording, a relative measure of soil temperature (T_{rel}) was calculated to compare between plots (soil T_{rel} = soil temperature - ambient temperature; ambient temperature was registered by a meteorological station located in an open field in the study area).

The SWP was calculated using the filter-paper method (Leong et al. 2002), which allows measurements down to -100 MPa. Soil samples (0–10 cm depth) were taken within an overcast day in all plots, from the edge of six quadrates of a plot. The samples were individually sealed in 150 cm^3 plastic jars with three Whatman No. 42 filter paper discs (55 mm diameter; Whatman plc, Maidstone, Kent, UK) placed in the middle of the jar. Samples were left to equilibrate during two weeks inside an isolated container. Afterwards, SWP was calculated following the methods of the D5298-03 American Society for Testing and Materials International standard and using the formulas of Leong et al. (2002).

Average conditions for all variables were obtained by calculating the daily means per quadrat/datalogger, averaging them to obtain the quadrat's/datalogger's mean, and averaging these in turn to obtain the final condition per fallow. As a measure of the fallow's environmental heterogeneity (in space), we calculated the coefficient of variation (CV) by dividing this final average by its standard deviation (×100). The CV for temperature was done using the absolute temperature data, as the CV of means equal to zero is undefined or varies disproportionately with small changes for means close to zero.

The successional trends of change of the understory environment were analyzed using average conditions and CVs plotted against fallow age. For a simple description of these trends that could account for curvilinear relationships, we used GraphPad Prism v. 5.00 for Windows to fit a series of nonlinear models with a maximum of three parameters, and used the Akaike's information criterion corrected for small sample sizes to select the model that best fitted the data with a minimum number of parameters (Motulsky and Christopoulos 2004). This included polynomial, logarithmic, power, and exponential models commonly used to describe biological responses in time (Ratkowsky 1990). The effect of seasonality on the average conditions and their heterogeneity was assessed by performing a repeated measurements ANCOVA using fallow age as covariate. The interaction of seasonality with fallow age was included in the analysis. If needed, variables were $\log_{10}$ or square-root transformed to improve normality and homoscedasticity. The test's sphericity condition was met in all cases (Quinn and Keough 2002).

To illustrate the daily march of environmental conditions we selected four plots representative of the successional gradient: a recently abandoned field, an early-mid successional fallow (9 yr-old), a mid-late one (42 yr-old) and an old-growth forest. Each point in time is the average of the measurements per quadrat/datalogger.

The relationship between forest structure and environment was analyzed using basal area (BA) as a measure of forest structure, as leaf area and aboveground biomass scale up with BA (Chiba 1998, Enquist 2002). Pearson's and Spearman's correlations were performed for this purpose. The same analyses were done using fallow age and the results compared to those of BA to evaluate its use in the context of successional development. The fallows' total basal areas were calculated using the data of individuals ≥ 1 cm DBH.

Finally, a PCA of environmental variables was performed to reveal the major gradients of environmental variation along succession. To include the variation in VPD (an important indicator of transpirational demand) we estimated missing VPD values from the plot's air T measurements. Interpolations were obtained from fitting a linear function to the data of the 10 plots in which both variables were evaluated (VPD = 0.287 × air T - 7.0581, $R = 0.95$, $P < 0.01$). The same procedure was used for RH but this variable was excluded from the PCA ordination and was afterwards overlaid on the PCA plot. BA was also overlaid to visualize its relationship with the gradients. As variables had different scales, they were relativized by their standard deviates (trait means=0, variances=1).

RESULTS

SEASSONAL AND SUCCESSIONAL CHANGES IN ENVIRONMENTAL CONDITIONS

For all environmental variables evaluated, the average environment differed strongly with season, and to a lesser extent with fallow age (Table 1). There was a significant season × fallow age interaction for all variables but SWP, indicating that successional trends varied with season. In most cases, abiotic conditions changed with fallow age in the wet season, but not in the dry season (Fig. 1). Spatial variation in abiotic variables differed with season only for three variables (%PAR, VPD, SWP), and for these variables the heterogeneity was higher in the wet than in the dry season (Table 1). Spatial variation was highest for SWP and %PAR, moderate for VPD, and relatively low for the other environmental variables (Fig. 1).

The amount of light reaching the forest understory reduced steeply within the first 10 yr of succession, more strongly so in the wet season (from ca. 75 to 15% PAR) than in the dry season (from ca. 95 to 45%). After the first 10 years, %PAR changed little (Fig. 1a). The within-plot heterogeneity in light availability was only below that of SWP. The average CV of light availability was 38% in the wet season vs. 19% in the dry season. In both seasons the CV increased with fallow age. It showed an optimum around 30 yr in the wet season, and a saturating response in the dry season (Fig. 1b).

TABLE 1. Results of the repeated measures ANCOVAs for the averages and the coefficients of variation of six environmental variables measured in 17 tropical dry forest fallows (secondary successional sites), plus a mature forest site in Nizanda (Oaxaca), Mexico, in two seasons (rainy and dry). Time since abandonment in fallows ranged from 1 to 65 yr. Fallow age was used as the covariate. Averages were obtained by calculating the daily means per quadrat/datalogger, averaging them to obtain quadrat/datalogger means, and then averaging these to obtain a final condition per fallow.

	Average		Coefficient of variation	
	$F_{(df)}$	P	$F_{(df)}$	P
PAR (percent of open sky)				
Season	$50.74_{(1,16)}$	<0.001	$53.40_{(1,16)}$	<0.001
fallow age	$10.53_{(1,16)}$	<0.01	$0.10_{(1,16)}$	n.s.
Season * fallow age	$7.77_{(1,16)}$	<0.05	$6.46_{(1,16)}$	<0.05
Air temperature				
season	$85.76_{(1,16)}$	<0.001	$0.20_{(1,10)}$	n.s.
fallow age	$7.81_{(1,16)}$	0.01	$0.10_{(1,10)}$	n.s.
season * fallow age	$4.74_{(1,16)}$	<0.05	$0.46_{(1,10)}$	n.s.
Relative humidity				
season	$315_{(1,8)}$	<0.001	$1.69_{(1,7)}$	n.s.
fallow age	$4.17_{(1,8)}$	n.s.	$2.76_{(1,7)}$	n.s.
season * fallow age	$15.49_{(1,8)}$	<0.01	$0.04_{(1,7)}$	n.s.
Vapor pressure deficit				
season	$27.17_{(1,8)}$	<0.001	$6.74_{(1,7)}$	<0.05
fallow age	$1.56_{(1,8)}$	n.s.	$1.73_{(1,7)}$	n.s.
season * fallow age	$13.01_{(1,8)}$	≤0.01	$1.04_{(1,7)}$	n.s.
Relative soil temperature				
Season	$5.18_{(1,16)}$	<0.05	$1.68_{(1,16)}$	n.s.
fallow age	$2.29_{(1,16)}$	n.s.	$0.57_{(1,16)}$	n.s.
season * fallow age	$5.06_{(1,16)}$	<0.05	$2.15_{(1,16)}$	n.s.
Soil Water Potential				
Season	$470_{(1,16)}$	<0.001	$33.24_{(1,16)}$	<0.001
fallow age	$0.04_{(1,16)}$	n.s.	$1.19_{(1,16)}$	n.s.
season * fallow age	$0.00_{(1,16)}$	n.s.	$0.00_{(1,16)}$	n.s.

The wet season understory environment was hotter (overall mean daily air temperatures = 30.5°C) than the dry season one (28.8 °C). With increasing fallow age the understory environment became cooler, though this trend was only significant in the wet season.

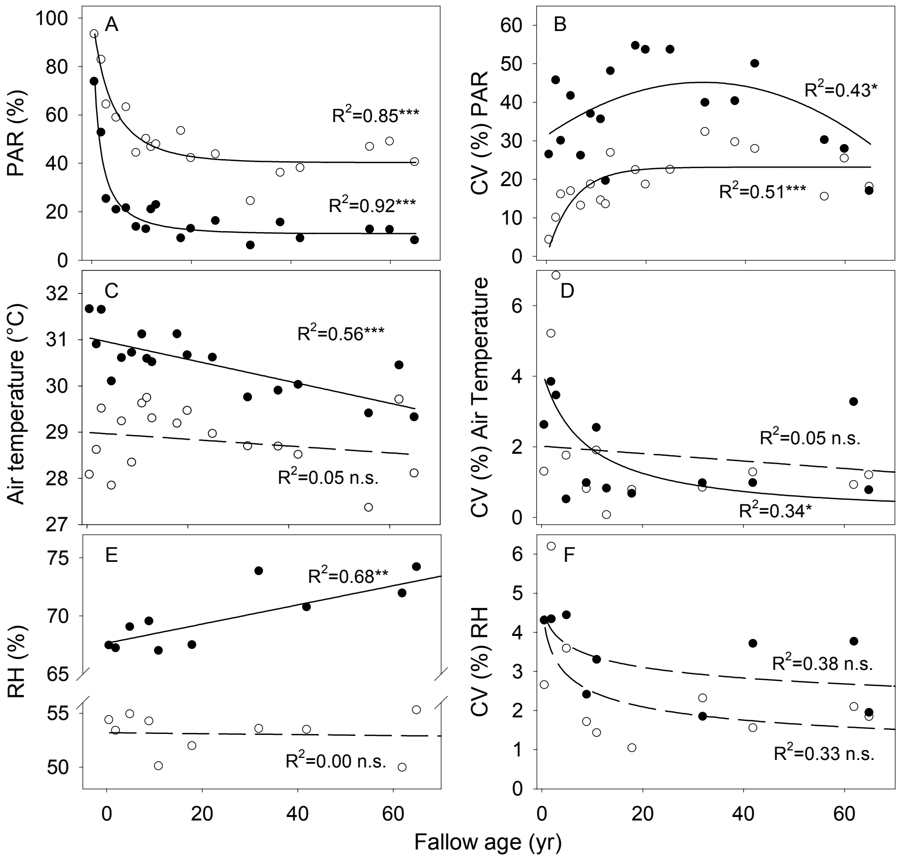


FIGURE 1. Developmental trends of averages (left) and coefficients of variation (CV; right) of environmental conditions in 17 tropical dry forest fallows plus a mature forest site. Fitted models (polynomial, logarithmic, power or exponential) had a maximum of three parameters and were chosen through Akaike's information criterion adjusted for small sample sizes. Black circles indicate data from the wet season, open circles are data from the dry season (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). PAR = photosynthetically active radiation; RH = relative humidity; VPD = vapor pressure deficit; T = temperature; and SWP = soil water potential.

The spatial heterogeneity in air temperature did not vary between seasons and was generally low (highest CV < 7%). Nonetheless the dry season showed a curvilinear decrease in spatial temperature variation with fallow age (Fig 1d).

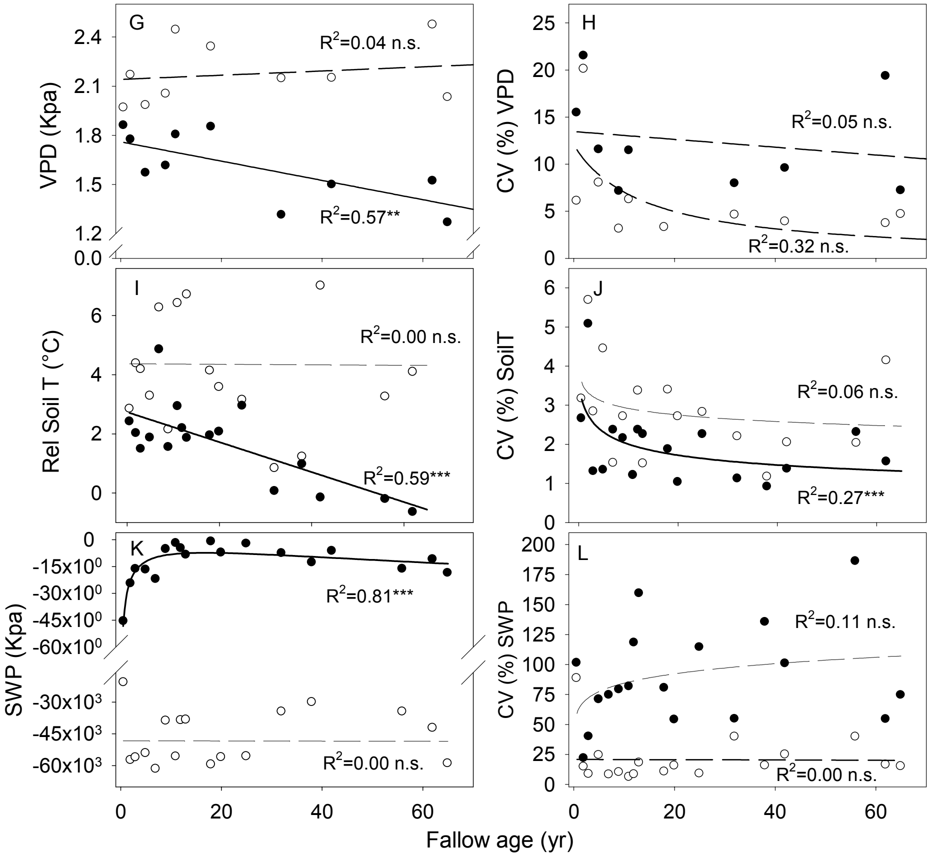
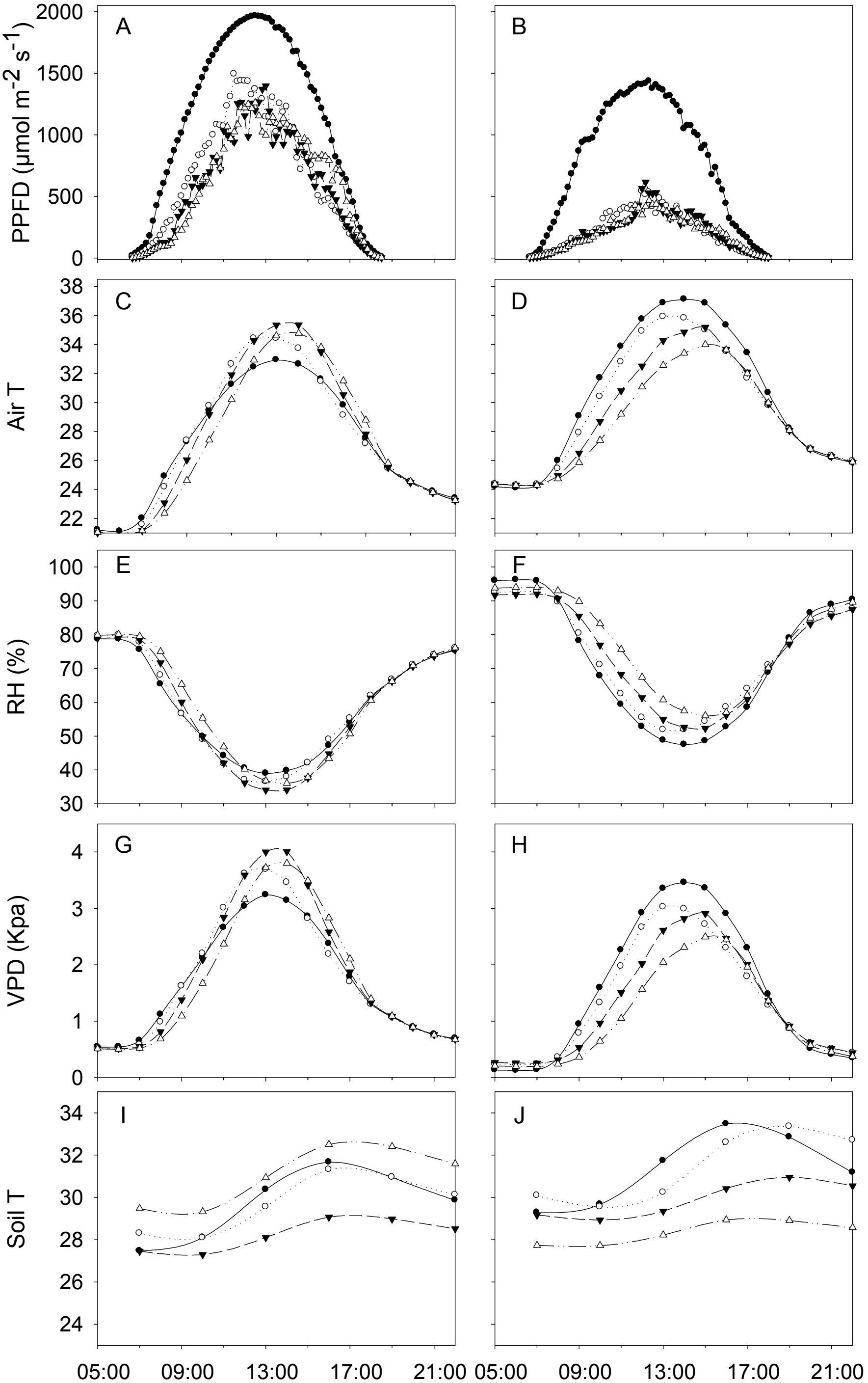


FIGURE 1 (continued).

As expected, the wet season was more humid (Av RH = 70%) and with lower VPD (Av = 1.6 KPa) than the dry season (Av RH = 53%, Av VDP = 2.2 KPa). In the wet season RH increased and VPD decreased with fallow age, whereas in the dry season no successional trend was observed (Fig. 1e,g). From young to old fallows, mean RH increased ca. 10%, and mean VPD decreased ca. 0.5 KPa. The spatial variation of VPD was below %PAR and SWP but yet considerable (with CVs up to 22%) while that of RH was low (Fig. 1f,h). The general pattern of higher heterogeneity in the wet season was only significant for VPD (Av CV = 11.7 and 5.3% for the wet and dry season; Table 1). The heterogeneity of RH or VPD was independent of fallow age in either season.


A
B
C
D
E
F
G
H
I
J
PPFD (μmol m^{-2} s^{-1})
0
500
1000
1500
2000
Air T
22
24
26
28
30
32
34
36
38
RH (%)
30
40
50
60
70
80
90
100
VPD (Kpa)
0
1
2
3
4
Soil T
24
26
28
30
32
34
05:00
09:00
13:00
17:00
21:00
Hour

Patterns in soil temperature mirrored those of air temperature (Fig. 1i; Table 1). Relative soil temperatures in the wet season were in average 1.6 °C above ambient temperature while their average in the dry season was much higher: 4.4 °C above. The wet-season soil-temperature decreased with fallow age from above ambient temperature in early and mid succession to below ambient temperatures in late successional and old-growth forests (Fig. 1i). Soil water potentials were considerably lower in the dry season (Av = -48 MPa) compared to the wet season (Av = -13 KPa). SWP sharply increased within the first ten years of succession and declined gradually afterwards (Fig. 1k). The spatial heterogeneity of soil temperature did not differ between seasons but showed a significant logarithmic-decline with fallow age in the wet season (Fig. 1l). The spatial heterogeneity of SWP in the wet season was very high throughout succession (Av CV= 89%; Fig. 1j).

DIURNAL PATTERNS

The daily course of light levels in two young and two old plots (< 1 yr, 9yr and > 40 yr-old) illustrate that, despite the significant dry-season decline in mean percentage PAR with fallow age, a considerable amount of light reaches the understory. The three older plots had several hours with PAR levels between 1000-1500 µmol photons m^{-2} s^{-1}. Most of the day, these dry-season PAR levels were well above the midday maxima in the wet season (ca. 500 µmol photons m^{-2} s^{-1}; Fig. 2 a,b). This variability with fallow age and between seasons implies large differences in total daily PAR: the youngest fallow had a total daily PAR of 48.9 and 32.5 mol m^{-2} for the dry and wet season while in the oldest plot (mature forest) this was 26.3 mol m^{-2} in the dry and 8.2 mol m^{-2} in the wet season.

FIGURE 2. Daily marches of environmental conditions measured in four plots selected to represent the successional gradient of the tropical dry forest in Nizanda, Oaxaca, Mexico. Closed circles = recently abandoned fallow; open circles = 9-yr old fallow; closed triangles = 42-yr old fallow; open triangles = mature forest. PPFD = Photosynthetic photon flux density; T = temperature; RH = relative humidity; VPD = vapor pressure deficit. Left panels = dry season; right panels = wet season.

Around midday hours of a dry-season day, differences between the youngest and oldest plots reached up to ca. 3°C for air temperature, 6% for RH and 1 KPa for VPD (Fig. 2 c,d,e). The two oldest plots were hotter, less humid and had higher VPD than the two youngest plots. These dry season rankings were, however, not consistent during the course of the day. In early hours young plots were less humid and had higher temperatures and VPD than older plots. Wet season daytime patterns in contrast, not only showed large differences for longer times but also consistent rankings that clearly exemplified the successional gradient. From 09:00-16:00 h, the young fallow and the old-growth forest showed clear differences: 2.9 to 4.7 °C for air temperature (mean air T ranges = 29.1-37.1 and 25.8-34.0 °C, respectively), 7.5 to 16.3% for RH (mean RH ranges = 47.5-78.1 and 57.4-89.81%), and 0.6 to 1.4 KPa for VPD (mean VPD ranges = 1.0-3.5 and 0.4-2.5 KPa; Fig. 2d,f,h).

Day courses for absolute soil temperatures show that they were not necessarily higher in the wet than in the dry season (Fig. 2i,j). Only in the wet season both old plots had absolute lower temperatures than the young plots. Daily oscillations in the wet season were higher in the youngest than in the oldest plots (between 3.8-4.2 °C for the young plots and 1.7-2.0 °C for the old plots) but this was not the case in the dry season (e.g. 3.2 °C for both a young and an old plot). Daily courses for the four plots were more similar in the dry than in the wet season. In the wet season the youngest plot followed more closely the daily cycle for air temperature and heated and cooled down notably faster than the older plots (Fig. 2i,j).

ARE ENVIRONMENTAL CONDITIONS BETTER RELATED TO FALLOW AGE OR FOREST STRUCTURE?

All environmental variables but SWP showed a strong correlation with the fallows' basal area. Most correlations were in fact stronger with BA than with fallow age (Table 2). PAR was the exception probably because the development of an understory with stems < 1 cm DBH is not taken into account in the BA calculations. The successional trend in SWP indicated that the relationships of the environment with community structure are not always linear: SWP showed a strong non-linear relationship to basal area (Fig. 3).

TABLE 2. Results of Pearson's (first five variables) or Spearman's (soil water potential) correlation analyses between environmental variables and fallow's age and basal area (BA) for 17 tropical dry forest fallows plus a mature forest site in Nizanda (Oaxaca), Mexico. Asterisks next to figures for soil water potential indicate that they represent the non-parametric correlation coefficient ρ.

	Age		BA	
Environmental variable	*r*	*P*	*r*	*P*
PAR (percent open sky)	-0.84	<0.001	-0.74	<0.001
Air temperature	-0.76	<0.001	-0.81	<0.001
Relative humidity	0.79	<0.01	0.80	<0.01
Vapor pressure deficit	-0.73	<0.05	-0.74	<0.05
Relative soil temperature	-0.64	<0.01	-0.66	<0.01
Soil water potential	0.28*	n.s.	0.24*	n.s.

MULTIVARIATE AXES OF ENVIRONMENTAL VARIATION

The PCA of the environmental conditions during the wet season represented 60.4% of the variation on its first axis and 27.0% on its second axis. Environmental variables that significantly loaded (P < 0.05) with the first axis were in order of importance air T > VPD > RH > PAR > soil T (all loading ≥ 0.7; Fig. 4). SWP had a high significant loading with the second axis (-0.83), to which PAR also loaded significantly (0.54). The environmental vectors in the PCA further show that temperature variables, RH and VPD are highly correlated among themselves but less so to PAR (all correlations significant at P < 0.05; min R = 0.48 between PAR and soil T). PAR was the only variable significantly correlated to SWP (R = 0.65, P < 0.01). BA, as a measure of community structure, strongly correlated with the first

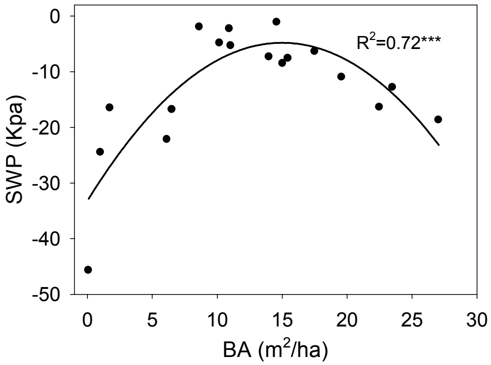


FIGURE 3. Model fitted to describe the relationship between soil water potential (SWP) and successional community structure, as indicated by basal area (BA); *** = $P < 0.001$.

PCA axis ($R= 0.88$, $P < 0.001$). The PCA for the dry season confirmed that the relationship between environmental gradients and fallow age or BA is lost. Yet, its major axis, which explained 48.5% of the environmental variation, still strongly and mainly represented air and soil T, VPD and RH (i.e. they loaded high on the main axis; data not shown).

DISCUSSION

AVERAGE CHANGES IN ENVIRONMENTAL CONDITIONS DURING TDF SUCCESSION

Significant environmental changes occur along succession but mainly during the wet season, when most species have leaves and are physiologically active (cf. Young and Mitchell 1994, Hennenberg et al. 2008). With forest development, the early successional environments changed from sunny to shady, hot to cool, and dry to moist (Fig. 1). These successional changes are parallel to those in other temperate and tropical forests in qualitative terms (e.g. Fetcher et al. 1985, Bazzaz 1996) but not in quantitative terms.

As in other forests, light availability declined sharply with the early and fast growth of pioneer trees (Chapter 4). Nonetheless, because TDF have a low canopy height, low vertical stratification and low leaf biomass production (Murphy and Lugo 1986), the light gradient created is much weaker than in temperate or tropical forests, where < 1 to 3.8% of full sunlight reaches the understory below closed canopies (vs. 6-22% in our fallows; Chazdon 1986, Canham et al. 1990, Brown and Parker 1994, Richards et al. 1996). Daily total PAR was at least 8 times higher in the

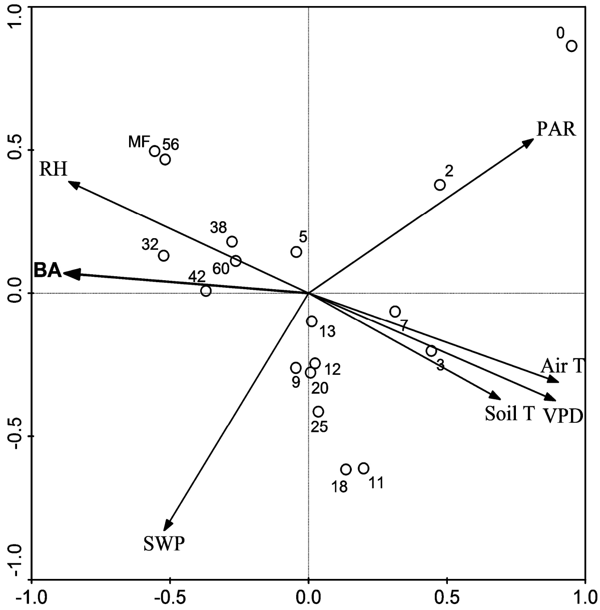


FIGURE 4. Principal Component Analysis (PCA) of 17 successional tropical dry forest fallows plus a mature forest site, based on a matrix of environmental data. The figures next to the circles indicate fallow age. All variables were relativized by their standard deviates. The scaling of the ordination diagram reflects the relationship between the environmental variables and their approximate loadings on the ordination axes.

understory of our old-growth forest than in that of tropical rain forests (TRF, *sensu latu)*, where it is generally less than one mol m^2 day^{-1} (Chazdon and Fetcher 1984, Ashton 1992, Brown 1993).

As with light, SWP changed fast at early succession. Depending on the balance between evaporation and transpiration, open areas can be moister, equal or drier than closed areas (Poorter and Hayashida-Oliver 2000, Marthews et al. 2008). The humpbacked relationship found between SWP with BA indicates that soils of early successional sites, when biomass is low and large patches of bare soil exist, are strongly dried by direct evaporation. The parallel increase in SWP with development reflects the reduction in soil drying by shading (SWP were highest when pioneer's crown cover peaks, at basal area of ca 10 m^2 ha^{-1}; Chapter 4). SWP drop again later in succession as the reduction in evaporation becomes less important than the increase in transpiration that occurs with further accumulation of biomass.

As the wet season SWP was measured during a period of frequent rainfall, SWP were as high as in TRF during this season (e.g. Camargo and Kapos 1995, Hoffmann et al. 2005, Santiago and Mulkey 2005). This is not always the case, however, as due to high rainfall variability wet season SWP can be notably drier (Bullock 1986, Murphy and Lugo 1986). As a result of that, crop fields in the area fail to yield harvests in years with a short wet season or in years with prolonged dry spells during the wet season, while up to two harvests can be obtained in more continuously wet years (pers. obs.). In the dry season fallow soils dry to SWP where water is unavailable to plants.

The linear patterns of change with fallow age in air and soil temperature, RH, and VPD reflect the influence of factors other than cover, such as stem biomass and soil litter. These factors have diverse effects in the environment and generally change more gradually than leaf area (Chapter 3, Guariguata and Ostertag 2001, Hertel et al. 2003). Forest soil and air temperatures largely drop as leaf cover increases the reflection and reduces the transmisivity of incoming radiation (Lorenzen and Jensen 1988, Asner 1998). Yet, a considerable amount of radiation still passed through the low-statured forest canopy of the fallows (as shown by understory PAR levels). A large part of the radiation penetrating the canopy is absorbed by stems and large amounts of heat flow back to the canopy (outflow), but also to the surrounding air and the soil (inflow; Haverd et al. 2007, Michiles and Gielow 2008). Gradual cooling through succession may also derive from heat storage by soil litter. This keeps the soil below the litter layer cool but warms the air above it (Felton 1979, Daubenmire 1974, Uhl et al. 1981). Together with canopy development, soil litter and organic matter development also enhance water retention below the canopy and rise understory RH (Felton 1979).

As expected from the effects of forest structure and biomass on the environment, other differences in gradients between tropical forests types exist. Air temperature ranges in open and closed areas are very similar between forests (22-38°C) but maximum temperatures of 12 different old-growth wet forests, at 0.7 to 1.5 m above the forest floor and below closed canopy, are 2-12°C lower than in any of our closed canopy forest (Schulz 1960, Denslow 1980, Chiarello 1984, Fetcher et al. 1985, Ashton 1992, Brown 1993, Whitmore 1998). Temperatures in wet forest understories are hence from 3.4 to 9.5°C cooler than in surrounding open areas vs. only 3.1°C in our forest, which is very similar to the difference found by Pinker

(1980) for a dry forest in Thailand (3°C). Relative humidity and VPD show similar patterns. The understory of closed wet forests is notably more humid and less desiccating than the understory of our closed forests (more than 12% difference in minimum RH and from 0.8 to 2.6 KPa difference in maximum VPD; Schulz 1960, Denslow 1980, Chiarello 1984, Kapos 1989, Fetcher et al. 1994, Camargo and Kapos 1995, Whitmore 1998). The same qualitative differences between forest types apply for their open areas (from 2-24% difference in minimum RH and 0.4 to 2.25 KPa difference in maximum VPD). Differences between open and closed areas are also larger in TRF than in our forest. Unlike in our forests, the environmental differences between open and closed areas in wet forests are very short-lasting due to the fast re-growth of vegetation (e.g. < 2yr for VPD and air T; Fetcher et al. 1985).

Soil temperature comparisons are complicated by differences in sampling depths among studies, as marked changes in temperature occur within a few centimeters. Soil temperature is also the integrated response of other microclimatic factors (e.g. irradiance, air temperature, moisture) and is affected by several factors such as soil type, soil cover type (e.g. litter), and canopy cover (Schulz 1960, Marthews et al. 2008). The qualitative response of soil temperature to vegetation cover is nevertheless the same between tropical forest types (but not temperate, cf. Bazzaz and Wayne 1994). In open areas, soil temperatures are higher than air temperatures, while the opposite is true in closed forests. Absolute soil temperatures in both open and closed areas in our forests get higher than in TRF. While mean annual temperature in our forest is within the range of compared forests (25-28.5 °C), the maximum soil temperatures at 5 cm soil depth below the closed canopy of TRF are 2.5-3.4 °C cooler than ours (at 12 cm depth); open areas in TRF are 2-3 °C cooler than in our TDF (absolute differences are conservative as values at same depth would be larger; Schulz 1960, Lawson et al. 1970, Ashton 1992, Marthews et al. 2008).

Differences in the magnitude of daily oscillations between forests types also exist. Oscillations of environmental conditions are generally larger in open than in closed areas (e.g. Schulz 1960, Ashton 1992). Nonetheless, as early-morning air is cool and close to saturation in all forests, and as average conditions are less extreme in TRF, daily oscillations in temperature, RH and VPD within the TRF understory are more damped than in our forest (e.g. 2-7.5°C vs. 9.7°C for air temperature). Even for open areas, daily oscillation of RH and VPD were larger in our forest than in TRF. This stresses the differences that exist between the patchy vs. uniform ways of regeneration between tropical dry and rain forests (Ewel 1980).

The link between the particularities of the tropical dry forest structure with the environmental conditions below its canopy is strengthened by the similarity of dry and wet season conditions between our forest and other deciduous and evergreen TDF (cf. Kieft 1994 for SWP in drought stressed systems, McLaren and McDonald 2003b, Asbjornsen et al. 2004 for PAR, Ishida et al. 2006, Cervera et al. 2007 for VPD).

ARE ENVIRONMENTAL CONDITIONS DRIVEN BY COMMUNITY STRUCTURE OR FALLOW AGE?

The correlations between fallow age and understory environment show that there is a clear relationship between successional and environmental change. The strength of the relationship of BA with the environmental gradients further shows that changes in the forest structure drive the changes in the environment. It also shows that a simple measure of structural development is an adequate proxy for the several plant-community factors that affect the microenvironment and that can be used to infer understory environmental conditions. This is in contrast to findings in tropical and temperate forests where light environments were unrelated to BA (Brown and Parker 1994, Kabakoff and Chazdon 1996). Brown and Parker (1994) did find a significant relationship with the vertical arrangement of leaves, indicating that differences in vertical structuring among forests imply significant differences in the creation of environmental gradients.

SPATIAL HETEROGENEITY IN ENVIRONMENTAL CONDITIONS

Besides such major successional changes, the variable's CV's demonstrate that the regeneration environment can differ considerably at a given successional stage.

Heterogeneity was not uniform across succession. In general, heterogeneity was higher in the wet than in the dry season, and larger for resources (i.e. water and light) than for conditions (air and soil temperatures, RH and VPD). These results stress the relevance of leaf phenology as a seasonal microenvironment driver and have implications for the differential growth and survival of species (discussed below).

The heterogeneity of light in early succession is relatively low due to the scarce and patchy re-growth of vegetation in TDF. The light reduction caused by the high leaf area of such vegetation patches (Ewel 1980) is attenuated by the strong penumbra effect of the surrounding open areas. Such contrasts nevertheless increase as the vegetation clumps expand vertically and horizontally in size with succession. Simultaneously, pioneers' senescence and mortality increase, which may explain the maintenance of a high heterogeneity until mid-late succession (Chapter 4). Thereafter, the spatial distribution of mature forest trees that recruit into the canopy becomes more regular (Hiroaki et al. 2004). PAR's heterogeneity decreased accordingly at late successional stages. As in temperate and tropical forests, these changes show that even when mean light availability may be very similar after canopy closure, light environments are yet different (e.g. Brown and Parker 1994, Nicotra et al. 1999).

The large and constant heterogeneity in SWP most likely responds also to a complex set of changes that simultaneously occur along succession. Heterogeneity in early succession may mainly correspond to differences in evapotranspiration rates between patches of vegetation and bare soil. As the leaf area index increases, heterogeneity may also result from marked differences in water consumption (and thus transpiration) by species belonging to different functional groups, which coexist mostly at mid succession (Chapter 4), and by individuals of different sizes (Huc et al. 1994, Küppers et al. 2008), whose frequency distribution reaches its highest variation in old-growth forests (Clark 1996).

The patchy structure of early successional vegetation is also responsible for the tendency of early environments to be more heterogeneous in their environmental conditions than later successional stages. Heating of the soil by direct radiation is more localized in such early open-areas. In relation to this, the variation of air temperature in the open tends to be greater than under shade due to a more localized vertical turbulence and mixing of the air (Daubenmire 1974, Felton 1979).

IMPLICATION FOR SPECIES PERFORMANCE

The soil drought (SWP) but also the atmospheric drought (RH, VPD) registered during the dry season illustrate the harshness of this characteristic TDF season. It explains also why the majority of woody species and individuals in this TDF are drought avoidant (deciduous) and only a limited number of (evergreen) drought tolerant species and individuals occur, mostly in old-growth forests (cf. Eamus and Prior 2001, Givnish 2002). The wet season is thus mostly important for plant establishment and growth, while the dry season is for survival.

The interaction of seasons with successional development (and/or vegetation structure) show that seasonality in TDF means more than just suitable and unsuitable periods for plant development. The formation of microclimatic gradients and the increase in environmental heterogeneity in the rainy season may lead to large growth differences from place to place. Survival during the dry period will largely depend on the conditions of the establishment patch because plants that are taller at the end of the wet season have a survival advantage in the dry season. This, as they have access to water from deeper soil layers or because they have more carbohydrates and/or water reserves to survive and resprout if necessary (Lieberman and Li 1992, Lopez and Kursar 2007, Myers and Kitajima 2007). Though less marked, dry season gradients in light availability and in variation of light and air T may nonetheless be important for established individuals of species that remain active during the dry season (evergreens and succulents).

The levels, the gentle rates of change, and the concurrent variation of T, RH and VPD throughout succession indicate that these are key factors of TDF succession. High temperature and VPD compromise plant performance by their negative effects on carbon balance (e.g. decreased assimilation and increased respiration) and plant water status (e.g. increased transpiration; cf. Jones 1992, Larcher 2003). For instance, short periods with levels of VPD as those found, even under closed canopies (VPD> 2 Kpa), markedly reduce the net photosynthetic rate of tropical drought avoiding species, even if water is freely available (Shirke and Pathre 2004, Ishida et al. 2006).

The year-round harshness of the early successional environment could explain the low pioneer diversity common to TDF in the dry side of their distribution-range (Ewel 1977, Álvarez-Yépiz et al. 2008, Lebrija-Trejos et al. 2008). Furthermore, it is consistent with the observations that TDF species incapable of dealing with such harshness are filtered-out from early successional communities and benefit from shade and the improvement of soil and atmospheric moisture that occur with vegetation development (Chapter 5, Campbell et al. 1990, Lieberman and Li 1992, McLaren and McDonald 2003a, Aerts et al. 2007).

While the light attenuation occurring early in succession closes the regeneration window for the limited number of pioneer species in these forests (Chapters 4, 6), the moderate light gradient created echoes the ideas that in TDF plant adaptations to shade may not be as relevant as in wet forests (Swaine et al. 1990, Gerhardt 1996) or, perhaps more precisely, that they must be study in relation to edaphic and atmospheric drought (Valladares 2003). The complex environmental patterns that we found in our TDF successional plots indicate that such an integrated assessment of plant functional adaptations will be a great leap forward in our understanding of succession and the major driving processes.

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CHAPTER 6

Functional Traits and Environmental Filtering Drive Community Assembly in a Species-Rich Tropical System

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ABSTRACT

Mechanistic models of community assembly state that biotic and abiotic filters constrain species establishment through selection on their functional traits. Predicting this assembly process is hampered because few studies directly incorporate environmental measurements and scale up from species to community level, and because the functional traits' significance is environment-dependent. We analyzed community assembly by measuring structure, environmental conditions, and species traits of secondary forests in a species-rich tropical system. We found, as hypothesized, that community structure shaped the local environment and that strong relationships existed between this environment and the traits of the most successful species of the regeneration communities. Path and multivariate analyses showed that temperature and traits for its control were the most important factors of community differentiation. Comparisons between the trait composition of the forest's regeneration, juvenile, and adult communities showed consistent patterns of community assembly. These results allowed us to identify the major functional traits and environmental factors involved in the assembly of communities in the ecosystem and demonstrate that environmental filtering is a predictable and fundamental process of community assembly, even in a complex system such as a tropical forest.

INTRODUCTION

Understanding and predicting the key factors that drive community assembly have been major questions in ecology that are nowadays critical if we are to address or mitigate the problems imposed by global change (Naeem and Wright 2003, McGill et al. 2006). Mechanistic explanations of community assembly state that community membership is constrained to those species with the appropriate functional traits to reach a site (i.e., overcome a dispersal filter) and establish under the conditions set by the environment and other organisms (i.e., the biotic and abiotic filters, Belyea and Lancaster 1999).

Numerous studies show how plant traits affect the performance of individual species, but our ability to predict community assembly from these relationships is nevertheless limited. This is partly because the link between plant traits and function to the environment is mostly conceptualized and few studies directly correlate them (McGill et al. 2006, Vile et al. 2006). Also problematic is that the importance of traits differs with ecosystem conditions and the scale of study (Wright et al. 2005, Ackerly and Cornwell 2007). In tropical humid forests for example, species adaptations to vertical and horizontal light gradients can explain successional change and species coexistence (Poorter et al. 2006, Chazdon 2008). In tropical dry forests (TDF) however, adaptations to such light gradients are considered less relevant because of the short-statured and seasonally more open canopy (Ewel 1977, Lebrija-Trejos et al. 2008). Instead, adaptations to strong seasonal drought, high solar irradiance, and high potential evapotranspiration seem to largely determine the ecology of TDF species (Borchert 1994, Lüttge 2008, Poorter and Markesteijn 2008). Such adaptations must be specially important in the particularly open early-successional communities of TDFs (Ewel 1977), but other adaptations might become important when succession proceeds. Late-successional TDFs have a larger vegetation cover (implying a lower light and nutrient availability), a more complex structure (e.g., guild diversity), and more diverse agents of seedling mortality (e.g., predators, herbivores, pathogens) than early-successional ones (Lieberman and Li 1992, Hammond 1995, Pereira et al. 2003, Read and Lawrence 2003, Saynes et al. 2005). Hence, light capture and protection of acquired resources may become important for plant establishment as succession proceeds.

Scaling up from the species level to the community level is one of the steps needed to advance in understanding and predicting community assembly (McGill et al. 2006). Patterns of traits and tradeoffs at species level can differ from those at community level and may not correctly predict vegetation change or plant community structure (e.g., Murray and Leishman 2003, Wright et al. 2005). Recent community-level studies analyzing functional traits and species abundances have shown their predictive value but have further stress the need to incorporate environmental data to establish the precise effect that environmental factors have, by working as filters, in community change (e.g., Vile et al. 2006, Mouillot et al. 2007, Shipley et al. 2007). To date, as far as we know, no studies have empirically assessed the role of environmental filters and species traits in the assembly of diverse and complex communities such as tropical forests through the direct inclusion of environmental measurements. This would provide an acid test of the importance of functional traits in the structuring of species-rich (tropical) communities, where unpredictable chance events are proposed to play a leading role (Hubbell 2001).

Secondary succession is ongoing community assembly. It is a re-colonization process in which community structure, environment, and species composition change over time. If environmental filters and species traits are relevant for community assembly, then communities should have particular combinations of traits under different environmental conditions. This should occur in spite of the heterogenizing effect that factors such as random dispersal or competition may have in the assembly process (Weiher et al. 1998, Hubbell 2001).

We combined data on composition and structure of TDF differing in successional status (1–60 yr-old) with measurements of their abiotic environment and species' functional traits to address the following questions: First, does forest structural development during secondary succession lead to predictable changes in abiotic conditions at the forest floor? Second, do the average trait values of the regenerating communities vary with abiotic conditions at the forest floor? By answering these questions we could specify the significance of traits and environmental filters in community assembly. We hypothesized that (1) with the development of forest structure, the regeneration environment changes from hot, sunny, and dry, to more cool, shady, and moist; and (2) early-successional communities are dominated by species with traits related to fast growth and tolerance to hot and desiccating environments, while late-successional communities are dominated by species with traits related to acquisition and conservation of resources.

METHODS

The study area is located around Nizanda (16°39′30″ N, 95°00′40″ W), a village on the Pacific Slope of the Isthmus of Tehuantepec, Oaxaca, Mexico. Mean annual temperature is ca. 26°C and mean total annual precipitation is ca. 900 mm, with 90 percent of rainfall occurring between late May and mid October. The main forest matrix is formed by a low-statured (ca. 7–8 m) tropical deciduous forest (> 75% of the species are deciduous). Sensu Holdridge's life zone system, it is a transition from subtropical very dry forest to subtropical dry forest. From 920 species recorded in the area (90 km^2), 430 are present in the dominant deciduous forest, while 191 species are exclusive to it. The other species of the recorded flora are mainly distributed in diverse communities such as savannas, xerophytic scrubs, gallery forests and semi-evergreen forests (for more study area details see Pérez-García et al. 2001).

Species composition and abundance of trees and treelets of the regeneration communities (RC; individuals 0.3–1.0 m tall) of secondary TDFs were measured in 144 2x2 m quadrats placed regularly in 18 plots (8 quadrates/plot). These were formerly corn fields with abandonment times ranging from < 1 yr to ca. 60 yr, plus a mature forest. Abandonment times were obtained by interviewing plot owners and checked by dendrochronological analyses (Brienen et al. 2009). Structure and species composition of the juvenile community (JC; individuals 1– <5 cm DBH), and the adult community (AC; individuals ≥5 cm DBH), were also obtained. See

Lebrija-Trejos et al. (2008) for details in plot selection, layout and characterization.

Photosynthetic Photon Flux Density (PPFD), air temperature, relative humidity, soil temperature and soil water potential (Ψ_s) were measured during the rainy season (late May–November), when most growth occurs and when foliage development creates marked environmental gradients. Nonetheless, to evaluate the influence of seasonal drought, Ψ_s was measured once during the leafless period (in February). Soils of all but 1 plot were similarly dry by then (average Ψ_s = -49.9 MPa, SD = -12.5 MPa), and no significant relationships were found between dry season Ψ_s and time or forest structure; thus, this variable was omitted from further analyses.

Understory PPFD was measured with Licor quantum sensors (Li-190, LI-COR, Lincoln, Nebraska, USA) set at 50 cm above soil level in seven randomly-chosen quadrats per plot. Another sensor was raised above the canopy to calculate the percentage PPFD reaching the understory. PPFD measurements during one full day have been shown to provide good estimates of long-term light conditions of differing understory microsites (Engelbrecht and Herz 2001). Two full days per plot were used. Sensors were placed simultaneously in two plots to record 10 min averages with a 5 sec sampling interval. After recording a faultless two-day period, sensors were moved to two other plots until all plots were characterized.

Air temperature and relative humidity (RH) were logged every hour from June to October also at 50 cm above soil level. Two HOBO Pro Temp dataloggers (Onset, Bourne, Massachusetts, USA) were randomly placed in eight plots and three HOBO Pro Temp/RH dataloggers in ten plots. To emphasize the differences in stress conditions between the plots, mean daily maximum temperature (T_{Amax}) was used across all analyses (results using mean daily temperature were similar). Simultaneous records of temperature and RH were used to calculate air vapor pressure deficit (VPD; $VPD = VP_{saturated\ air} - VP_{air}$; $VP_{air} = VP_{saturated\ air} \times RH/100$) and correlate plot-averaged values of air temperature and VPD ($R = 0.95$, $P < 0.01$, $N = 10$). This corroborated the use of temperature both as an indicator of heat and evapotranspirational conditions [mean daily maximum VPD (KPa) = 3.3, SD = 0.5, range = 2.6–4.4]. All calculated averages included only daylight records.

Soil temperature was measured using waterproof digital thermometers with 12.7 cm-long probes. Thermometers were placed in the same quadrates where soil samples were taken. Temperature was registered every 3 h from 07:00 to 19:00 h during the second day of PPFD recordings. For each recording, a relative measure of soil temperature (T_{Srel}) was calculated to compare between plots (T_{Srel} = soil temperature - ambient temperature; ambient temperature was registered by a meteorological station located in an open field in the study area).

The Ψ_s was calculated using the filter-paper method (Leong et al. 2002), which allows measurements down to -100 MPa. Soil samples were taken within an overcast day in all plots (0–10 cm depth), from the edge of six quadrates of a plot. The samples were individually sealed in 150 cm^3 plastic jars with three Whatman No. 42 filter paper discs (55 mm diameter; Whatman plc, Maidstone, Kent, UK) placed in the middle of the jar. Samples were left to equilibrate during two weeks inside an isolated container. Afterwards, Ψ_s was calculated following the methods of the D5298-03 American Society for Testing and Materials International standard and using the formulas of Leong et al. (2002).

Thirty-one species were selected for measuring various functional traits related to plant establishment and persistence (Weiher et al. 1999, Westoby et al. 2002, Table 1). Traits for dealing with the characteristic environmental stresses of TDF were of particular interest. Selected species were the most common in the RCs as they accounted on average for 91% of individuals in a plot (range = 81%–100%), and represented on average 84% of the species (range = 67%–100%).

Leaf thickness, leaf size (lamina surface area), leaf slenderness (lamina length/lamina width), leaf mass per area (leaf dry mass/leaf area), leaf density (leaf mass per area/leaf thickness), leaf dry matter content (leaf dry mass/leaf fresh mass), and petiole length were calculated from field measurements of sun-exposed fully-expanded fresh young and undamaged leaves of adult trees. Five trees of comparable size per species were selected, and five leaves per each tree were sampled. Sampled leaves came from the outer layer of the crown, halfway its vertical length. Leaves were collected with their branches and transported in plastic bags to the *in situ* laboratory for immediate measurement.

TABLE 1. List of functional traits, grouped by their role in plant establishment and persistence, measured as surrogates of difficult to measure traits (in italics).

Measured trait	Abrv.[1]	Functional role	Variation[2]
Establishment			
Dispersion & germination			
Dispersal mode		Spatial dispersion (distance & probability)	(N)
Animal dispersal	AD		
Unassisted dispersal	UD		
Wind dispersal	WD		
Seed shape	SSh	Seed longevity and survival	0.003 – 0.228 (D)
Seed size	SSz	Dispersal distance, fecundity, seed longevity	0.003 – 0.642 cm^3
Persistence			
Stress resistance			
Deciduousness	De	Drought avoidance	(B)
Leaf compoundness	LC	Leaf cooling, light capture economics (structural investment)	(O)
Leaf density	LD	Leaf structure/water balance (modulus of elasticity)	0.2 – 1.1 g/cm^3
Leaf dry matter content	LDMC		0.21 – 0.64 g/g
Leaf pubescence	LPb	Leaf cooling, water balance	(B)
Leaf size	LSz	Leaf cooling, light capture efficiency (self-shading)	0.02 – 96.53 cm^2
Leaf slenderness	LS		0.71 – 5.76 cm/cm
Maximum height	H_{max}	Light competitive ability	3.7 – 8.8 m
Petiole length	PL	Light capture efficiency	0.24 – 8.89 cm
Leaf pulvination	LPl	Irradiance control	(O)
Seed size	SSz	Seedling resource supply	0.003 – 0.642 cm^3
Growth rate			
Leaf mass per area	LMA	Photosynthetic performance, light capture economics	43 – 160 g/m^2
Nitrogen fixation	N_{fix}	Photosynthetic performance	(B)
Defense			
Exudates (latex and resins)	Ex	Against herbivore attack	(B)
Leaf dry matter content	LDMC	Against mechanical and herbivore damage	0.21 – 0.64 g/g
Leaf pubescence	LPb	Against herbivore and fungi attack	(B)
Leaf thickness	LT	Against mechanical and herbivore damage	50.2 – 301.1 µ
Spininess (spines & thorns)	Sp	Against large herbivore attack and pruning	(B)

[1]abbreviations used throughout the paper. [2]indicates the range of values for each trait along all sampled species; B, N, O, and D, denote binary, nominal, ordinal or dimensionless variables.

Collected branches were put in water and the leaves detached individually for recording their fresh weight and dimensions. This prevented leaf wilting and the closing of compound leaves after collection. Measurements were performed on entire leaves (including petioles), with the exception of leaf length, width, and area, where leaflets were used in the case of compound-leafed species. Leaf area was calculated from images obtained with a desktop scanner and analyzed with pixel-counting software (Berloo 1998). For measuring dry weights, leaves were oven dried for 48 h at 75°C.

From specimens of the study area deposited in the Herbario Nacional (MEXU) of the Universidad Nacional Autónoma de México, we obtained leaf compoundness (degree of leaf segmentation; 1 = simple leaves, 2 = compound leaves, 3 = double-compound leaves; leaf pubescence (no = 0, yes = 1); leaf pulvination, ranked from 0 for leaves without pulvini to 3 for leaves with up to tertiary pulvini (i.e., at the petiole base, and first and second order petiolules); seed shape (variance of seed length, width, and depth, each divided by the maximum quantity so that one of them is unity, see Thompson et al. 1993), which ranged from 0.003 for nearly spherical seeds to 0.23 for disc shaped seeds; seed size (as an ellipsoid volume = $Pi/6\times$length×width×depth); and dispersal mode, classified as wind dispersal for propagules with wings, hairs, or plumes; as animal dispersal for propagules with fleshy pulp or an aril; and as unassisted dispersal for propagules with no obvious dispersal adaptation. For all seed traits, a minimum of three seeds per five individuals (fifteen seeds) were assessed.

Deciduousness (strictly deciduous species = 1, otherwise = 0), spininess (spines or thorns = 1, absent = 0), and exudates (latex or resins = 1, absent = 0) were determined from botanical expertise. Maximum height (H_{max}) was calculated following Thomas (1996) using data taken from unpublished regional databases of forest structure and composition (E.A. Pérez-García and J.A. Meave), and nitrogen fixation (yes = 1, no = 0) was obtained from the database of the Germplasm Resources Information Network (http://www.ars-grin.gov/~sbmljw/cgi-bin/ taxnodul.pl? language=). This information was unavailable for three species but, as taxonomy and phylogeny are good indicators of nodulation (Doyle 1994), they were considered to nodulate because most studied species within the genera do so.

The analysis of the hypothesized relationships was based on a path model (Fig. 1). The plots' total basal area (BA), crown area and density of individuals were calculated using individuals ≥ 1 cm DBH, and their successional development was analyzed by performing simple linear regressions against abandonment time. The relationship between forest structure and regeneration environment (hypothesis 1), and the relationship between regeneration environment and RC assembly (hypothesis 2; Fig. 1), were analyzed using forward multiple linear regressions.

The complete analysis of the environmental effects in community assembly comprised three steps. First, to reveal the traits' variability among the species, a species' Principal Component Analysis (PCA, McCune et al. 2002) was performed using the species × traits matrix (species ordination). Second, by combining species abundances with species functional traits, a plot × traits matrix was made to do a PCA of the RCs based on the community-level abundance-weighted trait data. This weighted-average ordination was used to detect combinations of traits within the RCs and test the relationships of these combinations with the environment (regressions between the PCA axes and the environmental variables; Fig. 1). A similar analysis using only species presence-absence data (i.e., all species weighted equally; unweighted-average ordination) was used to differentiate between the effects of filters on the probability to occur, and on the probability to become dominant. Third, a PCA using a size-stratified plot × traits matrix containing the abundance-weighted data of each plots' regeneration, juvenile, and adult communities, was done to analyze the relationships between their composition of traits. This was done by regressing the first PCA axis scores of the size-stratified communities against their fallow basal area using non-linear models. Selection of the best model depended on statistical methods for model comparisons, namely on R^2 differences when the models had equal numbers of parameters, on the results of an F test when one model was a simpler case of the other (i.e., nested), or on the difference between the models' Akaike's Information Criterion, corrected for small sample sizes, when models were non-nested (Motulsky and Christopoulos 2004).

Time, crown area, tree density, PPFD, T_{Amax}, and Ψ_s were transformed using square root, arcsine and logarithmic functions to improve normality and homoscedasticity. For simplicity, their original names were used throughout the paper and the back-transformed values were plotted in all graphs. As trait variables had different scales, they were relativized by their standard deviates (trait means=0, variances=1) for the multivariate analyses. The PCAs' validity was tested by redoing the ordinations using non-metric multidimensional scaling, which makes no assumptions on data distribution (MDS, McCune et al. 2002), and by performing Monte Carlo randomizations (500 runs). The sample scores obtained with PCA and MDS (stress < 11.1, for 2 dimensional solutions) were highly correlated (for all cases $R \geq 0.94$) and Monte Carlo tests P were < 0.01. This meant that PCAs' assumptions of linearity and normality were met and that ordinations were unlikely to result from chance.

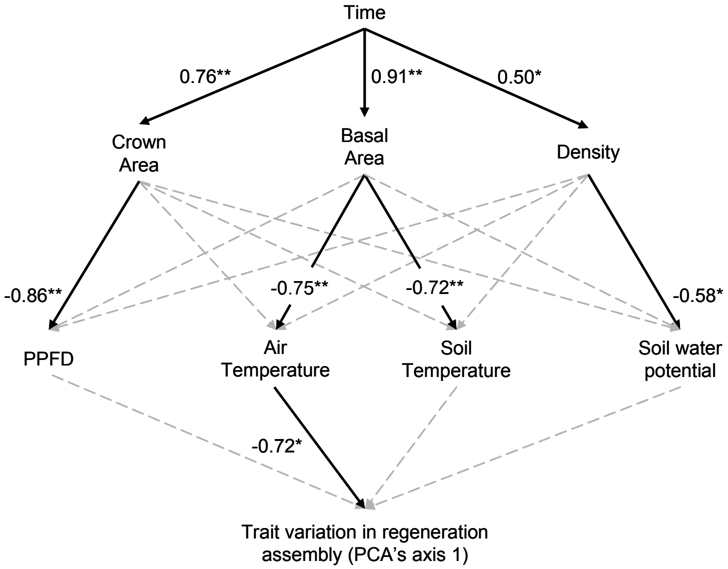

FIGURE 1. Path model showing the causal relationships (arrows) between abandonment time, structural development, environmental variability and trait composition of the regeneration assembly. Solid lines indicate significant effects (* $P < 0.05$, ** $P < 0.01$); shown values are standardized regression coefficients. Dashed lines show the full models tested by multiple linear regression. Time, crown area, air temperature and Photosynthetic Photon Flux Density were transformed to comply with linear models assumptions (see methods) but the original names are kept for simplicity.

RESULTS

FOREST STRUCTURE AND ENVIRONMENT

Forest structure changed significantly with time (Figs. 1 and 2a-c). Crown area increased rapidly (within 10 yr) while BA increased more gradually. These two patterns were remarkably regular and contrasted with the highly variable, though also significantly increasing pattern for density of individuals.

Significant environmental changes accompanied the structural changes (Fig. 1). The increase in crown area explained best the reduction in PPFD (74%–6%; Fig. 3a). Both T_{Amax} (39.8–34.2°C; daily mean temperature: 29.1–27.4°C) and T_{Srel} decreased with forest development. T_{Srel} changed from being higher than open-sky temperature (+3.1°C) in less developed fallows, to lower than open-sky temperature (-2.6°C) in more developed ones. BA explained best these changes in temperature (Fig. 3b,d). Differences in Ψ_s (-45.7 – -1.2 KPa) were only related to tree density; three early-successional plots with very low densities mainly caused the positive relationship (Fig. 3c).

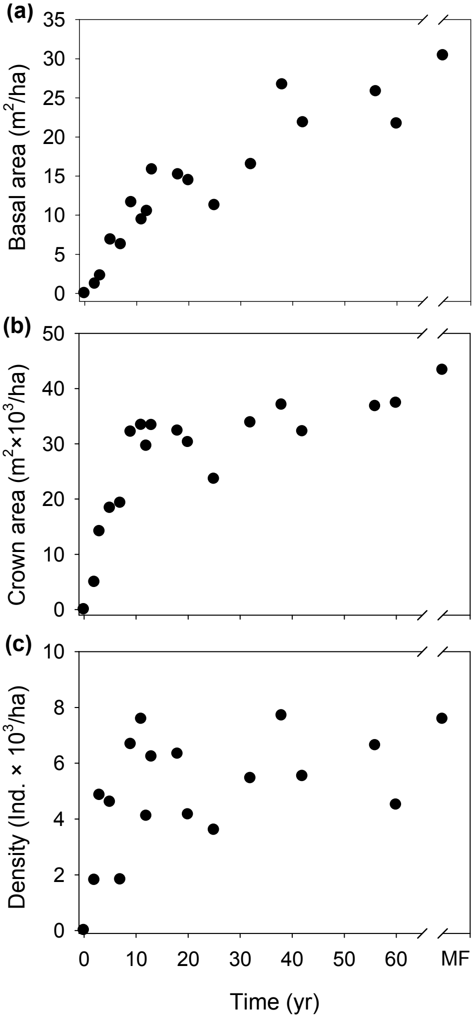

FIGURE 2. Structural characteristics of secondary forests stands (dots) with abandonment times ranging from < 1 yr to ca. 60 yr, and a mature forest (MF) at Nizanda, Mexico: (a) basal area, (b) crown area, and (c) density of individuals. All values are expressed per hectare and include individuals ≥ 1 cm dbh.

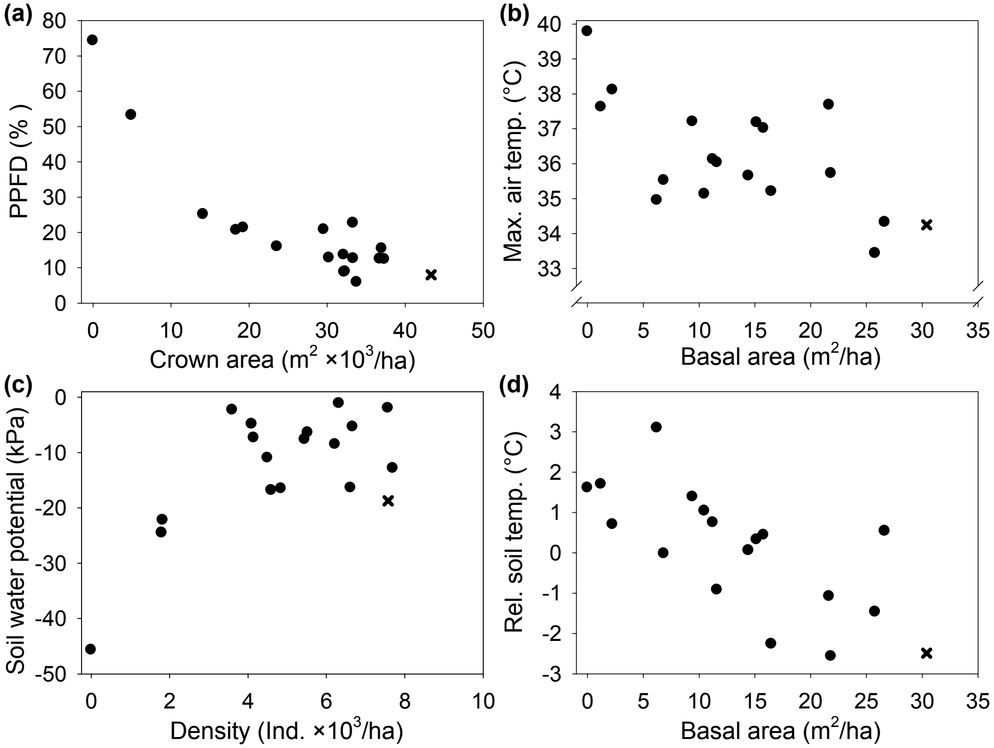

FIGURE 3. Regeneration environment of secondary forests (dots), with abandonment times ranging from < 1 yr to ca. 60 yr, and a mature forest (×) at Nizanda, Mexico, as a function of their canopy structure (individuals ≥ 1 cm dbh): (a) percentage of open-sky photosynthetic photon flux density (PPFD) reaching the forest understory (i.e. 50 cm above soil level); (b) maximum air temperature at the forest understory; (c) soil water potential (0–10 cm depth); and (d) soil temperature (ca. 13 cm depth) relative to ambient air temperature.

TRAITS AND SPECIES

The first two species PCA axes explained thirty-one and seventeen percent of the variation (Fig. 4a). Species with compound and slender leaves, high leaf pulvination, high leaf density and LDMC, N_{fix}, spininess, unassisted dispersal, and a flattened seed shape loaded high on the first PCA axis (loadings ≥ 0.5). Common early- and late-successional legumes had high species scores on the first axis.

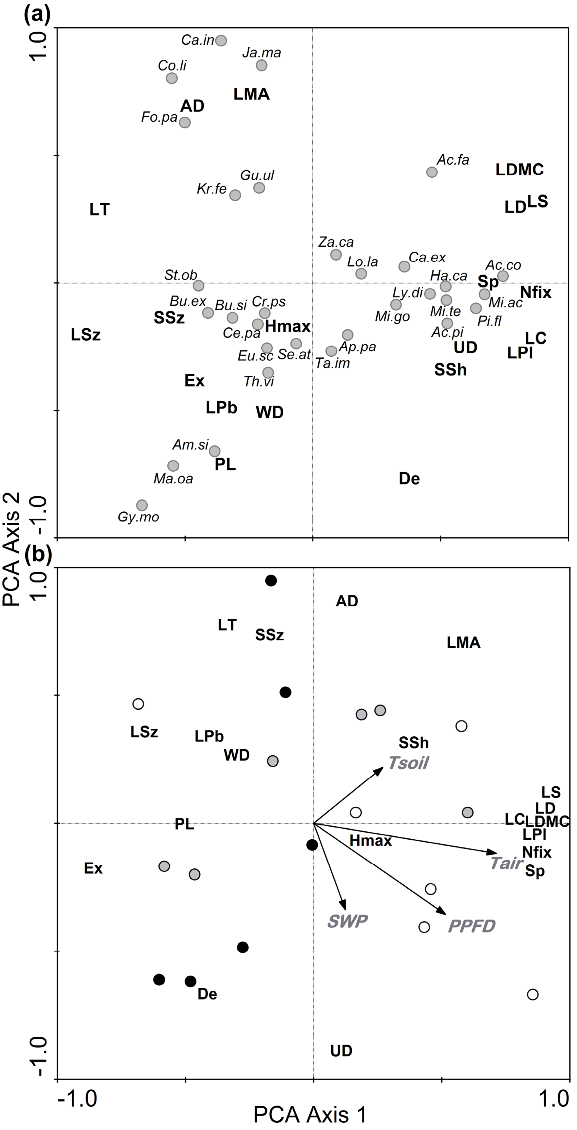

FIGURE 4. PCA ordination of Nizanda's tropical dry forest species (a), in the two-dimensional space of selected species traits, and (b) regeneration communities of secondary-forest plots and a mature-forest plot, based on the community-level abundance-weighted-mean of the traits of the most successful species in the regeneration assembly. The scaling of the ordinations reflects the relationships between the species traits (in bold) and their approximate loadings on the ordination axes: AD, animal dispersal; De, deciduousness; Ex, exudates; H_{max} maximum height; LC, leaf compoundness; LD, leaf density; LDMC, leaf dry matter content; LMA, leaf mass per area; LPb, leaf pubescence; LPl, leaf pulvination; LS, leaf slenderness; LSz, leaf size; LT, leaf thickness; N_{fix}, Nitrogen fixation; PL, petiole length; SSh, seed shape; SSz, seed size; Sp, spininess; UD, unassisted dispersal; WD, wind dispersal. Species (in italics and abbreviated) are: *Ac.co* = *Acacia cochliacantha*, *Ac.fa* = *A. farnesiana*, *Ac.pi*=*A. picachensis*, *Am.ad* = *Amphipterygium simplicifolium*, *Ap.pa* = *Apoplanesia paniculata*, *Bu.ex* = *Bursera excelsa*, *Bu.si* = *Bursera simaruba*, *Ca.ex* = *Caesalpinia exostemma*, *Ca.in* = *Capparis incana*, *Ce.pa* = *Ceiba parvifolia*, *Co.li* = *Coccoloba liebmannii*, *Cr.ps* = *Croton pseudoniveus*, *Eu.sc* = *Euphorbia schlechtendalii*, *Fo.pa* = *Forchhammeria pallida*, *Gu.u* =*Guazuma ulmifolia*, *Gy.mo* = *Gyrocarpus mocinnoi*, *Ha.ca* = *Havardia campylacantha*, *Ja.ma*=*Jacquinia macrocarpa*, *Kr.fe* = *Krugiodendron ferreum*, *Lo.la* = *Lonchocarpus lanceolatus*, *Ly.di* = *Lysiloma divaricatum*, *Ma.oa* = *Manihot oaxacana*, *Mi.ac* = *Mimosa acantholoba* var. *eurycarpa*, *Mi.go* = *M. goldmanii*, *Mi.te* = *M. tenuiflora*, *Pi.fl* = *Piptadenia flava*, *Se.at* = *Senna atomaria*, *St.ob* = *Stemmadenia obovata*, *Ta.im* = *Tabebuia impetiginosa*, *Th.vi* = *Thounia villosa*, *Za.ca* = *Zanthoxylum* aff. *caribaeum*. The symbols' fillings in (b) indicate the plots' time since abandonment (open circles: < 10 yr; gray circles: 10–30 yr; closed circles: > 30 yr) and the overlaid arrows represent the direction of increase of the environmental variables (in italics) and the approximate correlation (*R*) between the environment and the axes of variation. PPFD = percentage of open-sky Photosynthetic Photon Flux Density reaching the forest understory (i.e. 50 cm above soil level); Tair = maximum air temperature at the forest understory; SWP = soil water potential (0–10 cm depth); and Tsoil = soil temperature (ca. 13 cm depth) relative to ambient air temperature.

Species extending towards the PCA's left side had increasing leaf size, leaf thickness and seed size (1^{st} axis loads ≤ -0.5). Evergreen or brevi-deciduous species with high LMA and animal dispersal, and species with deciduous leaves, long petioles, and wind dispersal (all traits absolute loadings ≥ 0.5) were found on opposite sides of the second PCA axis.

TRAITS, ENVIRONMENT AND COMMUNITY ASSEMBLY

The RCs varied in their weighted-average trait composition (Fig. 4b), reflecting that combinations of species with different set of traits occur (cf. Fig. 4a). The first two PCA axes explained sixty-one percent of the variation (40% and 21%). Most of this variation (1^{st} axis) was strongly correlated (absolute loadings ≥ 0.75) to leaf traits involved in control of water and temperature status (LDMC, density, slenderness, leaf pulvination, compoundness), growth rate (N_{fix}) and defense (spininess and exudates; Fig. 4b, Table 1). T_{Amax} and PPFD were the only environmental variables significantly correlated with the first axis ($R = 0.72$, $P < 0.001$ and $R = 0.52$, $P < 0.05$, respectively), although only T_{Amax} was selected by the multiple regression (Fig. 1).

An increase in T_{Amax} concurred with an increase in the community weighted-average of traits such as LDMC, leaf slenderness, leaf density, leaf pulvination, leaf compoundness, spininess and N_{fix}. Traits strongly correlated with the second axis (absolute loadings ≥ 0.70) showed a gradual change from RCs dominated by individuals with small seeds, unassisted dispersal, and deciduous leaves, to RCs dominated by individuals with larger seeds, animal dispersal, and tick, high LMA, and evergreen or brevi-deciduous leaves (Fig. 4b). None of the environmental variables was significantly correlated with the second axis.

When only the traits unweighted-average was used for the community-level PCA (not shown), the variation explained was similar (38% and 23% for axis 1 and 2) and similar trait associations were found (correlation between trait loadings of the weighted- and unweighted- average PCAs $R = 0.93$, $P < 0.001$, and $R = 0.72$, $P < 0.001$ for axes 1 and 2). Nevertheless, the values of the trait loadings were lower (i.e., the strength of trait correlations with the axes declined) and no significant correlations were found between the axes and the environmental variables.

The weighted-average trait composition of the sized-stratified communities (i.e., their 1st PCA axis scores; ordination not shown) changed directionally during stand development, from high scores related to compound and dense leaves in low BA plots, to low scores, related to large leaves and exudates in high BA plots (Fig. 5). The trait composition of the RC shifted strongly within ca. 10 yr, with lower differences occurring afterwards (logarithmic fit), while in the JC and the AC the changes in time were gradual and continuous (linear fits). Regeneration, juvenile, and adult communities differed strongly in average-trait values early during stand development, but converged towards similar values in structurally fully-developed stands (Fig. 5). Additionally, the trends showed that the trait composition of the AC of the most developed stands was similar to that of the JC of mid-developed stands and to the RC of the least developed and recently-colonized stands.

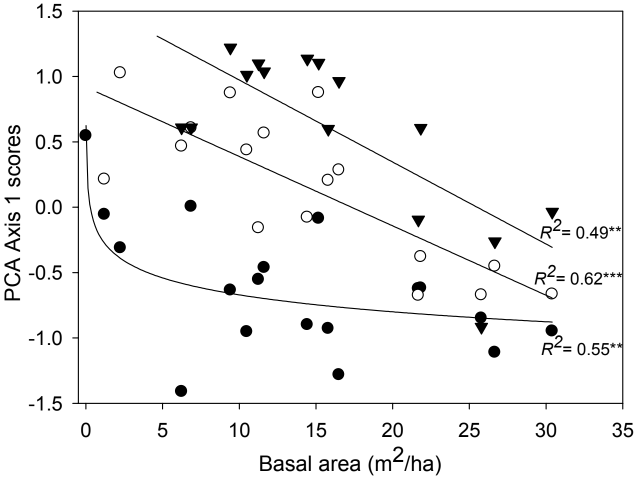

FIGURE 5. Community-level abundance-weighted-mean of traits (PCA axis 1 scores) of the regeneration (closed circles), juvenile (open squares), and adult (closed triangles) communities of secondary forests stands with abandonment times ranging from <1 yr to ca. 60 yr, and a mature forest (BA ca. 31 m^2) at Nizanda, Mexico, as a function of forest development (Basal area). Continuous lines represent modeled changes for each community strata (regeneration: logarithmic model, $R^2 = 0.49^{**}$; juvenile: linear model, $R^2 = 0.62^{***}$; and adult: linear model, $R^2 = 0.55^{**}$; $^{**}P < 0.01$, $^{***}P < 0.001$).

PATH ANALYSIS

Path analysis showed that an increase in abandonment time led to an increase of all forest structural variables (Fig. 1). The structural variables had, in turn, a different effect on the environmental factors; crown area led to a significant reduction in PPFD, basal area led to a reduction in air and soil temperature, and tree density led to a reduction in Ψ_s. Strikingly, air temperature was the only environmental variable leading to trait variation of the regeneration assembly, which indicates that it is the principal environmental filter that drives succession.

DISCUSSION

SUCCESSIONAL CHANGES OF FOREST STRUCTURE AND REGENERATION ENVIRONMENT

As expected, BA, crown area, and density of individuals showed directional developments with time. Although these successional changes can follow individual pathways of development (Chazdon 2008), our results prove that regeneration conditions at a site change predictably with overstory development. Increased crown area enhances absorption of light and, as expected, led to reduced PPFD levels at the forest floor (Fig. 3a). Soil and air temperatures dropped also as expected (Fig. 3b,d). As leaf area scales positively with BA, BA explained better the temperature changes probably because of the increased reflection and the decreased transmission of infrared radiation with increased stand leaf area, and the substantial infrared-reflective properties of wood (Asner 1998). The expected increase in Ψ_s was variable and caused by a few low-density stands (Fig. 3c). Reduced Ψ_s at depths < 20 cm are nevertheless common in open areas, even under rainy conditions (e.g., Ashton 1992). The more negative Ψ_s in open early-successional environments result from combined factors such as high evaporation because of high radiation loads and vapor pressure deficits, low water retention capacity of bare or poorly developed soils, and higher exposure to wind desiccation (Ashton 1992, Camargo and Kapos 1995). As hypothesized, from young to old-growth sites, forest structural development creates predictable environmental gradients that go from sunny to shady, hot to cool, and dry to moist.

FUNCTIONAL TRAITS, ENVIRONMENTAL CHANGE AND COMMUNITY ASSEMBLY

Abundant species had different sets of functional traits (Fig. 4a). The first PCA axis mostly reflected differences in traits for heat-load reduction and water-status control (leaf compoundness, slenderness, pulvination, leaf density and LDMC), while the second PCA axis reflected differences in species drought-coping strategies (cf. Givnish 2002), separating evergreen drought-tolerant species with high LMA from deciduous drought-avoidant ones.

The lack of relationship between the scores of the unweighted-average PCA of the RCs with the environmental variables suggests that species with different combination of traits can persist under the variety of abiotic conditions found along the plots. However, the abundance-weighted ordination showed associations of traits that were closely related to light and, primarily, temperature conditions (Figs. 1 and 4b), indicating that environmental filtering did make a difference. When community assembly is restricted by abiotic filters then this leads to convergence in the functional traits of the successful species (Holdaway and Sparrow 2006, McGill et al. 2006).

Adequate light and water availability do not necessarily guarantee carbon gain under high irradiance; short periods of high VPD (30–40 min, VPD > 3Kpa; cf. values in methods) may lead to strong reductions of net photosynthesis that parallel the effects of long periods (days) of drought (Shirke and Pathre 2004). As VPD increases exponentially with leaf temperature (Lambers et al. 1998), these results imply that plants incapable of keeping low leaf-temperatures under high irradiance face extended periods of virtual water stress, even if water supply is adequate. Accordingly, and as hypothesized, the sunny, hot, and dry early-successional sites in our system were dominated by species with traits to control irradiance load (leaf orientation by pulvinar movement), favor convective over transpirational cooling (compound leaves with small and slender leaflets) and maintain leaf structural integrity and low water potentials under water stress (high leaf density and LDMC, Koller 2000, Niinemets 2001, Westoby et al. 2002, Poorter and Markesteijn 2008). Many of these species were N-fixing legumes (with high N-content leaves) capable to photosynthesize and accumulate biomass at high rates (Wright et al. 2004). These traits further imply that the dominant early-successional species are able to enhance wet-season carbon gain, and hence increase dry-season survival, by (1) maximizing the use of high irradiance by keeping favorable photosynthetic leaf temperature and water balances for longer times; (2) avoiding the negative effects on net carbon gain of sharp temperature-induced increments in transpiration and respiration; and (3) enhancing water use efficiency through high N-content leaves that create steep CO_2 gradients by quickly depleting the internal C concentration (Lambers et al. 1998 and references therein, Wright et al. 2004).

Under the shady, cool and moist conditions of closed-canopy sites, the RCs were instead dominated by species with simple, large leaves with long petioles. Large leaves and long petioles reduce self-shading and enhance light interception per leaf area, which in turn increase net carbon gain under shaded conditions (Falster and Westoby 2003). Evidence of the expected increase of defensive traits with forest development was only found in the increased abundance of plants with exudates.

Although the second PCA axis of community-level traits was not related to the measured environmental variables, it separated RCs with combinations of average traits linked to drought-avoidant and drought-tolerant species, which implies that the RCs were dominated by species of either one strategy or the other. Such variation in dominance might be related to local scale variation in soil nutrient status and deep soil water availability, as deciduous species are favored by drier environments through an increased advantage of reducing water and carbohydrate losses during dry periods, while evergreen species are favored in nutrient-poor environments trough an increased advantage of reducing nutrient losses with leaf shedding (Givnish 2002 and references therein).

Additionally to the evidence provided by the close link between the environment and the traits of the most successful species in the RC (Fig. 4b), two more facts support that environmental filters and plant traits consistently shape community assembly. First, JCs of early–mid successional fallows (BA ca. 10–15 m^2) and ACs of mid–late successional fallows (BA ca. 20–25 m^2) have similar average-trait values compared to RCs in recently colonized area (BA ca. 0 m^2), suggesting that they passed through similar environmental filters (Fig. 5). Second, regeneration, juvenile, and adult communities converge towards similar community-level average-trait values when succession proceeds (Fig. 5).

The rapid shift in the RC attributes implies that the regeneration window for early-successional species is short, just as the open-canopy period with high light (Figs. 3 and 5). Reductions in light availability and temperature during succession are likely to decrease the carbon-gain advantage of early-dominant species both as a result of a loss in the trait advantages and their intrinsic high costs (see Koller 2000, Niinemets 2001, Vitousek et al. 2002, Falster and Westoby 2003). The early dominance and later decrease of legumes with functional traits like ours is common in other secondary TDFs (Donfack et al. 1995, Pereira et al. 2003, Saynes et al. 2005, Romero-Duque et al. 2007). The gradual decline in air temperature with forest development is paralleled by a gradual increase in dominance of species with simple and large leaves (Figs. 3 and 5), which are typical mature-forest dominants (Pérez-García et al. 2001). Other studies have shown that in temperature and water-stressed systems, the establishment of late-successional species is conditional on facilitation by early-successional species that reduce such abiotic stresses (Holmgren et al. 1997, Aerts et al. 2007), and that seedlings of mature TDF species survive better in shaded than in open sites (e.g., Lieberman and Li 1992, McLaren and McDonald 2003a).

In this study, community assembly was best predicted by temperature (which is strongly related to VPD), rather than by light or Ψ_s (Fig. 1). H_{max}, important for the species' competitive performance in systems with stronger vertical light gradients (100–1 % PPFD, Thomas 1996, Westoby et al. 2002, Poorter et al. 2006), was therefore irrelevant for succession in this TDF community. LMA was only of secondary importance during succession, and was related to drought tolerance rather than to shade tolerance (see Wright et al. 2005 for changes in the significance of LMA with climate stress). Drought tolerance is just an alternative to survive the dry season that all species in our system will eventually experience. The key for seedling survival during periods of negative carbon balances produced by resource shortages (like light and water) is previous growth and accumulation of sufficient carbohydrate and water reserves (Lieberman and Li 1992, Lopez and Kursar 2007, Myers and Kitajima 2007). Our results indicate that along the successional gradient, it is specially the interaction between the effects that the environmental conditions (temperature and light) have on plant growth and carbon gain during the rainy season, with its implications for plant survival during the dry season, what determines species establishment success and the relative importance of plant traits.

CONCLUDING REMARKS

Successional changes in the forest structure lead to predictable changes in the understory environment, which in turn molded community assembly on the basis of specific plant functional traits. Our findings highlight the importance of community-level analyses that include environmental measurements to identify the functional traits and environmental factors that are responsible for mayor ecological responses in an ecosystem. Although several other processes such as landscape configuration, disturbance history, biotic interactions, and dispersal limitation, may shape community structure, with such analytic focus we show, for the first time as far as we know, that environmental filtering is a fundamental process of community assembly even in a complex system such as a tropical forest.

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CHAPTER 7

General Discussion and Summary

When a disturbance opens-up a site for colonization by removing nearly all aboveground biomass, it initiates secondary succession: a process of vegetation re-growth in which community structure, environment, and species composition change over time. This so simply described process of vegetation change is one of the most intensively studied yet largely contended ecological phenomenon. On the one hand, this is because of the large amount of complex (interacting) factors both intrinsic and extrinsic to plants that determine the course and outcome of succession (see Pickett et al. 1987 for a comprehensive mechanistic framework). On the other, it results from the inconsistencies encountered in generalizations built from (incomplete) knowledge obtained from a limited range of biological systems and circumstances (Ewel 1980, Horn 1981, McIntosh 1981, Finegan 1984, McCook 1994).

Prior to our study, it had been suggested that tropical dry forest secondary succession could substantially differ from that in wet forests due to contrasting climatic, structural and functional attributes (Ewel 1980, Murphy and Lugo 1986, Guariguata and Ostertag 2001). Nonetheless, the scarcity of secondary succession studies in dry forests, and the complete lack of data on their successional dynamics has prevented solid analyses on their generalities and particularities. Theoretical models of secondary succession in the tropics have thus, so far, largely neglected tropical dry forests (TDF) and their characteristic ecology.

Within such framework, the present study aimed at understanding what makes a distinct group of species to be present, dominate, and eventually disappear from a certain space and moment in time throughout secondary succession in TDF. For this purpose, I combined the classical chronosequence approach with the direct study of successional changes over time (longitudinal approach). To reduce a major uncertainty of the chronosequence approach (the fact that fallow age determination in many cases is somewhat uncertain) a dendrochronological study was performed and allowed us to cross-check fallow ages obtained from interviewing land-owners. At the same time, it introduced dendrochronology as a complimentary technique to the study of tropical secondary succession (Chapter 2). Starting from the basics, successional patterns were studied using a chronosequence approach to gain insight into the particularities of TDF secondary succession and underlying processes (Chapter 3). This, led to the distinction of successional phases and groups of species, which were then used to analyze secondary forest dynamics and evaluate the suitability of mechanisms and concepts in models of tropical secondary succession (Chapter 4). Taking the environmental modification of resources and conditions by early colonizing species as a fundamental cause of species replacement, we also analyzed the change in understory environmental conditions as a function of community development (Chapter 5), and tested the hypothesis that these changes determine community assembly by filtering species according to their functional traits (Chapter 6).

In this final chapter we provide a synthesis of the main results and discuss the source of similarities and differences in the patterns and processes with successional studies from temperate and tropical systems. The applicability of two widely accepted tropical successional models to dry systems is finally assessed and suggestions for their improvement are given.

TESTING THE VALIDITY OF THE CHRONOSEQUENCE APPROACH

Because succession is a lengthy process, it has been traditionally studied by means of chronosequences: sites differing in age since disturbance are used to infer long-term vegetation change. For chronosequence studies to be valid, selected sites need to share a (relatively) similar landscape structure, landform, substrate conditions, and disturbance history and regime (Foster and Tilman 2000). An additional requirement is that reliable data on the age of the fallows are needed, which may be difficult to obtain. Many successional studies have not met these requirements sufficiently, thus the validity and value of the chronosequence approach has been seriously questioned (e.g. Johnson and Miyanishi 2008).

An important condition to be met by this study was hence to carefully address chronosequence requirements. We used dendrochronology as a new tool to determine fallow age. The occurrence of annual rings in both pioneer and mature forest species allowed us to verify and adjust interview-based estimates of fallow ages, which proved the use of dendrochronology as a complimentary technique to the study of tropical secondary succession (Chapter 2).

How valid is the chronosequence approach if all conditions of site selection are carefully addressed? To answer this question we compared the time-dependent changes of individually monitored plots with the predictions made by the static chronosequence approach (Chapter 4). Qualitatively and quantitatively, we found a remarkable agreement between the longitudinal and chronosequence approach, especially when developmental patterns were analyzed for two successional groups of species (pioneers and mature-forest species) that are expected to have similar ecological responses; 85% of all observations of plot-time combinations (i.e. individual plot censuses) fell within the 95% confidence intervals of the chronosequence models, and most individual-plot development trajectories closely paralleled the chronosequence trends (Chapter 4, Figs. 2, 5). These results prove that as long as the methodological requirements of the chronosequence approach are carefully addressed, chronosequence results are not only valid but highly valuable, as they allow to define basic development patterns, and contribute to the formulation and testing of successional hypotheses (e.g. Debussche et al. 1996, Foster and Tilman 2000, Capers et al. 2005).

PATTERNS OF FOREST RECOVERY AND RESILIENCE

The study of fallows with abandonment times covering from early to late stages of succession (< 1 - ca. 65 yr) revealed that with increasing abandonment time, species richness and diversity as a whole increased, the forest became taller, and basal area and crown cover accumulated continuously (Chapters 3, 4). Forest structural recovery followed classical patterns of secondary succession (cf. Brown and Lugo 1990, Barbour et al. 1998), with the exception of stem density, which is relatively low in dry forests and did not show the classical declining trend produced by competition-driven thinning (cf. Swaine and Hall 1983, Niklas et al. 2003, Breugel et al. 2006).

Patterns of species dominance across fallows also followed the classical replacement sequence from short-lived plants with high colonization and growth rates being replaced by long-lived plants with increasing size at maturity (Huston and Smith 1987, Finegan 1996). A short-lived stage of herbs and shrubs (0-3 yr) was hence followed by a mid-term stage (3-40 yr) dominated by a few (5) pioneer species, the understory of which was increasingly populated by larger-sized, longer-lived mature forest species (Chapter 3; Chapter 4, Fig. 2). In turn, late successional fallows (> 40 yr) had a mixture of senescent pioneer trees and small to mid-sized trees of mature forest species. The analysis of species abundance patterns, stratified in upper- and understory, strengthened the idea that species composition followed such sequence and was changing towards that of old-growth and mature forests (Chapters 3 and 4, Figs. 5). This is also in compliance with classical successional theory but in contrast to patterns of compositional change in many tropical wet forests, in which recovery of species composition may take over a century or it may never occur (Finegan 1996, Peña-Claros 2003, Chazdon et al. 2007).

Altogether, these results supported the hypothesis that, because of a reduced pool of pioneer species adapted to the harsh early-successional environment, succession in TDF involves fewer seral stages (Ewel 1977, 1980). The relative rapid successional changes in species composition also supported the hypothesis that tropical dry forests could be more resilient than wet forests because of a more simple community structure. This idea nonetheless did not apply to other structural attributes that showed similar or even slower relative recovery rates (measured as the percentage of recovery of mature forest values), compared to secondary tropical wet forests that established after similar disturbance intensity (Chapter 3). Drought stress and seasonality reduce plant growth and establishment rates to levels that make recovery of mature-forest conditions slow, even if the tropical dry forest structure is indeed simple.

Based on the patterns of successional replacement of species observed in the chronosequence study, we were able to distinguish two major successional groups (a pioneer- and a mature-forest species guild), which were used in the longitudinal study to analyze successional dynamics (Chapter 4). The successional trajectories of individual plots closely matched the overall trends predicted by the chronosequence study, and most trajectories fell within the 95% confidence interval of the chronosequence models (Chapter 4, Figs. 2, 5). Furthermore it was seen that the functional group distinction clearly explained long-term community level patterns. These results challenge current ideas that secondary succession is highly stochastic and unpredictable (Vandermeer et al. 2004, Chazdon 2008, Johnson and Miyanishi 2008). What appears as stochastic at the community level becomes highly predictable at the functional group level. The directionality in patterns of forest structural development and the sequential replacement of species through succession indicates that a common set of deterministic underlying forces strongly drive and form the backbone of successional development (cf. McCook 1994, Rees et al. 2001).

ENVIRONMENTAL CHANGE, COMMUNITY DYNAMICS AND SUCCESSIONAL MECHANISMS

Our results showed that secondary succession in TDF does not only depend on the life history traits of the species (i.e. growth rates and longevity) but also on biotic interactions (Chapter 4), and environmental filters, which are modified by vegetation development itself (Chapter 5).

As expected, the dry season TDF environment was characterized by high soil and atmospheric drought (soil water potentials below -30MPa, minimum RH < 35%, and VPD > 4 KPa). These harsh dry season conditions explain why the majority of woody species and individuals in this TDF are drought avoidant (deciduous) and why only a limited number of (evergreen) drought tolerant species and individuals occur in the system, mostly in old-growth and mature forests (cf. Eamus and Prior 2001, Givnish 2002). Significant environmental changes occur due to leaf deployment in the rainy season. In this season, soils reached water potentials close to soil field capacity and the forest understory became overall shadier, cooler and moister than in the dry season (Chapter 5, Figs. 1, 2). The intensity of these changes is diminished compared to tropical wet areas because of the lower above ground biomass and vertical stratification of TDF.

Despite the seasonal changes, the early successional environment of TDF is characterized by high irradiance, high temperatures, low RH, high VPD, and hence high soil desiccation (Chapter 5, Figs. 1, 2). These early-successional conditions therefore act as a strong filter for species establishment. Vegetation re-growth is characteristically patchy under such conditions (cf. Ewel 1980) and was dominated by deciduous pioneer species with traits to deal with such stressful environments (e.g. control irradiance load through leaf orientation by pulvinar movement, favor convective cooling over transpirational cooling, and maintain leaf structural integrity and low water potentials under water stress; Chapters 4, 6). Pioneers showed initially a high recruitment and growth rate, which led to a strong reduction in light availability. As a result, they made conditions unfavorable for their own regeneration, which was reflected in declining recruitment rates and increasing mortality rates. Pioneers nonetheless recruited and increased in density almost during the first ten years. Only then the mortality of pioneer trees was high relative to their recruitment. Thus, their density decline due to self-thinning largely overlapped with the density decline produced by the death of large senescent trees (Chapter 4, Fig.2). The rates of pioneer recruitment are markedly slow, and the self-thinning density decline was attenuated compared to tropical wet forests (e.g. Swaine and Hall 1983, Breugel et al. 2006).

Pioneers do not only inhibit their own regeneration but also facilitate the regeneration of mature-forest species by improving the moisture and temperature conditions of the atmosphere and soil. A reduced air temperature, vapor pressure deficit, and irradiance, facilitates the regeneration of mature-forest species with simple, large leaves (Chapter 6). Such large leaves are detrimental early in succession because they hamper heat reduction by convective cooling but they are advantageous late in succession because they reduce self-shading and enhance light interception per leaf area (Jones 1992, Falster and Westoby 2003). Recruitment and growth of mature-forest species were unrelated to the structural development of pioneers, but their survival was higher when the pioneers were most abundant (i.e. before pioneers reached full ontogenetic development; Chapter 4, Figs. 2, 4).

Hence, for strongly drought-stressed tropical forests, shade emerges more as a need than as a limitation for survival of most species; suppression due to low light levels plays a minor role, and direct facilitation emerges as an important mechanism in early succession (Chapter 4, Hammond 1995, Gerhardt 1996, McLaren and McDonald 2003a,b). At later stages, nonetheless, the more classical view of competition-driven succession emerged: as mature forest species continued filling up space and growing into the canopy, competition among them intensified and their mortality increased.

Because of the extended time of successional development covered, these results further show that plant interactions as mechanisms of successional replacement are indeed varied and dynamic (Finegan 1984, McCook 1994). Interactions occurred within and between the pioneer and mature-forest species guilds with different intensities, durations, and timings, and the shifts in interactions resulted from variations in environmental conditions, and the developmental stages and functional relatedness of coexisting plants (cf. Holmgren et al. 1997, Brooker et al. 2008, Valiente-Banuet and Verdú 2008).

MODELS OF SECONDARY FOREST SUCCESSION REVISITED

As most of our knowledge on tropical secondary succession comes from forest types that are markedly different from tropical dry forests, how do our results compare then to two of the most used and widely consented conceptual models of forest succession?

One of these models, the guild-dynamics model, focuses on the sequential changes of dominance by four well-defined functional groups: herbs and shrubs, short-lived pioneers, long-lived pioneers and shade-tolerants (Gómez-Pompa and Vázquez-Yanes 1981, Finegan 1996). The structure-dynamics model, in fact successfully adopted from secondary succession in temperate mesic forests, describes four development-phases based on stand structural changes, i.e.: (1) a stand initiation phase marked by abundant tree recruitment and packing of the available site; (2) a stem exclusion phase in which thinning notably reduces stem density and tree recruitment is largely inhibited; (3) a transition or understory reinitiation phase in which the senescence and death of the first cohort of trees creates gaps that improve the recruitment of species of the understory and the canopy of old-growth forests; and (4) an old-growth stage characterized by mixed-cohorts of trees not present in early stages, high vertical and horizontal structure, and high diversity of understory and canopy vegetation (Peet 1992, Oliver and Larson 1996, Denslow and Guzman 2000, Kozlowski 2002, Chazdon 2008).

In these two models, competition, suppression and increasing shade tolerance of the species are the main drivers of succession. The models largely reflect the individualistic concept of succession of Gleason (1939): changes in the understory environment by colonizing vegetation are considered to be the result rather than the cause of successional change, i.e. environmental changes are neutral or inhibitory but do not facilitate species replacement (see McIntosh 1981, Finegan 1984 for reviews on successional viewpoints). To include the successional process of drought-stressed systems like ours, these models should then incorporate the interrelated changes in both patterns and processes that occur along the water availability gradient in which tropical forests occur. While these changes in patterns and processes are probably numerous, here we point out to the most relevant ones that emerge from this dissertation.

Species diversity in our forests is low compared to other tropical forest types, which is in line with other studies that show that diversity declines with an increase in dry season stress and a decrease in water availability and productivity (Currie and Paquin 1987, Gentry 1988, Trejo and Dirzo 2000). Our forest is particularly poor with respect to pioneer species (only a handful of them; Chapter 3), which is clearly reflected in the simplicity by which structural changes were explained (Chapter 4). A straight forward consequence of it is that any general model based on the sequential replacement of functional groups should take into account that in more arid systems it is likely that the life-history variation of successional species is reduced, and thus the number of successional stages (Chapter 3, Ewel 1977, Álvarez-Yépiz et al. 2008).

As a consequence of an increase in environmental harshness and a decrease in productivity, processes such as recruitment, growth, and filling up of space, are slowed down in dry forests compared to wet forests (Chapter 4, Ewel 1980, Murphy and Lugo 1986). The high light availability, in combination with slow process rates (Chapters 4 and 5) leads to a reduced density-dependent mortality (self-thinning) of pioneers and to no recruitment limitations under closed forests for species other than pioneers. Therefore, the stem exclusion and understory reinitiation phases in TDF are less marked than in wet systems (Chapter 4, Read and Lawrence 2003, Álvarez-Yépiz et al. 2008). Theoretical studies indeed predict such a reduction in resource-based competition and in density-dependent mortality (thinning) in stressful environments (Huston 1979, Menge and Sutherland 1987, Niklas et al. 2003). In fact, such reductions have also been observed in wet tropical forests experiencing environmental stresses such as drought spells or soil nutrient impoverishment (Bunker and Carson 2005, van Kuijk et al. 2008). This implies that the incorporation of the effects of stress gradients on plant interactions into successional models would not only expand their validity to dry forests but also to wet forests with circumstantial environmental stress (e.g. van Kuijk et al. 2008).

In summary we found that: (1) a low number of species are successful under the harsh conditions of TDF early successional environments and, unlike in wet forests, only one pioneer phase is found; (2) competition between pioneers is diminished due to slow absolute recovery rates compared to wet forests so self-thinning in TDF is largely reduced; (3) the shift in dominance from pioneers to mature-forest species is facilitated by the pioneers themselves: heat-tolerance rather than shade-tolerance drives succession; and (4) recruitment of mature-forest species is not hampered by the canopy of pioneers, and canopy gap dynamics does not play therefore an important role in the shift in dominance between these groups in TDF succession.

Although we have found clear differences between dry and wet tropical forests these findings should not be ultimately seen as clear-cut differences. The change from wet to dry forests is undoubtedly gradual and so would be the shift in relevance between the different mechanisms responsible for successional change.

To fully understand a complex phenomenon like succession, our current "sample size" (this is the number of studies on different sites along environmental and disturbance gradients) is largely insufficient. Thus, to improve our theoretical models on secondary forest succession and to make sound generalizations, traditional successional research (e.g. chronosequences) should not be discouraged but continued to be used, in combination with longitudinal studies, new analytical approaches (e.g. looking at different community properties and components), and the use of diverse techniques to assure that chronosequence requirements are met (e.g. dendrochronology).

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ALGEMENE DISCUSSIE EN SAMENVATTING

Secundaire successie begint wanneer een verstoring bovengrondse biomassa verwijdert en daardoor ruimte creëert voor kolonisatie: hergroei van vegetatie waarbij de structuur, groeiplaats en soortensamenstelling van de plantengemeenschap verandert met de tijd. Dit proces van vegetatieverandering is een van de meest intensief bestudeerde ecologische fenomenen. Het is bovendien een fenomeen dat nog steeds veel debat veroorzaakt. Aan de ene kant is dit omdat er heel veel elkaar beïnvloedende factoren zijn die bepalen hoe de successie verloopt (zie Pickett et al. 1987 voor een uitgebreid mechanistisch raamwerk). Aan de andere kant is dit een resultaat van het feit dat veel successiemodellen zijn gebaseerd op onvolledige kennis van een beperkt aantal biologische systemen en omstandigheden (Ewel 1980, Horn 1981, McIntosh 1981, Finegan 1984, McCook 1994). Theoretische modellen van secundaire successie van tropische bossen zijn tot nu toe voornamelijk gebaseerd op successie in vochtige klimaatzones. Er is vaak gesuggereerd dat ecologie van de droge tropische bossen (DTB) vele typische kenmerken heeft en dat daarom successie in de droge tropen substantieel verschilt van successie in de natte tropen. Het aantal studies naar secundaire successie in droge tropische bossen is echter, tot nu toe, zeer beperkt waardoor we weinig gegevens hebben om deze stelling te ondersteunen.

De doelstelling van deze studie is om te begrijpen waarom verschillende groepen van bomen en struiken aanwezig zijn, domineren en uiteindelijk verdwijnen op specifieke momenten gedurende secundaire bossuccessie in de droge tropen. Hiervoor hebben we de traditionele chronosequentiebenadering gecombineerd met een directe studie van veranderingen over de tijd (longitudinale benadering). Onze chronosequentie bestond uit een reeks verlaten, braakliggende, landbouwgronden met verschillende periodes sinds braaklegging (vanaf nu "leeftijd" genoemd). Een belangrijke onzekerheid van de eerste benadering zit in de bepaling van de leeftijd van een secundair bos, daarom hebben we een dendrochronologische studie gedaan die ons in staat stelde om de leeftijdsinformatie uit interviews met landeigenaren te controleren. Tegelijkertijd introduceert deze studie dendrochronologie als een complementaire techniek in het onderzoek naar tropische secundaire successie (Hoofdstuk 2).

We hebben de chronosequentiebenadering gebruikt om de typische patronen van secundaire successie van DTB en hun onderliggende processen te bestuderen (Hoofdstuk 3). Deze studie heeft geleid tot een indeling in successiefasen en soortengroepen. Deze indelingen zijn vervolgens gebruikt om de dynamiek van secundaire successie te analyseren en te testen in hoeverre enkele gangbare modellen van tropische secundaire successie toepasbaar zijn op de situatie in de droge tropen (Hoofdstuk 4). Vervolgens hebben we aangenomen dat de door de eerste kolonisten veroorzaakte veranderingen in beschikbaarheid van hulpbronnen en van groeiplaatsomstandigheden fundamentele oorzaken zijn van het proces van veranderende soortensamenstelling gedurende successie. We hebben de veranderingen in groeiplaatsomstandigheden geanalyseerd als functie van de opstandontwikkeling en de hypothese getest dat deze veranderingen de soortensamenstelling sturen doordat ze er toe leiden dat steeds andere soorten weggefilterd worden, afhankelijk van hun functionele eigenschappen (Hoofdstuk 6).

In dit laatste hoofdstuk geef ik een synthese van de belangrijkste resultaten en bediscussieer ik de oorzaak van overeenkomsten en verschillen in de patronen en processen die de secundaire successie in verschillende klimaatszones kenmerken. Uiteindelijk beoordeel ik de toepasbaarheid van twee veel geciteerde successiemodellen voor droge tropische systemen en geef suggesties voor hun verbetering.

HET TESTEN VAN DE GELDIGHEID VAN DE CHRONOSEQUENTIE-BENADERING

Omdat successie een langdurig proces is wordt het traditioneel bestudeerd door middel van chronosequenties: percelen met secundair bos van verschillende leeftijden worden gebruikt om vegetatieontwikkeling op de lange termijn af te leiden. Chronosequentiestudies zijn alleen geldig als de geselecteerde percelen een (relatief) gelijke landgebruik – en verstoringgeschiedenis, topografie, bodem en omliggende landschapsstructuur delen (Foster en Tilman 2000). Een extra vereiste is de beschikbaarheid van betrouwbare leeftijdsgegevens en die zijn vaak lastig te verkrijgen. Vele chronosequentie studies voldoen niet aan deze vereisten waardoor de geldigheid van deze benadering serieus ter discussie gesteld wordt (zie bijvoorbeeld Johnson en Miyanishi 2008).

Het was voor ons dan ook belangrijk om de bovengenoemde vereisten zorgvuldig mee te nemen in deze studie. Daartoe hebben we dendrochronologie gebruikt als een nieuwe techniek om leeftijd van de secundaire bossen te bepalen. Het voorkomen van jaarringen in zowel pionier- als schaduwboomsoorten maakte het mogelijk om de op interviews gebaseerde schattingen van braakligperiodes te controleren en aan te passen. Hiermee was het nut van het gebruik van dendrochronologie als aanvullende techniek in de studie van tropische secundaire bossuccessie bewezen (Hoofdstuk 2).

Hoe geldig is de chronosequentiebenadering als alle voorwaarden ten aanzien van de selectie van de studiepercelen zorgvuldig zijn nageleefd? Om deze vraag te beantwoorden hebben we individuele percelen in de tijd gevolgd (longitudinale studie) en de veranderingen vergeleken met de voorspellingen van de statische chronosequentiebenadering (Hoofdstuk 4). De werkelijke veranderingen kwamen kwalitatief en kwantitatief opmerkelijk goed overeen met de voorspellingen van de chronosequentie, vooral als de ontwikkelingspatronen van twee successiegroepen (pioniers en schaduwtolerante soorten) apart werden geanalyseerd. In dat geval viel 85% van alle individuele perceel-census combinaties (in andere woorden, alle censuses gedurende de studieperiode van alle percelen) binnen de 95% betrouwbaarheidslimieten van het regressiemodel dat de chronosequentie beschrijft. Bovendien liepen de ontwikkelingstrajecten van de meeste individuele percelen parallel aan het regressiemodel (Hoofdstuk 4, Fig. 2, 5). Deze resultaten bewijzen dat, zolang de methodologische vereisten van de chronosequentiebenadering zorgvuldig nageleefd worden, chronosequenties niet alleen geldig zijn, maar ook zeer waardevol. Chronosequenties stellen ons in staat om basale successiepatronen vast te stellen en dragen bij aan de formulering en het testen van successiehypotheses (e.g. Debussche et al. 1996, Foster en Tilman 2000, Capers et al. 2005).

HERSTEL EN VEERKRACHT VAN BOSSEN

Onze studie naar hergroei op braakliggende gronden omvatte secundaire hergroei met leeftijden variërend van < 1 tot 65 jaar en daarmee de vroege tot en met late fases van bossuccessie. De resultaten laten zien dat soortenrijkdom en diversiteit, hoogte van het bos, grondvlak en kroonbedekking continue toenemen met toenemende leeftijd (Hoofdstuk 3 en 4). Het herstel van de opstandstructuur volgde hiermee het klassieke patroon van secundaire successie (cf. Brown en Lugo 1990, Barbour et al. 1998). Een uitzondering vormde de stamdichtheid die niet het klassiek patroon volgde van een snelle afname veroorzaakt door concurrentiedunning (cf. Swaine en Hall 1983, Niklas et al. 2003, Breugel et al. 2006).

Patronen van soortendominantie volgden de typische vervangingsreeks waarbij kortlevende planten met hoge kolonisatie- en groeisnelheden worden vervangen door langlevende planten met toenemende maximale grootte (Huston en Smith 1987, Finegan 1996). Een korte initiële fase gedomineerd door kruidachtigen en struiken (0-3 jaar) werd gevolgd door een periode met dominantie van enkele (5) pioniersoorten en een ondergroei met steeds meer en grotere oude-bossoorten (Hoofdstuk 3; Hoofdstuk 4, Fig. 2). De oudere secundaire bossen (> 40 jaar) bestonden uit een menging van aftakelende pionierbomen en kleine tot middelgrote bomen van volwassen-bossoorten. De abundantiepatronen van verschillende soorten in het kronendak en in de ondergroei ondersteunden de idee dat de soortensamenstelling aan het verschuiven was richting die van ‘volwassen’ bossen volgens de hierboven beschreven successiepatronen (Hoofdstuk 3 en 4, Figs. 5). Dit is in overeenstemming met de klassieke successietheorie, maar contrasteert met de successieperiodes van meer dan 100 jaar die nodig lijken te zijn om tot herstel van de originele soortensamenstelling in natte tropische bossen te komen (Finegan 1996, Peña-Claros 2003, Chazdon et al. 2007).

Al deze resultaten ondersteunen de hypothese dat successie in DTB minder successiefasen kent doordat slechts een beperkte groep van pioniersoorten aangepast is aan de moeilijke omstandigheden gedurende de vroegste successiefase (Ewel 1977, 1980). De relatieve snelheid waarmee de soortensamenstelling verandert ondersteunt ook de hypothese dat bossen in de droge tropen veerkrachtiger zijn dan in de natte tropen dankzij de relatief simpele structuur van hun plantengemeenschappen. Het herstel van andere aspecten van de opstandstructuur (gemeten als percentage van volwassen bossen) was echter vergelijkbaar – of langzamer dan het herstel van bossen op verlaten landbouwgronden in de natte tropen. Het lange droge seizoen en droogtestress zijn hier waarschijnlijke oorzaak van.

Gebaseerd op de succesionele vervangingsreeks in de chronosequentiestudie konden we twee belangrijke succesionele groepen onderscheiden, namelijk één groep van pioniersoorten en één van volwassen-bos-soorten. We gebruikten deze twee groepen om successiedynamiek te bestuderen in onze longitudinale studie en vonden dat de successietrajecten van de meeste individuele percelen, voor beide groepen, goed overeen kwamen met de trends zoals voorspeld door de chronosequentie studie. Dit resultaat daagt het tegenwoordig prevalerende idee uit dat secundaire bossuccessie willekeurig en onvoorspelbaar is (Vandermeer et al. 2004, Chazdon 2008, Johnson en Miyanishi 2008); wat stochastisch lijkt op gemeenschapsniveau is zeer voorspelbaar op het niveau van functionele groepen. De duidelijke richting waarin bosstructuur zich ontwikkelt en de opeenvolgende vervanging van soorten gedurende successie geeft aan dat successie gestuurd wordt door een aantal onderliggende deterministische mechanismen (cf. McCook 1994, Rees et al. 2001).

VERANDERING VAN DE GROEIPLAATS, DYNAMIEK VAN DE PLANTENGEMEENSCHAP EN SUCCESSIEMECHANISMEN

Onze resultaten laten zien dat secundaire bossuccessie in de droge tropen niet alleen afhangt van typische eigenschappen van soorten zoals potentiële groeisnelheid en levensduur, maar ook van biotische interacties (Hoofdstuk 4) en omgevingsfactoren. Deze interacties and factoren veranderen op hun beurt weer onder invloed van de succesionele vegetatieontwikkeling (Hoofdstuk 5).

Zoals verwacht worden de groeiplaatsomstandigheden van DTB gedurende het droge seizoen gekenmerkt door een lage luchtvochtigheid en vochtgehalte van de bodem (bodemwater potentiaal -30MPa, minimum relatieve luchtvochtigheid < 35% en dampdrukspanning > 4 KPa). Deze moeilijke omstandigheden gedurende het droge seizoen verklaren waarom de meerderheid van de houtige soorten en planten in deze DTB droogtemijdend (bladverliezend) zijn en waarom slechts een beperkt aantal soorten en individuen droogtetolerant (altijdgroen) zijn, vooral in de oudere bossen (cf. Eamus and Prior 2001, Givnish 2002). Belangrijke veranderingen in de groeiplaats vinden plaats aan het begin van het natte seizoen wanneer de bomen weer bladeren krijgen. Gedurende dit seizoen komt het waterpotentiaal van de bodem in de buurt van de veldcapaciteit van de bodem en de ondergroei wordt schaduwrijker, koeler en vochtiger dan in het droge seizoen (Hoofdstuk 5, Figs. 1, 2).

Ondanks de seizoensgebonden veranderingen is de groeiplaats van jonge secundaire bossen in de droge tropen over het algemeen gekenmerkt door veel licht, hoge temperaturen, lage relatieve vochtigheid, hoge dampdrukspanning en dus een droge bodem. Deze vroeg-successionele omstandigheden zijn daarom een sterke filter voor de vestiging van individuen en soorten. Hergroei van vegetatie is meestal fragmentarisch onder zulke omstandigheden (cf. Ewel 1980) en wordt gedomineerd door bladverliezende pioniersoorten die in staat zijn zich te handhaven onder dergelijke stressvolle omstandigheden. Voorbeelden van eigenschappen die hun hiertoe in staat stellen zijn (1) het controleren van de hoeveelheid ontvangen straling door aanpassing van de bladoriëntatie door pulvinaire beweging, (2) het bevoordelen van convectieve koeling boven koeling door transpiratie en (3) het handhaven van de integriteit van de bladstructuur en van een lage waterpotentiaal onder waterstress (Hoofdstukken 4 en 6).

In het begin van successie ontwikkelde zich snel een hoge dichtheid aan snelgroeiende pionierbomen en dit resulteerde in een sterke afname in lichtbeschikbaarheid. Als gevolg daarvan werden de omstandigheden ongunstiger voor deze pioniersoorten waardoor rekrutering af- en mortaliteit toenam. Desondanks duurde het 10 jaar voordat mortaliteit hoger was dan rekrutering, zodat gedurende die periode de dichtheid van pioniers toenam.De rekruteringsnelheid was erg langzaam en zelfdunning onbelangrijk vergeleken met de situatie in secundaire bossen in de natte tropen (e.g. Swaine en Hall 1983, Breugel et al. 2006).

Pioniersoorten onderdrukten niet alleen hun eigen regeneratie maar bevorderden tegelijkertijd de regeneratie van volwassen-bossoorten doordat ze de vochtigheid en temperatuur van zowel bodem als lucht verbeterden. Een lagere luchttemperatuur, dampspanningstekort en directe zonnestraling faciliteerden de regeneratie van volwassen-bossoorten met grote enkelvoudige bladeren (Hoofdstuk 6). Dergelijke grote bladeren zijn nadelig in de vroege fase van secundaire successie omdat ze slecht convectief afkoelen, maar ze zijn voordelig in oudere secundaire bossen omdat ze minder zelfbeschaduwing veroorzaken en daardoor efficiënter licht onderscheppen (Jones 1992, Falster en Westoby 2003).

Rekrutering en groei van volwassen-bossoorten waren niet gerelateerd aan de structurele ontwikkeling van de door pioniersoorten gevormde opstand, maar hun overleving was hoger wanneer het stamtal van de pioniers het hoogste was, dus voordat de pionierbomen volledig ontwikkeld waren (Hoofdstuk 4, Figs. 2, 4). In deze tropische bossen met sterke droogtestress blijkt schaduw voordelig te zijn voor de overleving van de meeste soorten en speelt onderdrukking van groei en overleving door de lage lichtbeschikbaarheid dus slechts een beperkte rol. Facilitatie is dus een belangrijk mechanisme gedurende de vroegste successiefase (Hoofdstuk 4, Hammond 1995, Gerhardt 1996, McLaren en McDonald 2003). Gedurende latere fasen komt het klassieke beeld van doorichtconcurrente gedreven successie sterker naar voren: terwijl volwassen-bossoorten steeds verder groeien en het kronendak domineren neemt de onderlinge concurrentie toe en daardoor de mortaliteit.

Omdat de chronosequentie de successie gedurende een lange periode vertegenwoordigt laten de resultaten zien dat de interacties tussen planten een zeer variabele en dynamisch successiemechanisme vormen (Finegan 1984, McCook 1994). Interacties vonden plaats binnen en tussen de groepen van pionier- en volwassen-bossoorten. Deze interacties verschilden met betrekking tot intensiteit, duur en timing. Veranderingen in deze interacties waren het resultaat van variatie in groeiplaatsomstandigheden gedurende de succesionele ontwikkelingsfases en de functionele verwantschap tussen de samenlevende planten (cf. Holmgren et al. 1997, Brooker et al. 2008, Valiente-Banuet en Verdú 2008).

EEN HERZIENING VAN MODELLEN VAN SECUNDAIRE BOSSUCCESSIE

Aangezien onze kennis van tropische secundaire bossuccessie grotendeels gebaseerd is op studies van bostypen die duidelijk verschillen van tropische droge bossen is het de vraag hoe onze resultaten zich laten vergelijken met twee van de meest gebruikte conceptuele modellen van secundaire bossuccessie.

Een van deze modellen, het functionele soortsgroep-dynamiekmodel, beschrijft de opeenvolgende dominantie van vier functionele soortsgroepen: kruidachtigen en struiken, kortlevende pioniers, langlevende pioniers en schaduwtolerante soorten (Gómez-Pompa en Vázquez-Yanes 1981, Finegan 1996). Het structuurdynamiek model, gebaseerd op secundaire bossuccessie in gematigde klimaatzones, beschrijft vier ontwikkelingsfasen gebaseerd op veranderingen in de opstandstructuur: (1) een opstandsinitiatiefase met overvloedige rekrutering en hoge stamtallen; (2) een dunningsfase met afnemend stamtal en weinig tot geen rekrutering; (3) een overgangs- of ondergroei-inititatiefase waarin de aftakeling en dood van veel bomen van het eerste cohort resulteert in gaten in het kronendak, waardoor de rekrutering van ondergroei- en kronendaksoorten toeneemt; en (4) een volgroeide fase die bestaat uit een mix van soorten en leeftijden met een complexe verticale en horizontale structuur en een hoge soortenrijkdom in ondergroei en kronendak (Peet 1992, Oliver en Larson 1996, Denslow en Guzman 2000, Kozlowski 2002, Chazdon 2008).

In deze twee modellen wordt successie gestuurd door lichtgerelateerde concurrentie, onderdrukking en een toenemend aandeel van schaduwtolerante soorten. Zij reflecteren grotendeels het individualistische concept van Gleason (1939): veranderingen van de groeiplaatsomstandigheden in de ondergroei worden vooral gezien als het resultaat van successie en minder als oorzaak van successionele veranderingen. Er wordt in feite aangenomen dat groeiplaatsveranderingen neutraal zijn of een remmende werking hebben en niet dat ze de vervanging van soorten gedurende successie faciliteren (zie McIntosh 1981 of Finegan 1984 voor een overzicht van successiemodellen). Om deze modellen aan te passen aan de realiteit in de droge tropen moeten de veranderingen in patronen en processen langs de regenvalgradiënt meegenomen worden in deze conceptuele modellen. Waarschijnlijk zijn dergelijke veranderingen van patronen en processen talrijk, maar hier behandelen we slechts de belangrijkste die in dit proefschrift naar voren zijn gekomen.

Soortenrijkdom is onze bossen is laag vergeleken met andere tropische bossen en dit is in overeenstemming met eerdere studies die een afnemende diversiteit hebben laten zien met een toename van intensiteit en lengte van het droge seizoen en de daaraan gerelateerde afname in waterbeschikbaarheid en productiviteit (Currie en Paquin 1987, Gentry 1988, Trejo en Dirzo 2000). Ons bos heeft met name weinig pioniersoorten (slechts een handvol, Hoofdstuk 3). Een duidelijk gevolg is dat een algemeen successiemodel gebaseerd op de opeenvolgende vervanging van functionele soortengroepen rekening zou moeten houden met een gereduceerde variatie in levensstijlen en dus met minder successiefasen (Hoofdstuk 3, Ewel 1977, Álvarez-Yépiz et al. 2008).

Als gevolg van een hardere leefomgeving en afname van productiviteit zullen processen zoals rekrutering, groei en kronendaksluiting langzamer gaan in droge bossen dan in natte bossen (Hoofdstuk 4, Ewel 1980, Murphy en Lugo 1986). De hogere lichtbeschikbaarheid, in combinatie met de tragere vegetatiedynamiek leiden tot een verminderde dichtheidsafhankelijke mortaliteit (zelfdunning) van pioniers minder rekruteringsproblemen voor alle soorten behalve de pioniersoorten. Hierdoor zijn de dunnings- en overgangsfasen minder duidelijk aanwezig in de droge – dan in de natte systemen (Hoofdstuk 4, Read en Lawrence 2003, Álvarez-Yépiz et al. 2008).

Theoretische studies voorspellen inderdaad een dergelijke vermindering in concurrentie voor hulpbronnen en in dichtheidsafhankelijke mortaliteit in een stressvolle omgeving (Huston 1979, Menge en Sutherland 1987, Niklas et al. 2003). Vergelijkbare waarnemingen zijn ook gedaan in natte tropische bossen met korte droogteperiodes of verarming van de bodemvruchtbaarheid (Bunker en Carson

2005, van Kuijk et al. 2008). Dit betekent dat als we de effecten van een stressgradiënt op plantinteracties meenemen in successiemodellen, dit niet alleen hun geldigheid vergroot ten aanzien van droge bossen, maar ook ten aanzien van natte bossen waar stress af en toe een rol speelt (zie bijvoorbeeld van Kuijk et al. 2008).

Samenvattend hebben we gevonden dat: (1) een klein aantal soorten succesvol is onder de harde omstandigheden gedurende de initiële fase van successie in DTB, en dat er, anders dan in natte bossen, slechts één pionierfase is; (2) concurrentie tussen pioniers relatief zwak is vanwege het langzame herstel vergeleken met natte bossen en het daarmee samenhangend beperkte voorkomen van zelfdunning; (3) de vervanging van pioniersoorten door volwassen-bossoorten gedurende successie grotendeels gefaciliteerd wordt door de pioniers zelf: het is eerder de hittetolerantie dan de schaduwtolerantie die successie stuurt; en (4) recrutering van volwassen-bossoorten wordt niet gehinderd door het kronendak van pioniers. Daardoor speelt de dynamiek van kronendakgaten geen belangrijke rol in de verschuiving in dominantie tussen deze twee functionele groepen die plaats vindt gedurende de successie van DTB.

De duidelijke verschillen die we hebben gevonden tussen successie in droge – en natte tropische bossystemen reflecteren zonder twijfel een geleidelijk gradiënt waarlangs het belang van verschillende mechanismen die de successie sturen verschuift. Om een complex fenomeen als successie te begrijpen is de beschikbare "steekproef" – het aantal gepubliceerde studies in verschillende locaties langs milieu- en verstoringgradiënten – bij lange na niet groot genoeg. Om onze conceptuele modellen van secundaire bossuccessie te verbeteren en te komen tot goedonderbouwde generalisaties zouden we dus niet de traditionele manier om successie te bestuderen, bijvoorbeeld door middel van chronosequenties, moeten ontmoedigen. In plaats daarvan zou deze benadering gecombineerd moeten worden met longitudinale studies, nieuwe analytische benaderingen (bijvoorbeeld de studie van verschillende eigenschappen en componenten van de plantengemeenschappen) en met het gebruik van nieuwe technieken om te garanderen dat de vereisten van de chronosequentiebenadering worden nageleefd (bijvoorbeeld dendrochronologie).

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SHORT BIOGRAPHY

Edwin Eduardo Lebrija-Trejos was born to Mexican father and Panamanian mother in Panama City, Panama, on April 5, 1975. At the age of ten he moved to Mexico where he finished his high school education in 1993 and registered at the Universidad Nacional Autónoma de México (UNAM) to study Biology from 1994 to 1998. He obtained his Bachelor of Science *cum laude* after defending his thesis entitled: Structural Analysis of the Riparian Forest in the Nizanda Region, Oaxaca, Mexico, in 2001. After graduating, he worked as research assistant in the Department of Physical Geography, Institute of Geography, UNAM, as editor assistant of the *Boletín de la Sociedad Botánica de México*, and as lecturer in ecology for undergraduate students at the Faculty of Sciences, UNAM.

In 2002 he received a grant from the National Council of Science and Technology of Mexico (CONACYT) to study a MSc in Forest and Nature Conservation at Wageningen University, The Netherlands. He was awarded his master degree *cum laude* in 2004. Supported further by CONACYT and in cooperation with the Department of Ecology and Natural Resources of the Faculty of Sciences, UNAM, he continued his research in secondary succession of tropical dry forests as a PhD student in the Forest Ecology and Forest Management Group of the Center for Ecosystem Studies, Wageningen University. That research resulted in this thesis.

Since Edwin Lebrija-Trejos obtained his BSc he has been a faculty-appointed reviewer of two BSc and one MSc theses at UNAM, and co-supervised one minor thesis at the Universidad Autónoma Metropolitana and two MSc theses at Wageningen University. He is interested in processes and mechanisms of plant community dynamics, restoration and conservation ecology, natural resource management and vegetation change in relation to climate change and desertification. In early 2009, he moved with his wife to Israel where he became Post-doctoral fellow in the Department of Plant Sciences of the Faculty of Sciences, Tel Aviv University, to study the effects of climate change on vegetation dynamics. Following his bicultural background he is passionate for intercultural exchange and an enthusiastic traveler.

PUBLICATIONS

Lebrija-Trejos, E., F. Bongers, E. A. Pérez-García and J. A. Meave. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. Biotropica 40: 422-431.

Brienen, R. J. W., E. Lebrija-Trejos, M. van Breugel, E. A. Pérez-García, F. Bongers, J. A. Meave and M. Martínez-Ramos. 2009. The potential of tree rings for the study of forest succession in southern Mexico. Biotropica 41:186-195.

Lebrija-Trejos, E., E. A. Pérez-García, J.A. Meave, F. Bongers and L. Poorter. Functional traits and environmental filtering drive community assembly in a species-rich tropical system (revision submitted to Ecology).

Pérez-García, E. A., J. A. Meave, J. L. Villaseñor, J. A. Gallardo-Cruz and E. Lebrija-Trejos. Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, Mexico (submitted to Folia Geobotanica).

Brienen, R. J. W., E. Lebrija-Trejos, P. A. Zuidema and M. Martínez-Ramos. Rainfall and ENSO sensitivity of a tropical dry forest tree indicate future growth decreases due to climate change (submitted to Global Change Biology).

PE&RC PHD EDUCATION CERTIFICATE

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

REVIEW OF LITERATURE (5.6 ECTS)

- Secondary succession in the tropics: the tropical dry forest case (2005)

WRITING OF PROJECT PROPOSAL (7 ECTS)

- Dry forest secondary succession in Mexico: mechanisms and differential species performance (2005)

LABORATORY TRAINING AND WORKING VISITS (4.3 ECTS)

- Vascular plants and their microenvironment (theory and practice of plant ecophysiology); Centro de Investigación Científica de Yucatán (2004)

POST-GRADUATE COURSES (3 ECTS)

- Multivariate analysis; PE&RC (2005)
- Advanced statistics; PE&RC (2005)

COMPETENCE STRENGTHENING / SKILLS COURSES (2.1 ECTS)

- Project & time management; DLV academy (2005)
- Scientific writing; CENTA (2005)
- PhD Competence assessment; Maas Assessment & Development (2005)

DISCUSSION GROUPS / LOCAL SEMINARS AND OTHER SCIENTIFIC MEETINGS (4.3 ECTS)

- Discussion group on plant community ecology; Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, UNAM (2005, 2006, 2007)

- Discussion group on forest and conservation; PE&RC (2005, 2008)
- Mini symposium: patterns and mechanisms of facilitation in plant and animal communities; Resource Ecology (2008)

PE&RC ANNUAL MEETINGS, SEMINARS AND THE PE&RC WEEKEND (1.2 ECTS)

- PE&RC Introduction weekend (2005)
- PE&RC day: accelerate scientific progress – expect the unexpected (2008)

INTERNATIONAL SYMPOSIA, WORKSHOPS AND CONFERENCES (7 ECTS)

- Ecological Society of America / International Association for ecology joint meeting (2005)
- Association for Tropical Biology and Conservation annual meeting (2006)
- Congreso Mexicano de Ecología (2007)
- Annual meeting of the Netherlands Research Network (2008)

COURSES IN WHICH THE PHD CANDIDATE HAS WORKED AS A TEACHER

- Ecological methods; Resource Ecology; 8 days (2005 & 2007)
- Forest ecology and forest management; FEM; 2 days (2005 & 2008)

SUPERVISION OF MSC STUDENTS: 20 DAYS

- Morphological leaf traits that distinguish pioneers from late colonizers in a tropical dry forest in Mexico
- Agricultural practices and tropical dry forest regeneration in southern Mexico