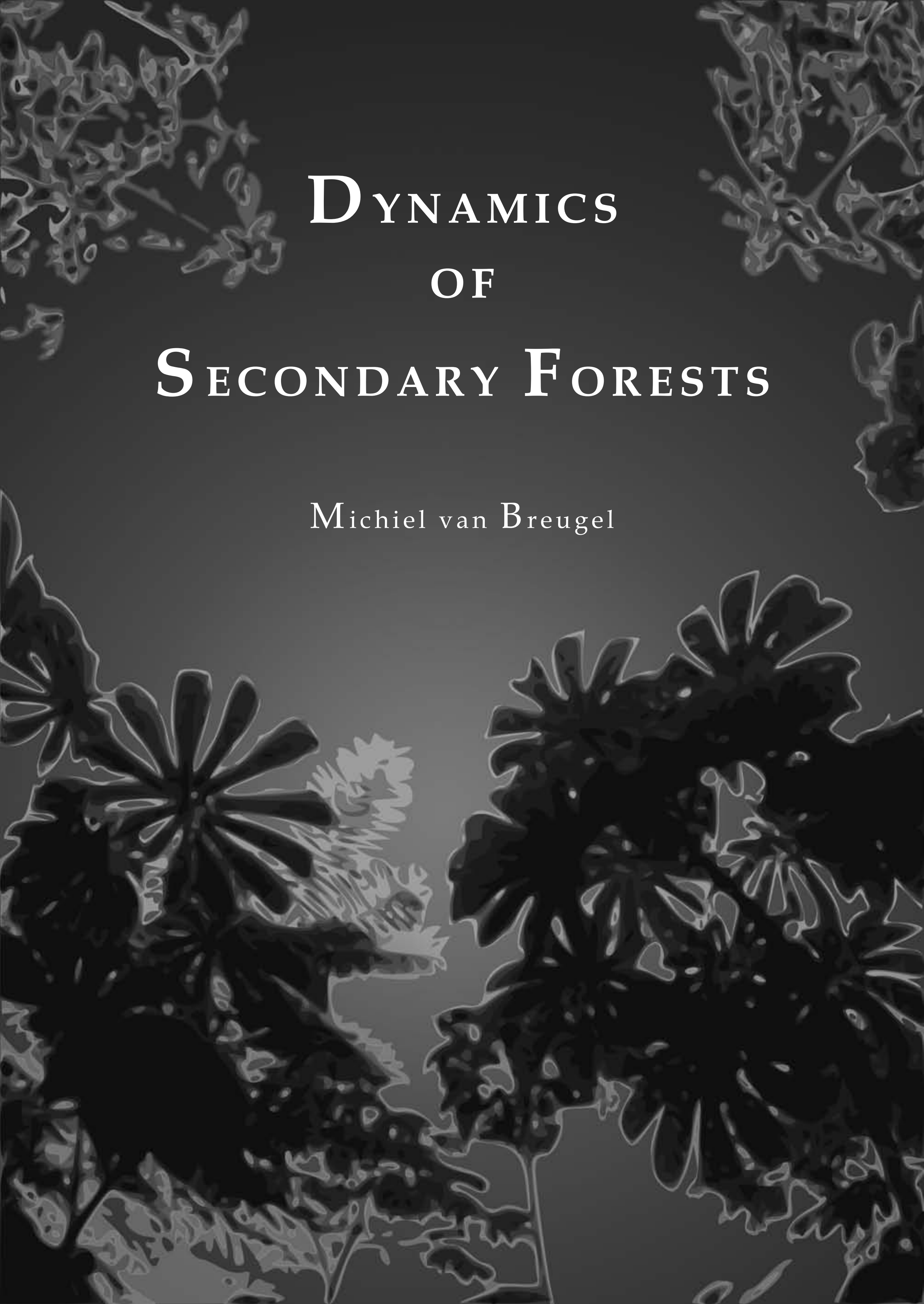
DYNAMICS OF SECONDARY FORESTS

Michiel van Breugel



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OF

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DYNAMIEK VAN SECUNDAIRE BOSSEN

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Voor mijn ouders
Voor Paulo, Yvonne en Lisanne
& hun families

&

voor mijn vrienden

para mis amigos,

for my friends

CONTENTS

Chapter 1

GENERAL INTRODUCTION

SECONDARY FORESTS IN THE TROPICS: A GENERAL CONTEXT

Tropical forest landscapes are changing rapidly. A growing human population and economy lead to rising resource demands and hence increasing and intensifying land-use (Geist & Lambin 2002; DeFries *et al.* 2005; Foley *et al.* 2005; Perz *et al.* 2005). Agricultural expansion and timber extraction have already caused the net loss of over half of the original tropical old-growth forests, although estimations of total accumulated deforestation and current rates of deforestation vary much due to differences in definitions of forest, methods and interpretations (Achard *et al.* 2002; Hansen & DeFries 2004; Wright 2005; FAO 2006; Wright & Muller-Landau 2006). Estimations of deforestation rates in the 1990s and the first five years of this decade vary between 5.8 million (Achard *et al.* 2002) and 13 million hectares (FAO 2006). Natural old-growth forests are also being replaced by intensively managed plantations for the production of *e.g.* timber, pulpwood or palm-oil (Sampson *et al.* 2005; FAO 2006), or degraded because of practices such as selective logging, infrastructure development, hunting, or over-harvesting of NTFP's (Robinson & Bennett 2000; Hassan *et al.* 2005). Although such changes may imply serious degradation in terms of structure, species diversity and ecosystem services, they hardly appear in statistics on forest cover changes (Foley *et al.* 2005; Shvidenko *et al.* 2005; Foley *et al.* 2007). At the same time forest planting and especially natural regeneration of secondary forests led to significant reforestation; secondary forest succession on abandoned lands is estimated to have reclaimed one of each six to seven deforested hectares in the Tropics (Wright 2005).

There is, however, considerable ambiguity and confusion in the use and perception of the term 'secondary forest'. Two primary considerations may lead to divergent views (and therefore statistics) on secondary forests (Chokkalingam & Jong 2001; Geldenhuys *et al.* 2003). A first question is whether we should refer to secondary forest only when they are the result of anthropogenic disturbances, or also of large-scale natural disturbance, such as by hurricanes, fires or landslides. A second question is whether intensity and scale of disturbance matters. The prevailing view is that secondary forest is regrowth occurring on land that was totally cleared from its original vegetation on a scale larger than naturally occurring disturbances (*e.g.* tree-fall). Particularly in tropical Asia, however, logged-over forests are also considered to be secondary forests (Sist *et al.* 1999; de Jong *et al.* 2001). As large-scale statistics on the extent and dynamics of secondary forests are mainly based on satellite imagines, definitions of secondary forests seem to be based on technical possibilities and restraints as much as on conceptual issues though (*e.g.*, Kuntz & Siegert 1999; Helmer *et al.* 2000).

Patterns, causes and dynamics of forest cover changes differ greatly within and between regions (Lambin *et al.* 2001; Geist & Lambin 2002; DeFries *et al.* 2005; FAO 2006). In consequence, the context of land-use dynamics in which secondary forest succession takes place can be very different from one location to another. Most secondary forests are part of swidden fallow or shifting cultivation agricultural systems. These systems are, broadly speaking, any temporally and spatially cyclical agricultural system that involves clearing – usually with assistance of burning – of land followed by phases of cultivation and secondary forest regeneration during fallow periods for the purposes of soil restoration. This type of agriculture is very common throughout the Tropics and held responsible for deforestation and the formation of secondary forests in large areas in the tropics (*e.g.*, Myers 1993; Richards *et al.* 1996; Brown & Schreckenberg 1998; Fox *et al.* 2000). An extensive review of 152 case studies on net losses of tropical forest cover indicated that shifting cultivation is associated with 48% of deforestation cases, although underlying economic, institutional, political, social, and demographic driving forces were manifold and highly variable between regions (Geist & Lambin 2002).

Furthermore, the term 'shifting cultivation' lumps a wide variety of very different systems (Fig.1; Sunderlin 1997). On one side there still exists a large variety of small-scale traditional systems by indigenous communities. Indigenous people over vast – if not all - parts of the Tropics practiced shifting cultivation over centuries, and still do so in many areas. Their systems mostly consist of a sequence of short cultivation and long fallow periods, combined with complex management of - and the use of a range of products from fallow vegetation (*e.g.* Gómez-Pompa 1991; Remmers & Koeijer 1992; Wal 1998; Cairns & Garrity 1999; Schmidt-Vogt 1999; Coomes *et al.* 2000; Floret & Pontanier 2000). In many regions these land use systems are becoming increasingly unsustainable as a consequence of a complex interplay of economic, social, demographic and political pressures, acting in various combinations in different regions. Population increase is mostly mentioned, but is not always the main driving variable. Whatever combination of variables may play a role, the result is generally an expansion or intensification of agriculture, based either on the clearing of old-growth forest or an increasingly intensive use of agricultural areas, the latter normally through reduction of the fallow period (Remmers & Koeijer 1992; Cairns & Garrity 1999; Coomes *et al.* 2000; de Jong & Chokkalingam 2001; Geist & Lambin 2002; Metzger 2002; Shriar 2002; Choudhury & Sundriyal 2003; Toledo *et al.* 2003; Perz *et al.* 2005).

An important factor is also the growing incorporation of cash crops (*e.g.* Lawrence *et al.* 1998) and livestock in the farming systems. Both encompass more extensive, (semi-) permanent and intensive types of land-use. In Latin America for example, large scale land-use conversion to pastures for cattle raising is among the major factors in tropical deforestation (Nepstad *et al.* 1997; Mendoza & Dirzo 1999; Walker *et al.* 2000). This may affect the extent and dynamics of (secondary) forest cover through different processes. Rates of secondary forest development, in terms of biomass, canopy structure, soil properties and species composition may be considerably slower on abandoned pastures compared to abandoned agricultural fields, due to stronger absence of - and

	Land-use intensity		
Fallow period	>> Cultivation period	Decreasing, often < 5 y	(Semi) permanent
Fields	Small	Small – large (pastures)	Large
Forest cover	High OGF, old SF	Decreasing Less OGF, decreasing SF age	Low Only OGF
Land-use types			
- Spatial context	Small scale, mixed	Transition	Large-scale, separated
- System complexity	One complex system	Transition	Separated components
- relation to environment	Well adapted	Deteriorating	Often bad
- fallow management	Intensive	Decreasing	No fallows
- Field management			
Crops	Subsistence Diverse Multipurpose From field and fallow	Subsistence / cash crops Decreasing diversity Focus on staple and cash crops Decreasing use of fallow	Cash crops One - few crops Cash crops Only field

FIGURE 1. Schematic typology of shifting cultivation farming systems. Elaborated from Sunderlin (1997), based further on references on shifting cultivation mentioned in the text. OGF = Old Growth forest, SF = secondary forest. Most agricultural landscapes are highly dynamic, with continuously changing patterns of land-use. Arrows give the direction of changes that appear to prevail in tropical regions (see discussion in text).

isolation from propagule sources and more severely degraded soils (Nepstad *et al.* 1991, see next sections). Furthermore the extensive nature of cattle farming may cause or add to land scarcity, and hence to old-growth forest clearance and shorter fallow periods..

At the other end of the gradient of shifting cultivation systems (Fig. 1) are the so-called frontier communities, consisting of recent settlers from other areas. Over-populations and shortage of land elsewhere generally drives such migration, often stimulated by government resettlement and transmigration schemes. Immigrants are usually associated with large-scale deforestation in areas such as the Amazon (Walker & Homma 1996; Nepstad *et al.* 1997) and the Lacandon and El Peten regions in Mexico and Guatemala (Mendoza & Dirzo 1999; Cairns *et al.* 2000; de Jong *et al.* 2000; Shriar 2002). Often – but not always – they apply extensive forms of shifting cultivation with very short fallow periods with a preference for old-growth forests for field establishment and without management or further use of fallows (Myers 1993;

Sunderlin 1997; Schmidt-Vogt 1999). In-migration is often from other ecological regions, for example from highlands and temperate zones to lowland tropical zones as in Mexico (Mendoza & Dirzo 1999). Hence knowledge on ecological conditions might be limited among migrants and their agricultural practices less productive and sustainable.

A particular case of land-use dynamics consists of natural post-abandonment forest succession in areas where rural-urban migration, following socio-economic and demographic changes, leaves marginal agriculture. In this case, the driving factors are the decreasing local labor demand and crop prices due to large-scale high-input agriculture, the increasing job opportunities in the cities due to developing industry and services, and a range of local or regional problems including natural catastrophes, conflicts, and environmental degradation (*e.g.*, Aide & Grau 2004). Large scale agricultural land abandonment and forest regrowth occurred before in the eastern United States and in parts of Europe since as early as the late 19th and the early 20th centuries, resulting in what is now part of the permanent forest cover in these regions (Flinn & Vellend 2005). Puerto Rico and the Dominican Republic provide examples from the Tropics. Formerly a large part of their land was under agricultural use, but since the 1940s (Puerto Rico) and 1970s (Dominican Republic) economic changes caused the abandonment of most of these areas (Thomlinson *et al.* 1996; Pascarella *et al.* 2000; Aide & Grau 2004; Lugo & Helmer 2004). In the Amazon (Moran *et al.* 1994; Moran *et al.* 1996) and Costa Rica (Helmer 2000) other examples of long-time abandoned pastures exist. However, similar processes seem not always to result in land abandonment. In colonization zones in the Ecuadorian Amazon, short-cycle shifting cultivation of crops for expanding urban and export markets were found to replace semi-permanent land-use practices such as cattle ranging (Rudel *et al.* 2002). The result was a net reforestation, but, different from the examples from Puerto Rico, consisting of temporal young secondary vegetation.

Viewpoints on the role of shifting cultivation agriculture and secondary fallow vegetation in the maintenance of biodiversity and sustainable local livelihood diverge widely. Arguments that they are essential for the long term conservation and management of forests and biodiversity (*e.g.*, Kammesheidt 2002; Finegan & Nasi 2004) are based on examples from the left-hand end of the continuum depicted in Fig. 1. Moreover, optimism on recovery of forested landscapes and accompanying environmental services by natural secondary forest succession on abandoned farmlands seem to lean strongly on the many publications on such developments in Puerto Rico, the Dominican Republic and some few other sites (*e.g.* Foster *et al.* 1999; Grau *et al.* 2003; Aide & Grau 2004). In contrast, examples from the right-hand end or cases in which a shift to the right is occurring may have fueled the opinion of many of those who consider shifting cultivation a threat to forests and secondary forests of limited value (*e.g.*, Green 2005). These widely divergent views underline that perspectives on the role of secondary forest in maintaining ecosystem services on landscape scale must be seen in the context of the local and regional land-use dynamics (Chazdon 1998; Kammesheidt 2002; Finegan & Nasi 2004; DeFries *et al.* 2005).

PATTERNS OF TROPICAL FOREST SUCCESSION

Within the field of secondary forest succession in the Tropics, changes in community structure and species composition with fallow age have been documented by numerous studies (Brown & Lugo 1990; Guariguata & Ostertag 2001). Most commonly studied variables are basal area, biomass, stem density, species richness and species diversity. The most common approach to study such successional patterns is to select a range of plots with different times since abandonment, assuming that they represent different stages of a similar successional development; the so-called chronosequences (see below). A classic example of such a chronosequence study is the work of Saldarriaga and co-workers (1988). They studied the patterns of stem density, basal area, biomass and species richness over a chronosequence of 80 years and their findings are exemplary for the fairly general trends found across most studies (Fig. 2).

STEM DENSITY

Saldarriaga *et al.* (1988) found decreasing stem density with fallow age (Fig. 2A), although age explained only a small proportion of between-plot variation. Quite different patterns were observed in other studies. In a chronosequence on central Amazonian abandoned pastures that covered 15 years post abandonment succession, tree stem density followed a modal distribution over time with a peak between 6-8 y (Feldpausch *et al.* 2005). In Puerto Rico, stem density increased up to ca. 25 years post-abandonment and then stabilized for the next 35 years of succession (Aide *et al.* 1995). In Panama, Denslow & Guzman (2000) found that density decreased over the first 70 years and increased over the following 30 years. Studies on succession on abandoned agricultural fields (*e.g.* Peña-Claros 2003: 0-40 y; Toledo & Salick 2006: 1-36 y), on abandoned pastures (*e.g.* Moran *et al.* 1996: 0-20 y; Rivera *et al.* 2000: 15-35 y), or on coffee plantations (*e.g.* Marcano Vega *et al.* 2002: 10-40 y) however failed to find a relation between stem density and fallow age, as did most comparable studies I am aware of.

Hence, stem density does not appear to follow a predictable pattern with successional age. Density is the result of recruitment, growth and mortality; i.e., it is potentially influenced by a wide variety of factors, operating at a range of spatial and temporal scales that vary in their effects on different size classes. For example, competition may result in thinning among the smallest individuals, while growth of the survivors results in an increasing stem density in larger size classes (Compare Fig. 2A with Fig. 2B). Pioneer trees may attract dispersal vectors (*e.g.* bats and birds) (Guevara *et al.* 1992;

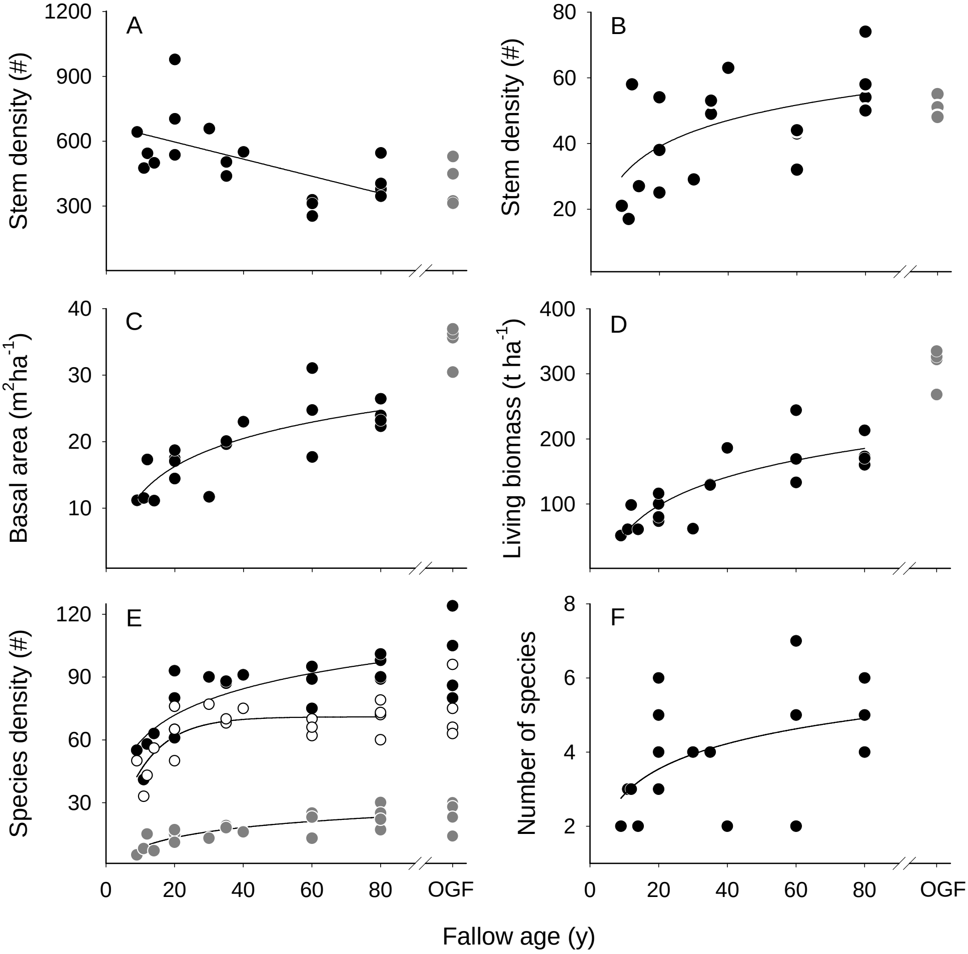

FIGURE 2. Successional trends on abandoned agricultural fields in the Colombian and Venezuelan Amazon near San Carlos de Rio Negro. Plot size was 0.09 ha^{-1}, inventory included all woody stems with dbh ≥ 1 cm. A) Stem density of stems with dbh ≥ 1 cm (R^2 = 0.37, P = 0.006). B) Stem density of stems with dbh ≥ 10 cm (R^2 = 0.64, $P < 0.001$). C) Basal area (m^2 ha^{-1}, R^2 = 0.64, $P < 0.001$). D) Living above and belowground biomass (Mg ha^{-1}, R^2 = 0.70, $P < 0.001$). E) Species density (species 0.09 ha^{-1}, R^2 = 0.65, $P < 0.001$) of stems with dbh ≥ 1 cm (black dots); of stems stems with 1 cm ≤ dbh < 10 cm (open dots, R^2 = 0.60, $P < 0.001$), and of stems with dbh ≥ 10 cm (grey dots, R^2 = 0.65, $P < 0.001$). F) Number of species whose relative importance values accumulated up to 50% (R^2 = 0.24, P = 0.033). Data from Saldarriaga *et al*. (1988, their Tables 1 and 2 and Appendix 1).

Duncan & Chapman 1999; Garcia Queila *et al.* 2000; Wijdeven & Kuzee 2000; Holl 2002), or eliminate competition from forbs and grasses (Aide & Cavelier 1994; Zimmerman *et al.* 2000), enhancing subsequently recruitment of more shade tolerant species below them and thus increasing understory density. Stem density will also depend upon which species was able to colonize the area first, as some species form and/or tolerate much denser stands than others. As early secondary forests are mostly dominated by only few secondary forest species of similar age (Finegan 1996), processes affecting these cohorts may add to an erratic behavior of stem density during succession. A species that establishes itself at high densities at a particular site might experience subsequently high mortality due to density dependent factors such as competition or outbreaks of specific pathogens (Castello *et al.* 1995; Toyohara & Fujihara 1998). At the end of the maximum lifespan of a dominant species, high mortality could open up the stand for a new wave of recruitment (Saldarriaga *et al.* 1988). Analyzing stem density of specific functional groups or within specific size classes therefore might be more informative (*e.g.* Saldarriaga *et al.* 1988; Peña-Claros 2003), especially when actual dynamics over time are included.

BASAL AREA AND BIOMASS

Changes of basal area and biomass during succession appear to be much more predictable than stem density. In the calculation of stand biomass, allometric equations for relating stem diameter to total biomass are commonly used, including regularly tree height and wood density. Most of such equations are not species-specific, but developed from a mix of species (Brown *et al.* 1989). In addition most studies used generic regression equations that were developed elsewhere (*e.g.* Jepsen 2006). Obviously there are problems and limitations to such an approach, and especially between-site comparisons have to be done cautiously (Overman *et al.* 1994; Brown *et al.* 1995; Ketterings *et al.* 2001; Chave *et al.* 2004; Chave *et al.* 2005). Nonetheless the method is widely used in assessing biomass accumulation in secondary forests, as it was for the calculation of the values of figure 2C. It might therefore not be much of a surprise that successional trends for biomass and basal area are generally found to be very similar. Most studies are limited to estimations of aboveground living biomass, but several others include belowground living biomass and dead organic matter (*e.g.* Uhl & Jordan 1984; Hughes *et al.* 1999; Hughes *et al.* 2000a).

The findings of Saldarriaga *et al.* (1988; see Fig. 2B, C) are qualitatively the same as have been found by most comparable studies. In general, both variables increase linearly or asymptotically with fallow age (see overviews of Brown & Lugo 1990; Moran *et al.* 2000; Silver *et al.* 2000; Guariguata & Ostertag 2001). These trends appear to be rather robust: Lumping 134 plots differing in past land-use (pasture, agriculture fields, only cleared) and life-zones (wet, moist, dry) from a wide range of tropical chronosequence studies, Silver *et al.* (2000) found a good and highly significant fit ($R^2 = 0.66$, $p < 0.0001$) between aboveground biomass and fallow age. Accumulation rate was much higher during the first 20 y (6.2 Mg ha^{-1} y^{-1}) than over a larger period (2.9 Mg ha^{-1} y^{-1} over the first 80 y).

The shape of the trend will always depend to some extent on which part of the development trajectory is covered by the chronosequence (See Fig. 4 and accompanying discussion below). In the youngest plot (9 y) of Saldarriaga *et al.* (1988) basal area and biomass already reached values of respectively 12 m^2 ha^{-1} and 51 Mg ha-1, indicating that the accumulation rate in the first years must have been much higher than in the following years. In contrast, the chronosequence of Feldpausch (2004) on light-moderately used pastures in central Amazonia did cover the first 12 years of succession. He found hardly any biomass accumulated in the first 2 yrs; then, following 12 years, biomass increased almost linearly to 128 Mg ha^{-1}. Biomass accumulation can also slow down very early in succession. In swidden fallows from 1 to 12 y old in Kalimantan, Indonesia (Hashimotio *et al.* 2000) and from 2 to 15 y old in Sarawak Malaysia (Jepsen 2006), accumulation stagnated in respectively 12 and even 5 years after abandonment.

As with density, dynamics of basal area and (living) biomass is the outcome of the patterns of recruitment, growth and mortality, hence it may be governed by a variety of factors. The slowing down of biomass accumulation may be related to size- or age-related diminishing growth rate of the dominant trees, while trees in the understory are still suppressed as found in temperate forest succession (Peet & Christensen 1980; Oliver & Larson 1996). Saldarriaga *et al.* (1988) proposed that the accumulation of basal area and biomass was offset by the death of the dominant long-lived successional species after ca 40 years of succession (Fig. 2B, C). Results of Fehse and colleagues (2002) suggest that productivity, expressed as annual aboveground biomass accumulation, was highest during the establishment phase (14.2-15.0 Mg ha^{-1} y^{-1} at 6-8 y) due to high recruitment of saplings, and then slowed down significantly as number of saplings decreased substantially (5.9 -6.9 Mg ha^{-1}y^{-1}, at age 30). As chronosequence data are not actually measuring processes of mortality, growth and recruitment, any of these explanations are merely hypotheses. In one of the very few studies that followed successional dynamics in time, Uhl (1987) concluded that the rate of biomass accumulation declined beyond ten years because the dominant tree species began to die out and to be gradually replaced by more slow-growing, primary forest species.

SPECIES

Across a wide range of studies, ranging from small swidden fallow fields, abandoned coffee and cacao plantations to extensive pastures, species density has been found to be related to fallow age (see *e.g.* Fig. 2 and Aide *et al.* 1995; Chinea & Helmer 2003; Gemerden *et al.* 2003b; Peña-Claros 2003; Toledo & Salick 2006). Species density can increase very fast, and has been found to reach old-growth forest values in 40 y in abandoned pastures (Aide *et al.* 1996), in 25-30 y in abandoned pastures and coffee plantation (Pascarella *et al.* 2000) and within 20 y on abandoned agricultural fields (Dewalt *et al.* 2003; Peña-Claros 2003). In all cases however, species composition was still very distinct and estimated to take much longer (>100 y) to get to resemble the species composition of nearby old-growth forests (see also Turner *et al.* 1997).

The patterns generally observed in tropical forest succession is that initial colonization is dominated by relatively short-lived, fast-growing, pioneer species that dominate the canopy of secondary forests during the first decades after abandonment, after which they are succeeded by long-lived pioneer species that dominate the canopy until senescence or disturbance cause their dead (see overviews in Finegan 1996; Richards *et al.* 1996; Guariguata & Ostertag 2001). Cronosequences that covered a period long enough (> 40-50 years) to observe these trends confirmed such trends (*e.g.* Saldarriaga *et al.* 1988). In general, stands are dominated by only very few species in the sense of stem density and basal area. Saldarriaga (1988) found an across-plot average of 4 species whose relative importance value accumulated to 50%, and this number was only weakly related to fallow age over a age range of 9-80 year (Fig. 2F). Other studies had similar findings (*e.g.*, Rivera *et al.* 2000). As some pioneer species can be very long lived, their dominance may persist for decades or even centuries. In nine of sixteen 1-ha old-growth – apparently 'primary' – forest plots in Cameroon, the tree species that dominate the canopy preferred shifting cultivation fields for recruitment while trees of species below the canopy preferred gaps and closed forest conditions (Gemerden *et al.* 2003a). Several species of the first group, like Lophira alata, are among the main (in terms of quantity and economic value) timber species of the region (Parren 2003). This indicates that, even several centuries after human land-use, this forest can be considered to be a secondary forest (Gemerden *et al.* 2003a).

Some studies explicitly examined patterns of species richness and composition separately for canopy and understory (see *e.g.* Figs. 2E). They found invariably that understory species density was much higher and species composition approached the species composition of old-growth forest more rapidly (*e.g.* Guariguata *et al.* 1997; Peña-Claros 2003; Toledo *et al.* 2003; Lawrence 2004). This reflects two processes: the sequential canopy dominance of a few pioneer species, and a continuous recruitment of shade tolerant species in the understory. Species of the first group often occur at very low numbers in old-growth forests, while the second group represents species that may be more typical for old-growth forests. Just as successional patterns in stand structure mainly reflect the dynamics of the larger trees, patterns of diversity and composition appear to reflect largely the dynamics (recruitment and mortality) of the smaller individuals. The latter may only very slowly grow into the canopy, hence canopy species may add substantially to stand diversity only relatively late in succession (see *e.g.* Fig. 2E). Rates of recruitment, dead and growth may vary much between sites, and hence the resulting patterns of species accumulation and replacement.

Few studies on tropical forest succession examined individual species distribution along a succession gradient, despite the fact that the individualistic nature of succession has been stressed since long by many ecologists (*e.g.* Gleason 1939; Peet & Christensen 1980). Two studies in Bolivia assessed patterns of relative abundance with fallow age (Peña-Claros 2003; Toledo & Salick 2006). Both found various trends, including a rise, a decline, an optimum and no change in abundance, indicating that species achieve their highest abundance at different times during succession. Kammesheidt (2000) compared functional traits of 21 early and late successional species with abundance patterns. Finding of these studies broadly confirm earlier classifications in functional groups of tree species, but clearly suggest that across and within classes a continuum of responses exist.

Patterns of species richness, composition and abundance are the net results of species dynamics, i.e. recruitment, growth and mortality, and the subsequent population changes of the constituent species. However, very few studies actually monitored either community or population dynamics over time. Findings from permanent plot studies in stands with initial fallow age ≥ 55 years (Lang & Knight 1983; Milton *et al.* 1994), in sites with initial fallow age between 12–25 y (Chazdon *et al.* 2005; B. Fingegan unpublished data), and two further studies that monitored the first years of post clearance succession (Uhl *et al.* 1981; Swaine & Hall 1983; Uhl 1987), confirm largely the general patterns found by chronosequences. However, the detailed descriptions of species dynamics of Uhl and co-workers (1981; 1987) and Swaine & Hall (1983) indicate that population dynamics of individual species, interactions between species and individuals, and stochastic processes may result in community dynamics that are much more complex and more erratic than can be inferred from the chronosequence studies. Comparing the latter studies with the studies in older secondary forests also suggest decreasing rates of change in community parameters with time.

Observations on secondary forests seem to suggest that secondary forests within a certain region are dominated by the same early or long-lived pioneer species (Finegan 1992; Richards *et al.* 1996). Moreover, many of these species appear to occur over a wide range of environmental conditions and have a wide geographical distribution (Finegan 1996; Richards *et al.* 1996). Some typical pioneer genera such as *Cecropia* and *Vismia*, that are widely distributed throughout the Neotropics, have been found to be dominant (in terms of relative number or basal area) in many studies. Within the Amazon basin, studies near Manaus (Steininger 2000; Mesquita *et al.* 2001; Lucas *et al.* 2002), in Para (Uhl *et al.* 1988; Parrotta *et al.* 1997), in Rondondia (Alves *et al.* 1997), in Bolivia (Steininger 2000; Peña-Claros 2003), in the upper Rio Negro region in Venezuela (Uhl *et al.* 1981; Uhl 1987) and in Colombia (Vester 1997) found dominance of species from one or both genera in a significant proportion of their sample plots. Much further north, the same was found in the Los Tuxtlas region (Purata 1986) and southern Chiapas (this thesis), both in Mexico. See Finegan (1992) for examples on other species. Within regions, most studies report a small number of dominant species across their sample plots. It remains the question, however, how typical such observations are for the secondary forests and the pioneer species in a region. In other words, are the species that dominate individual secondary forests also the most frequent across the secondary forests of a particular region, and are most or only few pioneer species widely distributed and dominant across a region? Surprisingly very few studies addressed these question explicitly and quantitatively, likely because only few chronosequences included enough plots to assess such patterns of dominance and frequency across a region (but see Saldarriaga *et al.* 1988; Finegan 1992; Rivera & Aide 1998; Aide *et al.* 2000).

FACTORS INFLUENCING SUCCESSIONAL TRENDS

The rate of successional stand development may depend on a wide array of factors. In a survey across five regions of the Amazon basin, inter-regional differences in the average rates of basal area and height growth were best explained by differences in soil types, reflecting differences in soil fertility (Moran *et al.* 2000). Similar findings were reported before by Tucker *et al.* (1998). Zarin *et al.* (2001) found soil texture to be a nearly unbiased linear predictor of forest regrowth in terms of biomass across seven Amazonian sites, while they did not find a significant difference between regrowth on abandoned pasture land vs. slash-and-burn agricultural fields. Within regions, the type, duration and intensity of land-use prior to abandonment has been demonstrated to have a strong effect on rate of forest regrowth, most commonly expressed in basal area, biomass or canopy height (*e.g.* Chinea 2002). Regrowth on pastures for example has been found to be delayed in comparison with regrowth on agricultural fields (*e.g.* Moran *et al.* 2000; Steininger 2000) or coffee plantations (*e.g.* Zimmerman *et al.* 1995; Pascarella *et al.* 2000).

Differences between land-use types relate to typical practices that differentiates them, such as the prolonged use and large extent of pastures compared with swidden fallow fields. Purata (1986) compared the effects of different crops (maize, coffee, pasture), length of the past cropping period, fallow age and forested perimeter on stand structure and composition. All variables except crop type significantly influenced species richness and composition, while only fallow age and cropping period had (opposite) effects on structure. Within one land-use type, differences in management and cultivation practices influence rates of regrowth. Secondary forest regrowth varied between areas in Thailand that had similar edaphic conditions, but were farmed by different ethnic groups. Major factors influencing these differences were cultivation period; fallow length and mode of site preparation prior to cultivation, which were on their turn related to the socio-economic and demographic factors discussed earlier (Schmidt-Vogt 1999). When fallow periods are long enough, soil fertility can be maintained, even after centuries of shifting cultivation. Lawrence & Schlesinger (2001) found no significant differences in total soil phosphorus across 24 sites in West Kalimantan, Indonesia, although number of prior cultivation cycles differed between 2 and 10. In this region fallow periods were on average 20 year. In the Amazon and in Mexico, increasing intensity of cattle-grazing (Uhl *et al.* 1988), length of the land-use prior to abandonment (Hughes *et al.* 1999; Steininger 2000), and different clearing treatments such as burning, weeding and bulldozer treatments (Uhl *et al.* 1982; Moran *et al.* 2000; Chinea 2002) had a negative impact on rates of forest regrowth (basal area and biomass). At the same time, environmental factors and patterns of land use history will be easily confounded. After all, land-use type and variables such as intensity and duration of land-use are closely linked farmer decisions and, on their turn, these are strongly related to soil conditions (Chinea 2002).

Duration and intensity of land-use affect rates of secondary forest regrowth through different processes. First, they strongly affect depletion of soil organic matter and nutrient and alter soil physical properties prior to regrowth (Buschbacher *et al.* 1988; Aide & Cavelier 1994; Reiners *et al.* 1994; Hughes *et al.* 2000b; Hughes *et al.* 2002), which directly affects site productivity and therefore tree growth (Buschbacher *et al.* 1988; Aide & Cavelier 1994; Fetcher *et al.* 1996; Lawrence 2001). Moreover, adverse soil properties may impede the establishment of species, or affect one species stronger than another, thus giving it a relative competitive advantage (Bazzaz 1996). Across studies, results are equivocal with respect to the influence of soil conditions on species diversity. Lawrence (2004) found no effect of soil fertility on species density across and within sites. In several studies in near Manaus, in the Amazon, *Vismia* species occurred on more deteriorated sites that had more intensive or prolonged land-use, while *Cecropia* species occurred more abundantly on sites with less intensive land-use (Uhl *et al.* 1988; Mesquita *et al.* 2001; Lucas *et al.* 2002).

Secondly, the on-site availability of propagules in the form of a seed bank and resprouts will be greatly reduced by intensive or prolonged land-use (Uhl *et al.* 1981; Nepstad *et al.* 1999). Resprouting can be an important regeneration mechanism that influences stand development (Kammesheidt 1999; Bond & Midgley 2001). An extreme example is given by comparing post-agricultural - with post-hurricane succession (Boucher *et al.* 2001). The abundant presence of residual vegetation and propagule sources at the beginning of the post-hurricane succession, steered forest development in a very different direction compared to post-agricultural, considering both structure and composition. Rates of forest regrowth and biomass accumulation has been found to decline when residual vegetation and propagule sources are lacking due to the nature of former land-use, *e.g.* burning, intensive and long-term use as rangeland (Hooper *et al.* 2004).

Thirdly, in highly disturbed sites such as abandoned pastures, various other factors may constitute major selective barriers on colonization of woody species, even 'typical' pioneer species, (Aide *et al.* 1995). Elevated seed predation (Holl *et al.* 2000; Wijdeven & Kuzee 2000; Myster 2003), low germination success due to unfavorable soil (Aide & Cavelier 1994) and microclimate conditions (Holl 1999), and slow growth and high mortality of seedlings due to strong competition from grasses and forbs (Aide *et al.* 1995; Holl *et al.* 2000) may be important barriers preventing tree establishment and inhibiting fast secondary forest development.

When past land-use eliminated most on-site propagules, regeneration will depend largely on seed rain from outside (Wijdeven & Kuzee 2000; Benitez-Malvido *et al.* 2001; Cubina & Aide 2001). The abundance and species richness of seeds is found to be strongly negatively related to distance from (old-growth) forests. In abandoned pastures (Aide & Cavelier 1994; Wijdeven & Kuzee 2000) seed rain of woody species was concentrated near forest edges and dropped sharply beyond 10-20 m distance. In 9-12 year old swidden fallows, seed rain of woody species was much higher and species richer in sites close (< 100 m) to old-growth forests than in sites beyond 300 meter distance from old-growth forests (Lawrence 2004). Seed rain has also been found to be much higher below remnant trees and shrubs than elsewhere in pastures, due to their attraction of seed-dispersing birds and bats (Guevara *et al.* 1986; Guevara *et al.* 1994; Harvey & Haber 1998; Duncan & Chapman 1999; Galindo-Gonzalez *et al.* 2000; Holl *et al.* 2000; Slocum 2001; Holl 2002). Generally, seed rain (of woody life forms) is overwhelmingly dominated by pioneer species, with a smaller proportion of small-seeded, bird and bat dispersed late successional species, and a near absence of large-seeded species (references above). Such results demonstrate the major importance of the landscape matrix (how much forest and where).

However, a chain of events, from seed dispersal through seedling establishment and subsequent survival, controls recruitment (Houle 1995). As stated before, various barriers may prevent tree establishment after on-site arrival. Hence the question is if a higher and more diverse seed rain translates in faster regrowth with higher tree diversity. In seven 9-12 year old swidden fallows, Lawrence (2004) found highest species density in sites close to old-growth forests. This pattern of declining species density with distance from old-growth forests could largely be accounted for by a similar pattern of stem density. Within 6-10 years old secondary forest patches (Mesquita *et al.* 2001) and in 10-year old plantations, (Parrotta *et al.* 1997) in the Amazon, similar patterns were observed. In the latter study, the dominance of small-seeded, animal-dispersed late successional tree species among the colonizing species and the mere absence of large-seeded species were consistent with the results of the wildlife surveys. These indicated that the most common frugivorous bat and bird species fed on small-seeded plant species, while typical dispersers of larger-seeded tree species were absent or rare. Thus, the relationship between distance to old-growth forest and species density in part reflected long-distance dispersal limitation of late successional species.

After woody colonizers grow big enough, interactions between individual neighbor trees will start to play a role as well. Any factor that steers initial stand composition may thus influence further stand development, due to the differential effects of dominant species on smaller individuals. An example is given by the *Cecropia*- and *Vismia*-dominated stands near Manaus that I discussed earlier in this section. Regeneration in *Cecropia*-dominated stands was more divers than in *Vismia*-dominated stands. Several mechanisms may have played a role (Mesquita *et al.* 2001). In a permanent plots study, establishment of a variety of species with significant numbers started only with the decline of the dominant *Vismia*, suggesting competitive suppression (Uhl 1987). *Cecropia* litter was more effective than *Vismia* litter in restoring soil properties such as organic matter content, water retention capacity and micro-arthropod biomass (Betsch & Betsch-Pinot 1983 in Maury-Lechon 1991). Hence, facilitation may have played a role as well. Studies in plantation forests in Amazonia (Parrotta 1995) and in Costa Rica (Guariguata *et al.* 1995; Powers *et al.* 1997) found that understory species richness and seedling densities were affected significantly by overstory composition. This effect was attributed to differences in canopy openness (suppression of grasses), humus depth and attraction of seed-dispersing birds and bats.

The preceding review demonstrates that the rate and direction of post-agricultural secondary forest succession are regulated by a complex set of interactions between landscape configuration, local site factors, biotic interactions and species life histories (see also Pickett 1976; Chazdon *et al.* 2003). Keddy (1992) defined assembly rules – that determine which components of a regional species pool will form a local community – as a hierarchical set of filters removing species which lack traits for persistence under a particular set of circumstances. Following his approach, landscape configuration, site factors and biotic interactions can be considered examples of such filters (Fig. 3). The nature of regional shifting cultivation agriculture is particularly important in such a framework. The spatial-temporal scale, patterns and intensity of agricultural practices shape landscape configuration and influence local site factors (Lawrence *et al.* 1998; Helmer 2000). Along a gradient of intensifying agriculture as depicted in figure 1, the proportion of agricultural fields, pastures and young secondary forests will increase at the expense of older secondary and old-growth forest. There will be thus an increasingly selective filter, screening strongly for specific traits such as early prolific reproduction, efficient dispersal mechanisms, seed dormancy and resprouting capacity, and short lifespan. A more intensive agriculture (*e.g.* stronger site preparation, prolonged land-use, shorter fallows) will have an adverse impact on soil properties and survival of on-site propagules. Among the individuals that were able to arrive at the site (or survived), a next filter will select for those physiological and morphological traits enabling establishment under the prevailing conditions. One of the main biotic interactions may be competition for resources, which can be between woody seedlings and aggressive grasses or ferns, between seedlings and earlier established overstory trees, or between the trees of the overstory. Local site conditions and the nature of biotic interactions will continuously change as a secondary forest develops. Established vegetation may change soil properties, eliminate competition from grasses, change the microclimate and increase the degree of competition for resources. Moreover a developing stand structure may favor attraction of seed dispersers, implying a changing role in the landscape matrix. Traits being selected for will thus depend on both phase of secondary forest development and of tree phase being considered.

MODELS AND PROCESSES OF SPECIES REPLACEMENT

A strong focus in the studies on forest succession has been on the patterns of floristic change. Egler (1954) proposed two alternative models of forest succession. In the "relay floristics" model, successive groups of species arrive and replace earlier groups as a result of site modification. According to the 'Initial floristic composition" model (IFC), all species may be present or arrive at the onset of succession in the form of seeds or propagules. Species come to prominence at different times due to differences in life history traits such as growth rate, longevity and shade tolerance reach peak

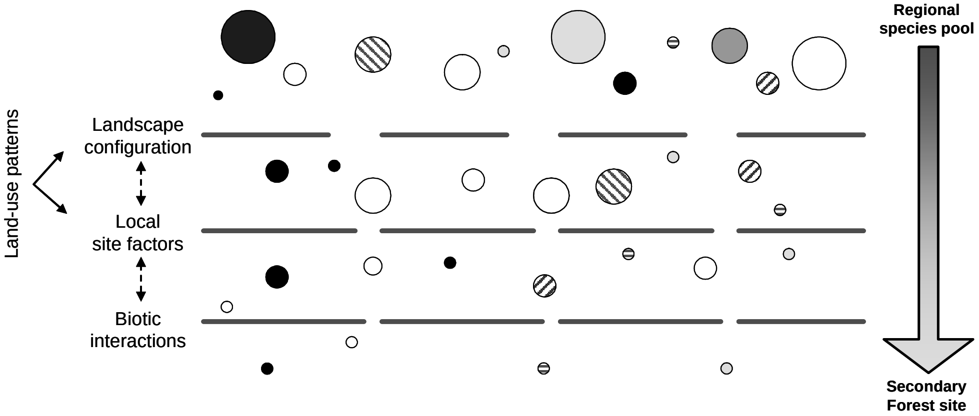

FIGURE 3. Assembly rules - that determine which components of a regional species pool will form a local community – may be defined as a hierarchical set of filters removing species that lack traits for persistence under a particular set of circumstances (Diaz, 1998; Keddy, 1992). The combination of nature and intensity of the environmental filter and the specific traits of a species affect the probability that a species establishes and/or survives as part of a specific secondary forest site.

abundances at different points in succession. Connell and colleagues (Connell & Slatyer 1977; Connell *et al.* 1987) proposed three models – representing a continuum of possible interactions – in which succession is steered by the net effects of earlier species on later ones: facilitation, tolerance and inhibition. In the first two models, competition for resources kills the earlier species, while disturbance or age kills the dominant species in the last model. According Gomez-Pompa & Vazquez-Yanes (1981) and Finegan (1984; 1996), tropical post-agricultural secondary succession resembles most the IFC model. They described succession in terms of four phases, characterized by different sets of species. The initially dominant grasses, forbs and shrubs are replaced within a few years by early pioneers that dominate the canopy for 10-30 y, depending on their lifespan. Long-lived pioneers then replace them and dominate the canopy for a period that depends again on their lifespan. The more shade tolerant species colonize the site continuously from the beginning of succession, but likely at a slow pace due to dispersal limitations, while early and late pioneers only establish under the high light conditions early in succession (Henceforth the GVF-model).

Which of the models most adequately describes succession in a certain area depends on factors such as site conditions and species availability. Real succession will likely be a mixture of models. Finegan (1984; 1996) recognized explicitly that the GVF-model represents succession under a specific set of conditions, viz. low-intensity past land-use and proximity of seed sources. Such conditions are found where small-scale shifting cultivation practices still prevail (left side Fig. 1).

Findings of studies on succession under such conditions indeed indicate that species from all functional groups (including shade-tolerant species) established very early in succession, that pioneer trees come to dominance within 1-2 years, that many species of early successional pioneers fail to recruit after canopy closure, and that shade tolerant species continued to establish after canopy closure (*e.g.* Swaine & Hall 1983; Uhl & Jordan 1984; Uhl 1987; Peña-Claros 2003). In more severely degraded or more isolated sites however, unfavorable site conditions and absence of (off- and on-site) seed sources can slow down succession, as discussed in the former section. Under such conditions facilitation by the earliest colonist or remnant vegetation can be important not only by attracting seed-dispersers but also by modifying soil and microclimate conditions and suppressing competition from grasses and forbs (see references in former sections)

In a critical review of these and a series of other successional models, McCook (1994) pointed out that most of them are implicitly based on a whole range of species interactions and trade-offs between species attributes such as wide dispersal, fast growth, longevity, maximum size, and shade tolerance. Qualitatively similar interactions will govern succession in all situations, and facilitation and inhibition

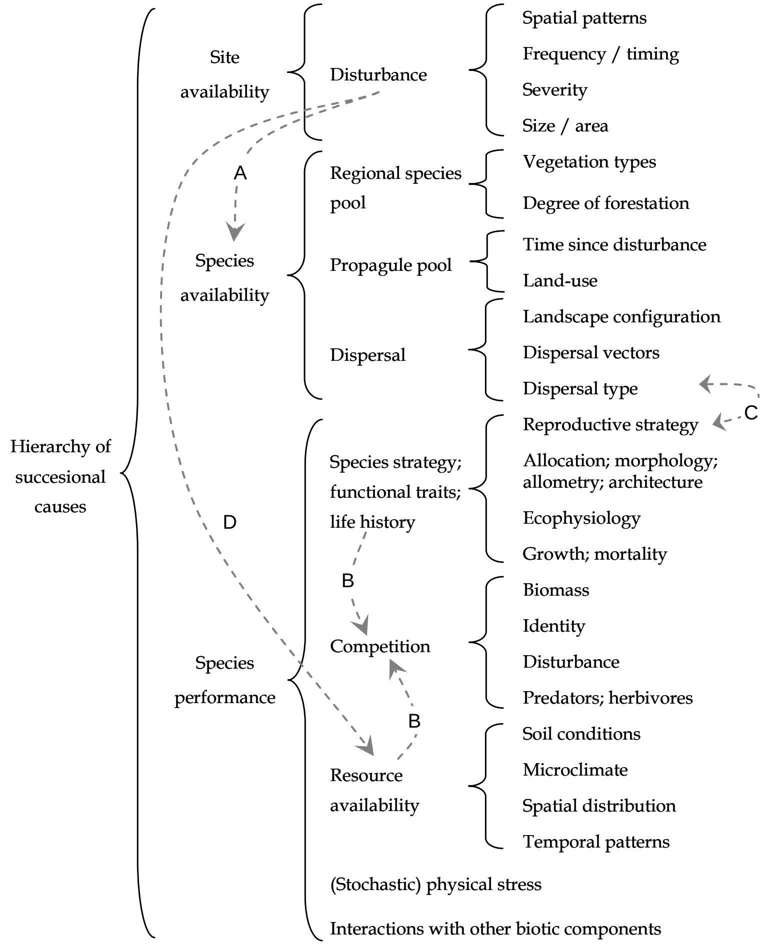

FIGURE 4. A hierarchy of successional causes, going from the most general phenomenon of community dynamics, through the intermediate level of aggregated processes of site availability, differential species availability, and performance to specific interactions, constraints, and resource conditions that govern the outcome of intermediate-level processes at particular sites (Based on Picket *et al.* 1987). The factors at each level are related and/or interacting. As an illustration, some of such relationships are indicated. A) The different aspects of disturbance affect, or even determine, the different aspects of species availability, e.g. landscape configuration is determined by the spatial and temporal patterns of disturbance. B) Competition between individuals or between species is determined by both resource availability and the characteristics of the participating species. C) One aspect of the reproductive strategy of a species is its dispersal type; there are many more of such links. D) Resource availability will for example depend on the severity and intensity of the disturbance. The effects of each factor or process and their relative importance in shaping succession will vary between sites and in time.

effects are the empirical summaries of their relative effects (see for extensive discussion McCook 1994). In an earlier modeling study (Huston & Smith 1987; Smith & Huston 1989), recruitment, growth and dead of individual trees was modulated by competition for light, which on its turn was modulated by neighbors. In this model, an inverse correlation between traits favoring rapid colonization (*e.g.* wide dispersal, fast growth, early reproduction,) and favoring long term dominance (*e.g.* longevity, shade tolerance, height) across a range of simulated species resulted in a sequential species replacement. Varying the nature of the initially dominant species, *e.g.* succession without typical pioneer species, resulted in sequential succession patterns only as long as the before-mentioned trade-off was maintained. It did also result in differences in dominance patterns and rates of species replacement, as relative impacts of species on each other shifted (see Huston & Smith 1987; Huston 1994). Such an approach goes back to the earlier ideas of for example Gleason who saw succession as the result of individualistic species responses to temporal gradients of changing conditions (Gleason 1926, 1939). Similarly, Peet & Christensen (1980) described succession as a population process, with species replacement occurring through differences in species performance at each point along the succession gradient and through stochastic means, resulting in different establishment and mortality rates.

The concept of secondary forest succession is thus based on the fundamental idea that plants have different capacities to match with the prevailing environmental conditions at any moment. When an agricultural field becomes available because it is abandoned or left in fallow, differential availability of species and differential performance of the species that were able to arrive will drive secondary forest succession, i.e. a change in vegetation structure and composition. On their turn, these processes are composed of a combination of more specific conditions, constraints, interactions and mechanisms such as regional species pool, resource availability, and competition. Pickett *et al.* (1987) organized these causes, processes and factors that drive succession in different hierarchical levels in an orderly framework (Fig. 4). The different hypotheses on succession may not be conflicting hypotheses, but indicate different possible outcomes of the processes and mechanisms that are listed in figure 4. Thanks to the numerous studies on secondary forest succession, reviewed in the preceding sections, general successional patterns are well-established by now. In particularly they contributed to our understanding of the role and importance of specific constraints and conditions (*e.g.* time since disturbance, propagules availability, soil properties) with regard to community-level patterns of vegetation structure and composition. Much less understood are, still, the dynamics of secondary forest succession, inclusive spatial-temporal patterns of dispersal, recruitment, growth and mortality and their relationship to the factors and interactions by which they are governed.

STUDYING SECONDARY FOREST DYNAMICS

As I put forward earlier, a large proportion of research efforts have focused on the evaluation of patterns of *e.g.* species replacement or stand structure development using chronosequences. Such an approach is based on assumptions of the same successional processes in stands with similar conditions (*e.g.* land-use history, soil), i.e. sites represent points along a continuum, rather than points on independent trajectories. This basic assumption of chronosequence studies has been questioned (Pickett 1989; Bakker *et al.* 1996; Foster & Tilman 2000). Because chronosequence studies are based on single-time information from a range of sites, these data emphasize cumulative or net effects of ecological processes. Chronosequence data, however, only permit inferences of successional changes rather than the direct analysis of the underlying processes mediating these changes (growth, mortality, and recruitment). Long-term studies in the temperate zone demonstrated that actual developments may diverge considerably form chronosequence patterns because of many reasons that may reflect specific processes on a very local spatial scale in vegetation dynamics (Hibbs 1983; Pickett 1989; Pickett *et al.* 2001). The complexity of interrelated factors and processes that influence the course of succession on any particular place (Fig. 4), and the probabilistic nature of many of these ecological processes can not be captured by evaluating their net effects.

From the few permanent plot studies on forest succession in the Tropics that are published, a picture emerges of highly dynamic patterns of growth, mortality and recruitment, resulting in complex patterns of stand structure development and species replacement. Complexity was found to be very high in the first years of succession (Swaine & Hall 1983; Uhl 1987) and after many decades (Sheil *et al.* 2000). Ecological theory stresses that successional changes in stand structure and species replacement are driven by differential patterns of recruitment, mortality and growth, and that these may be driven by intrinsic species life-history differences (*e.g.* in shade tolerance, recruitment requirements and maximum growth) and competition for resources (*e.g.* Peet & Christensen 1980; Huston & Smith 1987). The patterns of chronosequence studies are often implicitly or explicitly interpreted to be the result of density-dependent processes and interspecific variation in tolerance to competition for resources. However, many different mechanisms act in succession and each of these mechanisms is affected by a range of conditions. The intensity and relative importance of any of them will differ between successions and change during a succession. Moreover, competition, as most processes, act on individual level, and may have different effects on different levels (population, community) or spatial-temporal scales. Longitudinal studies are thus necessarily to advance our understanding of successional dynamics and underlying ecological processes beyond the interpretation of static data.

As yet permanent plot studies have been much less common in the research on tropical forest succession. Even less studies examined the role of competition in successional population and community dynamics. Recently, however, permanent plot studies have been initiated in various parts of the Neotropics. Permanent plot studies in the humid tropics of Costa Rica (Capers *et al.* 2005; Chazdon *et al.* 2005; B. Finegan 2006, personal communication) and Brazil started some years ago. More recently permanent plots were established in dry tropical regions in Oaxaca (E. Lebrija and F. Bongers 2007, personal communication), Yucatan (J. Dupuy 2006, personal communication) and Jalisco (P. Balvanera, M. Martínez-Ramos and co-workers 2007, personal communication), and in the humid tropical region of southern Chiapas (this thesis; M. Martínez-Ramos, F. Bongers and co-workers 2007, personal communication) promise important advances in our understanding of secondary forest dynamics, and an exiting framework for future comparative studies of the role of processes and mechanisms in very different successional settings.

AIM OF THIS STUDY

In the humid Tropics, secondary forest succession on abandoned agricultural fields is highly dynamic and directed by a complex set of factors and interactions. Furthermore, theory and field observations predict that competition for resources, and specifically for light, is one of the main mechanisms that direct these dynamics in the humid Tropics. Therefore the focus of this study is on the processes of growth, mortality and recruitment of trees and species in young secondary forests and how these processes are influenced by competition for resources on individual, population and community level.

The aims of the present study are:

To evaluate the dynamics of young secondary forests on abandoned agricultural fields in terms of community changes and to asses how these dynamics changes with time since abandonment.

To evaluate the dynamics of young secondary forests in terms of growth, mortality and recruitment, and how community changes are related to these processes.

To examine the role and importance of competition in the dynamics of young secondary forests and, more specifically, to examine the degree to which competition can account for (a) variation in growth and mortality of saplings within a population and (b) variation in population dynamics across distinct populations.

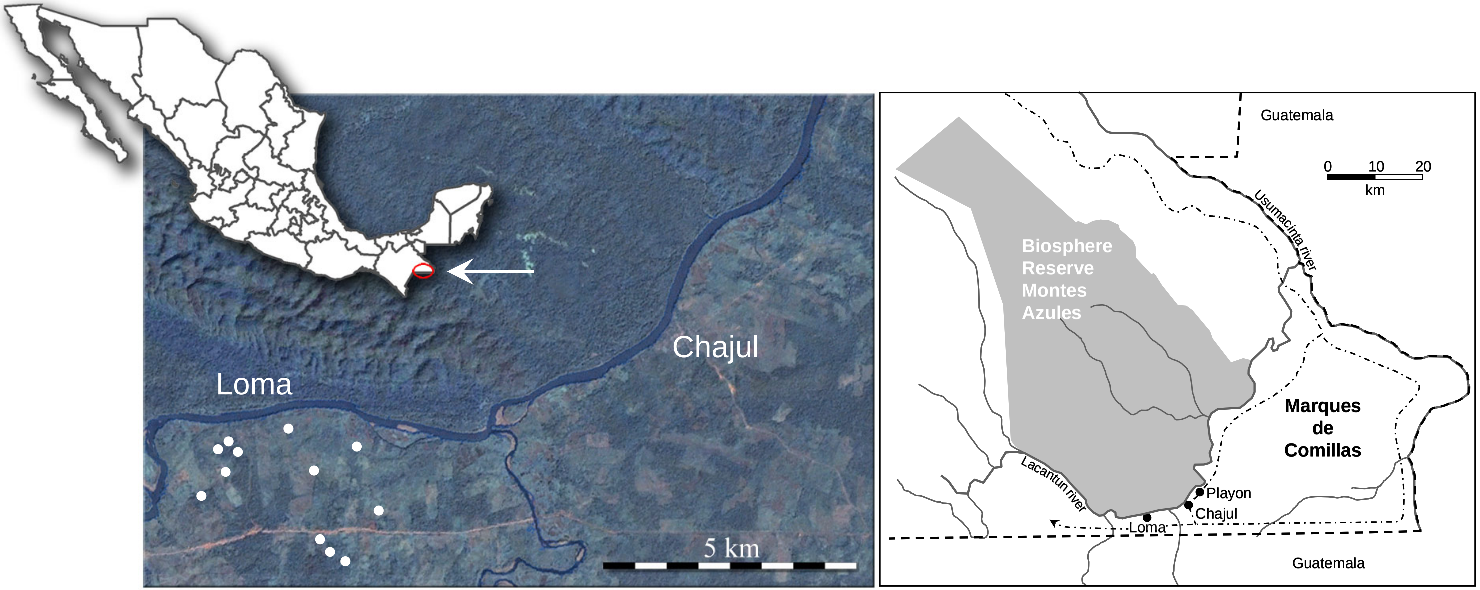

FIGURE 5. A) General overview of the study area. The image is derived from the NASA global OnEarth 15m Landsat (Visible Color) satellite image mosaic, accessed via NASA World Wind on 21 February 2007. Satellite images were taken from 1999 to 2003, with 2000 being the most active year. The river is the Lacantún River with the study area south of the river and Montes Azules Biosphere reserve on the northern banks. The inlet gives the state and national boundaries of Mexico, with the arrow indicating the location of the study area. The white dots indicate the approximate positions of the permanent sample plots. B) The map on the right gives the location of the region Marques de Comillas, the Biosphere Reserve Montes Azules, de location of the three ejido's, the national border (dashed lines), roads (dashed-dotted lines) and rivers (continuous lines).

REGIONAL CONTEXT

The study was carried out in the south-western part of the Marqués de Comillas (approximately between N16 º08' - 16 º 16′ and W90 º 860′ – W91 º 02′), in the eastern extreme of the state of Chiapas, Mexico (see Fig. 5). Field work was done in the ejido's[1] of Chajul, Loma Bonita and Playon de Gloria, south of the Lacantun river and adjacent to the Biosphere Reserve Montes Azules on the northern side of the Lacantun (Fig. 5). The region is part of the Selva Lacandona that contains the northernmost remaining extensive track of tropical rain forests on the American continent. It continues into the Péten region of Guatemala and Belize. Together these regions contain the most extensive continuous rainforest in Mesoamerica (Challenger 1998; Mendoza & Dirzo 1999). About one-fifth of the original Selva Lacandona and 70% of the remaining original vegetation is in the Montes Azules Biosphere Reserve, which encompasses 3312 km². Adjacent to the north-east an additional 663 km² of the forest is protected in the Lacan-tún Biosphere Reserve and Bonampak Natural Monument (Challenger 1998).

The climate of the Marqués de Comillas region (henceforth MdC) is humid tropical. The average annual temperature is 24 ºC. The mean annual rainfall is ~3000 mm, with the greatest concentration in June-September, and a dry period with less than 100 mm month^{-1} in February-April. In the study region four broad geo-morphological units are defined based on soil and topographic criteria (Siebe *et al.* 1996; Celedón-Muñiz 2006): Alluvial terraces along the rivers are flat, fertile soils along the margins of the Lacantun River. Low hills consist of undulating hills with moderate-steep slopes (15°–30°). This is the most common geo-morphological unit in the region and characterized by complex nutrient-poor sandy and limestone soils. Flood plains are old meandric areas with hydromorphic soil characteristics that are flooded for at least three months a year. The Karst-formations consists of limestone rock outcrops and is only found north of the Lacantun River in the Biosphere Reserve Montes Azules. Table 1 summarizes the main soil and vegetation characteristics of these units.

The original vegetation consists mainly of tropical evergreen and semi-deciduous forests that form a mosaic of vegetation types including lowland evergreen rain forest, semi-deciduous forests on Karst formations, and savannah-like vegetation (Martínez *et al.* 1994). Around 3400 species of vascular plants have been recorded for this region, of which 573 are trees (Martínez *et al.* 1994). *Dialium guianense* (Leguminosae) and *Brosimum alicastrum* (Moraceae) are among the most dominant canopy species. Other dominant canopy tree species include *Guarea glabra* (Meliaceae), *Ampelocera hottlei* (Ulmaceae), *Spondias radlkoferi* (Anacardiaceae*), Licania platypus* (Chrysobalanaceae); and *Cupania dentata* (Sapindaceae). The structure and composition of the lowland rain

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[1] Land vested in peasant communities by agrarian reform for communal usufruct, portions of which are often worked by individual farmers.

TABLE 1. Characteristics of two dominant geomorphologic units of the study region, southeast Mexico. Soil data from Siebe *et al.* (1996) and Celédon-Muñiz (2006). Tree community attributes are based on censuses of trees with a DBH ≥ 10 cm in three 0.5 ha plots on alluvial terraces and five plots in the low hills (M. Martinez-Ramos, unpublished data). Canopy height was measured above a 5x5m grid in the 0.5 ha plots, means (± s.d.) are based on data lumped per unit (M. van Breugel unpublished data).

		Habitat	
	Units	Alluvial terraces	Low Hill
Soil			
HC (FAO)		Haplic luvisol	Humic acrisol
Soil depth	cm	77.6 ± 6.7	57.6 ± 4.6
Field Capacity	L m^{-2}	472.3 ± 115	241.6 ± 63.5
Available Water Capacity	L m^{-2}	220.6 ± 55.6	103.1 ± 24.1
P availability	mg kg^{-1}	0.65 ± .29	0.1*
N availability	mg kg^{-1}	29.4 ± 5.6	20.2 ± 7.05
pH		6.1 ± .5	4.7 ± .7
Tree community			
Species richness	0.5 ha^{-1}	43-58	50-81
Canopy height	m	23.09 ± 9.8	16.8 ± 8.9
Tree density	ind ha^{-1}	347 ± 29	434 ± 90
Basal area	m^2 ha^{-1}	30.1 ± 7.5	23.2 ± 6.6

* Data from one study plot only.

forest varies with soil and topography (Siebe *et al.* 1996). The Karst-formations and low hills sustain highest stem densities and species richness, while basal area and canopy height are highest in the alluvial terraces (Tabel 1).

Between the late 1960s and early 1990s, governmental programs stimulated migration from other parts of Chiapas and central Mexican states to the then largely inhabited MdC region (de Jong *et al.* 2000). Colonization started from the northwest and moved rapidly towards the southeast, developing mainly along the rivers and roads. This resulted in large scale deforestation, reducing the area of closed forest from 95% in 1976 to 56% in 1996 (de Jong *et al.* 2000). Since then deforestation continued and current forest cover is probably much lower. Moreover, uncontrolled fires affected considerable parts of the region, most notably in the El Niño year of 1998, but also at several earlier occasions (Román-Cuesta *et al.* 2003; Román-Cuesta *et al.* 2004). Currently, a large part of the landscape consists of temporarily and permanent grazing pastures, young secondary forest and cultivated land (de Jong *et al.* 2000).

In the study area, initial colonization was largely confined to the proximities of the river Lacantun until a regional road was constructed in the late 1990s that connected the area with the regional centers. The fertile alluvial terraces were the first to be cultivated. The low hills followed mostly later, although at an accelerated pace since the construction of the regional road. Currently, the prevailing land use types in the three ejido's are the cultivation of maize and some other crops, cattle ranging and some permanent crop cultivation on the alluvial terraces. The cultivation of maize and other crops generally imply the use of irregular slash-and-burn shifting cultivation practices with usually one harvest followed by a short fallow of a few years. Most production is for subsistence or regional use. Only few farmers cultivate cash crops such as the jalapeño pepper (*Capsicum annuum* var. *annuum*). This happens mainly on the alluvial terraces. However, high costs and labor input, and uncertain price developments keep most farmers from such activities. Most farmers invest in cattle, which are maintained in extensive pastures, and as a result pastures now occupy the larger proportion of the study area. A consequence of this development appears to be reduced fallow periods, as farmers have an increasing shortage of available land (i.e. old-growth forest and secondary forest) for crop cultivation. For example, 18 of 19 secondary forests that were sampled in 1995 (see chapter 2) were already cleared in 2000, and mostly converted to pastures. These past and current land-use patterns result in considerable deforestation and in a landscape currently dominated by pastures and young secondary forests, mixed with agricultural fields and patches of old-growth forests. (Information based on personal communication with various long-term inhabitants from the three ejido's, 2000-2004).

THESIS OUTLINE

CHAPTER **2** describes patterns of species richness and of frequency and abundance of tree species across a wide range of secondary forests sites. Patterns of species richness are related to former land-use (pasture vs. crop cultivation) and soil types (Alluvial terraces vs. Low hills). Differences in across-site frequency and dominance between pioneers, and late-successional canopy and understory species are analyzed.

CHAPTER **3** examines patterns of species recruitment and mortality over a period of 18 months in 8 secondary forest sites with fallow age between 1 and 5 years to test the hypotheses that: (i) both pioneer and shade-tolerant species colonize a site directly after abandonment; (ii) as the canopy closes, the recruitment of pioneers sharply declines, while recruitment of shade-tolerant species continues; (iii) mortality among pioneers is highest; (iv) as a consequence from the preceding, recruited and dead trees are expected to differ in species composition, with highest species richness for the recruits.

CHAPTER **4** relates relative rates of change in stand structure variables during early secondary forest succession to (i) fallow age and initial stand structure and (ii) to community-level patterns of mortality, growth, and recruitment rates. This study uses a combination of a chronosequence and a longitudinal study by following stand dynamics over a two-year period in 11 secondary forest sites with fallow age ranging from 2 to 17 years.

CHAPTER **5** reviews patterns and rates of change in tree communities of secondary Neotropical forest and the factors and processes that direct them in the broader context of different types of major disturbances, but with an emphasis on post-agricultural succession. Furthermore the results of chronosequences and annual tree dynamics studies are evaluated and compared with the use of two case studies in northeastern Costa Rica and Chiapas, Mexico.

CHAPTER **6** tests the hypothesis that variation in asymmetric neighborhood competition for light is the main factor that determines within-site variation in tree growth and survival. The effect of neighborhood basal area on diameter growth, height growth, height-diameter ratio, and survival is examined for saplings of two *Cecropia peltata* and *Trichospermum mexicanum*, the two most abundant tree species in the secondary forests of the study region.

CHAPTER **7** relates the between-site differences in demographic behavior of four pioneer species (*Cecropia peltata*, *Trichospermum mexicanum*, *Trema micrantha* and *Schizolobium parahyba*) to variation in population size structure and neighborhood structure. Specifically, the hypothesis is tested that differences in growth and mortality between the biggest and smallest trees of a population are related to differences in the average level of asymmetric neighborhood competition in both size groups.

CHAPTER **8** summarizes and connects the different studies from this thesis.

Chapter 2

DIVERSITY PATTERNS ACROSS YOUNG SECONDARY FORESTS

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Abstract

Patterns of species diversity and dominance across the secondary forests of an agricultural landscape, characterized by a mosaic of pastures, crop fields and patches of secondary and primary forests, were examined using a chronosequence of 72 plots ranging in age from 0.5 to 18 years, and 7 disturbed old-growth forest plots.

Diversity varied widely between the plots, which could be partly explained by differences in time since abandonment and substrate while the influence of former land use was more ambiguous. Changes of species diversity with time since abandonment could largely be attributed to changes in species richness, with similar dominance between plots of different ages. Similarly, species richness, but not dominance, differed between secondary forests on low hills and alluvial plains.

Only a very small sub-set of the regional species pool dominated secondary forests, all of them pioneer species. The variation in frequency and abundance patterns was very high among pioneer species, with many of them occurring at very low frequencies. A few shade tolerant canopy species were relatively frequent, but the majority had very limited distribution and occurred at low abundance.

The observed patterns of species diversity across our study sites are broadly in accordance with the expected tropical post-agricultural secondary succession observed in many parts of the world. However, there is a need for a more integrated approach combining information on patterns of frequency and abundance of species across the secondary forests of a region and life history attributes and functional traits of species to better understand developments of species diversity and composition under current and future conditions.

INTRODUCTION

Secondary forests occupy a large and growing proportion of the forest cover in the tropics. Combined with the rapid decrease in primary forest (Achard *et al.* 2002; FAO 2006; Wright & Muller-Landau 2006; Foley *et al.* 2007), this expansion leads to increasing importance of secondary forests for biodiversity conservation (Kammesheidt 2002; Blay 2003) as well as for their regulatory functions (Corlett 1995). Furthermore, secondary forests can be important sources of timber and non-timber products and services (Chazdon & Coe 1999), thus providing alternative sources of income for local communities (Dourojeanni 1987; Brown & Lugo 1990; Pereira & Vieira 2001). Moreover, interest in their role in carbon sequestration is growing (Silver *et al.* 1996; Fearnside 2000; Salimon & Brown 2000; Silver *et al.* 2000; Richards & Stokes 2004).

Secondary forests are the result of a multitude of interacting variables that determine, at different spatial and temporal scales, their start and successional development (Chokkalingam *et al.* 2001; Bongers & Blokland 2003; Chazdon 2003). One of the land use practices that is responsible for the establishment and formation of secondary forests in large areas in the Tropics is shifting cultivation (Fox *et al.* 2000; Chazdon 2003; Geldenhuys *et al.* 2003). Shifting cultivation has been a common land use type for ages throughout the tropics, including the Americas (Whitmore & Turner 1992; Richards *et al.* 1996). However, the conditions that historically underpinned the sustainability of rotations with long fallows have largely vanished in many parts of the world, with increasing population and competition for land leading to land-use intensification and increasingly short fallow periods (*e.g.*, Cairns & Garrity 1999; Geist & Lambin 2002; Metzger 2002; Choudhury & Sundriyal 2003; Perz *et al.* 2005). In many regions, fallow periods are already as short as five years; and as a consequence, the secondary forests become increasingly younger.

Tree species density can recover quickly to values of old growth forest (Finegan 1996; Guariguata & Ostertag 2001). As soon as in 25-30 y on abandoned pastures and coffee plantation (Pascarella *et al.* 2000) and within 20 y on abandoned agricultural fields (Dewalt *et al.* 2003; Peña-Claros 2003), species density was found to have reached or surpassed values from nearby old-growth forests. Species composition, in contrast, remains distinct for much longer or may never fully recover (*e.g.*, Corlett 1991; Turner *et al.* 1997; van Gemerden *et al.* 2003). In a system with small scale shifting cultivation with long fallow times in the Amazon, species composition was almost identical to those of primary forest after approximately 80 years (Pavlis 2000). Most other studies come to estimation of over 100 years and possibly much longer for species composition in secondary forests to resemble that of the original old growth forests (*e.g.*, Aide *et al.* 1996; Turner *et al.* 1997; Peña-Claros 2003). On the other hand, in many regions secondary forests will become rarely older than a few decades and often much less (see former paragraph). In order to understand the potential role of secondary forests in the maintenance of biodiversity and environmental services under such conditions, it is relevant to focus on the dynamics and diversity of secondary forests in those younger age classes that prevail across the landscape.

Across sites, species richness and composition may vary considerably, depending on forest type, land use intensity and biophysical conditions, among other factors (Guariguata & Ostertag 2001). Across different regions, variation in community structure are found to relate to differences in soil types and attributes (Tucker *et al.* 1998; Moran *et al.* 2000; Zarin *et al.* 2001). Within regions, the differences in land-use type prior to abandonment, for example pastures vs. agricultural fields, have been demonstrated to affect strongly species composition and rate of forest development (*e.g.* Moran *et al.* 2000; Steininger 2000). A wide variety of studies, covering very different land-use systems and environmental conditions, found strong effects of, *e.g.*, mode of site preparation prior to cultivation, length of land-use, intensity of cattle grazing and fallow length (Uhl *et al.* 1982; 1986; Uhl *et al.* 1988; Hughes *et al.* 1999; Schmidt-Vogt 1999; Moran *et al.* 2000; Steininger 2000; Mesquita *et al.* 2001; Chinea 2002; Lucas *et al.* 2002).

Species richness is only one component of diversity. It gives the same weight to all species, irrespective of their relative abundance; hence it is strongly influenced by the number of rare species. Evenness, the other component of diversity, is strongly influenced by the relative frequencies of the dominant species (Legendre & Legendre 1998; Magurran 2004; Kindt *et al.* 2006). Species density generally is much higher among the smaller trees of a secondary forest community, while dominance of a few (pioneer) species is stronger among the larger trees. Moreover, rates of change of species density and composition are generally much slower among the larger trees (*e.g.* Guariguata *et al.* 1997; Peña-Claros 2003; Toledo *et al.* 2003; Lawrence 2004). As a consequence the use of different diversity indices will emphasize different diversity patterns that emphasise different processes.

Observations on secondary forests seem to suggest that secondary forests within a certain region are dominated by the a small group of pioneer species (Finegan 1992; Richards *et al.* 1996). Surprisingly very few studies, however, examined explicitly patterns of frequency and dominance across the secondary forests of a region, likely because only few chronosequences included enough plots to assess such patterns (but see Saldarriaga *et al.* 1988; Finegan 1992; Rivera & Aide 1998; Aide *et al.* 2000). Most studies report, indeed, a small number of dominant species across their sample plots. It remains the question, however, how typical such observations are for the secondary forests and the pioneer species in a region. There is very scant information whether the species that dominate individual secondary forests are also the most frequent across the secondary forests of a particular region, if most or only few pioneer species are widely distributed and dominant across a region, and if they differ much from shade tolerant species with regard to these patterns.

This study examines patterns of species diversity as well as patterns of abundance and frequency of the most abundant tree species in young secondary forests in the Marques de Comillas region in Chiapas, Mexico, in relation to fallow time, land use before abandonment and site conditions. The aim is to get a better insight in patterns and dynamics of species diversity in and across the secondary forests of the study region. More specifically, we address the following questions: (1) How variable is species diversity across young (≤ 18 y) secondary forests in a region and to what extent this is related to fallow age, land-use and substrate origin? (2) Are successional changes in diversity in these forests due to an increase in species richness, a shift in dominance or both? (3) Are the species that dominate individual secondary forests also the most frequent across the secondary forests of a particular region, are most or only few pioneer species widely distributed and dominant across a region, and does the frequency and dominance patterns of pioneers differ from those of shade tolerant species?

METHODS

STUDY AREA

The study area of roughly 60 km^2 is located in the in the Marqués de Comillas region between N16.08^0 - N16.16^0 and W90.86^0 – W91.02^0 in Chiapas, Mexico (Fig. 5, chapter 1). In the region, a mixture of lowland evergreen tropical rain forest, semi-deciduous forests and rangelands can be found. For a more extensive description of the natural vegetation in the region, see Ibarra-Manríquez & Martínez-Ramos (2002) and Pennington & Sarukhán (2005). Average annual rainfall is about 3000 mm, and mean annual temperature about 22^o C. There is a dry season from February to April (< 100 mm month^{-1}) that accounts for less than 10% of the total annual rainfall. The area is characterized by (i) alluvial terraces along the rivers and (ii) undulating hills with moderate-steep slopes (15°–30°) and altitudes between 115 and 300 m.a.s.l. The alluvial terraces are characterized by flat and fertile soils with good availability of N, P and water. The hill type is the most common geo-morphological unit in the region and characterized by sandy Humic Acrisols with low pH (4-5), and low nutrients and water availability (Siebe *et al.* 1996; Celedón-Muñiz 2006).

In the 1970s and -80s many people migrated from central Mexican states to new lands in Chiapas, contributing to doubling of the population since the 80s (Ramírez León & Carrera Pola 2004). This has resulted in large scale deforestation, strongly reducing the total area of closed forest. In the Marqués de Comillas region mature forest coverage decreased from 95% in 1976 to 56% in 1996. In the same period the secondary forests and shrub coverage increased from 1.5% in 1976 to 27% in 1996 (de Jong *et al.* 2000). Currently irregular shifting cultivation practices with short rotation cycles are the prevailing land use type, alongside pastures for cattle breeding, resulting in a mosaic of pastures, crop fields and patches of secondary and primary forests. Moreover, uncontrolled fires affected considerable parts of the region, most notably in the El Niño year of 1998, but also at several earlier occasions (Román-Cuesta *et al.* 2003; Román-Cuesta *et al.* 2004).

DATA COLLECTION

We selected 79 secondary forest patches on abandoned agricultural fields, pastures or disturbed old-growth forest. Nineteen plots were sampled in 1995 and 60 in 2000. In each site, three transects of 2 x 25 m were located randomly within a 0.5 ha area in the centre of the forest patch. All trees with a diameter at breast height (1.30 m, dbh) of ≥ 1 cm were identified to species and their dbh and height were measured. Unnamed species were numbered and matched within sites, but across sites only for the 19 plots sampled in 1995. Of the in total 8643 individuals 7.5 % (655 trees) could not be identified to their scientific name. Identification and nomenclature was based on (W3TROPICOS; Pennington & Sarukhán 2005). In the text, repeatingly mentioned species will be refered to by genus name only after the first time they are mentioned.

As far as possible, species were classified into three functional groups (pioneers, shade tolerant canopy species and shade tolerant understory species). The classification was based on data and observations from long-term studies conducted at Los Tuxtlas Tropical rain forest (Bongers *et al.* 1988; González-Soriano *et al.* 1997; Ibarra-Manríquez *et al.* 2001) and in our own study region (M. Martínez-Ramos *et al.*, unpublished data) using maximum stature and the distribution of seedlings and young saplings as criteria. We defined pioneers as those light-demanding species that establish and persist only under higher-light conditions and, accordingly, their distribution as seedlings and saplings is largely confined to gaps and early secondary vegetation. We defined shade-tolerant species as those able to establish and persist below the closed canopy of old-growth forests. Note that this classification includes a wide array of alternative life-histories (Martínez-Ramos *et al.* 1989). Of identified trees and species, we could classify 76% and 73% into one of the functional groups respectively.

We used semi-structured informal interviews with the landowner and/or relatives to determine the time since last abandonment (fallow time) and type of land use before abandonment of the plots. We distinguished two main groups of former land use: pasture (18 plots) and milpa (54 plots). Seven additional plots were selected in disturbed old-growth forest (showing signs of extraction of forest products, indications of wind damage or a burnt understorey). Furthermore, plots were selected in the two contrasting geo-morphologic units described (i) alluvial terraces along the rivers (20 plots), and (ii) low hills (52 plots).

ANALYSIS

Diversity

Diversity is made of two components, the number of species and the evenness of their frequency distribution (Legendre & Legendre 1998; Purvis & Hector 2000; Magurran 2004). There are many ways to combine richness and evenness, each with its own merits and pitfalls; see *e.g.*, (Magurran 2004) for an extensive discussion. As argued by (Ricotta & Avena 2002; Ricotta 2005), diversity indices such the Shannon Wiener index and Fisher alpha supply point descriptions of community structure with one specific combination of these two diversity components. Alternatively, a whole array of indices representing varying sensitivities to the presence of rare and abundant species can be used (Ricotta 2003). One such array is given by the Rényi's generalized entropy (Rényi 1961). This is one of the several diversity ordering techniques (Tóthméresz 1995) available and is calculated using equation 1 (Legendre & Legendre 1998):

$$H_\alpha = \frac{\ln\left(\sum_{i=1}^{s} p_i^\alpha\right)}{1-\alpha} \qquad \textit{Equation 1}$$

where s is the total number of species and pi is the proportion of the ith species in the sampling unit (Orlóci 1991). Alpha is a scale parameter that can range from 0 to infinity (Tóthméresz 1995; Legendre & Legendre 1998). Hα thus gives a continuum of possible diversity measures, which differ in their sensitivity to the rare and abundant species in the community. With increasing alpha Hα becomes increasingly dominated by the commonest species (He & Orlóci 1993; Ricotta & Avena 2000).

A convenient property of H_α is that a number of traditional diversity indices are special cases of H_α. When $\alpha = 0$, H = ln S, where S is species richness. For $\alpha = 1$, H equals the Shannon Wiener index and for $\alpha = 2$, H = ln 1/D, where D is the Simpson dominance. Finally, when $\alpha = \infty$, H = ln 1/p, where p is the relative abundance of the most frequent species in the assemblage (Lövei 2005; Ricotta 2005). Another desirable property of H_α is that it conforms to the definition of diversity by combining species richness and evenness (Kindt 2002; Kindt *et al.* 2006).

We constructed so-called 'diversity profiles' by plotting H_α against α for different values of alpha (α = 0, 0.25, 0.5, 1, 2, 4, 8, and ∞). Where H_0 gives information about species richness (see above), the shape of the profile gives information about the evenness; from equation 1 it can be deduced that more equality in the relative frequencies of the different species (is more evenness) will give more horizontal profiles. It is thus possible to order communities from lowest to highest diversity explicitly based on number of species and evenness. A community X is more diverse than community Y if all values of the diversity profile ($H_0 \leq \alpha \leq \infty$) of X are larger than for Y. Two communities that have intersecting profiles consist of one community that is richer but not more evenly distributed than the other, and consequently cannot generally be ordered in diversity (Kindt 2002; Oksanen *et al.* 2007).

To account for the effects of tree abundance on diversity (Sanders 1968; Denslow 1995; He *et al.* 1996; Chazdon *et al.* 1998), we calculated rarefied diversity profiles. For each plot we calculated the mean H_α of 10.000 random samples (without replacement). Sample size was equal to the number of trees in the plot with the lowest abundance (N = 36, the number of stems varied between 36 and 299 stems). All calculations were carried out with the vegan package (Oksanen *et al.* 2007) for R (R Development Core Team 2006).

To analyse the effect of fallow time on species diversity and whether this differed between old pastures and old milpa fields and between alluvial plains and low hills, we carried out ANCOVA' s of $H_0 \leq \alpha \leq \infty$ against fallow time, with as covariates former land use (LU) and substrate (ST). Because of the low sample size for the combination old pastures – alluvial plains (two plots) we did not use a two-way ANCOVA. Instead the following one-way ANCOVA'S were carried out to examine the effect of LU and ST respectively: (1) H_α vs. fallow time and LU for all plots on low hills and (2) H_α vs. fallow time and ST for all plots on former milpas. First we tested whether there was a significant interaction between fallow time and LU (first model) and ST (second model). If this interaction was not significant, then the analysis was repeated excluding the interaction effect.

Residual error and quantile-quantile plots of the models were examined for heteroscedasticity and departure of normality. When needed, H_α was transformed using the Box-Cox power transformation (Box & Cox 1964; Sokal & Rohlf 1995). When within the 95% log-likelihood confidence interval for λ (Venables & Ripley 2002), rounded values of -1, 0.5, 0, 2, or 1 were used. Given the strong heteroscedasticity between plots on different LU, fitting of the parameters in the first model was done by weighted least squares (Venables & Ripley 2002) with the weight W_i, being defined as the squared sum of the standard deviations of H_α within LU group i.

Species composition and distribution

We used non-metric two-dimensional scaling (Legendre & Legendre 1998) with the Bray–Curtis dissimilarity to examine dissimilarities in species composition of the most abundant species (species in ≥ 10 plots and with ≥ 20 individuals in total). The run was initiated from the ordination obtained using principle coordinate analyses (Legendre & Legendre 1998). The species abundance data were square root transformed, and then submitted to Wisconsin double standardization prior to the MDS (Oksanen *et al.* 2007). In the ordination plot, weighted averages scores of the species for the ordination axes were plotted. The same was done for fallow time, LU and ST and their significance was calculated based on 5000 random permutations of the data (Oksanen *et al.* 2007).

To examine if species that are widely found across the secondary forests of a region are the same species that dominate (most/many of) the secondary forests in terms of stem number or basal area, we examined across-sites frequency patterns of the most abundant species and compared this with their within-site dominance. Therefore we determined for each species the number of plots in which it occurred with (i) ≥ 1, 2 or 5 individuals per plot; and (ii) ≥ 1%, 2%, 5% or 10% of plot basal area. For each set of frequency data, we constructed rank-frequency curves.

Furthermore we tested whether the three functional groups (pioneers, shade tolerant canopy species and shade tolerant understory species) differed in their medians of across-plots frequencies using the non-parametric Kruskal-Wallis test and Dunn's multiple comparison tests. We used the chi-square test to examine if abundant species (occurrence in ≥ 10 plots) did occur significantly more in (1) plots on alluvial plains or in low hills and (2) in plots on old milpa fields or old pastures. P-values were computed by Monte Carlo simulation with 10000 replicates (R Development Core Team 2006).

TABLE 1. Averages and standard deviation of forest structure indices for three fallow time (FT) classes, two land-use classes (*LU*) and two soil type classes (*ST*). H$_{mean}$ = average height, H$_{90}$ = 90% quantile of the height, BA = basal area, Density = number of trees / ha. Means of respectively the *FT* and *LU* classes with the different letter super script did differ significantly from each other (Tukey-Kramer test, $p < 0.05$). Similarly, means of the two *ST* classes with the different letter super script did differ significantly (Welch Two Sample t-test, $p < 0.05$).

	H$_{mean}$	H$_{90}$	BA (m^2/ha)	Density (#/ha)
FT[i]				
[0,5]	3.9 ± 0.9 ^{A}	6.2 ± 2.2 ^{A}	9.2 ± 6.7 ^{A}	8533 ± 4577 ^{A}
(5,10]	5.2 ± 1.0 ^{B}	9.2 ± 2.2 ^{B}	16.3 ± 6.0 ^{B}	6252 ± 2478 ^{A}
(10,18]	5.1 ± 0.8 ^{B}	8.7 ± 1.7 ^{B}	25.7 ± 15.9 ^{B}	6115 ± 2205 ^{A}
ST[i]				
alluvial	5.1 ± 0.9 ^{A}	9.0 ± 2.4 ^{A}	20.4 ± 13.6 ^{A}	5403 ± 1843 ^{A}
low hills	4.4 ± 1.2 ^{B}	7.2 ± 2.8 ^{B}	13.4 ± 10.6 ^{B}	7945 ± 4228 ^{B}
LU				
milpa	4.4 ± 1.0 ^{A}	7.5 ± 2.6 ^{A}	15.1 ± 11.0 ^{A}	8001 ± 4283 ^{A}
pasture	4.4 ± 1.4 ^{A}	6.9 ± 2.4 ^{A}	9.6 ± 7.2 ^{A}	6214 ± 2357 ^{AB}
disturbed	6.1 ± 0.7 ^{B}	11.1 ± 2.9 ^{B}	31.5 ± 14.4 ^{B}	4342 ± 1390 ^{B}
All plots[i]	4.6 ± 1.2	7.7 ± 2.8	15.3 ± 11.8	7260 ± 3895

[i] plots in disturbed old-growth forest excluded

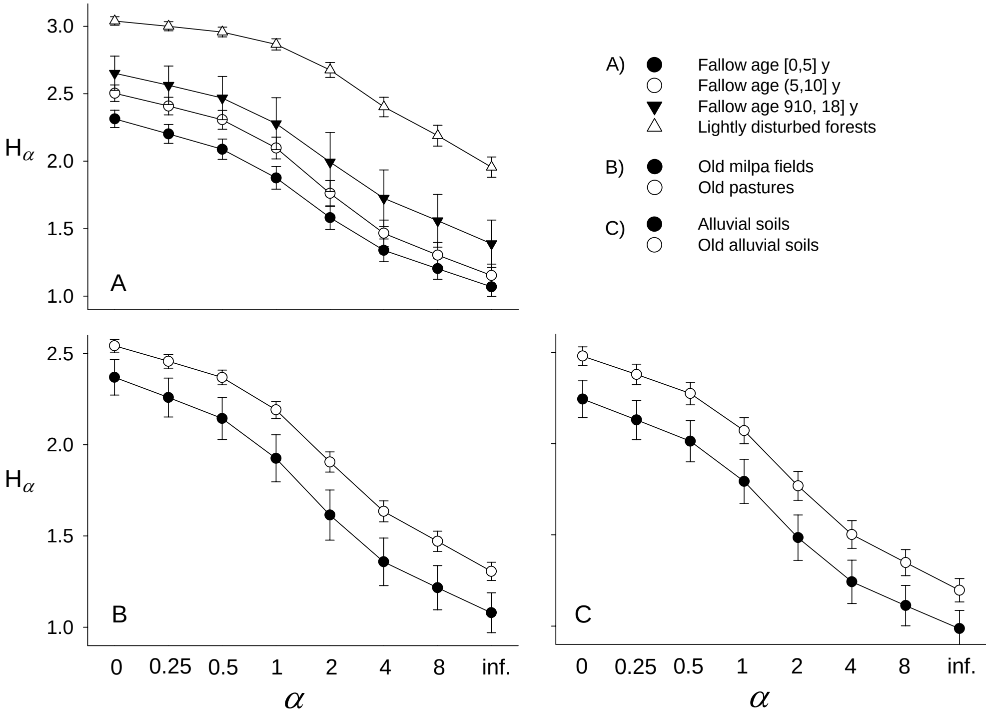

FIGURE 1: (A) Average Renyi diversity profiles for the age classes 0-5 (43 plots), 5-10 (19 plots) and 10-18 yr (11 plots). Additionally, the average diversity profile for the forests that underwent some light form of perturbation (6 plots) is given. (B) Average Renyi diversity profiles for plots on former milpa fields (54 plots) and former pastures (19 plots). Differences in mean H_α are significant for all alpha (Welch two sample t-test, $p < 0.05$). (C) Average Renyi diversity profiles for plots on alluvial terraces (21 plots) and low hills (58 plots). Differences in mean H_α are significant for all alphas (two sample t-test, $p < 0.05$ for $0 \le \alpha \ge 1$ and $p < 0.1$ for $2 \le \alpha \ge \infty$). The error bars give the standard error. Note that all profile values were calculated for the same scales, but graphs were presented at slightly divergent scales for better discrimination.

RESULTS

STAND STRUCTURE CHARACTERISTICS

Plots were in general characterized by high tree densities (108 ± 58 trees / plot, see Table 1 for trees / ha). Basal area, average tree height and 90% quantile tree height were (mean and standard deviation): 15.3 ± 11.8 m^2 ha^{-1}, 4.6 ± 1.16 m and 7.7 ± 2.79 m respectively. Forest structure parameters differed significant between plots on alluvial plains and low hills, with secondary forests on alluvial plots being characterized by larger trees and lower tree densities than those on low hills (Table 1). There were no significant differences between secondary forests on old milpa fields and old pastures. Both, however, had significant higher tree densities and smaller average tree height and basal area than the disturbed old-growth forests.

Differences in forest structure between young [0.5 y], intermediate (5,10 y] and older (10,18 y] plots were mostly significant. Average tree height, 90% quantile of the tree heigh and basal area differed between the first and second and first and third classes, but not between the second and third (Table 1), suggesting a particularly fast increase

TABLE 2: Linear models of H_α against fallow time (*FT*) and substrate (*ST*) and fallow time and land use (LU). For all four models the interaction term was not significant (F-test, $p < 0.05$), hence results of ANCOVA's without interaction term are presented. *FT* gives the slopes. *ST* gives the differences in intercept between low hills and alluvial plains and *LU* the differences in intercepts between former pastures and old milpa fields. Variables were excluded when their inclusion did not give a significant improvement of the model (F-test, $p < 0.05$), in which case the results of a reduced model is presented.

	FT	*ST*	R^2		*FT*	*LU*	R^2
H^2_0	0.19 ***	1.23 **	0.22	H^2_0	0.17 **	0.83 *	0.17
$H^2_{0.25}$	0.19***	1.25 **	0.21	$H^2_{0.25}$	0.17 **	0.90 *	0.17
$H^2_{0.5}$	0.19 **	1.26 **	0.20	$H^2_{0.5}$	0.17 **	0.95 *	0.16
H^2_1	0.19 **	1.24 *	0.18	H^2_1	0.16 **	0.98 *	0.15
H_2	0.04 *	0.33 *	0.13	H_2	0.04**	0.32*	0.14
H_4	0.04 *	0.30 *	0.12	H_4	0.03*	0.30 *	0.12
H_8	0.04 *	0.30 *	0.12	H_8	0.03 *	0.28 *	0.12
H_∞	0.03 *	0.24 *	0.11	H_∞	0.03 *	0.25 *	0.11

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns $P > 0.1$

TABLE 3: Across–plot averages of species density (SD) and four species-richness/diversity indices related to special cases of H_α, viz. species richness (SR =exp (H_0)), the Shannon Wiener index (SW = H_1), the Simpson dominance (D = exp(-H_2)), and the relative abundance of the most frequent species in the assemblage (P_{max} = exp(-H_∞)).

	SD	SR	SW	D	P_{max}
FT[i]					
[0,5]	18.0	10.1	1.9	0.21	0.34
(5,10]	18.7	12.2	2.1	0.17	0.32
(10,18]	23.7	14.2	2.3	0.14	0.25
ST[i]					
alluvial	14.9	9.4	1.8	0.23	0.37
low hills	21.9	11.9	2.1	0.17	0.30
LU					
milpa	19.0	10.7	1.9	0.20	0.34
pasture	19.4	12.7	2.2	0.15	0.27
disturbed	28.7	20.1	2.9	0.07	0.14
All plots[i]	20.0	11.2	2.0	0.18	0.32

[i] plots in disturbed old-growth forest excluded

in canopy height and basal area in the first years after abandonment. Variation in tree density within the fallow time classes was higher than between the fallow time classes.

CHANGES IN DIVERSITY WITH TIME SINCE ABANDONMENT

The average Renyi diversity profiles for the age classes 0-5, 5-10 and 10-18 y show that H_α values increased with fallow time over the whole range of alpha (Fig. 1), i.e. diversity increases with time along the whole gradient of sensitivities to the presence of rare and abundant species. However, the increase in Hα with fallow time is considerably weaker for high alpha (Table 2), showing that i) the increase in diversity is largely due to an increase in species richness, ii) the increase in species richness resulted only in relative small changes in the proportions of the dominant species.

Renyi diversity profiles are not commonly used in similar studies, making it more difficult to compare these results with those of other studies. Some special cases of H_α can be easily converted to more traditional diversity indices, including species richness (exp(H_0)), the Shannon Wiener index (H_1) and the Simpson dominance (exp(-H_2)). Moreover, the proportion of the most frequent species in the assemblage is given by (P_{max} = exp(-H_∞)) (Table 3). So to take the extremes of the profiles: species richness increases from 10 species in the 0-5 y age class to 14 species in the 10-18 y class, while the proportion of dominant species decreased from 0.34 to 0.25 respectively (Table 3). Note the large difference with lightly disturbed forests, were species richness was on average 20 and the most dominant species contained only 14% of all trees.

Rate of change of H_α with fallow time was independent of both LU and ST as indicated by the non-significant interaction terms (i.e. fallow time x ST or fallow time x LU) in all models. Differences in intercepts between plots on alluvial plains and low hills and between plots on old milpa fields and old pastures were significant for all alpha (Table 2), thus providing some evidence for the observed higher diversity of old pastures (Fig. 1B) and higher diversity for low hills (Fig. 1C). However, when abandoned milpas on alluvial and low hill sites were compared, only for $H_0 \leq \alpha < 1$ differences in intercepts of ST remained significant (Table 4). On the other hand, analyses carried out for plots on low hills did not yield any significant difference between the two LU classes (Table 4). Thus, only evidence for the observed differences in species richness between plots in secondary forests on alluvial plains and low hills remained strong.

COMPOSITION AND DISTRIBUTION OF DOMINANT SPECIES

The composition of the most abundant (≥ 20 individuals) and frequent (≥ 10 plots) species changed significantly with fallow time. Differences in species composition between plots on former milpa fields and pastures and between plots on alluvial plains and low hills were also significant (Fig. 2). Amongst these species, species composition

TABLE 4: The same models as in Table 2, but for old-milpa fields only (FT + ST) and for low hills only (FT + LU). For all models the interaction term was not significant (F-test, p < 0.05) and results of ANCOVA's without interaction term are presented.

	FT	ST	r^2		FT	LU	r^2
H^2_0	0.21 ***	1.1 *	0.22	H^2_0	0.20 ***	ns	0.2
$H^2_{0.25}$	0.21 **	1.1 *	0.21	$H^2_{0.25}$	0.21 ***	ns	0.18
$H^2_{0.5}$	0.20 **	ns	0.15	$H^2_{0.5}$	0.22 **	ns	0.18
H^2_1	0.19 **	ns	0.13	H^2_1	0.22 **	ns	0.16
H_2	0.05 *	ns	0.10	H_2	0.05 *	ns	0.12
H_4	0.04 *	ns	0.09	H_4	0.05 *	ns	0.11
H_8	0.04 *	ns	0.09	H_8	0.04 *	ns	0.10
H_∞	0.04 *	ns	0.09	H_∞	0.04 *	ns	0.10

* P < 0.05; ** P < 0.01; *** P < 0.001; ns P > 0.1

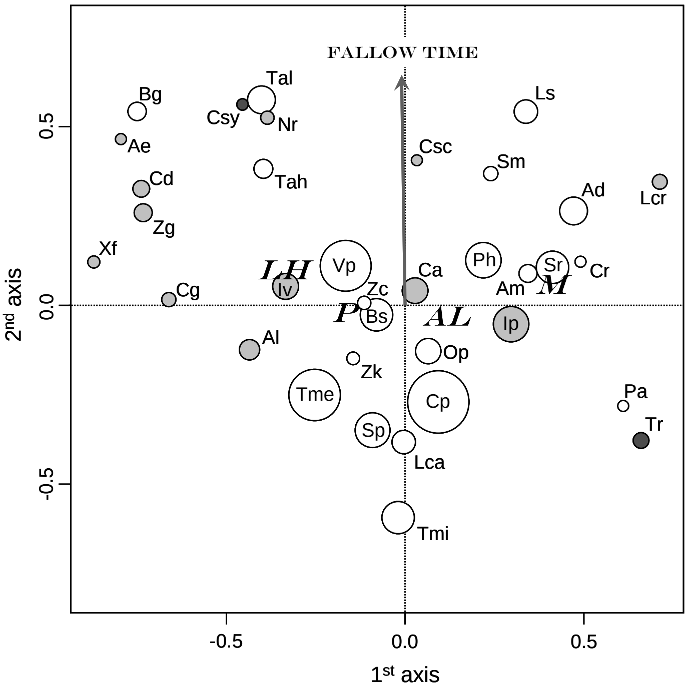

FIGURE 2. Ordination graph for two-dimensional NMS based on the Bray–Curtis distance (stress = 27) for dominant species (species in $\geq$ 10 plots and with $\geq$ 20 individuals in total). The circles give the weighted average scores of the species, with their size proportional to the percentage of plots in which the species occurs (species frequency). White = pioneer species (21 species), light grey = shade tolerant canopy species (12 species), dark grey = shade tolerant understorey species (2 species). The arrow gives the direction of fastest change in time. R^2 between ordination and fallow time is 0.23 ($p < 0.01$, based on 10000 permutations). *P*, *M*, *AL* and *LH* give the weighted averages ordination scores for plots on old pastures, old milpa fields, alluvial terraces and low hills respectively. Goodness of fit (R^2, p-values based on 10000 permutations) for differences between the land use types *P* and *M* and substrate types *AL* and *LH* are respectively 0.15 ($p < 0.01$) and 0.22 ($p < 0.01$).

was characterized by a stronger association of the less frequent species with plots with longer fallow time (small circles, Fig. 2, *e.g.*, *Alibertia edulis*, *Bellucia grossularioides*, *Casearia sylvestris*, *Luehea speciosa* and *Nectandra reticulata*), while weighted average ordination scores of the more frequent species (larger circles, Fig. 2) were in general closer to zero (*e.g.*, *Vernonia* patens, Bursera simaruba) or negative (*e.g.*, *Trema micrantha*, *Cecropia peltata*, *Trichospermum mexicanum*). Many of the shade tolerant canopy species, which are in general less frequent, seemed to be closely associated with low hill plots, some in plots with longer fallow time (*e.g.*, *Alibertia edulis*, *Nectandra reticulata*), and others appear not to have a preference (*e.g.*, *Cupania glabra* and *Xylopia frutescens*; Fig. 2).

Not all relations suggested by the ordination graph (Fig. 2) are significant though. A total of only 10 species showed a weak to strong preference for one of the substrate types, of which 5 were pioneer (including the very abundant *T. micrantha* and *T. mexicanum*, both with a strong preference for LH) and 5 shade tolerant canopy (inc., *Alchornea latifolia* (LH) and *Lonchocarpus cruentus* (AL)). Even less species showed a preference for a particular former land use type, viz., 2 pioneer (*Bellucia grossularioides* and *Ochroma pyramidale*) and 3 shade tolerant canopy species (inc., *Lonchocarpus cruentus*, Table 5).

FREQUENCY PATTERNS

Only few species are widely distributed (i.e., high frequency of occurrence in sample plots). Even less species are frequently abundant (i.e., occurring with ≥ 2 or with ≥ 5 individuals in sample plots) and/or relatively dominant (in terms of basal area) in the secondary forests of the region (Fig. 3). These frequency patterns are not related to fallow age as rank frequency curves (both with abundance and basal area) for three separate age classes (<5 y, 36 plots; <10 y, 24 plots; >= 10 y, 15 plots) did show very little of no differences.

The species that are widely distributed across the secondary forests are also the species that dominate in individual forests (Fig. 4). However, only a few species were "top-ranked" in all cases, most notable *Trichospermum* and *Cecropia*. As noted above, *Cecropia* was distributed independent of LU and ST, while *Trichospermum* was found significantly more often in plots on low hills (Table 5). Shrub species such as *Acalypha diversifolia* and *Vernonia patens* occurred frequently at relatively high stem densities but with relatively low contributions to total plot basal area. *Ochroma pyramidale*, on the

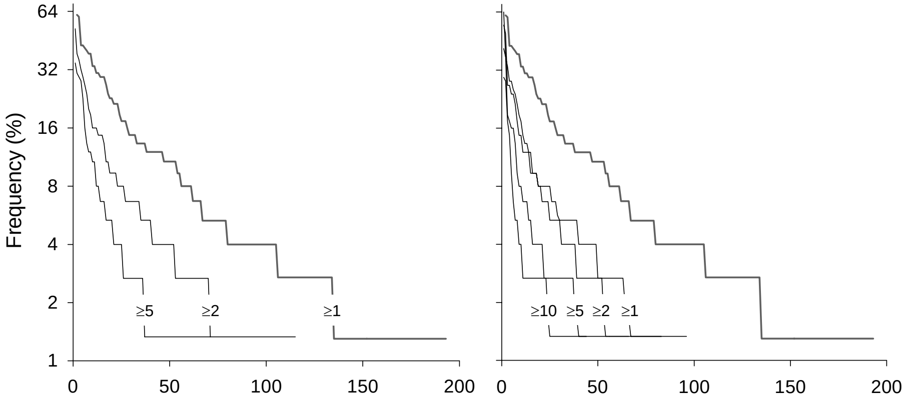

FIGURE 3: Rank frequency curves. Frequency based on number of plots in which a species occurs with the on the corresponding lines indicated (A) number of individuals, and (B) percentage of plot basal area. Not-identified species are not included.

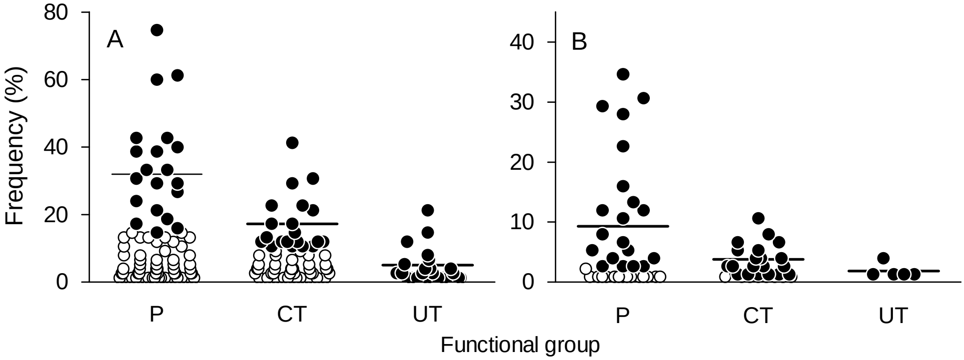

FIGURE 5: Comparison between the median rank of across-plot frequencies (A) of occurrence with at least one individual per plot and (B) with >= 10 trees/plot. P = Pioneers, CT = Canopy shade Tolerant species; UT = Understorey shade Tolerant species (UT). Black dots: 20 most frequent species per group; open dots: other species. Horizontal line: median of the black dots. Medians of the three group differ significantly from each other A) Kruskal-Wallis statistics 40.94, $p<0.0001$. Dunn's multiple comparison test, P-CT: difference in rank sum 16.15, $p<0.05$; P-UT: 35.23, $p<0.001$; CT-UT: 19.08, $p<0.01$. B).

other hand, occurred in several plots at low stem density but representing an important part of plot basal area (Fig. 5B). Most other widely-distributed species occur at low (relative) numbers and with low basal area in most of the sites (Fig. 4, Table 5).

In all three functional groups, most species occurred at low frequencies across the sample plots (Fig. 5). Respectively 44%, 48% and 75% of the pioneer -, canopy shade tolerant - and understory shade tolerant species occurred at frequencies of < 5%, and respectively 75%, 87% and 96% at frequencies < 15%. We could only classify part of the species into one of the functional groups. Of the unclassified species 76% occurred at frequencies of < 5% and all at frequencies < 15%, indicating that these percentages are still underestimations. The groups differed most with regard to the most frequent species in each group (Fig. 5). When only occurrences with at least 10 stems were taken into account, differences became even more pronounced, with only 5 pioneer species with a frequency of > 20% (Fig. 5B).

The medians of the percentages of pioneer species and of individuals of pioneer species in the understory differed significantly between age-classes (Kruskal-Wallis rank sum test, $\chi_2^2 = 10.1$, $p = 0.007$ and $\chi_2^2 = 10.1$, $p = 0.011$ respectively). The medians of the percentages in the age classes 0-5, 5-10, and 10-18 year decreased from 83%, 70% to 59% (percentage of individuals) and 84, 70 and 59% (percentage of species). Medians of the percentages of pioneer species and of individuals of pioneer species in the canopy did not differ, with in both cases an overall average of 81%.

TABLE 5: All species with minimum frequency of 10 (out of 72 plots) and total number of individuals over all plots ≥ 20. Regeneration type (RT): Pioneer (P), Shade tolerant canopy (CT), and shade tolerant understory (UT); # trees: number of trees across all plots; Freq = proportion of sites where the species occurs; P = average relative abundance ± standard deviation (only plots were the species was found); ST: Observed number of plots on alluvial plains (AL) and low hills (LH). Expected values are 20/72 and 52/72 x total number of trees of given species. LU: Observed number of plots in old milpa fields (Mi) and abandoned pastures (Pa). Expected values were 54/72 and 18/72 x total number of trees of given species. The values that are significantly higher than expected are underlined.

						ST		***LU***	
species	**Code**	**RT**	**No**	**Freq**	**P**(%)	***AL***	***LH***	***M***	***P***
Acalypha diversifolia	*Ad*	*P*	1092	0.33	40.2 ± 27	$\underline{12}^{*}$	12	21	3
Aegiphila monstrosa	*Am*	*P*	86	0.22	6.4 ± 9.6	2	14	15	1
Alchornea latifolia	*Al*	*CT*	65	0.25	4.9 ± 4.5	0	$\underline{18}^{***}$	13	5
Alibertia edulis	*Ae*	*CT*	46	0.14	10.3 ± 15.4	1	9	6	4
Bellucia grossularioides	*Bg*	*P*	64	0.24	8.1 ± 8.0	0	$\underline{16}^{***}$	6	$\underline{10}^{**}$
Bursera simaruba	*Bs*	*P*	63	0.39	4.8 ± 4.9	8	20	21	7
Casearia sylvestris	*Csy*	*UT*	44	0.14	6.5 ± 5.3	1	9	6	4
Cecropia peltata	*Cp*	*P*	507	0.74	11.9 ± 14.1	13	40	44	9
Cestrum racemosum	*Cr*	*P*	29	0.14	5.3 ± 5.5	5	5	9	1
Cordia alliodora	*Ca*	*CT*	78	0.31	5.0 ± 3.9	2	$\underline{20}^{*}$	18	4
Croton schiedeanus	*Csc*	*CT*	116	0.14	9.3 ± 8.1	2	8	9	1
Cupania dentata	*Cd*	*CT*	103	0.21	12.0 ± 12.6	0	$\underline{15}^{***}$	9	6
Cupania glabra	*Cg*	*CT*	74	0.18	7.6 ± 11.2	1	12	11	2
Inga pavoniana	*Ip*	*CT*	94	0.43	3.3 ± 2.9	9	22	$\underline{29}^{*}$	2
Inga vera	*Iv*	*CT*	136	0.31	8.1 ± 9.1	5	17	18	4
Lonchocarpus cruentus	*Lcr*	*CT*	48	0.18	10.5 ± 12.5	$\underline{11}^{***}$	2	$\underline{13}^{***}$	0
Luehea candida	*Lca*	*P*	91	0.28	5.8 ± 8.1	3	17	16	4
Luehea speciosa	*Ls*	*P*	185	0.29	12.6 ± 19.1	8	13	19	2
Nectandra reticulata	*Nr*	*CT*	27	0.17	2.9 ± 1.8	1	11	9	3
Ochroma pyramidale	*Op*	*P*	275	0.31	10.0 ± 13.2	4	18	$\underline{22}^{***}$	0
Piper aequale	*Pa*	*P*	34	0.14	8.0 ± 15.0	3	7	8	2
Piper hispidum	*Ph*	*P*	232	0.43	11 ± 13.7	10	21	22	9
Schizolobium parahyba	*Sp*	*P*	251	0.42	7.3 ± 9.9	6	24	24	6
Spondias mombin	*Sm*	*P*	30	0.17	3.5 ± 1.9	6	6	9	3
Spondias radlkoferi	*Sr*	*P*	136	0.39	6.6 ± 6.5	10	18	25	3
Tabernaemontana alba	*Tal*	*P*	85	0.33	5.9 ± 6.3	3	21	16	8
Thevetia ahouai	*Tah*	*P*	52	0.24	5.3 ± 10.9	2	15	10	7

TABLE 5. *continuation*

Trema micrantha	*Tmi*	*P*	579	0.39	17.0 ± 19.7	3	$\underline{25}^{*}$	24	4
Trichospermum mexicanum	*Tme*	*P*	1099	0.61	20.2 ± 20.9	5	$\underline{39}^{**}$	36	8
Trophis racemosa	*Tr*	*UT*	34	0.19	3.8 ± 4.8	7	7	13	1
Vernonia patens	*Vp*	*P*	352	0.61	12.1 ± 15.8	6	$\underline{38}^{*}$	29	15
Xylopia frutescens	*Xf*	*CT*	27	0.15	4.9 ± 4.3	0	$\underline{11}^{***}$	6	5
Zanthoxylum caribaeum	*Zc*	*P*	37	0.17	3.5 ± 4.1	2	10	8	4
Zanthoxylum kellermanii	*Zk*	*P*	40	0.15	4.9 ± 7.6	2	9	7	4
Zuelania guidonia	*Zg*	*CT*	44	0.22	8.7 ± 17.2	2	14	8	$\underline{8}^{*}$

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

DISCUSSION

SPECIES DIVERSITY

Changes with fallow time

Diversity and especially species richness increased with time since abandonment, similar to what has been found in a wide range of sites that ranged from small swidden fallow fields, abandoned coffee and cacaoplantations to extensive pastures (*e.g.* (Aide *et al.* 1995; Aide *et al.* 2000; Kennard 2002; Gemerden *et al.* 2003b; Peña-Claros 2003; Toledo & Salick 2006). Species richness and diversity have been found to approach similar levels as that of mature forests in as little as a few decades ((Saldarriaga *et al.* 1988; Grau *et al.* 1997; Franklin *et al.* 1999; Aide *et al.* 2000; Pascarella *et al.* 2000) or even less than twenty years (Kappelle *et al.* 1995; Peña-Claros 2003). Our secondary forests were young (0-18 y) and diversity was still much lower than in some disturbed old-growth forest sites. These sites were similar to three 500m^2 sample areas in old-growth forests in the nearby Montes Azules Biosphere Reserve (unpublished data M. Martínez-Ramos) with regard to average species richness (number of species/25 stems: respectively 16.4 ± 1.3 SD and 17.0 ± 1.1), tree densities (respectively 4480 ± 763 and 4343 ± 1390 individuals/ha) and basal area (26.7 ± 1.4 and 31.5 ± 14.4 m^2 ha^{-1} respectively).

Where other studies report a fairly strong relation between diversity and fallow time, the explanatory power of our models of H_α vs. fallow time were not particularly strong (Table 2). The small size of our sites likely accounted for part of the large variation observed. On the other hand, many chronosequences cover periods of several decades with a relatively lower number of plots (*e.g.* Saldarriaga *et al.* 1988; Aide *et al.* 1996; Peña-Claros 2003), while our study included a relatively larger number of plots, and covered a shorter gradient of time since abandonment than most studies. Purata (1986) sampled 32 sites with fallow age between 0.5 year and ~6 year, and found that species density varied almost 8-fold. These observations demonstrate that diversity may vary very much between sites of relatively similar age, suggesting (i) the importance of factors that operate on a very local scale and hence (ii) the importance of replicates within age classes. Direct comparisons between studies remain difficult, however, because the large differences in plot lay-out and size, lower size limits, range of times since abandonment, and variation included with regard to site and landscape factors.

Influence of land use and substrate differences

Secondary forests on low hills appear to have higher species diversity than those on alluvial plains and diversity on abandoned pastures appear to be higher than on abandoned milpa's (H_α for the whole range of alpha). Since only two abandoned pastures were found in the alluvial planes, we were not able to examine the interaction of both factors. Instead, we compared (i) abandoned milpa's from the alluvial planes with abandoned milpa's from the low hill areas and (ii) abandoned pastures and milpa's from the low hills areas. In the first case only differences in H_0 and $H_{0.25}$ remained significant, i.e. species richness differed between substrate types. In the second case there were no differences between land-use types. So, average species richness on abandoned milpa's is higher in low hill sites than in alluvial sites, while across low hill sites, former pastures and milpa's had similar diversity. The differences between sites were constant, i.e. initial species richness was higher on low hill areas, but the rate at which species richness increased was similar on both substrate types. Many earlier studies found a strong effect of land use history on the actual recovery of species diversity of a secondary forest (Pascarella *et al.* 2000; Rivera

et al. 2000; Mesquita *et al.* 2001; Chinea & Helmer 2003). Purata (1986) For example, changes in terms of species composition and species density have been reported to be slower on abandoned pastures compared to abandoned agricultural fields (Nepstad *et al.* 1991; Aide *et al.* 1995). Effects of substrate type seem less clear. Across different regions, soil type has been found to account for differences in stand structure development (Tucker *et al.* 1998; Moran *et al.* 2000; Zarin *et al.* 2001). Within regions, however, effects of soil type on species richness or composition has been demonstrated by few studies only (*e.g.*, Chinea 2002), while other studies did not find effects of soil fertility (*e.g.*, Lawrence 2004).

Factors such as former land-use, substrate type, and landscape configuration are often correlated, confounding possible processes and mechanisms that influence patterns of species richness and composition (Fuller *et al.* 1998; Lawrence 2004). In the research area, low hills have generally poorer soils than alluvial soils (Siebe *et al.* 1996; Celedón-Muñiz 2006). Species richness was found to be higher in nearby old-growth forests on low hills than in alluvial planes (Ibarra-Manríquez & Martínez-Ramos 2002), suggesting that differences in local species pools may play a role. Finally, past and present land-use patterns and the resulting landscape configuration differ between both substrate types. The settlement history followed the general settlement pattern described by de de Jong *et al.* (2000) for the whole Marques de Comillas region (see Chapter 1, section 'regional context'). As a consequence alluvial planes generally have a longer history of land-use and a lower old-growth forest cover than low hill sites, although there is important local variation (information from local villagers 2000-2003; pers. obs. M. van Breugel 2003).

Size of the secondary and old growth forest patches and their configuration in the landscape have a strong influence on local species diversity (Iida & Nakashizuka 1995; Benitez-Malvido *et al.* 2001; Hill & Curran 2003), amongst others because it determines proximity to nearby seed sources which in turn influences colonization rate (Cubina & Aide 2001; Mesquita *et al.* 2001; Chinea 2002). Moreover, the landscape matrix of a site may be constantly changing and diversity in a landscape will thus reflect present as well as past conditions of the surrounding landscape matrix. Adding to the spatial and temporal complexity of the landscape matrix, the region has experienced uncontrolled fires that affected considerable parts of the region, most notably in the El Niño year of 1998, but also at several earlier occasions (Román-Cuesta *et al.* 2003; Román-Cuesta *et al.* 2004). From local farmers we have fragmentary records of repeated burning of secondary forests on both abandoned pastures and milpas, which sets back the successional age and can affect further succession by inhibiting resprouting ability (Hooper *et al.* 2004) or severely reducing the available seed in the soil seed bank (Miller 1999).

SPECIES COMMUNITY STRUCTURE

Rate of changes with fallow time differed considerably between H_α for low and high order α, with a much lower rate of increase (and lower significance) for $H_{\alpha>1}$. Because increasing the order α diminishes the relative weight of rare species in the resulting index (Hill 1973), this results signifies that changes in diversity are driven by the influx of relative rarer species in the community and to a lesser extent by decreasing dominance of the most abundant species. These results underpin the importance to consider a whole continuum of possible diversity measures with shifting sensitivities from the rare to the abundant species in the assemblage. When only taking into account species that were relatively frequent (≥ 10 plots) and abundant (≥ 20 individuals) across plots, composition changed with fallow age, with an increasing importance of the less frequent species. Species from all three functional groups were, in general, represented in all plots, including the youngest plots. The proportion of shade tolerant species increased with time since abandonment in the understory (both in terms of individuals and species), but not in the canopy.

These results are in concordance with the typical tropical post-agricultural secondary succession pattern described by Gomez-Pompa & Vazquez-Yanes (1981) and Finegan (1984): Species from different light requirements recruit at the onset of succession (Swaine & Hall 1983; Uhl 1987; Chapter 3). Then, species dynamics during the first phases of tropical forest succession reflects two processes: continuous recruitment of shade tolerant species, resulting in accumulating species densities or richness in mainly the understory and the sequential canopy dominance of pioneer species that all established at the start of succession, mediated by differential growth rates and longevity (*cf.* Finegan 1996). Various chronosequence studies have demonstrated that species density and composition change faster towards old-growth forests values in the understory than in the main canopy (Saldarriaga *et al.* 1988; Guariguata *et al.* 1997; Peña-Claros 2003; Lawrence 2004; Toledo & Salick 2006), providing support for the first two points. Observed changes in the few studies that monitored early successional species dynamics in permanents plots were also in line with these points (Swaine & Hall 1983; Uhl 1987; Chapter 3), but also indicated that the processes of recruitment, mortality and growth underlying these patterns may be more dynamics and complex than can be inferred from chronosequence data (see Chapter 3).

PATTERNS OF DOMINANCE AND FREQUENCY

Observations on secondary forests seem to suggest that a small group of pioneer species dominate the secondary forests within a certain region and age range (Saldarriaga *et al.* 1988; Finegan 1992; Richards *et al.* 1996). The steep rank-frequency curves demonstrate that there are sharp differences between species frequencies, and support the notion that only few species are frequent across the secondary forests in a region. The next question was whether frequently occurring species are generally occurring at high stem density (abundance) and/or with a relative large proportion of the plot basal area (dominance). The slopes of the rank-frequency curves increase rapidly as higher abundance or dominance threshold values are applied, indicating that even less species are frequently abundant and/or dominant. For example, species with a frequency of ≥ 20% included six shade-tolerant and sixteen pioneer species, but only five pioneer species occurred in more than 20% of the plots with at least ten stems. Only three pioneer species (*Cecropia*, *Trichospermum* and *Vernonia*) occurred in ≥ 50% of the plots, and only the first two were also relatively dominant (>10% of plot basal area) and/or abundant (> 10 stems) in many of the plots they were found.

Striking is the large variation in frequency patterns between pioneer species. We found *Ochroma pyramidale* in stands of all ages, but always in the main canopy and only very rarely as smaller individuals below the canopy of other trees, hence the higher frequency as dominant (> 10% of plot basal area) than as abundant (>10 stems/plot) species. Other species are frequent or locally abundant without contributing significantly to plot basal area. Examples are the shrub species *Acalypha diversifolia*, that occurs locally in very high densities but is less frequent across the landscape, and *Vernonia patens* that is frequent across the landscape but occurs in low densities in most plots. Yet, most other species are neither frequent nor abundant. For a pioneer species, a high frequency assumingly implies that a species must, first of all, be present at many sites when these become available for establishment, and may thus reflect species attributes such as a wide ecological range, an efficient and long-distance dispersal mechanism, and/or persistence in the soil seed bank. These elements are thought to be part of the trade-off typical for pioneer species (Swaine & Whitmore 1988; Whitmore 1990), but results of this study suggest that only few pioneer species comply with most of them.

However, data from chronosequences have to be interpreted cautiously, as they may capture only a part of the underlying dynamics (Chapters 3-5; Bakker *et al.* 1996; Herben 1996). Patterns of dominance in individual plots can change rapidly due to interspecific differences in mortality and recruitment (Swaine & Hall 1983; Uhl 1987; Chapters 3-5). Part of such dynamics may be explained by differences in lifespan. Some species have a maximum lifespan that exceeds the length of our chronosequence (*e.g. Cecropia*, *Trichospermum*, *Ochroma*), others do have a shorter maximum lifespan (*e.g. Vernonia patens*), and for most species there is no information available. However, several of the species that dominated (in number of stems or in basal area) our secondary forests belong to the first group, indicating that other factors play an important role, such as competition for resources (see Chapters 6, 7). Additionally, episodic mass mortality, apparently caused by pathogen outbreaks, has been observed to cause abrupt change in canopy composition and dominance (Chapters 3-4).

CONCLUSIONS

The patterns of species diversity and composition across our study sites are broadly in accordance with the expected tropical post-agricultural secondary succession observed in many parts of the world (Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1984; 1996). The chronosequence of this study covers a relatively small range of successional ages (0-18 y), yet across-site variability in species diversity and composition was very high. Part of the observed variation in diversity between plots could be explained by differences in time since abandonment, substrate and, more ambiguously, former land use. However, they only captures a small part of the complex set of interactions between landscape factors (*e.g.* local species pool, mature forest cover), local site factors (*e.g.* land-use history, substrate), biotic interactions (*e.g.* competition, pathogens) and species life histories that governs the species diversity in such sites (see *e.g.*, Chazdon 2003; Pickett & Cadenasso 2005).

The results of this study explicitly demonstrate that the patterns of frequency, and the abundance at which species occur, vary highly between species. As expected, a very small sub-set of the regional species pool dominates secondary forests (*cf.* Finegan 1992), and all of them are pioneer species. There are a few shade tolerant canopy species that are relatively frequents, but the majority has a limited distribution and occurs at low abundances. But, also a large proportion of the pioneer species has a limited distribution, and even a larger proportion occurs mostly at low densities. Understanding patterns of frequency and abundance of species across the secondary forests of a region is an important challenge. As yet, only few studies on tropical secondary forest succession have explicitly examined regional patterns of species frequencies across secondary forests (but see Aide *et al.* 1995; Rivera & Aide 1998). Moreover, we have very little or no data on life history attributes and functional traits of most species. The combination of such data would allow us to better understand the patterns (and variation) of species diversity and composition across secondary forests.

Chapter 3

SPECIES DYNAMICS DURING EARLY SECONDARY FOREST SUCCESSION: RECRUITMENT, MORTALITY AND SPECIES TURNOVER

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ABSTRACT

The "Initial Floristic Composition" hypothesis is applied to secondary tropical rain forest succession in abandoned agricultural fields with light previous land-use and close to seed sources. This hypothesis predicts that both pioneer and shade-tolerant species colonize a site directly after abandonment, and as the canopy closes, the recruitment of pioneers sharply declines, while recruitment of shade-tolerant species continues. It also predicts higher mortality among pioneers. Consequently, recruited and dead trees are expected to differ in species composition, with highest species richness for the recruits. During 18 months, we monitored recruitment and mortality of trees with height ≥ 1.5 m in eight plots in abandoned corn fields with initial fallow age of 1 to 5 y, in southeast Mexico. Shade-tolerant species established in the first years of succession, albeit in low numbers. As predicted, recruited and dead trees differed in species richness and composition, and in shade-tolerant frequency. In contrast to our expectations, over 50% of recruits were from pioneer species, as high stand-level mortality opened new opportunities for continued pioneer colonization. Species turnover starts very early in succession but is not always a gradual and continuous process, complicating prevailing succession models. The strong spatial and temporal variability of succession emphasizes the need to monitor these dynamics in permanent plots across a range of initial stand ages, with multiple plots in a given age class.

INTRODUCTION

Secondary forest succession on abandoned agricultural fields has been described as the colonization and replacement of functional groups of species, which differ in life history attributes such as seed dispersal rates, establishment requirements, growth rates, longevity and size at maturity (*e.g.*, Huston & Smith 1987; Bazzaz 1996). The variety of temporal patterns of species colonization and replacement is immense, and depends on site and species availability and characteristics (Pickett & Cadenasso 2005). Across-site variation in these patterns has been related to environmental factors such as soil characteristics (*e.g.*, Donfack *et al.* 1995; Chinea 2002; Lu *et al.* 2002), previous land-use (*e.g.*, Uhl *et al.* 1988; Pascarella *et al.* 2000), distance to seed sources (*e.g.*, Purata 1986; Mesquita *et al.* 2001), and characteristics of dominant species (Lucas *et al.* 2000; Mesquita *et al.* 2001).

The Initial Floristic Composition hypothesis (IFC) of Egler (1954) is predicted to apply to tropical post-agricultural secondary succession where previous land-use was of low-intensity and seed sources are nearby (Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1984). Such conditions are found in many regions of the tropics, especially where traditional small-scale shifting cultivation practices still prevail or where agricultural colonization is recent (*e.g.*, Lawrence *et al.* 1998; Kammesheidt 2002; Gemerden *et al.* 2003b). According to the IFC hypothesis most species that will later dominate the community will colonize the site at the onset of succession. The proposed sequential physiognomic dominance of species, first light demanding species of increasing longevity, and finally shade-tolerant species, unfolds largely due to differences in growth rates, longevity, and shade-tolerance among tree species that happen to colonize the site at abandonment (Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1984).

The IFC hypothesis does not provide an unambiguous testable hypothesis, and accordingly it has been interpreted in different ways (Wilson *et al.* 1992; McCook 1994). Therefore, to address this hypothesis clear predictions have to be formulated about successional replacement among functional groups, making interpretations and assumptions explicit. In this study we formulated and evaluated the following predictions. Both pioneer and shade-tolerant species are present in the first phase of succession although pioneer species are more abundant (Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1996). After canopy closure, recruitment of the dominant pioneer species becomes limited, while recruitment of shade-tolerant species continues (Swaine & Whitmore 1988). Mortality is relatively high among the dominating pioneer species compared to shade-tolerant species (*e.g.*, Alvarez Buylla & Martinez Ramos 1992; Davies 2001). In consequence of these three aspects, recruits and dead trees constitute distinct groups of species, while the surviving initial assemblage can be expected to represent a transitional species composition (i.e., high potential of species replacement).

Shade-tolerant taxa form a much larger species pool than pioneer taxa (Budowski 1965; Saldarriaga *et al.* 1988; Finegan 1992), though pioneer species seem to be more widely distributed than many shade-tolerant species (Holmgren & Poorter in press). Unlike shade-tolerant taxa, few pioneers have narrowly localized or disjunctive areas, and generally occur at much higher densities (Richards *et al.* 1996; Holmgren *et al.* 2004). Hence, we expect that species richness and evenness of recruits will be higher than that of the species assemblage of earlier established trees. For the same reasons, we expect that species richness and evenness of the group of trees that die will be lower than that of recruited trees.

We know of only one community-level study that explicitly, but partially, addressed these predictions in the context of tropical rain forest succession. This chronosequence study in the Bolivian Amazon demonstrated that the understory had higher species diversity and approached the composition of nearby old-growth forests faster than the canopy (Peña-Claros 2003). However, a complete examination of the rate and patterns of species colonization and replacement requires monitoring of permanent plots (Pickett 1989; Bakker *et al.* 1996; Foster & Tilman 2000). We are aware of only two studies focussing on advanced (initial fallow age ≥ 55 y) secondary succession (Lang & Knight 1983; Milton *et al.* 1994), and of two studies in sites with initial fallow age between 12–25 y (Chazdon *et al.* 2005; Chazdon *et al.* 2007; B. Finegan, unpublished data), and two further studies that monitored the first years of post clearance succession (Swaine & Hall 1983; Uhl 1987). These studies monitored mortality, recruitment and changes in species composition over periods ranging between 5–17 y, but none explicitly addressed the above stated predictions on species colonization and replacement.

In this study we examine in detail community-level species dynamics in the initial years of secondary tropical rain forest succession. We analyze mortality, recruitment and subsequent changes in species abundance, diversity and evenness and composition in eight 1–5 y old fallows in a swidden agricultural landscape with light previous land-use and in proximity of old-growth forest remnants over a period of 18 months. Our specific objectives were: (1) to describe early secondary patterns of species richness and composition and short-term changes therein; (2) to test the predictions derived from the IFC hypothesis.

METHODS

STUDY AREA

The study was conducted at the Marquéz de Comillas region, to the south of the Montes Azules Biosphere Reserve (approximately 16° 04' N, 90° 45' W), Chiapas, Mexico. Annual temperature and rainfall is ca 23ºC and 3000 mm. There is a dry season from February to April (< 100 mm/month). The original vegetation consists mainly of lowland tropical rainforests and semi-deciduous forests. A more extensive description of the natural vegetation in the region is given by Ibarra-Manríquez and Martínez-Ramos (2002).

The region is a mosaic of small-scale agriculture, pastures, mostly young (< 10 y) secondary forests, and remnants of old-growth forests. In Chapter 2, some indications are found that secondary vegetation succession in the study region varied with former land-use, more specifically abandoned pastures vs. abandoned cornfields, and with geomorphology. It was not our objective to study such relationships; therefore, we selected secondary-growth plots with similar geomorphology and land-use history. Plots were selected on abandoned cornfields ('milpas') in areas with undulating hills, between 115–300 m asl., with a complex acidic soil (pH 4–5), derived from sedimentary rocks (sandy and clay) that have low total nitrogen and phosphorous content (Siebe *et al.* 1996; Celedón-Muñiz 2006). The cornfields had been established after clear-cutting the original old-growth forest, used for corn cultivation once, and subsequently abandoned. Initial fallow age ranged from 1 to 5 y. All plots were bordering remnants of old-growth forest or connected to them by another secondary forest plot. Fallow age and land use history was determined based on information of landowners and other local residents.

INVENTORY

We selected eight secondary forests, and established plots of 10 x 50 m in each of them. At the beginning of the study all free standing woody perennials (trees, shrubs and treelets) with a diameter at 1.3 m above ground (dbh) ≥ 1 cm were recorded, tagged, and identified to lowest possible taxonomic level. In the case of individual plants with multiple stems, all stems with dbh ≥ 1 cm were included. Henceforth we will refer to individual plants as 'trees', independent of their life form, for convenience. After six months, a census was conducted to record mortality and recruitment. At this time all trees with dbh ≤ 1 cm but height ≥ 1.5 m were included as well, but dbh was not measured. Hereafter we will refer to the first census as 'census 0' and to the latter as 'census 1'. Approximately 18 months (± 15 days) after census 1, recruitment and mortality were monitored again (census 2). Here we report data from this 18-month study period. Henceforth, we will deal with five tree groups: (i) trees with height ≥ 1.5 m at census 1, initial assemblage (IA); (ii) trees with height ≥ 1.5 m at census 2; (iii) trees of census 1 that survived until census 2 (surviving trees, ST); (iv) trees alive at census 1 and recorded dead at the end of the study period (dead trees, D); and (v) trees that grew over the lower size limit of 1.5 m height after census 1 and were alive at census 2 ('recruitment', R).

Based on data and observations from long-term studies on the distribution of seedlings and young saplings, conducted at Los Tuxtlas Tropical rain forest (Ibarra-Manríquez *et al.* 2001) and in our own study region (M. Martínez-Ramos *et al.*, unpublished data), 118 of a total of 142 species were classified in two broad regeneration groups (pioneer and shade-tolerant). We defined pioneers as those light-demanding species that establish and persist only under higher-light conditions and, accordingly, their distribution as seedlings and saplings is largely confined to gaps and early secondary vegetation. We defined shade-tolerant species as those able to establish and persist below the closed canopy of old-growth forests. Note that this classification includes a wide array of alternative life-histories (Martínez-Ramos *et al.* 1989). For example, within the pioneer group we included short- and long-lived species, and within the shade-tolerant group understory, mid- and upper-canopy species.

ANALYSES

To measure species evenness we used Smith and Wilson's index (E_{var}) (Smith & Wilson 1996):

$$E_{\mathrm{var}} = 1 - 2/\pi \arctan\left\{ \sum_{S=1}^{S} \left(\ln(x_s) - \sum_{t=1}^{S} \ln(x_t)/S \right)^2 \Big/ S \right\}$$

With S = the number of species in a plot, x_s = the abundance of the s^{th} species, and arctan in radians. Values range from 0–1, with 0 representing minimum evenness, and 1 the maximum (Smith & Wilson 1996).

We compared the similarity of species composition of groups (census 1 vs. census 2; recruitment vs. dead trees; recruitment and dead trees vs. surviving trees from census 1) using the Chao-Jaccard abundance-based similarity estimator (Chao *et al.* 2005). Standard errors and confidence intervals were calculated by a bootstrapping procedure, with 200 resample trials. The estimator varies from 0 (no similarity) to 1 (complete similarity). Similarity index values differed significantly from complete similarity when the value 1 fell outside the calculated confidence intervals. Note that the Chao Jaccard Abundance Index provides a conservative estimate of similarity; the Jaccard Index based on presence-absence data and the Morisita Index based on abundance data (Krebs 1999) give much lower similarity values.

To evaluate whether these plot-wise analyses reflected a general pattern of successional species replacement, we performed a detrended correspondence analysis (DCA) on species abundance by plot x group combinations (24 combinations). Groups were: Recruited (R); Dead (D); and Surviving trees from census 1 (ST). We performed the DCA using the CANOCO (version 4.5) software (Ter Braak & Smilauer 1998), with abundance data square-root transformed prior to analysis. We included only species with five or more sampled individuals per plot (76 species). These species represented

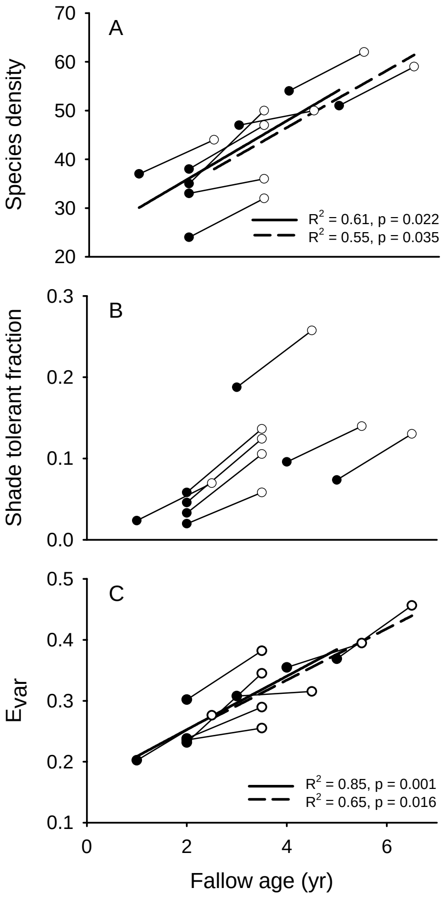

FIGURE 1. Early secondary succession trends in community attributes of trees ≥ 1.5 m height at Marquéz de Comillas, Southern Mexico. (A) Species density (number of species/$500m^2$); (B) Fraction of total number of trees belonging to shade tolerant species; and (C) Smith & Wilson´s measure of evenness (E_{var}). Closed circles: census 1; Open circles: census 2. The bold continuous and dashed lines give the linear regressions of the variables of census 1 and 2 respectively on fallow age.

99 and 97% of the sampled individuals and 61 and 75% of the total number of species of the initial assemblage and recruits respectively.

Differences in species richness might proceed from differences in tree density (Denslow 1995; Chazdon *et al.* 1998). Therefore, when indicated in the results, we compared species richness at the lowest abundance level among groups using a bootstrapping procedure (Krebs 1999; Quinn & Keough 2002). This procedure implies random resampling, with replacement, from the original group to calculate test statistics. Calculations were done in the EcoSim 7.0 package (Gotelli & Entsminger 2001), using its rarefaction procedure. Calculated test statistics were the mean and 95% confidence intervals. We used the same bootstrapping procedure (using 1000 repetitions) to calculate the expected species richness and E_{var} assuming random mortality, and we tested differences between expected and observed values with one-sample t-tests (Quinn & Keough 2002).

RESULTS

SPECIES RICHNESS

Across plots tree density varied between 426 and 1786 (mean 906 ± 155 SE), and variation in species richness can simply be a consequence of these large differences (Denslow 1995; Condit *et al.* 1996). There was no significant relationship, however, between tree density and species richness in any of

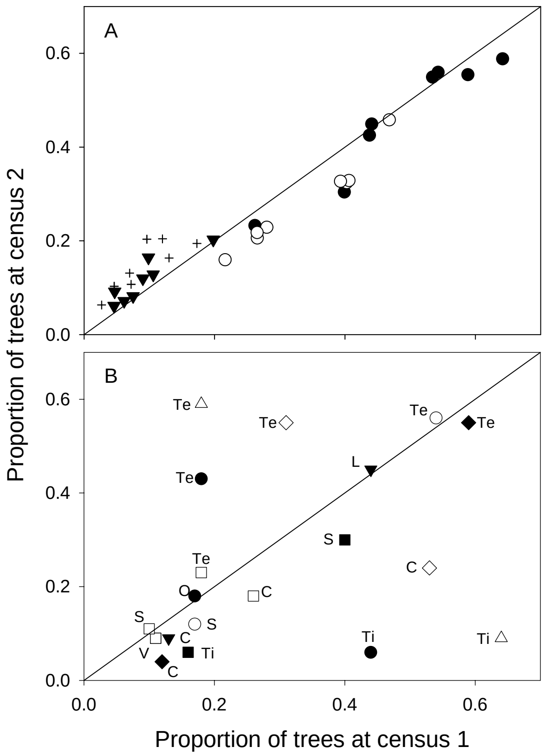

FIGURE 2. Change in proportional abundance of pioneer tree species during 18 months (from census 1 to census 2) in young secondary forest at Marquéz de Comillas, Southern Mexico. (A) Species are grouped according to dominance and every symbol represents a group-plot combination. Closed circles: single most dominant species per plot; open circles: 2nd to 5th most dominant species: triangles: 6th to 10th most dominant species; crosses: all other species. (B) Individual species that had a relative abundance of at least 10 percent in one or both censuses. Every point is a species-plot combination and different symbols represent different plots. Species are indicated as follows: Te = *Trichospermum mexicanum.*; Ti = *Trema micrantha*; C = *Cecropia peltata*; L = *Luehea speciosa*; S = *Schizolobium parahybum*; O = *Ochroma pyramidale*; V = *Vernonia patens*

the two censuses (least square linear regression, census 1: P > 0.95, census 2: P > 0.47), and therefore we used actual observed species richness for across-plot comparisons.

At census 1 the number of recorded species in the plots (S_i) ranged from 24 to 54 (mean 40 ± 3.6 SE) and was positively related to fallow age (Fig. 1A). During the 18-m study period, species density increased to 32–62 species/plot (mean 47.5 ± 3.6 SE), representing a 20% increase on average (6.4–42.9%). Species density continued to be significantly related to fallow age (Fig. 1A), with statistically similar regression slopes (F = 0.00, df = 12, P = 0.95) and interception points (F = 0.10, df = 13, P = 0.75) compared with those of the first census.

Shade-tolerant species constituted on average 7% (± 2 SE) of the total number of individuals, but 42% (± 5 SE) of all species. The fraction of shade-tolerant trees increased on average 2.3 (± 0.3 SE) times to an average of 13% (± 2 SE). In neither of the two censuses was the shade-tolerant fraction related to fallow age (Fig. 1B), but the increase of this fraction was negatively related to fallow age (R^2 = 0.59, P = 0.025).

SPECIES DOMINANCE AND EVENNESS

Evenness (E_{var}) values were low, varying between 0.20 and 0.37 (Fig. 1C), but increased during the 18-m study period in all plots. At the beginning and end of this period, E_{var} was positively related to fallow age (Fig. 1C) with statistically similar regression slopes ($F = 0.01$, $df = 12$, $P = 0.91$) and interception points ($F = 0.07$, $df = 13$, $P = 0.80$).

Low evenness values reflect the dominance (high relative abundance) of few species in these early successional assemblages. Across plots only 11 species (9% of total number of species) had more than 50 individuals in census 1, while 62 species (51%) had less than five individuals. Only seven species had a relative abundance (RA) ≥ 10 % in at least one plot (Fig. 2B), of which *Trichospermum mexicanum* (DC.) Baill. (mean RA 26%, range: 1.5–59%), *Trema micrantha* (L.) Blume (mean RA 19.6%, range: 0–64%) and *Cecropia peltata* L. (mean RA 16.4%, range: 1–53%) were by far the most abundant ones. At census 1, in one plot the single most abundant species alone comprised on average 48% (± 4 SE) of total number of trees and the group of five most abundant species on average 82% (± 3 SE; Fig. 2A).

Changes in dominance over the 18 months study period seem to have been small, with only a slight decline of the share of dominant species in all plots (circles in Fig. 2A). However, the relative abundance of individual dominant species changed rather drastically in several plots (Fig. 2B) due to high mortality (see below). Populations of the early pioneer species *T. micrantha* dominated two plots (closed circles and open

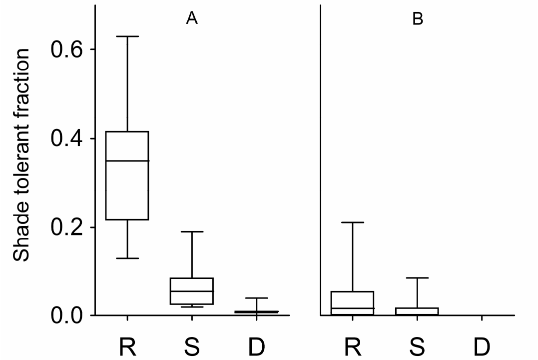

FIGURE 3. Dynamics of the fraction of shade tolerant trees in early successional communities. Shade tolerant fraction of the trees of the initial assemblage that survived the study period (S) and of the groups of trees that recruited (R) and that died (D) between census 1 and 2. Different lower size limits were used to define the initial group of trees as well as recruitment: (A) height ≥ 1.5 m; (B) dbh ≥ 2.5 cm. Boxes show median, the 25th and 75th percentiles and the whiskers give the extent from lowest to highest values.

TABLE 1. Similarity between species assemblage of census 1 (C1) and 2 (C2), and between recruitment (R), dead trees (M) and surviving trees (S) assemblages. Chao-Jaccard abundance-based similarity estimators are given ± standard error. Bold values indicate that the value is significantly different from 1. The number in the plot names indicate plot age at census 1.

Plot	C1 x C2	S x M	S x R	M x R
R1	0.98 ± 0.04	0.90 ± 0.14	0.83 ± 0.16	**0.35 ± 0.16**
F2	0.95 ± 0.05	0.87 ± 0.10	0.86 ± 0.15	0.74 ± 0.23
H2	1.00 ± 0.03	0.83 ± 0.17	0.96 ± 0.10	0.78 ± 0.27
P2	0.98 ± 0.04	0.83 ± 0.14	0.94 ± 0.14	0.73 ± 0.30
R2	0.97 ± 0.03	0.99 ± 0.07	**0.54 ± 0.14**	**0.57 ± 0.20**
G3	1.00 ± 0.00	0.98 ± 0.13	1.00 ± 0.06	0.85 ± 0.28
F4	1.00 ± 0.01	0.93 ± 0.17	0.78 ± 0.19	**0.38 ± 0.21**
R5	1.00 ± 0.01	0.97 ± 0.08	**0.39 ± 0.13**	**0.39 ± 0.20**

triangles in Fig. 2B) but collapsed due to extreme high mortality (89% and 93%) and were replaced by the early pioneer *T. mexicanum* as the most dominant species. The latter was partly the result of a high absolute increase (260% and 126% respectively) due to recruitment, and partly a direct consequence of the decrease of *T. micrantha*. In one plot (open diamonds, Fig. 2) 76% mortality of the most abundant species C. *peltata* resulted in an increase of the relative dominance of T. *mexicanum*, even while absolute number of *T. mexicanum* trees decreased by seven percent.

RECRUITMENT AND MORTALITY

On average, 59% (± 6 SE) of the recruits was classified as pioneer, 34% (± 6 SE) as shade-tolerant, and 7 % (± 3 SE) was unclassified, although among-plot variation was high (Fig. 3A). This variation is partly explained by among-plot differences in stand basal area mortality. Between 22% and 74% of the initial basal area in our study plots was lost due to the death of canopy trees during the study period, and the proportion of pioneers among the recruits was positively related with this percentage (least square linear regression, $R^2 = 0.69$, $P = 0.01$).

Most recruits (across plot average 77% ± 7 SE) belonged to species with less than 1% of total plot basal area at census 0 (including new species). Ten percent (± 7 SE) of recruits belonged to species that constituted between 1–10% of the plot basal area, and 13% (± 5 SE) to the group of species that constituted at least 10% of the plot basal area (Fig. 4A). For convenience we will refer to the latter group as 'canopy dominants'. Only six species belonged to this group in at least one of the study plots, all of them pioneer species. Four of these species hardly recruited in the plots were they formed the canopy dominants, with across-plot averages (± SE; number of plots) of: T. *micrantha* 0.7% (± 0.5; 4); *Schizolobium parahyba* (Vell.) S. F. Blake 1.1% (± 1.1; 3); *Ochroma pyramidale* (Cav. ex Lam.) Urb. 0.4% (± 0.4; 4); *C. peltata* 2.6% (± 1.2; 4). These averages were much higher for two other pioneer species: *T. mexicanum* 17% (± 8.5; 4); and *Luehea speciosa* Willd. 18% (–; 1). In five plots the canopy dominants were represented by > 10% of the recruits (Fig. 4A), and these percentages were largely due to high recruitment of these two species.

Redefining the size class to take into account only larger stems with dbh > 2.5 cm resulted in rather different recruitment patterns. A lower fraction of the recruitment in this class was shade tolerant (Fig. 3B) and, on average, most recruits in this class belonged to the group of species with more than 10% of total plot basal area (at census 0), with considerably higher between-plot variation (Fig. 4B). Comparing figures 3A and 3B, on one hand, and 4A and 4B, on the other hand, show that most of the species dynamics discussed in the former paragraph occurred in the lower size classes (notably stems < 2.5 cm dbh) .

Mortality was high, ranging between 17% and 63% (mean 39% ± 6 SE) of the initial individuals. The Smith & Wilson index (E_{var}) of the group of dead trees was lower than expected by random mortality in all plots (bootstrap procedure, with plot-wise repeated random sampling of a number of individuals equal to the number of dead

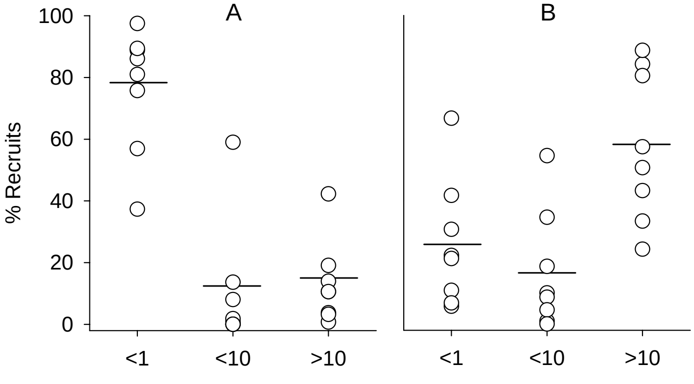

FIGURE 4. Frequency distribution of recruitment among relative basal area classes. Relative basal area: percentage of the plot basal area at census 0. Species were grouped in classes according to their relative basal area, with class limits as indicated on the x-axis, and the percentage of total number of recruits in a plot was calculated for each class. The among-plots means are indicated by horizontal lines. Different lower size limits were used to define the initial group of trees as well as recruitment: (A) height ≥ 1.5 m; (B) dbh ≥ 2.5 cm

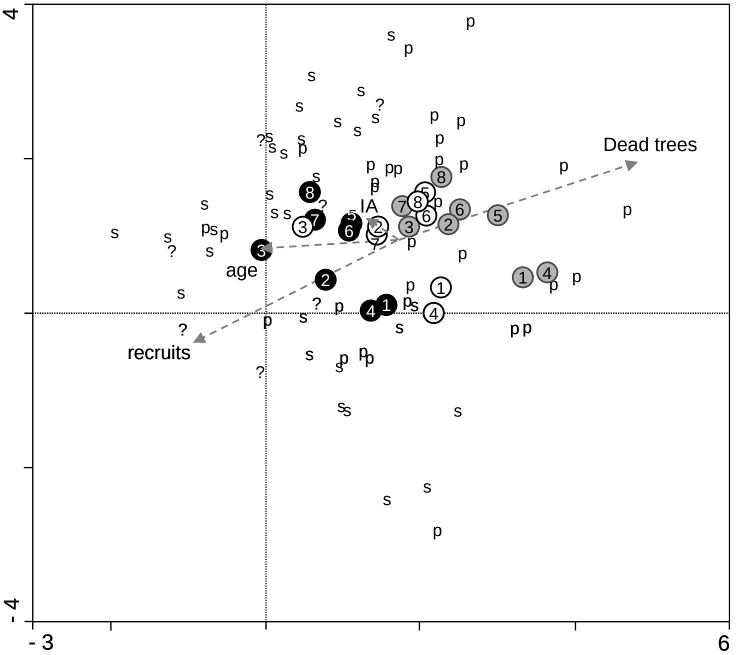

FIGURE 5. Ordination of groups in secondary forest plots with species (letters) and samples (circles). P: pioneer species; S: shade tolerant species; ?: not classified. Samples were plot x group combinations, with groups being: open circles: trees from the initial assemblage (census 1) that survived the study period (IA), black circles = recruits, and grey circles = trees of the census 1 that died during the study period. Numbers indicate plots. Groups were included as dummy variables (arrows). A detrended correspondence analysis (DCA) was used, and species numbers were square root transformed prior to analysis.

trees in the plot, t-test, df = 999, $P < 0.001$). This suggests relatively high mortality among the most abundant species in each plot. In all plots mortality among the pioneer species (mean = 43.3% ± 5.8 SE) was more than three times higher than the across-plot mean of the shade-tolerant group (13.0% ± 2.6 SE). Across plots this difference was highly significant (paired samples t-test, $t = 5.6$, $P = 0.001$).

Species richness of the dead trees (S_d) ranged from 12 to 20 (mean 16) species, and between one and six species per plot disappeared during the 18-months interval (mean 2.8 ± 0.6 SE). Species richness of recruited trees (S_r) varied between 19 and 40 (mean 28). Between 5 and 19 new species entered the plots (mean 10.4 ± 1.4 SE) which constituted on average 38% (23-61%) of the species richness of the recruited trees. In all plots, the number of new species surpassed the number of species lost, and consequently absolute species richness increased (Fig. 1A). The recruited community was not only richer in species than the group of dead trees, but also had higher evenness values (mean ± SE = 0.63 ± 0.06, and 0.27 ± 0.02, respectively).

When the species richness of the initial assemblage (S_i) was compared pair-wise with S_r and S_d, considering the lowest abundance level of recruitment and dead trees ($S_{i(rarefied)}$, Gotelli & Entsminger 2001), S_r was significantly higher than $S_{i(rarefied)}$ in seven out of eight plots, and S_d was in all cases lower than $S_{i(rarefied)}$. Likewise we compared S_r with S_d at the lower abundance level of the recruitment, and S_r was significantly higher than $S_{d(rarefied)}$ in all cases (data not shown).

SPECIES COMPOSITION AND TURNOVER

None of the eight plots showed a significant change in species composition over 18 months. Similarity values (Chao Jaccard Abundance Estimator; Chao *et al.* 2005) ranged from 0.95–1.00 with none being significantly different from 1 (Table 1). In all but two plots species composition of the assemblage of recruits did not differ significantly from the assemblage of surviving trees. Similarity between dead and recruited trees was on average lower, but the difference was only significant in 4 of the 8 plots (Table 1).

The three groups did differ with respect to the share of shade-tolerant trees. In all plots, the fraction of shade-tolerant trees in the recruitment group was higher than in the group of survivors from the initial assemblage (after log transformation, paired sample t-test, $t = -5.93$, $P = 0.006$). The shade-tolerant fraction of the surviving trees was higher than that of the dead trees (after log transformation, paired sample t-test, $t = 4.81$, $df = 7$, $P = 0.002$ (Fig. 3).

The variation explained by the first two axes of the DCA was only 27.6% (axis 1 = 19.8%; Fig. 5). The first axis was most strongly correlated with the variables 'recruits' and 'dead', but with opposite sign ($r = -0.55$ and 0.63 respectively), indicating a separation between the composition of species that entered (recruitment) and left (mortality) our secondary succession plots. Correlation of the first axis with fallow age was $r = -0.47$. The shade-tolerant species had a significant lower mean score on the first axis than the pioneer species ($t = -4.8$, $df = 66$, $P < 0.001$). These results suggest a pattern of species turnover, starting the replacement of pioneer species by shade-tolerant species as succession progresses.

DISCUSSION

In this study we addressed species colonization and replacement dynamics during the first years of secondary succession. More specifically we evaluated the prediction that the initial floristic composition (IFC) hypothesis (Egler 1954) applies to succession on abandoned agricultural fields with light use and proximity to old-growth forests patches (Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1984, 1996). To meet these conditions, all sites were selected on abandoned milpas that had been in use for one single harvest, and adjacent or close to other forest fragments. There is no clear consensus regarding how to understand and interpret the IFC hypothesis (Wilson *et al.* 1992; McCook 1994). Therefore we formulated specific predictions concerning species dynamics on community level that will be examined in the following paragraphs.

PATTERNS OF SPECIES RICHNESS AND COMPOSITION

Species density was as high as 54 species/500m^2 in these very early stages of secondary succession (Fig. 1B). When differences in density were taken into account, species richness reached about one third of the values of old-growth forest within the same region: after rarefaction, the mean old-growth forest species richness was 56 species/188 trees (M. Martínez-Ramos, unpublished data), while the average secondary forest value was 17 species/188 trees (range 9–22, census 1). About 60% of the species encountered in our sites were also found in five 0.5-ha old-growth forest plots in the in the same region on similar soils (M. Martínez-Ramos, unpublished data). Dominance of the species differed, however, between secondary and old-growth forests. While the five most dominant species in the secondary forest plots represented 66% of all trees, they represented less than 1.3% of all trees with dbh ≥ 10 cm in the old-growth forest. On the other hand, five of the six most abundant species in the old-growth forest (together representing 33% of total stems with dbh ≥ 10 cm in 2.5 ha), were present in 1 to 6 of our 8 secondary forest plots. They occurred in low numbers however (1–5 individuals per plot).

The relationships between species density and fallow age were the same for census 1 and census 2, suggesting that the chronosequences gave a good estimate of general trends of increasing species density, at least over a time-interval of a few years. Despite such consistent results, however, rate of increase of species richness varied considerably among plots (Fig. 1B). This supports the suggestion that time-studies are very much needed to recognize such variation and to analyse the underlying patterns of mortality and recruitment, as advocated earlier by Swaine & Hall (1983), Finegan (1996) and Chazdon *et al.* (2005).

RECRUITMENT

The predictions that both pioneer and shade-tolerant species co-occur since the initial phase of succession is supported by our data. Because of differences in criteria used and a degree of subjectivity in species grouping, comparisons between studies have to be made with care. However, the 2% shade-tolerant trees in our one-year old site is in the same order of magnitude as those in one-year old plots in Ghana (5.4%; Swaine & Hall 1983), and in the Venezuelan Amazon (2%; Uhl 1987).

Resprouting from surviving stumps from trees of the original forest can be an important regeneration mode (Kammesheidt 1998; Bond & Midgley 2001, 2003) that might make it inherently more likely that a succession will fulfill IFC predictions, as opposed to a situation in which "shade-tolerant" species have to recolonize mainly or totally through seed dispersal. Data on resprouting in secondary forest succession is scarce though. In the Venezuelan plot of Uhl (1987) five years after abandonment 21% of the shade-tolerant individuals were sprouts on stumps of trees from the original forest. In the study site in Ghana (Swaine & Hall 1983) one year after abandonment all shade-tolerant plants (13% of all plants) were coppice shoots of trees of the original forest, but in the 5 years following the initial census no more resprouting was observed. In our three-year-old site resprouts on surviving trunks constituted at least 32% of the stems and represented 65% of the shade-tolerant species in the plot. In the other sites resprouting from original vegetation seemed to be rare or absent. This was, however, difficult to assess reliably, since resprouting also occurred from surviving below ground root systems (M. van Breugel 2003, personal observation).

Our results contrast with the IFS prediction that dominant pioneer species recruit poorly after initial canopy closure (Finegan 1984, 1996). All our plots had a closed canopy at the time of the first census, yet on average more than half of the recruitment belonged to pioneer species. Uhl (1987) also reported recruitment of pioneer species in year 2–5 of post-agriculture succession, despite the presence of a relatively high leaf area index in these years. High stand-level mortality in young secondary forests, however, results in a highly dynamic stand structure (Chapter 4), and we found a positive relationship between stand-level mortality and the proportion of pioneers among the recruits. Uhl (1987) reports enhanced recruitment of pioneer trees following increased mortality of the dominant *Vismia* spp. four year after succession started. These findings suggest that high mortality rates during early succession might provide new recruitment opportunities for pioneer species after initial canopy closure.

Swaine & Hall (1983) found that none of the species that dominated the canopy at the end of the first year recruited thereafter, while the dominating *Vismia* spp. in Uhl's (1987) study plot continued to recruit in relatively large numbers up to the fourth year. The contrasting results of these early single-plot studies could lead to different conclusions, but in fact they fit well within the variation at local scale that we found in this study (Fig. 4), stressing the necessity of using multiple plots within the same age class.

MORTALITY

As predicted, mortality among pioneers exceeded mortality of shade tolerant species in all plots. Moreover, mortality was biased towards the dominant species. These and similar observations in 12–25 year old plots (Capers *et al.* 2005; Chazdon *et al.* 2005) and in a 60 year old plot (Lang & Knight 1983) indicate a gradual shift in canopy dominance from pioneers to shade-tolerant species.

In the first years of succession shade-tolerant species are still mainly confined to the understory (Peña-Claros 2003) and competition for a canopy position is mainly between species with the same early successional status. In this study, all plots were dominated by pioneer species with a maximum life span that exceeds the 6.5 years covered by our chronosequence study system. Nonetheless inter-specific variation in mortality rates was very high, and caused a strong shift in canopy dominance in five out of eight study plots, despite the short study period (Fig. 2). Illustrative is the 1-year old plot, where relative abundance of *C. peltata* and *T. mexicanum* was 53 and 31%, respectively. Both species are early successional species with about the same maximum life span of 25–35 years, and abundance and often co-occur in our study region. The two species accounted for 86% and < 5% of total stem mortality respectively and, in consequence, *T. mexicanum* replaced *C. peltata* as the canopy dominant. Similar patterns were also reported for early succession in Ghana, where the initially dominating *Musanga cecropioides* gave way to *Harungana madagascariensis* due to differences in mortality rates (Swaine & Hall 1983). A different example is given by the catastrophic mortality among the dominant *Trema micrantha* (> 90% of trees) in two other plots. Mortality affected these trees irrespective of their size or canopy position (M. van Breugel, unpublished data), suggesting an outbreak of pathogens as the more likely cause of death, as has been shown earlier for cohorts of pioneer species in old growth tropical forest (Augspurger 1984; Augspurger & Kelly 1984). This enabled another pioneer (*T. mexicanum*) to recruit massively and dominate the canopy within 18 months. In old-successional (*e.g.*, Lussier *et al.* 2002) and young-successional temperate forests (Fujihara 1996; Toyohara & Fujihara 1998) pathogen outbreaks have been shown to alter succession in a similar fashion. These examples indicate that inter-specific differences in mortality rates play an important role in the dynamics of early years of secondary forest succession.

SPECIES TURNOVER

The recruitment group showed consistently higher species richness and evenness than the dead tree group, as predicted. On average, four times more new species entered than disappeared from the plots, hence species diversity increased strongly in all plots. Nonetheless, similarity estimates suggested that species composition hardly changed after 1.5 years. An explanation of this lies in the strong dominance by few species, as a result of which the numerical influence of the recruitment of new species was low. In one plot with an initial richness of 35 species, for example, the 19 new species recruited were represented by only 42 individuals, about 10% of the initial tree density in that plot.

A more sensitive indication for an ongoing shift in species composition was therefore given by the dissimilarity between the species composition of the trees that entered (recruitment group) and left (dead group) the tree community. The differences between these two groups indicated successional species replacement that was not evident when only net changes from census 1 to 2 were considered. The separation of the composition of recruits and dead trees along the first axis of the correspondence analysis suggested similar successional patterns. The shade-tolerant fraction was relatively high in the recruitment group, while mortality was almost entirely confined to pioneer trees. These results indicate that successional species turnover, in which pioneer species are being replaced by shade-tolerant species as a consequence of differential recruitment and mortality rates, already starts at the very early years of succession.

Species composition of the recruited and dead tree groups did not, however, differ in all plots. In some plots still a considerable fraction of recruits belonged to pioneer and canopy dominant species. Consequently the degree of species turnover and functional group replacement varied considerably among plots. Further studies should disentangle effects of species differences (*e.g.*, seed dispersal modes, establishment requirements, susceptibility to natural enemies affecting growth and mortality rates) and landscape factors (dispersal limitations, local species pool available for colonization). Applying a larger size limit (2.5 cm dbh instead of 1.5 m height) clearly showed that most of species and functional group recruitment in these initial years are confined to the smaller size classes, in line with earlier suggestions from Okimori & Matius (2000) and Peña-Claros (2003). This stresses the need to include small size limits in the study of successional species dynamics, at least in these early communities.

CONCLUSION

We conclude that the highly dynamic and spatially variable nature of secondary succession makes it difficult to explain successional species replacement patterns based on static data, and support calls (Finegan 1996; Chazdon *et al.* 2005) for community-level studies that monitor recruitment, mortality and growth. This study demonstrates the benefits of setting up permanent plots across a range of initial stand ages. This approach effectively complements direct observation with space-time substitution when long-term monitoring of secondary sites is problematic, and addresses questions on community dynamics in different phases of secondary forest succession.

Successional species turnover, resulting in replacement of pioneer species by shade-tolerant species already started in the beginning of succession. However, the fraction of canopy dominants and pioneer species among recruits, and consequently the species turnover rate, varied considerably among sites. We suggest that secondary succession is not always a gradual and continuous process of functional group replacement, but that high mortality during the first years of secondary forest succession may open new recruitment windows for pioneer species. Overall, our study supports the IFC hypothesis, but we urgently need the development of new approaches (stochastic and/or deterministic) to explain the high levels of inter-site variation observed in the early stages of the secondary succession process in tropical abandoned agricultural fields.

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Chapter 4

COMMUNITY DYNAMICS DURING EARLY SUCCESSION IN MEXICAN TROPICAL RAIN FORESTS

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ABSTRACT

Stand structure dynamics during early secondary forest succession were related to mortality, growth, and recruitment rates, and the dependence of these demographic processes on fallow age and initial stand structure attributes was evaluated. In 11 secondary tropical rain-forest sites (1.5-19 y) in Chiapas, Mexico, one plot of 10 × 50 m was established. Diameter and height were measured for all trees ≥ 1 cm dbh, and their survival, growth, and recruitment was monitored over a 2-y period. Changes in stand structure were especially fast in the first 5 y of succession, and decreased rapidly afterwards, which resulted from similar stand-level changes in relative mortality, growth, and recruitment rates. Demographic processes were negatively related with initial stand basal area, but independent of initial tree density. Basal area was a better explanatory variable of the among-stand variability in these rates than fallow age. Results suggest that asymmetric competition and resulting patterns of tree-thinning are major driving forces determining secondary forest successional pathways. Fallow age per se is a compound variable reflecting community organization at a certain point along the successional axis, while community structure drives succession. Sudden mass mortality among dominant species in some stands showed that early secondary forest succession is not always a gradual and unidirectional process.

INTRODUCTION

Succession in tropical secondary forests on abandoned fields has been studied with a strong emphasis on describing temporal trajectories of community structure and composition (Guariguata & Ostertag 2001). These studies, mostly based on chronosequences, have shown that community structure and composition approach those of old-growth forest as fallow age increases (Brown & Lugo 1990; Guariguata & Ostertag 2001). However, recovery rates vary widely among sites of the same fallow age and with the structural parameter being considered. Basal area and species density sometimes attain the values of old-growth forest within a few decades (Saldarriaga *et al.* 1988; Uhl *et al.* 1988; Guariguata *et al.* 1997; Tucker *et al.* 1998), while species composition takes over a century to recover (Aide *et al.* 1996; Finegan 1996; Aide *et al.* 2000; Dewalt *et al.* 2003). Explaining variation in successional pathways has been another major concern of studies of secondary forest, and important advances in linking such variation with environmental heterogeneity and land-use history has been made (Purata 1986; Uhl *et al.* 1988; Aide *et al.* 1996; Pascarella *et al.* 2000; Mesquita *et al.* 2001; Chinea & Helmer 2003; Ferguson *et al.* 2003).

Considering the asymptotic behavior of most successional trends, we could predict a decreasing rate of change of community attributes with fallow age, i.e. community dynamics lessen with fallow age. Until now, such a prediction has not been examined explicitly and directly. Community dynamics (the temporal change in the structure and composition of communities) emerge from the aggregated demographic changes of constituent species in terms of growth, recruitment and mortality. For example, a change in basal area of a tree community within a certain time period (ΔBA) results from the aggregated differences in growth, recruitment and mortality of all trees (i.e., $\Delta BA = \Delta BA_{growth} + \Delta BA_{recruitment} - \Delta BA_{mortality}$). Species turnover is a result of differential patterns of recruitment and of mortality. Therefore, we propose that analysis of these components of community-level dynamics is crucial to understanding the mechanisms that determine secondary forest succession.

Studies of growth, mortality and recruitment in secondary forests are manifold, but they chiefly cover a selection of species, and mostly under manipulated conditions (*e.g.*, Gerhardt 1993; Guariguata *et al.* 1997; Pearson *et al.* 2003b; Pearson *et al.* 2003a; Walker *et al.* 2003; Iriarte Vivar Balderrama & Chazdon 2005). To our best knowledge, examples of studies on community-level dynamics and underlying mechanisms in young secondary tropical forests are much less common. Recently Chazdon *et al.* (2005) monitored recruitment, growth and mortality of trees ≥ 5 cm dbh annually for 6 y in four 12-25-y-old sites on abandoned cattle pastures. In the same sites, Capers and co-workers (2005) studied recruitment and mortality of the seedling communityEarlier Uhl (1987) examined growth, mortality, and recruitment over 5 y following slash-and-burn agriculture in one plot in the Amazon of Venezuela.

A current debate links community structural attributes (*e.g.* basal area and plant size hierarchies) to concepts of asymmetric competition and density-dependent growth and mortality (Condit *et al.* 1998; Enquist & Niklas 2001; Midgley *et al.* 2002; Coomes *et al.* 2003). These concepts have been studied extensively in even-aged monocultures (Yoda *et al.* 1963; White 1980, 1981; Westoby 1984; Begon *et al.* 2006), and the debate concerns the validity of extending them to mixed-species, mixed-aged forests (alien-thinning sensu White 1980). Because life-history traits such as survival, growth and mortality rates, longevity, and shade tolerance vary widely among species (Sarukhán *et al.* 1985; Condit *et al.* 1995; Martínez-Ramos & Álvarez-Buylla 1995b; Davies 2001), the question is if tree-thinning under size-related competition has a similarly important role in species-rich successional forests as in single-species stands.

If so, we would expect to observe a relationship between successional dynamics and forest community structure operating at a given time of succession. It has been predicted that under asymmetric competition growth concentrates in the largest individuals and smaller individuals suffer higher mortality rates, resulting in declining density and an increasing average and maximum tree diameter (Huston 1994; Niklas *et al.* 2003a; Niklas *et al.* 2003b). So community structure would determine the degree and nature of competitive pressures operating on growth and survival of individual trees. The aggregated response of these trees, in turn, would determine how community structure changes during successional stand development.

In this study we monitored tree successional dynamics over 2 y in a chronosequence of 11 sites in young secondary tropical rain forests, with fallow age ranging from 1.5 to 17 y. First, we evaluate dynamics at tree-community level by quantifying mortality, growth, and recruitment rates as well as the changes in community structure. Second, we examine the effect of fallow age and community structure on these components of forest dynamics. More specifically, we address the following questions:

1) Do rates of change of community structural attributes (such as basal area, mean canopy height, stem density, and species density) decrease with fallow age as expected from the asymptotic behavior of successional trends in chronosequence studies?

2) How do such structural changes relate to mortality, growth and recruitment rates?

3) Do community-level growth, mortality and recruitment rates depend on community structure (basal area and tree density)?

4) Do growth and mortality show the patterns that would be expected under the assumption that asymmetric competition plays an important role during successional stand development?

METHODS

STUDY AREA

The study was conducted at the Marquéz de Comillas region, to the South of the Montes Azules Biosphere Reserve (approximately 16º04′ N; 90º45′ W), within the Lacandona rain forest area, Chiapas, Mexico. Average annual rainfall is about 3000 mm, and mean annual temperature about 22 ºC. There is a dry season from February to April (< 100 mm month^{-1}) that accounts for less than 10% of the total annual rainfall. The research area consists mainly of three geomorphologic units defined on soil and topographic criteria (Siebe *et al.* 1996). This study was conducted within the most common geomorphologic unit in the region. This unit consists of topographically irregular areas at 115-300 m a.s.l. with small hills and valleys with sandy and limestone soils of low pH (< 5.5). The original vegetation consists mainly of lowland tropical rainforests and semi-deciduous forests. For a more extensive description of the natural vegetation in the region, see Ibarra-Manríquez & Martínez-Ramos (2002) and chapter 1.

SITE SELECTION AND PLOT LAYOUT

We selected the study sites in order to obtain as much environmental homogeneity as possible with regard to soil, topography and management history. Earlier studies demonstrated differences in secondary vegetation among the geomorphological units present in the region ((Méndez-Bahena 1999; Chapter 2). The same studies

TABLE 1. Characteristics of the study sites at the time of the initial census. Column 'SV' (surrounding vegetation): OGF = old-growth forest; OSF = old secondary forest (±15 y); YSF = young secondary forest (< 10 y); P = pastures; r = remnant OGF trees. Column 'Land-use history': F = fallow; m = milpa (corn field, one harvest only in all cases); OGF = old-growth forest. Fallow length is indicated between brackets (in y). Symbols can be used to identify the sites in Figures 1 and 4.

	Site	Age (y)	Area (ha)	SV	Land-use history
○	F2	1.5	8.5	OGF, P	F (1.5) - m - F(16) - m - OGF
□	H2	1.5	1.1	OSF, P, r	F (1.5) - m - F(16) - m - OGF
◇	P2	1.5	4.0	OGF, P, YSF	F (1.5) - m - OGF
▲	R2	1.5	3.0	OGF, P, YSF	F (1.5) - m - OGF
▽	G3	3	10.0	OGF, P, r	F (3) - m - OGF
●	E4	4	1.0	P, r	F (4) - m - OGF
▼	F4	4	1.0	OGF, P	F (4) - m - F(13) - m - OGF
△	R4	4	2.8	OGF, P, r	F (4) - m - OGF
⬢	S8	8	2.3	OSF, P, r	F (8) - m - F(?) - m - F(?) - m - OGF
◆	H10	10	6.0	P, YSF, r	F (10) - m - OGF
■	H17	17	5.5	OGF, P	F (17) - m – OGF

demonstrated that former land use, more specifically abandoned pastures vs. abandoned cornfields ('milpas'), exerted an influence on vegetation succession. In this region most secondary forest was found on abandoned cornfields. Consequently we decided to select our study sites on abandoned cornfields within the Low-Hill geomorphological unit.

Secondary forest sites were selected with fallow age ranging from 1.5 to 17 y, which represents the most common ages of secondary forests found within the study region. Fallow age and land-use history was determined based on information of landowners and other local people. We measured the perimeter with measurement tape to calculate site area and determined the land-use type of the adjacent fields (Table 1). Because the study area was opened to human colonization only three decades ago (Dichtl 1988; see also chapter 1), availability of sites was unbalanced with respect to fallow age, with abundant presence of young forests (< 10 y) and scarcity of sites older than 15 y. Site selection was in accordance with such availability. In each selected site, we rented an area (0.5 ha) for a period of more than 2 y. One plot of 10 × 50 m was laid out within each site. The plots were divided in 125 2×2-m quadrants. Plots and quadrants were permanently indicated with poles.

TREE INVENTORY

A total of five inventories were conducted over 2 y. At the first census (census 0), all trees with dbh ≥ 1 cm were recorded, tagged and identified to species as far as known, otherwise genus name and/or species number were recorded. The position of each tree was determined within 1 x 1-m quadrats and dbh (stem diameter at 1.3 m above ground) and height (from the stem base to the crown top) were measured. A stem was considered dead when it died back to below 1.5 m.

At approximately annual intervals (1 and 2 y after plot establishment, census 2 and census 4 respectively) complete re-censuses were done, including the recording of all dead trees and the dbh measurement of new recruits (trees reaching 1 cm dbh). Additionally, 6 and 18 mo after plot establishment, (census 1 and census 3, respectively), only mortality and recruitment were recorded. One plot (E4) burned between census 3 and census 4, so for this plot no data for census 4 are available.

ANALYSIS

Basal area (BA, m^2 ha^{-1}), mean stem diameter (D_m, cm), and mean canopy height (H_m, the mean of the tallest trees of the 2 × 2-m quadrants, m) were calculated for census 0, 2, and 4. Community density (NT, trees ha^{-1}) was calculated for all censuses. Diameter frequency distributions were calculated for each plot × census combination using dbh classes of 3 cm. We calculated the linear regression of the logarithm of the number of trees ($\log N_i$) against the logarithm of the mid-values of the dbh classes ($\log D_i$): $\log N_i$

$= \log \beta - \alpha \log D_i$ with α giving the slope of the linear regression. This regression model approximates the numbers of trees N_i into the different diameter classes D_i (Enquist & Niklas 2001; Niklas *et al.* 2003b). All regressions were highly significant with R^2 ranging between 0.83 and 0.99.

Annual relative rate of change (RRC) of each structural variable X_i was calculated over the two study years as the difference between the variable in the last (X_f) and the first census (X_i) as a proportion of X_i and corrected for the actual census period in days (t):

$RRC(X) = (X_f/X_i)^{365/t} - 1$ *Equation 1*

Net change of community basal area (BA) over the two study years can be calculated from basal area growth of surviving trees, basal area of the newly recruited trees surviving until the end of the period, and the initial basal area lost due to mortality of trees. For convenience we will further refer to these components as growth (G), recruitment (R), and mortality (M), respectively. Annual relative recruitment and mortality rates (R_{BA}, M_{BA}) were calculated as proportions of the community BA at census 0, corrected for the actual census period (see equation 2-3 below). Annual relative growth rates (G_{BA}) were calculated as proportions of the initial BA of the trees that survived the census period (see equation 4 below). Similarly, relative recruitment and mortality rates based on number of trees (NT) were calculated as the number of recruited trees and the number of dead trees at the last census (census 4) as proportion of the number of trees at census 0, corrected for the actual census period (equation 2-3).

$R_X = [(X_0 + R) / X_0]^{365/t} - 1$ *Equation 2*
$M_X = 1 - [1 - (M / X_0)]^{365/t}$ *Equation 3*
$G_{BA} = [(BA_{S(0)} + G) / BA_{S(0)}]^{365/t} - 1$ *Equation 4*

Where R_X and M_X can be expressed in BA or NT, X_0 is the community BA or NT at the initial census, $BA_{S(0)}$ is BA at the initial census of the trees that survived the census period; and t is the census period (census 0-census 4) in days.

For the plots S8 and E4, the annual relative rates of change of all variables and tree growth, recruitment and mortality were calculated over the first study year only. In plot S8 the dominant canopy species *Ochroma pyramidale* suffered sudden extraordinary high mortality in the second year, so strongly affecting all calculations. Plot E4 was burned in the second year.

We used ordinary least square regression analyses to examine the following relationships (dependent vs. independent variables): (1) BA, NT, D_m , H_m, α and species density (S) at census 0 vs. fallow age. (2) Annual rates of change of BA, NT, D_m , H_m, and α vs. fallow age and vs. initial basal area. (3) Growth, recruitment and mortality rates vs. BA, NT, and fallow age. All relationships with fallow age as independent variable were chronosequence analyses. The first analysis is the classical approach describing the state of the community as a function of time; the second and third analyses describe the rate at which the community is changing as a function of age, i.e. dynamics with fallow age. We chose basal area and tree density as they describe different but complementary aspects of community organization, i.e. number of individuals and size of these individuals, that are expected to be related to resource availability (*e.g.* light and soil nutrients).

Regression analyses for points 1 to 3 were performed using the curve estimation procedure of the SPSS 10 package, examining all available models with maximal two parameters and then selecting the curve with the best fit. Models examined were: Linear: y = a + b * x; Logarithmic: y = a + (b * ln(x)); Inverse: y = a + b/x; Power: y = a * xb; Compound: y = a * bx; S: y = e(a + b/x); Growth: y = e(a + b * x); Exponential: y = a * e(b * x). We had two reasons to use this procedure. First, we expected variables describing forest structure to reach mature forest values asymptotically in the course of succession, but for most variables it generally takes longer to reach the asymptote than the 17 y covered by our plots (Saldarriaga *et al.* 1988; Aide *et al.* 2000; Denslow & Guzman 2000; Guariguata & Ostertag 2001). Therefore, there is no reason to assume that one particular response function would describe the relationships best over the first two decades of succession. Second, we have a low number of independent observations (11). To evaluate the relative importance of fallow age, basal area and tree density as explanatory factors of the variation observed among stands in growth, recruitment and mortality rates, we applied forward stepwise multiple linear regression analysis. We log-transformed these rates to account for non-linearity.

Abundance of trees differed considerably among plots. When species density was significantly correlated to tree density, we 'rarefied' plot species density down to the lowest abundance level among plots to ensure appropriate among-plots comparisons. We used the rarefaction procedure available in the EcoSim package (EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear (http:// homepages.together.net /~gentsmin /ecosim.htm).

RESULTS

CHRONOSEQUENCE COMMUNITY TRAJECTORIES

The total number of recorded species in the plots ranged from 14 to 41 and was positively related with fallow age (Fig. 1a). Among plots, basal area ranged from 2.8 to 27.4 m^2 ha^{-1} (Fig. 1b), average canopy height from 3.2 to 9.9 m (Fig. 1c), and average diameter from 1.6 to 5.0 cm (Fig. 1d). All these variables showed a positive and asymptotic trajectory with fallow age. The slope of the log-log size-frequency

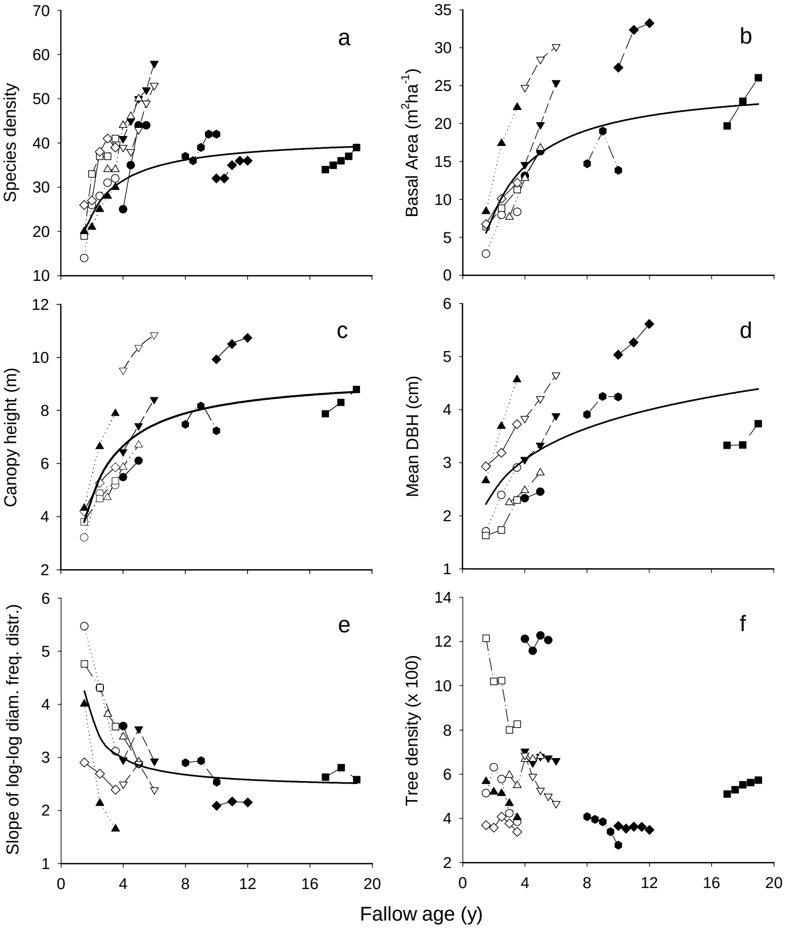

FIGURE 1. Successional trends of community structural attributes with fallow age in abandoned milpa's in south-east Mexico. a-f) For each one of 11 secondary forest 10 × 50-m plots, attribute values in three consecutive annual censuses (tree density, five 6-monthly censuses) are plotted against fallow age (lines connecting same symbols). a) species density in number of species per 500 m^2. b) Basal area, expressed as m^2 ha^{-1}. c) Mean canopy height, the average height (m) of the highest trees in 2 × 2-m quadrats. d) Mean stem diameter (cm) at 1.3 m height. e) The slope of the linear regression on the log-log diameter frequency distribution (α). f) Tree density in number of trees per 500 m^2. Continuous curves show adjusted non-linear models for the chronosequence relationships between community attributes and fallow age, based on data of the initial census. Model type, R^2, and P-values are as follows: (a) S model, $R^2 = 0.63$, $P < 0.01$; (b) S model, $R^2 = 0.71$, $P < 0.001$; (c) S model, $R^2 = 0.78$, $P < 0.0001$; (d) Logarithmic model, $R^2 = 0.5$, $P < 0.05$; (e) S model, $R^2 = 0.55$, $P < 0.01$; (f) no significant relation. Models were fitted using the best-fit estimation procedure of SPSS 10.1. Symbols represent study plots as in Table 1.

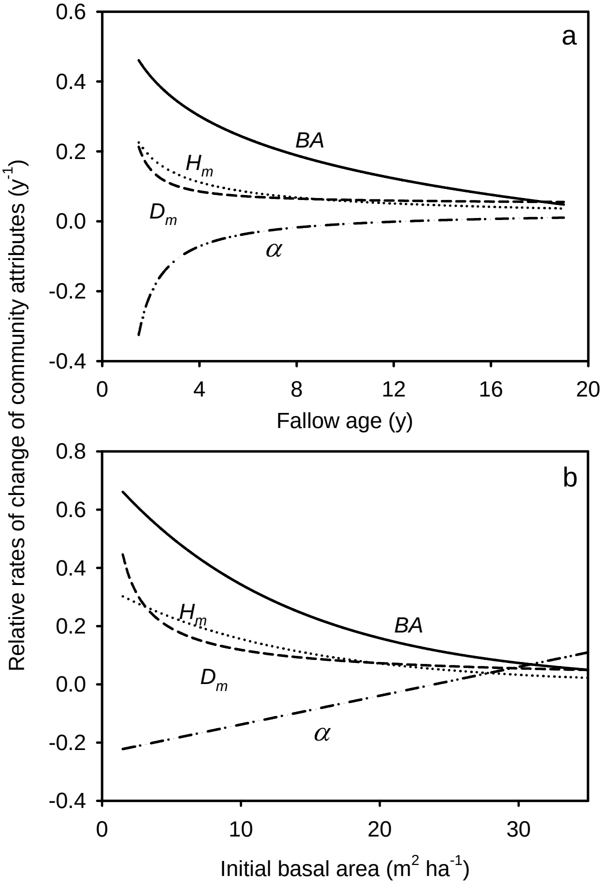

FIGURE 2. Relationships of annual relative rates of change (RRC) of tree community attributes with fallow age (a), and initial basal area (b) obtained for secondary forests in south-east Mexico. *BA* = basal area; H_m= mean canopy height; D_m= mean dbh; -α = slope of the log-log diameter frequency distribution. Best fit models obtained from the curve estimation (SPSS 10.1 package) are provided. Regression model type, R^2 and P-values are as follows: (a) RRC_{BA}: logarithmic, $R^2 = 0.54$, $P < 0.01$; RRC_{Hm}: Power, $R^2 = 0.78$, $P < 0.0001$; RRC_{Dm}: S, $R^2 = 0.72$, $P < 0.001$; $RRC_{-\alpha}$: Inverse, $R^2 = 0.56$, $P < 0.01$; (b) RRC_{BA}: Exponential, $R^2 = 0.86$, $P < 0.0001$; RRC_{Hm}: Exponential, $R^2 = 0.81$, $P < 0.0001$; RRC_{Dm}: Power, $R^2 = 0.54$, $P < 0.01$; $RRC_{-\alpha}$: Linear, $R^2 = 0.44$, $P < 0.05$.

distribution (α) varied between 2.1 and 5.5 and was negatively related with fallow age, indicating a more equal distribution of number of trees among dbh classes as successional time advances (Fig. 1e). Tree density ranged from 7320 to 24,240 trees ha-1, showed quite a large variation among youngest stands, and was not related to fallow age (Fig. 1f). H_m, D_m, α and BA were mutually and strongly correlated (Table 2).

COMMUNITY DYNAMICS

The change of community structural attributes over the 2 y of the study exhibited large variability among plots (Fig. 1). Overall, the general trend was an increase of species density, BA, H_m, D_m and a decline in stem density and α.

Species density per plot increased between 13% and 129% (mean 53%) in 2 y. Noteworthy, four of the younger sites (initial fallow age ≤ 4 y old) developed a higher species richer than the older plots (≥ 8 y old; Fig. 1a). Mean canopy height and basal area increased in all but one plot (Fig. 1b,c). In this plot (S8), massive mortality occurred in the second year among the 10-15-m-tall *Ochroma pyramidale* trees that initially dominated the canopy. Basal area showed an average increase of 77.9% (range among plots: 5.9-195.2%), H_m of 36.7% (3.1-82.7%), and D_m of 31.6% (8.5-71.5%).

Changes in tree density fluctuated considerably among and within plots in the 2 y of the study. Overall, tree density decreased in most plots (8 out of 10), particularly in the younger forests (Fig. 1f). On average, density decreased 14.2% (range among plots: -32.0% to +14.5%). In the youngest five plots, α decreased while in older ones it exhibited little variation (Fig. 1e).

The relative rate of change (RRC) of tree density was independent of fallow age. For the other attributes, regression models indicate rapid RRC values (between 0.2 and -0.5) in the first 2 y of succession followed by a steep decline towards values close to zero in plots with fallow ages more than 6 y (Fig. 2a). RRC of BA, D_m , α, and H_m were mutually related (Table 3), meaning that a rapid increase of one attribute was accompanied by a rapid increase (or decrease in case of α) of the other ones. The RRC of tree density was only weakly but significantly negatively related with the RRC of D_m (Table 3).

COMMUNITY LEVEL GROWTH, MORTALITY AND RECRUITMENT RATES

In terms of basal area, relative growth, recruitment and mortality rates declined significantly with fallow age (Fig. 3a, Table 4). Relative growth rates were higher than relative mortality and recruitment rates in all stands, more markedly so in the youngest

TABLE 2. Pair-wise relationships among tree community attributes obtained for secondary forests in south-east Mexico. R^2 and significance level of least square linear regressions are shown. *NT* = tree density; *BA* = basal area; H_m = mean canopy height; D_m = mean dbh; α = slope of the log-log dbh frequency distribution.

	NT	*BA*	H_m	D_m
NT	-			
BA	ns	-		
$\bar{H}$	ns	0.97 ***	-	
$\bar{D}$	ns	0.77 ***	0.82 ***	-
α	ns	- 0.70 **	- 0.72 **	- 0.79 ***

* = $P < 0.01$, ** = $P < 0.001$, *** = $P < 0.0001$

TABLE 3. Pair-wise relationships among annual rates of change (ACR) of community attributes obtained for secondary forests in south-east Mexico. R^2 and significance level of least square linear regressions are shown. *NT* = tree density; *BA* = basal area; H_m = mean canopy height; D_m = mean dbh; α = slope of the log-log dbh frequency distribution.

	RRC$_{BA}$	RRC$_{Hm}$	RRC$_{Hm}$	RRC$_{\alpha}$
RRC$_{NT}$	ns	ns	- 0.44*	ns
RRC$_{BA}$		0.87 ***	0.78 ***	- 0.66 *
RRC$_{Hm}$		-	0.86 ***	- 0.79 ***
RRC$_{Dm}$			-	- 0.66 *

* = $P < 0.01$, ** = $P < 0.001$, *** = $P < 0.0001$, ns = not significant

ones (Fig. 3a). Net differences among these three trajectories result in a sharp basal area gain during the first 2 y of succession and a subsequent decline in basal area gain which was still positive after 20 y of succession (Fig. 2a). Relative mortality rates based on number of trees (M_{NT}) declined significantly with fallow age, but relative tree recruitment rates (R_{NT}) varied independently of this time indicator (Fig. 3a, Table 4). R_{NT} and M_{NT} were positively correlated, i.e. recruitment was relatively high in sites with high mortality rates (linear regression, $R^2 = 0.51$, $P = 0.02$).

Modest net changes in community structure hid fast dynamics occurring in some sites. This was clearest in three of the sites (H2, F2 and S8). In the first two sites loss of basal area due to high mortality (M_{BA} = 0.44 and 0.48 m^2 m^{-2} y^{-1}, respectively) was overcompensated by high recruitment (R_{BA} = 0.36 and 0.38 m^2 m^{-2} y^{-1}, respectively) and growth (G_{BA} = 0.79 and 1.44 m^2 m^{-2} y^{-1}, respectively), which resulted in moderate positive RRC$_{BA}$ values. In the other plots, M_{BA} (mean = 0.12, 95% confidence interval (CI) = 0.06-0.17), R_{BA} (mean = 0.03, CI = 0.01-0.06), and G_{BA} (mean = 0.44, CI = 0.24-0.64) were much lower. In S8 sudden mass mortality exhibited by *Ochroma pyramidale* in the second year of the study resulted in a very high M_{BA} (0.46) that was not compensated by recruitment (R_{BA} almost zero) and growth (G_{BA} = 0.18). Overall, these changes resulted in a negative RRC$_{BA}$ value

The proportion of trees in the stand that accounted for 90% of basal area growth varied between 15% and 57% and declined with the initial stand basal area (Fig. 4). The smaller individuals, on the other hand, had a relatively high probability of mortality, as the proportion of trees that died among the 25% shortest trees (among-plot average = 0.27) was significantly higher than the proportion of trees that died among the taller trees (among-plot average 0.20) (Wilcoxin matched-pair signed rank test, n = 11, one-tailed P = 0.0049).

COMMUNITY DYNAMICS VS. INITIAL COMMUNITY STRUCTURE

The relative rates of change (RRC) of all community structural attributes were significantly related to initial basal area (Fig. 2b), except for the RRC of tree density (not shown). A similar analysis of the relation between the RRC of BA, H_m, D_m and *a* on the one hand and initial tree density on the other hand showed that the rate of change of community structure did not significantly depend on initial tree density (not shown).

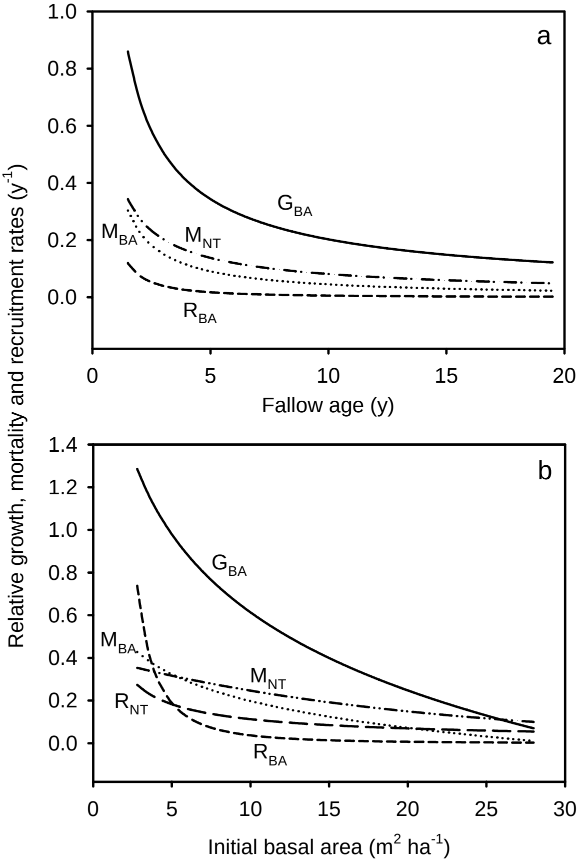

FIGURE 3. Relationships between annual relative rates of growth (G), mortality (M) and recruitment (R) on the one hand and and fallow age (a), and initial basal area (b) on the other hand obtained for secondary forests in south-east Mexico. Subscripts *BA* and *NT* indicate rates based on basal area and tree density, respectively. Showed curves are the best-fit models (model type, R^2 and P-values are given in Table 4) and only significant models are plotted. See text for further details.

TABLE 4. Relationship functions between growth (G), mortality (M), and recruitment (R) rates (dependent variables, rows) and initial fallow age, basal area, and tree density (independent variables, columns) for secondary forests in south-east Mexico. Rates are expressed in terms of basal area (*BA*) and number of trees (*NT*). For all cases, sample size was 11 and the curve fitting procedure of the SPSS 10.1 package was used to select the best-fit regression model. Pow = Power model; Log = Logarithmic model; Exp = Exponential model.

	Fallow age			*BA*			Tree density
	model	R^2	P	model	R^2	P	P
G_{BA}	Pow	0.71	**	Log	0.85	***	ns
M_{BA}	Pow	0.78	***	Log	0.67	*	ns
R_{BA}	Pow	0.62	*	Pow	0.85	***	ns
R_{NT}			ns	Exp	0.68	*	ns
M_{NT}	Pow	0.77	***	Pow	0.55	*	ns

* = $P < 0.01$, ** = $P < 0.001$, *** = $P < 0.0001$, ns = not significant

Relative growth, mortality and recruitment rates were not related to initial tree density but were quite sensitive to changes in BA_0 (Fig. 3b, Table 4). The recruitment rate per plot (R_{NT}) declined exponentially with increases in BA_0 while mortality rate (M_{NT}) declined with a power trajectory (Fig. 3b, Table 4). These curves did not intersect, mortality rates being higher than recruitment rates all along the basal area axis. Thus, a reduction over time in tree density occurred at any point within the range of BA_0 values of our plots.

In contrast, trajectories of the rates of gain (R_{BA}) and loss (M_{BA}) of basal area as a function of BA_0 intersect at an equilibrium point of ca. 4 m^2 ha^{-1} (Fig. 3b). However at any point, loss of basal area resulting from mortality was overcompensated by the basal area gains due to growth (Fig. 3b). Differences in G, M and R decline as the community basal area increases, but the net gain in basal area is still positive after 20 y of succession (*cf.* Fig. 2a).

Stepwise multiple linear regression showed that among-plot variation in relative growth, mortality and recruitment rates based on basal area (G_{BA}, M_{BA}, R_{BA},) and relative recruitment rate based on number of trees (R_{NT}) was best explained by BA_0 ($R^2 = 0.75$, $P = 0.001$; $R^2 = 0.56$, $P = 0.008$; $R^2 = 0.47$, $P = 0.021$; $R^2 = 0.57$, $P = 0.004$, respectively). Tree density and fallow age did not contribute significantly to the regression coefficient. In the case of mortality rate based on number of trees (M_{NT}), fallow age explained most of the variation ($R^2 = 0.41$, $P = 0.035$), while BA_0 and tree density did not contribute significantly to the regression coefficient. In both cases, the exclusion of BA_0 or fallow age was due to the fact that they were strongly related (see Fig. 1f).

DISCUSSION

SECONDARY VS. OLD-GROWTH FOREST

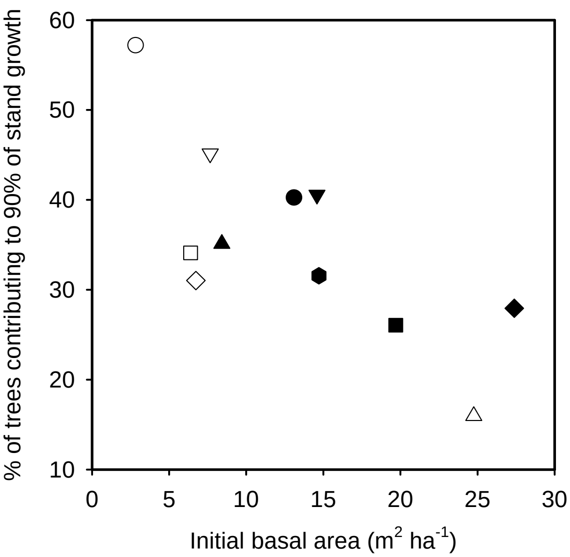

FIGURE 4. Relationship between percentage of fastest growing trees accounting for 90% of stand basal area growth) and the initial basal area (*BA_0*) in 11 secondary forests sites in south-east Mexico. Each point represents one study plot, symbols as in Table 1. Pearson correlation coefficient (r) = 0.73, P = 0.01.

The degree and rate of structural convergence of secondary forests with old-growth forests strongly depended on the parameter considered, as has been demonstrated earlier (Finegan 1996; Guariguata & Ostertag 2001). Species density in our plots was still far from reaching values of old-growth forest within the same Low-Hill study area. Rarefied species density values found in old-growth forest averaged 56 species per 188 trees (three 500-m^2 plots, trees with dbh ≥ 1, M. Martínez-Ramos, *unpublished data*) which was more than twice as high as our highest secondary forest value of 26 species per 188 trees. Basal area, on the other hand, reached and even surpassed basal area of old-growth forests very early in succession. For example, the estimated 30.3 m^2 ha^{-1} basal area of plot R4 at an age of 6-y was higher than the average of five old-growth forest stands (25.4 m^2 ha^{-1}, trees with dbh ≥ 1 cm, M. Martínez-Ramos *unpublished data*) within the same Low-Hill area. Such rapid and early successional increase of basal area has been observed in other studies (Saldarriaga *et al.* 1988; Denslow & Guzman 2000; Steininger 2000), but not for secondary forests as young as ours. This does not imply, however, that standing biomass of old-growth forest is reached rapidly in early successional stages as stature and wood density of pioneer species dominating young secondary forests is much lower than that of shade-tolerant species dominating old-growth forest (M. van Breugel, *unpublished data*). In the same region and forests, Balvanera *et al.* (2005) found that secondary forests 13 y old have less than 40% of the standing biomass (trees dbh ≥ 10 cm) of old-growth forest in Low-Hill areas.

In contrast to basal area, canopy height of the studied secondary forests (among plot mean ± SD = 6.1 ± 2.3 m) still remained well behind the old-growth forest average in the Low-Hill area (16.8 ± 8.9 m, five 20 × 250-m plots, M. van Breugel, *unpublished data*). The tree diameter distribution in the secondary forests was rather different from that of the old-growth communities, with small trees (< 10 cm dbh) constituting 30-100% of the total basal area. This is similar to the findings of Read & Lawrence (2003) in dry tropical forests, where the relative contribution of stems with dbh < 5 cm to total above-ground biomass ranged from 15% in mature forests to almost 80% in 2-5-y-old secondary forests. In all plots the slope of the log-log diameter frequency distribution (α) was higher than the average value of –2.0 that was found for the 226 forest stands of the Gentry forest transect database (Enquist & Niklas 2001), with a clear trend of decreasing α with fallow age. Tucker *et al.* (1998) made similar observations, and proposed that a high ratio of basal areas of saplings (< 10 cm dbh) to larger trees is a key indicator of early successional stage in the Amazon. Niklas *et al.* (2003b) similarly suggested that a high α reflects relatively short time since disturbance. Such observation implies that when trees with dbh < 10 cm are not included, as in Balvanera *et al.* (2005), relative basal area or relative biomass recovery in young secondary forests will be underestimated.

The fact that attributes such as tree density, canopy height, mean diameter and α were very different from old-growth values in our plots clearly indicates that similarity in basal area between young secondary and old-growth forests resulted from very distinct stand structure and composition.

COMMUNITY DYNAMICS

The obtained chronosequence trajectories indicate increasing basal area, canopy height, average diameter, and more uniform stem size distribution (smaller α) as succession advances. Similar patterns have been found elsewhere (Saldarriaga *et al.* 1988; Guariguata *et al.* 1997; Tucker *et al.* 1998; Denslow & Guzman 2000; Peña-Claros 2003). However, this study allowed the examination of successional processes underlying these trajectories; disentangling community dynamics in tree mortality, growth, and recruitment. Our results indicate, for example, that changes in tree community basal area in the first two decades of succession are driven, in absolute and relative scales, by tree growth more than mortality and tree recruitment. Also, although the relative rate of change in community structural attributes varied considerably among plots, a general pattern was found of very high rate values early in succession followed by a rapidly decline in these rates with age of succession.

Our study shows that the decline in the rate of change of most community attributes through succession is a consequence of reduction in recruitment, mortality, and growth rates. Very early in succession (< 5 y), relative mortality, recruitment, and growth rates were very high with highest relative annual growth rates even exceeding 100%. At 20 y, dynamics were much lower.

Basal area, strongly correlated with both fallow age and the other stand structural attributes (average tree diameter, canopy height and α), explained a large part of the among-plot variation in all three rates. Thus, our results support the hypothesis that community dynamics depend on the forest structure at a given time of succession. In this context, fallow age can be defined as a compound variable reflecting stand structure and related within-plot environmental heterogeneity at a certain point along the successional axis. On the other hand, growth, recruitment and mortality rates were independent of community tree density, which was related to neither fallow age nor to other community structural variables.

ASYMMETRIC COMPETITION AND SUCCESSIONAL COMMUNITY DEVELOPMENT

The dependence of community dynamics on community structure can be expected under size-asymmetric competition for limiting resources, such as a reduced light availability (Huston 1994; Schwinning & Weiner 1998; Enquist & Niklas 2001; Freckleton & Watkinson 2001). In early phases of secondary succession, plants would tend to compete symmetrically since most trees are similarly small and occupy similar positions in a low canopy (Schwinning & Weiner 1998). However early differences in size among trees can be caused by variation in emergence time (Connolly & Wayne 1996), environmental (related to differences in, for example, soil, topography, land-use history) and genetic heterogeneity (Hartgerink & Bazzaz 1984), and/or variation in spatial levels of competition intensity due to non-uniform spatial distribution of trees (Huston 1986; Huston & DeAngelis 1987; Miller & Weiner 1989). The heterogeneous starting environment and resulting plant size differences can be expected to result in increasingly asymmetric competition as the larger trees may gain an advantage and seize a relatively large part of the community biomass. As a result, larger trees improve their competitive position, exacerbating subsequently the differences in growth rates among interacting trees (Huston 1994; Schwinning & Weiner 1998). While the winners get the largest part of the pie, the individuals that lag behind in growth and stature will suffer from lower levels of light availability and are expected to experience higher mortality.

We found support for the operation of this asymmetric competition. Basal area growth was concentrated into a relatively small proportion of the trees, and this proportion declined with increasing initial stand basal area, while the smaller individuals had an increased probability of mortality. A direct result was that the slopes of the stem size distribution (α) decreased in most plots, which links asymmetric competition with successional stand development as discussed by Niklas *et al.* (2003b).

Relative mortality - and recruitment rates were not related to tree density, but were strongly related to initial basal area. These results suggest that the role of competition in successional stand development is more strongly related to the degree of asymmetry of competition than to the number of trees per se. Moreover the positive among-plot relationship between mortality and recruitment rates suggests that mortality continuously opens up space that can be occupied by recruits of other species, at least in the earlier phases of secondary forest succession. This is clearly demonstrated by two of the youngest sites (H2 and F2); both with very high initial tree density (*cf.* Fig. 1). Catastrophic mortality among the dominant early successional species *Trema micrantha* opened the canopy enough for the massive recruitment of another early successional species *Trichospermum mexicanum*.

Our results suggest that community structure and competition are driving factors underlying the observed successional patterns. However, when we extend the concept of self-thinning under increasing asymmetric competition (Weiner 1988) to mixed-species mixed-aged forests, we assume a similar dominant role of size-related competition in these forests as in even-aged single-species systems. As Coomes *et al.* (2003) and Midgley *et al.* (2002) pointed out; species composition can be expected to influence successional community dynamics since life history traits such as growth, mortality, longevity, and shade tolerance vary broadly among species (Sarukhán *et al.* 1985; Condit *et al.* 1995; Martínez-Ramos & Álvarez-Buylla 1995a, 1998; Davies 2001). An evaluation of the role of density-dependence mechanisms in organization of successional communities needs therefore to take such variation into account.

An analysis of species dynamics in our study plots indicates that shade-tolerant species were relatively abundant amongst smaller trees, similar to findings in successional forests in Bolivia (Peña-Claros 2003) and that such species exhibited relatively high recruitment and low mortality rates (M. van Breugel *unpublished data*). Inter-specific differences in species response to competition, in terms of growth, mortality and recruitment, may explain partially the deviation from expected patterns, such as the observed lack of relationship between mortality rate and tree density.

CONCLUSIONS

Rates of change of different community structure attributes are very fast in early phases of secondary forest succession (first 5 y since field abandonment) and slow down rapidly after a few more years. These dynamics result from similar underlying trends of high relative rates of mortality, recruitment, and growth early in succession, and slower rates at later ages. Direction and rate of change of most community attributes are related to community structure, i.e. forest community structure in a given successional time drives further community development. Therefore, to understand mechanisms of secondary forest succession, time since abandonment has to be considered as a compound factor integrating variables of community structure.

Our study suggests that processes of community-level thinning as a consequence of increasing asymmetric competition play a paramount role in community dynamics and underlying processes of mortality, growth and recruitment. The concept of asymmetric competition predicts specific changes in community structure along the successional gradient of which some were indeed observed in our secondary forests. Observations of community changes that were not in line with expectations from the concept of community-level asymmetric competition and thinning might be explained partly by life-history differences in the context of species replacement during succession. Overall, forest development can be gradual or show abrupt changes, depending on species composition and the degree of dominance by one or few species.

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Chapter 5

RATES OF CHANGE IN TREE COMMUNITIES OF SECONDARY NEOTROPICAL FORESTS FOLLOWING MAJOR DISTURBANCES

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ABSTRACT

Rates of change in tree communities following major disturbances are determined by a complex set of interactions between local site factors, landscape history and structure, regional species pools and species life histories. Our analysis focuses on vegetation change following abandonment of agricultural fields or pastures, as this is the most extensive form of major disturbance in Neotropical forests. We consider five tree community attributes: stem density, basal area, species density, species richness and species composition. We describe two case studies, in northeastern Costa Rica and Chiapas, Mexico, where both chronosequence and annual tree dynamics studies are being applied. These case studies show that the rates of change in tree communities often deviate from chronosequence trends. With respect to tree species composition, sites of different ages differ more than a single site followed over time through the same age range. Dynamic changes in basal area within stands, on the other hand, generally followed chronosequence trends. Basal area accumulation was more linked with tree growth rates than with net changes in tree density due to recruitment and mortality. Stem turnover rates were poor predictors of species turnover rates, particularly at longer time-intervals. Effects of the surrounding landscape on tree community dynamics within individual plots are poorly understood, but are likely to be important determinants of species accumulation rates and relative abundance patterns.

INTRODUCTION

Rates of change in tree communities following major disturbances are determined by a complex set of interactions between local site factors, landscape history and structure, regional species pools and species life histories. Our analysis focuses on vegetation change following abandonment of agricultural fields or pastures, as this is the most extensive form of major disturbance in Neotropical forests. We consider five tree community attributes: stem density, basal area, species density, species richness and species composition. We describe two case studies, in northeastern Costa Rica and Chiapas, Mexico, where both chronosequence and annual tree dynamics studies are being applied. These case studies show that the rates of change in tree communities often deviate from chronosequence trends. With respect to tree species composition, sites of different ages differ more than a single site followed over time through the same age range. Dynamic changes in basal area within stands, on the other hand, generally followed chronosequence trends. Basal area accumulation was more linked with tree growth rates than with net changes in tree density due to recruitment and mortality. Stem turnover rates were poor predictors of species turnover rates, particularly at longer time-intervals. Effects of the surrounding landscape on tree community dynamics within individual plots are poorly understood, but are likely to be important determinants of species accumulation rates and relative abundance patterns.

Disturbances are pervasive features of forest ecosystems, to the extent that there is no clear distinction between successional and mature-phase vegetation (Aubréville 1938; Whittaker 1972; Clark 1996). Structure and dynamics of forest vegetation reflect a complex interplay of disturbance events and regeneration processes taking place through time and space (Chazdon 2003). Vegetation structure and composition are often interpreted in terms of how forests have responded to recent and historic disturbance regimes (Whitmore & Burslem 1998). Several attributes of tropical forest structure and composition can recover following large-scale disturbances, natural or anthropogenic, such as hurricanes, fires, logging, swidden agriculture or cattle raising activities (see reviews by Brown & Lugo 1990; Guariguata & Ostertag 2001; Chazdon 2003; Finegan & Nasi 2004; Chazdon in press; Holl in press). Rates of change, however, vary considerably, depending upon what forest attributes are being measured and upon the intensity, duration and frequency of the disturbance. Ultimately, rates of forest change following major disturbances are determined by a complex set of interactions between local site factors, landscape history and structure, regional species pools (including non-native species) and species life histories (Pickett *et al.* 1987). In this review, we define major disturbances as those that result in the complete or nearly complete removal of vegetation, leading to the establishment of even-aged regrowth. These disturbances may occur at a range of spatial scales, from large gaps in a forest matrix, to small swidden agriculture fields, to large-scale deforestation. In most of the successional studies we discuss here, vegetation removal occurs at spatial scales ranging from 0.5 to 20 ha. 1.

COMPLEXITIES OF VEGETATION CHANGE FOLLOWING STAND-REMOVING DISTURBANCES

Following major disturbances, rates of change of forest structure and composition are strongly affected by the nature and extent of residual vegetation, in the form of resprouts, remnant trees or shrubs, seedling/saplings and/or the soil seed bank (Uhl *et al.* 1981; Guevara *et al.* 1986; Galindo-Gonzalez *et al.* 2000; Slocum & Horvitz 2000; Benitez-Malvido *et al.* 2001; Elmqvist *et al.* 2001; Chazdon 2003). Resprouting is the predominant form of regeneration following damaging windstorms, such as hurricanes or cyclones (Yih *et al.* 1991; Bellingham *et al.* 1994). The effects of large-scale wind disturbances on forest structure and species composition are therefore generally transitory (Dittus 1985; Walker 1991; Bellingham *et al.* 1995; Burslem *et al.* 2000; Vandermeer *et al.* 2000; Pascarella *et al.* 2004), with rapid recovery of forest structure and composition. Globally, tropical forests subject to frequent hurricanes/ cyclones have significantly shorter canopies compared with forests in similar environments that are not prone to such frequent wind-induced disturbances (Whitmore 1990; de Gouvenain & Silander 2003). When residual vegetation and propagule sources are lacking, destroyed by fires, or when soils are highly disturbed or compacted by heavy grazing, bulldozing or high-impact logging, rates of forest regrowth and biomass accumulation decline; under extreme conditions, successional processes may be arrested or diverted by exotic species (Hjerpe *et al.* 2001; Chinea 2002; Fine 2002; Zarin *et al.* 2005).

To add further complexity, site factors (such as soil fertility and texture) interact with landscape factors, such as forest cover spatial organization and extent, distance to forested areas and regional species pool, to determine rates of species colonization, accumulation of species and accumulation of biomass above- and belowground (Johnson *et al.* 2000; Moran *et al.* 2000; Zarin *et al.* 2001; Chazdon 2003). A complete understanding of the factors that influence forest vegetation change following major disturbances in tropical forests must incorporate analyses of site attributes as well as landscape configuration and regional species composition. Most studies to date, however, have focused on effects of site attributes (such as land-use history and soils), leaving many unanswered questions regarding the effects of landscape composition and regional land-use dynamics on local patterns and processes of forest succession (Helmer 2000; Chinea & Helmer 2003). These effects are not exclusively unidirectional, as secondary forest development can influence species composition and genetic structure of populations in nearby mature forests as well as in surrounding areas undergoing succession (U. Sezen 2006, unpublished work). As stated by Pickett (1976, p. 117), ‘Successional gradients and the evolutionary and functional responses of populations on them are part of a dynamic, regional process rather than a single site pattern.’

ASSESSING RATES OF CHANGE FOLLOWING MAJOR DISTURBANCES

Successional processes are not always directional or predictable, and multiple pathways can lead to a range of mature forest types rather than a single stable endpoint (Gleason 1926). Here, we describe the succession process in terms of rates of change in tree community attributes rather than as a recovery process, thereby avoiding the assumption that succession is orderly or deterministic and will eventually reach the original forest structure and species composition present before the disturbance.

Two general approaches have been used to assess rates of vegetation change during succession. Most information on tropical forest succession is derived from chronosequence studies, where temporal changes are inferred from a single-time investigation of a set of forest stands of different ages since disturbance. Rates of change are therefore estimated indirectly, based on assumptions that the same successional process takes place within each stand. The second approach directly documents the rates of change through monitoring vegetation dynamics over time in particular forest stands. Here, we describe results of studies using each approach and examine their strengths and limitations in terms of assessing rates of vegetation change following large-scale disturbance in tropical forest areas. Most of our examples are drawn from studies of wet and seasonally dry Neotropical forests. We then examine whether chronosequence trends can predict tree community changes as observed within individual secondary forest stands over time. We consider two case studies, from northeastern Costa Rica and Chiapas, Mexico, where both approaches are being applied in long-term studies of successional permanent plots. Since chronosequence studies are based on single-time information from a range of sites, these data emphasize cumulative or net effects of ecological processes. In contrast, vegetation dynamics examine incremental change over time and can therefore reveal more about the ecological processes that produce cumulative changes.

Our review focuses on vegetation change following abandonment of agricultural fields or pastures, as this is the most extensive form of major disturbance in tropical forests today, as well as historically. Secondary, degraded and logged forests now cover more area than mature forests within tropical regions (FAO 2006). We examine rates of change for five tree community attributes: stem density; basal area; species density; species richness; and species composition. In two case studies, we examine turnover rates of stems and species for different size classes and time-scales. Stem density and basal area are influenced by rates of tree growth, recruitment and mortality, whereas species density, richness and composition reflect processes of species turnover and community assembly. Collectively, these processes determine changes in species relative abundance, size distributions and dominance over time.

When assessing vegetation change in successional tropical forests, the standard for comparison is usually neighbouring areas of mature or old-growth forests. For many regions, however, these forests have become reduced to small fragments or are degraded to various degrees, and a suitable 'pristine' area may not be available for contemporaneous study (Chazdon in press). Moreover, edaphic variation may lead to local differences in forest structure and composition in mature forests (Fanshawe 1952; Duivenvoorden 1995; Clark *et al.* 1999; Harms *et al.* 2001; Potts *et al.* 2002; Valencia *et al.* 2004) and this is also the case in secondary forests (Herrera & Finegan 1997; Méndez-Bahena 1999; Chapter 2; Finegan & Delgado 2000). Many secondary forests are found in small patches isolated from continuous forest cover. As a result, it remains a major challenge to obtain robust data on vegetation change in secondary forests that matches the spatial extent of data collected for mature forest tracts, which are generally larger areas (at least for those that are investigated in ecological studies) and may therefore encompass greater edaphic heterogeneity.

RATES OF CHANGE BASED ON CHRONOSEQUENCE STUDIES

Originally framed as a tool for investigating primary succession, chronosequence studies have become a key component of research on secondary forest succession. A space-for-time substitution allows researchers to examine a much larger time frame than would be otherwise feasible and also corrects for potential interannual climatic variation that could confound a time-series (Foster & Tilman 2000). However, chronosequence data only permit inferences of successional change and do not facilitate direct analysis of the underlying processes mediating the change (growth, mortality and recruitment). In addition, the basic assumption of chronosequence studies –that the sites represent points along a continuum, rather than snapshots of independent trajectories– often remains untested.

Chronosequence sites must be carefully chosen to avoid bias in site selection. The best chronosequence studies are those that base their site selection on precise, independently verifiable estimates of site age. For example, Ruiz *et al.* (2005) selected a chronosequence of tropical dry forest sites on Providencia Island, Colombia, based on a sequence of available aerial photographs and remote sensing data. Ideally, site selection should remain unbiased by prior notions of successional rates, topography or ease of access, although these factors often restrict available study areas. Moreover, successional sites should encompass the same range of heterogeneity in soils and topography as mature forest sites that are being compared.

Chronosequence studies have contributed valuable data used to infer rates of vegetation change in regenerating tropical forests. Our review will largely focus on woody vegetation in moist/wet lowland forests, but we also include studies in tropical dry forests. Most studies have examined relatively young forests (less than 50 years old). Studies of more advanced secondary forests (50–200 years old) often focus on single forest sites in the absence of a chronosequence context (Lang & Knight 1983; Milton *et al.* 1994; Brearley *et al.* 2004).

(a) Basal area/aboveground biomass

Trends in basal area are closely linked to trends in aboveground biomass (ABM; Clark & Clark 2000). Both are generally calculated from stem diameters, but the equations used for ABM are often site specific (*e.g.*, Brown 1997; Nelson *et al.* 1999) and sometimes incorporate data on wood density and tree height. Owing to these factors, basal area is a more conservative metric for comparisons of regrowth across sites where site-specific allometric equations have not been developed. For both ABM and basal area, secondary tropical wet forests exhibit rapid growth in the first years of establishment. Biomass accumulation tends to be tree dominated (greater than 94% in Central Amazonia; Feldpausch *et al.* 2005), with lianas comprising only a small fraction (DeWalt & Chave 2004; Gehring *et al.* 2004). In a chronosequence of sites in Bolivia, Peña-Claros (2003) found that secondary forests reached 70% of mature forest basal area in the first 25 years of regrowth. Pascarella *et al.* (2000) found similar values in the first 25–30 years of regrowth in Puerto Rico.

Saldarriaga *et al.* (1988) found that ABM increased linearly with stand age up to 40 years in the upper Rio Negro, then levelled off due, they suggested, to mortality of long-lived pioneer species. The pantropical average rate of biomass accumulation in the first 20 years of forest succession has been estimated to be 6.2 mg ha^{-1} y^{-1}, although among-site variation is very high (Silver *et al.* 2000). Reported values are as high as 11 mg ha^{-1} y^{-1} in central Amazonia (Feldpausch 2004) and up to 15 mg ha^{-1} y^{-1} in high altitude forests (Fehse *et al.* 2002). In contrast to the linear increases in ABM found in other chronosequence studies, Jepsen (2006) reported sigmoidal increase in biomass accumulation in swidden fallows from 2 to 15 years old in Sarawak Malaysia, with initially rapid biomass growth up to 10 years followed by no net biomass accumulation. Based on fitted functions, biomass accumulation reached a maximum rate of 12.7 mg ha^{-1} y^{-1}, 4 years after abandonment (Jepsen 2006). In Chiapas, Mexico, secondary forests developed in abandoned pastures and with fallow ages of 12–13 years attained 20% of the carbon storage estimated for nearby undisturbed mature rainforest (94 mg C ha-1) sharing the same geomorphological properties (Balvanera *et al.* 2005).

The growth of secondary forests can be strongly affected by soil fertility (Moran *et al.* 2000), the duration and intensity of prior land use (Uhl *et al.* 1988; Steininger 2000; Finegan & Nasi 2004; Gehring *et al.* 2005) and fire frequency (Zarin *et al.* 2005). Swidden fallows and abandoned pastures may follow very different successional trajectories (Uhl *et al.* 1988; Steininger 2000). Unfortunately, comparisons among studies are hindered by methodological differences in plot size, minimum stem diameter and the need for site-specific allometric equations to calculate biomass (Clark & Clark 2000).

(b) Tree density

Successional changes in stem density may be driven by intrinsic species life-history differences (*e.g.* in recruitment, growth and mortality rates), density-dependent population processes and additional stand disturbances. Species life-history attributes can lead to episodic recruitment and the development of strong cohort structure in young secondary forests. For example, in the Neotropics, initial colonization is often dominated by relatively short-lived, fast-growing, pioneer genera such as *Cecropia, Vismia* and *Ochroma* (Finegan 1996; Vester 1997; Mesquita *et al.* 2001). When these species die off after 25–30 years, or sometimes much earlier, stem density may decline rapidly (see Chapter 4 and §4).

Tropical secondary forests are generally dense and highly productive, and density-dependent mortality is to be expected, as is the case in secondary forests in other climatic regions (Peet & Christensen 1987; Finegan 1996). Mortality and recruitment processes in mature tropical forests are often density- or frequency dependent (Wills *et al.* 1997; Harms *et al.* 2000; Niklas *et al.* 2003b; Uriarte *et al.* 2005b; Wills *et al.* 2006). The importance of density-dependent effects on stem density and species composition in tropical secondary forests remains unclear, however, due to the paucity of published information from permanent sample plot studies. Breugel *et al.* (2006, Chapter 4) found that stand-level growth, mortality and recruitment were negatively related to stand basal area, but not to stem density. A concentration of growth in the larger trees and relatively high mortality among the smaller trees indicated asymmetric competition, and the resulting pattern of tree thinning strongly influences vegetation dynamics in early succession. Successional changes in density of both trees and regenerating seedlings and saplings may indicate the potential for density dependent effects on mortality, growth and recruitment (Uriarte *et al.* 2004a). The relative importance of conspecific versus heterospecific effects of density on tree regeneration also remains to be determined in tropical secondary forests (Uriarte *et al.* 2004a; 2004b). Since shade-tolerant tree species are not yet reproductively mature in young stands, seeds must be dispersed from nearby or distant mature forests or forest fragments. The lack of locally produced seed shadows decreases the potential for conspecific density-dependent effects on seedling recruitment and growth (Connell 1971; Janzen 1971; Uriarte *et al.* 2005a) in young secondary forests. Therefore, if density-dependent processes are operating in young secondary forests, these effects are more likely to be heterospecific for all but the dominant pioneer species. Intraspecific density-dependence mechanisms may still operate in very early successional stages, however, when a single species dominates colonization in abandoned fields.

Unlike basal area and ABM, stem density does not appear to follow a predictable pattern with forest age. Density is potentially influenced by a wide variety of factors, operating at a range of spatial and temporal scales that vary in their effects on different size classes. Stem density in secondary forests is generally higher than in old-growth forests, even when comparing relatively large size classes (*e.g.* greater than or equal to 10 cm DBH). In Costa Rica, density of stems greater than or equal to 10 cm DBH ranged from 547 to 687 stems ha-1 in 15–20 years old secondary forests compared with 506–527 stems ha-1 in old growth (Guariguata *et al.* 1997). Stem density may peak at an intermediate age range, although these patterns will vary with diameter size limits. Feldpausch *et al.* (2005) detected a peak in stem density at 6–8 years post-abandonment in central Amazonian secondary forests. In Puerto Rico, stem density greater than 2.5 cm DBH increased up to ca 25 years post-abandonment (Aide *et al.* 1995) and then stabilized.

The overall pattern of stem density along chronosequences may yield few discernible trends, but analyzing the density of species, in particular functional groups or within specific size classes, will likely be a more fruitful line of inquiry. These comparisons will be facilitated using the same minimum stem diameter in sample plots at similar successional stages.

(c) Species density and species richness

As the forest develops, new species begin to colonize and recruit, leading to a gradual accumulation of species over time. We distinguish between species density (number of species per sample area) and species richness (number of species per standardized number of individuals sampled; Gotelli & Colwell 2001). Species density is highly sensitive to stem density (Denslow 1995; Chazdon *et al.* 1998), which varies during succession in an unpredictable manner as discussed above. An alternate approach is to use an index such as Shannon's H or Fisher's alpha to assess species diversity; these measures can also be influenced by sample size, however. Species richness can also be estimated from sample data using a variety of approaches (Colwell & Coddington 1994; Chazdon *et al.* 1998). Numerous studies have documented increasing diversity with forest age, although direct comparisons are difficult due to lack of standardization of diversity measures (see reviews by Chazdon in press; Holl in press). Aide *et al.* (1995) found a positive relationship between stand age and species density in a 60-year chronosequence in Puerto Rico, and Saldarriaga *et al.* (1988) found similar Shannon diversity in 40 years old secondary forest and old growth in very small plots. In the earliest study of secondary forest diversity, Eggeling (1947) found a peak in species density of stems greater than or equal to 10 cm at intermediate ages, followed by a decline later in succession. Sheil (2001) applied rarefaction methods to these data to correct for differences in stem density and confirmed the mid-successional peak. Andel (2001) found higher diversity (Fisher's alpha) in old secondary forests in northwest Guyana than in neighbouring old-growth forests.

Like basal area and ABM, species accumulation in secondary forests can be strongly influenced by soil fertility and land-use history (Finegan & Delgado 2000; Pascarella *et al.* 2000). Rates of species accumulation are often slower on abandoned pasture compared with abandoned crop cultivation in regenerating forests of Puerto Rico (Aide *et al.* 1995).

(d) Species composition

Whereas species density may quickly reach the level of old growth, species composition remains distinct for much longer or may never fully recover (Corlett 1992; Clark 1996; Finegan 1996). Pioneer species dominate the community during the first years of regeneration, leading to a forest composition very distinct from that of nearby old growth (Chazdon 2003; Peña-Claros 2003; Chazdon in press). The legacy of early species colonization may persist for decades or even centuries, as some pioneer species can be very long lived (Budowski 1970; Gemerden *et al.* 2003a).

One of the central questions regarding forest succession is whether floristic change follows a predictable pathway. Egler (1954) proposed two contrasting models of forest succession, which Gomez-Pompa & Vazquez-Yanes (1981) adapted for tropical forests. In the 'relay floristics' model, forest development proceeds via successive waves of colonization. The species composition of each wave is predictable, as is the sequence of replacement. In the 'initial floristic composition' model, most of the colonists arrive at the onset of forest regeneration, but reach peak abundances at different points in succession. Neither of these models adequately describes actual trends in species composition in successional tropical forests, however. Few chronosequence studies support the relay floristics model, although many species of early successional pioneers fail to recruit after canopy closure (Finegan 1996; Breugel *et al.* in press, Chapter 3; Chazdon in press; Holl in press). Studies in eastern Amazonia, Bolivia, and Mexico found that species from all functional groups (including shade-tolerant species) established very early in succession and continued to establish after canopy closure (Uhl *et al.* 1988; Peña-Claros 2003; Breugel *et al.* in press, Chapter 3), supporting the initial floristic composition model. In Mesoamerica, studies of tree life histories have revealed a number of distinct functional groups of tree species, which become abundant during different phases of succession (Budowski 1965, 1970; Finegan 1984, 1996; Dalling *et al.* 2001; Capers *et al.* 2005; Chazdon in press.). The resulting waves of recruitment and mortality may lead to wide fluctuations in stem density and may also account for the observed mid-successional peak in species richness (Sheil 1999a). Further study will reveal whether these waves reflect species differences (seed dispersal modes, seedling establishment requirements, growth rates, final size and longevity) and/or landscape effects (dispersal limitation and species pool available for colonization).

The initial floristic composition of successional forests may influence species composition for long periods of time, though the effects of early species composition are often confounded with those of prior land use. In the Brazilian Amazon, researchers have identified two different floristic pathways on abandoned lands. *Cecropia*-

dominated forests generally arise on less severely impacted lands, while *Vismia*-dominated forests develop on more heavily used or more frequently burned areas (Steininger 2000; Mesquita *et al.* 2001). *Cecropia* species are short lived, driving a rapid turnover in species composition at 25–30 years post-abandonment and potentially leading to a more rapid recovery of old-growth forest species. *Vismia* species, in contrast, are longer lived and resprout frequently and may arrest the floristic turnover (Vester 1997; Steininger 2000; Mesquita *et al.* 2001; Lucas *et al.* 2002). Detailed long-term studies are needed to evaluate the influence of land-use history and initial floristic composition on successional pathways and species turnover.

An important question in forest regeneration is whether secondary forests converge with the vegetation of nearby old-growth forests or whether the community composition remains distinct. Terborgh *et al.* (1997) found directional succession occurring on floodplain forests in Peru, returning to the composition of old-growth forests. A key factor in convergence here, however, would seem to be that the regional context of this study was that of forest cover with little or no human disturbance. Are successional trajectories more variable in human-influenced or -dominated landscapes? Sheil (1999b) re-evaluated Eggeling's (1947) plots in Budongo Forest, Uganda, and also detected directional changes in floristic composition conforming to Eggeling's (1947) predicted successional trajectory.

In other situations, the outcome of succession is less clear with measurable differences in floristic composition persisting for up to centuries after abandonment (Clark 1992; Clark 1996; Finegan 1996; Gemerden *et al.* 2003a). In some cases, succession can be arrested due to intensive land use. Fern thickets of Dicranopteris pectinata (Willd.) Underw. colonized large areas in the Dominican Republic after abandonment of agriculture in the early 1970s and inhibited forest regrowth since then (Slocum *et al.* 2004). Observations from the Montes Azules Reserve in southern Mexico suggest that fern thickets can arrest succession for very prolonged periods: pure and thick carpets (0.5–4 ha in extent) of D. pectinata are found immersed in old-growth rainforest in areas that were inhabited by ancient Mayan people. Ceramic pieces found beneath such carpets (ca 1300 years old) suggest that intensive crop cultivation in poor soil led to this long-lasting, arrested successional phenomenon (M. Martínez- Ramos 2006, personal observations). At present, no tree regeneration is occurring within the fern carpets even though they are completely surrounded by mature forest (Suazo-Ortuño 1998).

Chazdon (in press) points out another uncertainty inherent in inferring successional trajectories: the composition of 'mature' forest varies edaphically and harbours the legacy of ancient disturbances. Establishing appropriate reference points for mature forest composition may pose problems for reconstruction of late successional pathways.

(e) Rates of change in tropical dry forests

Tropical dry forests compose 42% of tropical forests worldwide, but are far less studied than tropical wet or moist forests (Mooney *et al.* 1995; Sanchez-Azofeifa *et al.* 2005). Dry forests are floristically and structurally simpler than wet forests, with fewer canopy strata, lower leaf area index and more frequent vegetative reproduction (Murphy & Lugo 1986). Highly seasonal rainfall distribution strongly limits conditions for seed germination and seedling establishment (Ceccon *et al.* 2006; Vieira & Scariot 2006). These differences are likely to affect rates of change in vegetation structure and composition following major disturbances (Ewel 1977; Vieira & Scariot 2006).

The prevalence of anemochorous species in dry forests (Sabogal 1992; Bullock 1995; Gentry 1995; Vieira & Scariot 2006) can have contrasting effects on rates of successional change. In seasonally dry tropical forests of Bolivia, 63% of the canopy tree species are wind dispersed (Justiniano & Fredericksen 2000). Small, wind-dispersed seeds arrive at higher densities than animal-dispersed ones (Holl 1999) and are more resistant to desiccation (Vieira & Scariot 2006). Seed dispersal in dry forests may therefore be less negatively affected by forest fragmentation than in wet forests (Gillespie 1999), although dispersal limitation is still a major limitation for dry forest regeneration (Janzen 1988). These factors may promote rapid structural regeneration in tropical dry forests (Ceccon *et al.* 2002; Ruiz *et al.* 2005; Vieira & Scariot 2006). If early regeneration of tropical dry forests is dominated by wind-dispersed species, however, the frugivore community of the area may be impoverished and rates of species accumulation may be negatively affected (Janzen 1988). Seedling survival is generally very low in tropical dry forests (Gerhardt & Hytteborn 1992; Swaine 1992; Ceccon *et al.* 2006), and the seed bank has a reduced role in seedling regeneration (Rico-Gray & García-Franco 1992; Ray & Brown 1994) compared with wetter forests. Rates of seed predation may be as high as in wet forests, although more studies are needed (Hammond 1995).

Fire likely plays a more important role in tropical dry forest succession (Murphy & Lugo 1987; Vieira & Scariot 2006). Owing to strong seasonality in moisture and nutrient availability, light conditions and gap dynamics are less important for tropical dry forests compared with wet forests (Gerhardt 1996). However, seedling growth and survival in a tropical dry forest of Yucatan, Mexico, was affected by light availability (Ceccon *et al.* 2003; 2004), and at Chamela, Mexico, seedlings of a wide array of tropical dry forest tree species, differing in seed mass and successional status, showed strong differential growth responses to experimental levels of light (Rincón & Huante 1993; Huante & Rincón 1997) and soil nutrients (Huante *et al.* 1995a; 1995b). Such seedling functional responses suggest that tropical dry forest species may be sensitive to environmental heterogeneity promoted by disturbance and forest regeneration.

Resprouting assumes a greater importance in secondary dry forest regeneration than in wet forests (Murphy & Lugo 1986; Kennard 2002; McLaren & McDonald 2003; Vieira &

Scariot 2006; Vieira *et al.* 2006). By allowing survival through a disturbance (Swaine 1992; Miller & Kauffman 1998; Marod *et al.* 2002), resprouting uncouples initial species composition from seed availability (Ceccon *et al.* 2006; Vieira & Scariot 2006). Consequently, resprouting lessens the impact of important barriers commonly related to seed regeneration —lack of seed sources and animal dispersers, short seed longevity, impoverished soil seed banks, lack of suitable microhabitats for seed germination, seed predation, seedling herbivory and competition with aggressive vegetation (Guariguata *et al.* 1995; Wunderle 1997; Wijdeven & Kuzee 2000; Zimmerman *et al.* 2000).

The small number of chronosequence studies conducted in tropical dry forest suggest that dry forests have fewer seral stages than wet forests (Ewel 1980; Kennard 2002; Lebrija-Trejos 2006, unpublished data). As in wet forests, basal area and ABM increase rapidly with stand age (Brown & Lugo 1990; Ray & Brown 1994; Kennard 2002; Ruiz *et al.* 2005; Toledo & Salick 2006). Based on nine secondary tropical dry forests, ABM increased significantly with stand age in young stands (0–20 years post-abandonment), but not in a wider age range (up to 50 years; Silver *et al.* 2000). Life zone (wet, moist and dry) did not significantly affect ABM during the first 20 years of succession, although rates of ABM accumulation were higher in wet versus moist forests (Silver *et al.* 2000). Generally, forest biomass in tropical forests increases with precipitation levels (Brown & Lugo 1982; Murphy & Lugo 1986), although more studies in secondary tropical dry forests are needed. In dry forests of Southern Yucatan, Mexico, ABM increased linearly with stand age in swidden up to 25 years old (Read & Lawrence 2003). Read & Lawrence (2003) projected that at the continuing rate of 2.3–3.4 mg ha^{-1} y^{-1}, ABM will reach levels observed in mature forests of the region within 55–95 years, similar to rates estimated by Hughes *et al.* (1999) for the humid region of Los Tuxtlas. The contribution of small stems (1–4.9 cm DBH) to ABM decreased during succession, whereas large stems (greater than 10 cm DBH) assumed an increasing importance. Increases in tree height during succession were important determinants of ABM changes (Read & Lawrence 2003).

Changes in stem density in tropical dry forests show inconsistent trends with stand age across studies. As in wet forests, much of the variation in stem density with age is due to fluctuations in the density of small stems (Kennard 2002; Toledo & Salick 2006). At the tropical dry forest of Chamela, a chronosequence study showed that stem density (DBH ≥ 1 cm) increased rapidly with fallow age, so that secondary forest plots (1000 m^2 in size) of 8–12 years have similar stem density than old-growth forest plots. Species richness in these secondary forest plots, however, was still 15% lower than that of the old-growth forest (P. Balvanera, G. Ibarra-Manríquez, A. Pérez-Jiménez & M. Martinez-Ramos 2006, unpublished data). Although species density showed a peak in 11–16 years old tropical dry forests of Providencia Island, Colombia, species richness of stems (number of species/187 stems greater than 2.5 cm DBH) increased linearly with stand age (Ruiz *et al.* 2005). As with wet forests, species composition in secondary dry forests lags behind species density and structural measures (basal area and biomass) in terms of relative rates of change during succession (Ceccon *et al.* 2002; Toledo & Salick 2006).

The effect of land use on secondary forest regeneration is poorly understood in dry forests. One recent study of 45–50-year-old subtropical dry forests in Puerto Rico showed strong effects of land use on rates of recovery of basal area, tree height and biomass (Colón & Lugo 2006). Species density and basal area recovered faster in areas used for charcoal production compared with abandoned home sites or farms. Severe disturbances that removed vegetation and disturbed soil and root systems promoted establishment of invasive, exotic species, with long-term effects on successional pathways (González-Iturbe *et al.* 2002; Colón & Lugo 2006). Further comparative studies are needed to draw conclusive comparisons between rates of change during succession in wet versus dry tropical forests. To our knowledge, no published studies have examined vegetation dynamics over time within secondary dry forest stands, although a few studies are now underway in Mexico (F. Bongers and M. Martínez-Ramos 2006, personal communication).

CASE STUDIES OF VEGETATION DYNAMICS IN RELATION TO CHRONOSEQUENCE STUDIES

Long-term vegetation dynamics studies are a necessary counterpart to chronosequence studies. While chronosequence studies may reveal patterns, studies of vegetation dynamics provide insight into the processes that drive vegetation change: recruitment, mortality, growth rates and species turnover (Bakker *et al.* 1996; Foster & Tilman 2000). One fruitful combination of approaches has been chronosequence resampling (Foster & Tilman 2000), in which individual sites within a chronosequence are followed over time. Currently, there is a paucity of time-series data on secondary tropical forest succession. The longest running set of observations come from Sheil's (1998; 1999b; 2001) re-examination of Eggeling's (1947) plots in Budongo forest, Uganda. Another long-term vegetation dynamics study documents forest recovery following anthropogenic and cyclone disturbance in the Solomon Islands (Whitmore 1974; Burslem *et al.* 2000).

Here, we describe successional vegetation dynamics based on case studies in northeastern Costa Rica and Chiapas, Mexico. These studies encompass different land-use histories, different stem size classes and different temporal scales. As we illustrate below, some of the community-level patterns observed in these dynamics studies are remarkably consistent with chronosequence predictions. However, these vegetation dynamics studies also reveal idiosyncratic patterns driven by initial species composition, site factors, landuse history and landscape composition. These studies also provide insight into the mechanisms and drivers of successional change following the abandonment of agricultural lands.

CASE STUDY: SARAPIQUÍ REGION, COSTA RICA

In wet lowlands of northeastern Costa Rica, Chazdon and collaborators have monitored vegetation dynamics annually for 8 years (1997–2004) in four 1 ha plots of secondary forest on abandoned pastures in the Caribbean lowlands (Capers *et al.* 2005; Chazdon *et al.* 2005), and Finegan and collaborators have monitored forest dynamics in four plots over 16 years (1987–2003); three plots are 1 ha and one plot (initially 1-year old) is 0.3 ha. These four plots studied by Finegan were not used for pasture, but were cleared and prepared for planting and then abandoned or were used for one cycle of cultivation. Although these sites had lighter land use than the sites studied by Chazdon, results from both the sets of plots are combined in some of the analyses presented here.

Lowland forests of the Sarapiquí region of northeastern Costa Rica are classified as tropical wet forest (sensu Holdridge *et al.* 1975), receiving ca 3900 mm of precipitation annually (Sanford Jr. *et al.* 1994). The driest months, February–April, still receive more than 100 mm of rain in most years (but see Chazdon *et al.* 2005). The average monthly temperature is 25.88C, with little annual variation. The region is a patchwork of cattle pastures, agricultural areas (bananas, heart of palm and pineapple), residential areas, forest fragments and second-growth forests. Soil fertility varies throughout this region due to erosion of old and more recent lava flows, nutrient-enriched alluvium associated with flood zones and phosphorus-enriched zones associated with geothermal waters at La Selva Biological Station (Pringle 1991; Sollins *et al.* 1994). These factors, as well as variation in land-use history (logging versus pasture versus crops), affect species composition and regeneration in both secondary and mature forests of the region (Herrera & Finegan 1997; Clark *et al.* 1999; Finegan & Delgado 2000).

In the time-series analyses shown here, we combine data for seven 1 ha plots and one 0.3 ha plot for basal area and stem density. Analyzing the plots as a chronosequence across the initial age range from 1 to 25 years, the tree basal area in the first 25 years of regrowth increased linearly with time since abandonment (R^2 = 0.79; Fig. 1a). Resampling these plots over time revealed few deviations from the initial chronosequence projection (Fig. 1a). These results, along with findings from many chronosequence studies, support the view that the basal area is a predictable emergent feature of regenerating forest communities on sites with low to intermediate intensities of agricultural use. At least for sites less than 40 years following abandonment – dominated by long-lived pioneers like *Goethalsia meiantha*, *Laetia procera*, *Simarouba amara* and *Vochysia ferruginea* – the basal area increases linearly with time. Basal area in secondary forests over 25 years is similar to or higher than values from mature forests of this area (Guariguata *et al.* 1997).The only site where basal area decreased over time was the youngest site (Fig. 1a); in this case, decreases in basal area from 6 to 9 years were due to the decline of the initially dominant pioneer species, *Ochroma pyramidale*.

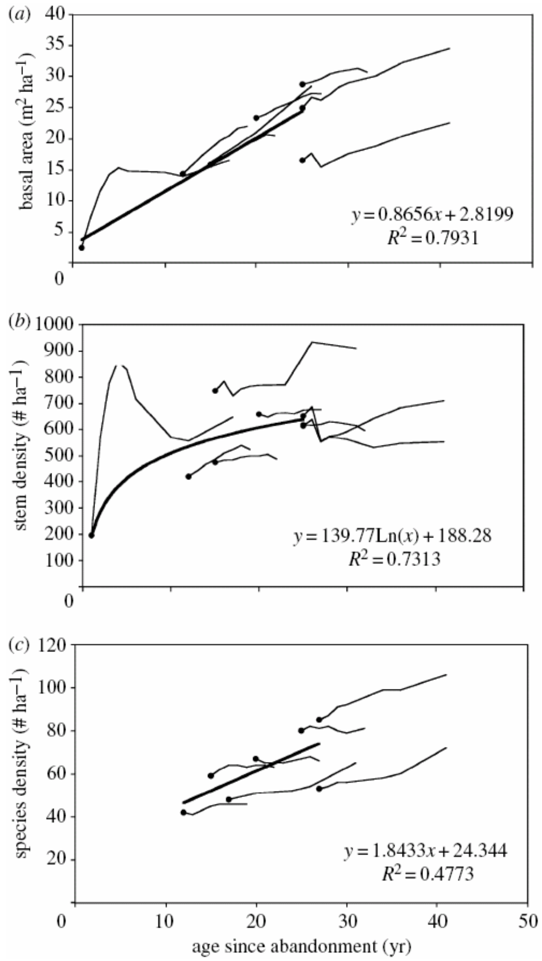

FIGURE 1. Chronosequence data for trees ≥10 cm DBH in 8 secondary forest monitoring plots in northeastern Costa Rica (black dots) and successional trajectories within the same set of plots. a) basal area (m^2/ha) ; b) stem density (#/ha); and c) species density (# species/ha). Data on species density were available for only 7 plots (each 1 ha).

Tree density also showed a clear chronosequence trend, but the increase with stand age was nonlinear (Fig. 1b). Within sites, however, tree density showed highly variable dynamics, and did not conform well to chronosequence trends. The youngest site showed a rapid increase for the first 4 years, followed by a rapid decline in density, due to the dynamics of the dominant species, *O. pyramidale*. Density changes in the older sites varied widely over time; some plots showed no changes in tree density, whereas others showed decreases or increases (Fig. 1b).

The remarkably consistent patterns in basal area despite the inconsistent temporal patterns of density suggest that at the stand level, basal area increments are driven by overall tree growth increments rather than by changes in stem density, a pattern also observed in even-aged temperate forests (Peet & Christensen 1987). Indeed, diameter growth rates in young forests are significantly higher than rates in older stands, even when comparing the same species and size classes (R. L. Chazdon 2006, *unpublished work*). In the Lindero Sur site (initially 12 years old), the per capita basal area increment for trees (≥ 10 cm DBH) was more than six times higher than in the Cuatro Rios site (initially 25 years old). Accumulation of basal area and biomass is driven by growth rates of large trees and can proceed rapidly even if stem density is declining (as occurs in even-aged stands during self-thinning; White

& Harper 1970). Tree mortality in these secondary forests is concentrated in the smaller stem size classes (< 10 cm; Chazdon *et al.* 2005) and has relatively little impact on basal area.

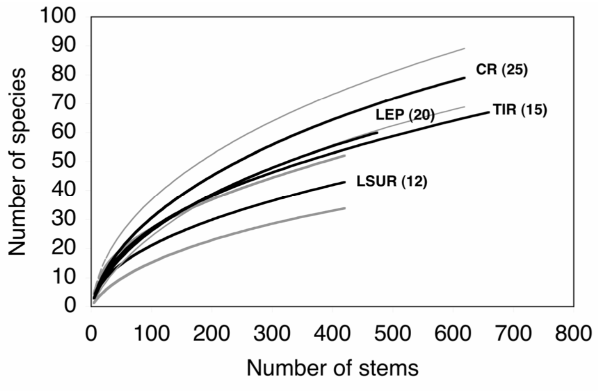

FIGURE 2. Sample-based rarefaction curves for trees>10 cm DBH in 1997 (initial census) for four second-growth forest 1-ha plots in northeastern Costa Rica on former pasture. Site ages are given in parenthesis next to each solid line. Gray lines indicate 95% confidence intervals for species richness based on sample-based rarefaction (Mao Tau; Colwell *et al.* 2004).

Species density rises during forest regeneration in this chronosequence, although the relationship is not as consistent as the pattern observed for basal area ($R^2 = 0.47$; Fig. 1c). Although there is a significant increase in species density with age since abandonment, the former-pasture sites showed little or no change in species density over time. In part, this stabilization of species density reflects species turnover within plots and replacement of early colonizing tree species with later recruiting species, with little or no net change in the number of species. These results show, however, that changes in species density over time cannot explain initial differences among plots in the chronosequence. Thus, chronosequence patterns in species density that appear to be based on plot age may actually reflect intrinsic differences in levels of tree diversity among plots that are predominantly unrelated to age.

Similar conclusions apply to comparisons of tree species richness ≥ 10 cm DBH for four former-pasture sites studied by (Chazdon *et al.* 2005), based on rarefaction analyses. In both 1997 and 2004, species richness was significantly higher in the oldest site (25 years, Cuatro Rios; 66 species/420 stems) compared with the youngest site (12 years, Lindero Sur; 43 species/420 stems; $p < 0.05$), but the two sites of intermediate age did not differ from the others (Fig. 2). Interpreting these trends as a chronosequence suggests that tree species richness increases slowly during succession compared with other forest structural characteristics. Within each plot, species richness (number of trees/420 stems) for trees ≥ 10 cm DBH was also compared between 1997 and 2004. Tree species richness did not change significantly within any of these plots over the 7-year study period, in parallel with observations on species density. Thus, for species richness, plot-level changes did not conform to the overall chronosequence trend.

Species richness remained stable or increased despite substantial turnover rates for stems and species (Fig. 3a). Younger forests (less than 15 years since abandonment) are certainly more dynamic in overall stem density and population sizes than older sites (Chazdon *et al.* 2005), but this dynamism at the level of stems and species does not necessarily translate into significant changes in species richness. For the former pasture sites, rates of stem gain were highest (31.6%) in the youngest site and decreased with forest age, whereas rates of stem loss remained relatively constant (13.5–16.5%) across sites (Fig. 3a). Rates of species turnover were lower than rates of stem turnover in all the four former-pasture plots (Fig. 3a). In the two younger plots (Lindero Sur and Tirimbina), rates of species gain exceeded rates of species loss, whereas the reverse was found for the two older plots (Lindero El Peje and Cuatro Rios; Fig. 3a).

A slightly different pattern of stem and species turnover was observed in the three 1 ha light-use sites studied by Finegan from 1989 to 2003, a 14-year period (Fig. 3b). Over this extended time period, rates of stem gain were higher than rates of stem loss in two plots (initially 15 and 25 years old). Rates of species gain exceeded species loss in all the three plots; in plot 1 (initially 25 years old), species gains were substantial despite no net change in stem density. In plot 2 (initially 25 years old), rates of stem gain exceeded rates of species gain, because most species of new recruits were already present in the plot. Higher rates of stem loss than species loss in all the three plots indicate cohort decline in species that were initially abundant. Half of the total species lost from the three sites belonged to pioneer genera (*Cecropia*, *Croton*, *Trema* and *Vismia*) and the family Melastomataceae. Plot differences in stem and species turnover rates may also reflect variation in soil fertility and proximity to seed sources. We lack a clear

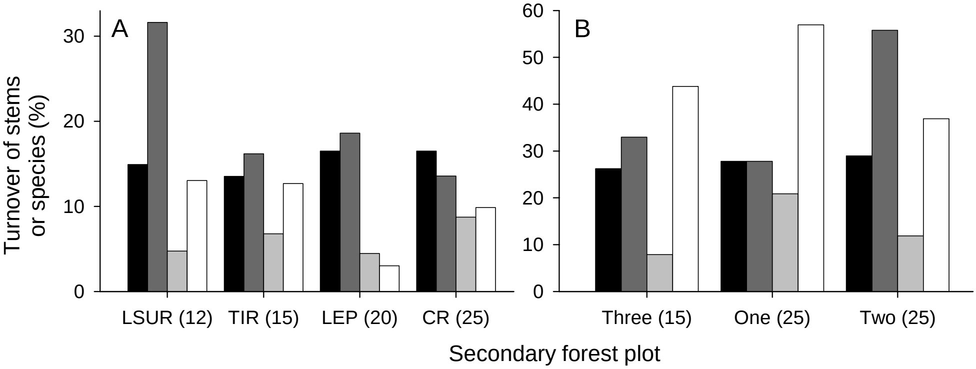

FIGURE 3. Percentage of stems ≥ 10 cm DBH lost through mortality (black bars) and gained through recruitment (dark grey bars) and percentage of species lost (light grey bars) and gained (white bars) in secondary forest plots in northeastern Costa Rica from (A) 1997 to 2004 in four plots on abandoned pasture; LSUR, Lindero Sur; TIR, Tirimbina; LEP, Lindero El Peje; CR, Cuatro Rios and (B) 1989 to 2003 in three plots abandoned after light land use. Initial plot age since abandonment is shown in parentheses.

TABLE 1. Pair-wise similarity for trees >10 cm DBH in four second-growth forest plots in Costa Rica in 2004, based on the Chao Jaccard Abundance Estimator ± 95% confidence limits (Chao *et al.* 2005). Plot age since abandonment is given in parentheses. Values along the diagonal are similarities within each site between 1997 and 2004. Tree species composition differed significantly across plots of different ages, but not over time within plots.

	Lindero Sur (12)	Tirimbina (15)	Lindero El Peje (20)	Cuatro Rios (25)
Lindero Sur	1.0 ± 0.0	0.48 ± 0.14	0.80 ± 0.12	0.61 ± 0.12
Tirimbina		1.0 ± 0.0	0.48 ± 0.16	0.44 ± 0.15
Lindero El Peje			1.0 ± 0.0	0.75 ± 0.09
Cuatro Rios				1.0 ± 0.0

understanding of how these factors interact with stand demography to bring about changes in species richness over time in tropical secondary forests. We do know, however, that these changes are slow and may take centuries (Finegan 1996; Chazdon 2003).

For trees ≥ 10 cm DBH, the four former-pasture plots differed significantly in species composition in 2004 ($p < 0.05$; Table 1). Similarity values (Chao Jaccard Abundance Estimator; Chao *et al.* 2005) ranged from 0.44 to 0.80. The 15-year-old plot (Tirimbina), which has the longest history of disturbance and isolation, was the most divergent. The same pairwise similarities were also computed within each site between 1997 and 2004 to determine whether species composition changed significantly over time (Table 2). None of the four sites showed a significant change in species composition over time, however, suggesting that age differences are not the major factor contributing to differences in species composition. Each plot appears to follow an idiosyncratic pathway of species accumulation, likely driven by edaphic factors, land-use history and landscape matrix.

CASE STUDY: CHIAPAS, MEXICO

The second case study took place in the Marquéz de Comillas region, Chiapas, Mexico, where Breugel, Martínez-Ramos, Bongers and collaborators have monitored secondary forest succession in ten 500 m^2 secondary forest plots since 2000. The climate of this region is cooler, drier and more seasonal than that of the Sarapiquí region. The average annual rainfall is ca 3000 mm, with less than 100 mm per month falling in the dry season (February–April). The mean annual temperature is ca 248C. The original vegetation consists mainly of lowland tropical rainforests and semi-deciduous forests (Ibarra-Manríquez & Martínez-Ramos 2002). Today, the region is a mosaic of small-

TABLE 2. Pair-wise similarity for trees ≥ 1 cm DBH in 10 second-growth forest plots, based on the Chao Jaccard Abundance Estimator ± 95% confidence limits (Chao *et al.* 2005). Values along the diagonal are similarities within each site between the first and last census (3-yr interval). Number in parentheses gives plot age since abandonment. Tree species composition was significantly different over time in three plots only (indicated in bold).

	R(1)	F(2)	H(2)	P(2)	R(2)	G(3)	F(4)	S(8)	H(10)	H(17)
R1	0.98 ± 0.03	0.93 ± 0.16	0.95 ± 0.25	0.92 ± 0.10	0.81 ± 0.13	0.87 ± 0.16	0.87 ± 0.14	0.69 ± 0.22	0.38 ± 0.28	0.29 ± 0.27
F2		**0.75 ± 0.17**	0.92 ± 0.22	0.49 ± 0.29	0.69 ± 0.17	0.34 ± 0.22	0.62 ± 0.22	0.74 ± 0.17	0.83 ± 0.23	0.04 ± 0.08
H2			0.83 ± 0.17	0.99 ± 0.15	0.96 ± 0.20	0.41 ± 0.26	0.98 ± 0.16	0.83 ± 0.17	0.85 ± 0.22	0.02 ± 0.08
P2				**0.85 ± 0.13**	0.94 ± 0.07	1.0 ± 0.17	0.92 ± 0.10	0.40 ± 0.21	0.90 ± 0.22	0.26 ± 0.19
R2					**0.78 ± 0.10**	0.86 ± 0.14	0.85 ± 0.11	0.67 ± 0.14	0.55 ± 0.22	0.21 ± 0.18
G3						1.0 ± 0.04	0.51 ± 0.24	0.41 ± 0.23	0.75 ± 0.28	0.33 ± 0.28
F4							1.0 ± 0.03	0.7 ± 0.21	0.87 ± 0.17	0.84 ± 0.17
S8								1.0 ± 0.05	0.87 ± 0.12	0.22 ± 0.19
H10									1.0 ± 0.03	0.28 ± 0.24
H17										1.0 ± 0.04

scale agriculture, pastures, mostly young (< 10 years) secondary forests and remnants of old-growth forests. In the area, three morphological units are found, of which the Low Hills topographic unit with sandy and limestone based soils with low pH (< 5.5; Siebe *et al.* 1996) is most common. Geomorphology and former land use, more specifically abandoned pastures versus abandoned cornfields, have been shown to affect successional patterns in this region (Chapter 2; Méndez-Bahena 1999). Sites were selected in Low Hills on former cornfields (milpas), with fallows ranging from 1.5 to 17 years post-abandonment and mostly with only one cycle of cultivation. In these plots, growth, mortality and recruitment of trees ≥ 1 cm DBH are being monitored annually; here we present data for the first 3 years examined. The vegetation in these sites is expected to exhibit faster dynamics than the larger size classes and older sites described in the case study of northeastern Costa Rica.

Both among-plot comparisons and within-plot dynamics showed high variability for all the three parameters (basal area, stem density and species density; Fig. 4). In contrast to the Sarapiquí study, fallow age was not a significant predictor of initial basal area when the plots were analyzed as a chronosequence (Fig. 4a). Initial basal area varied widely among plots with one of the highest values for the 1-year-old plot (due to extremely high density and fast growth of early recruits). Basal area increased in all but one plot by an average of 126% during the first 3 years of the study. The only exception to this trend was in one of the intermediate-aged plots (8 years at the beginning of the study), where, as observed in the youngest plot in the Sarapiquí study, massive mortality of the pioneer species, *Ochroma pyramidale*, drove an overall decline in basal area (Chapter 4). In every other case, there was an increase in basal area ranging from 33 to 304% in the 3-year period, resulting in several plots with basal area over 25 m². These are surprisingly high values, higher than the average basal area in neighboring old-growth forest plots on comparable sites (M. Martínez-Ramos *et al.* 2006, unpublished work). We have to realize however that this does not directly translate into a relatively high biomass, mainly owing to lower plant stature and low average specific wood density of the dominant species in our plots (Balvanera *et al.* 2005; M. van Breugel 2006, unpublished data).

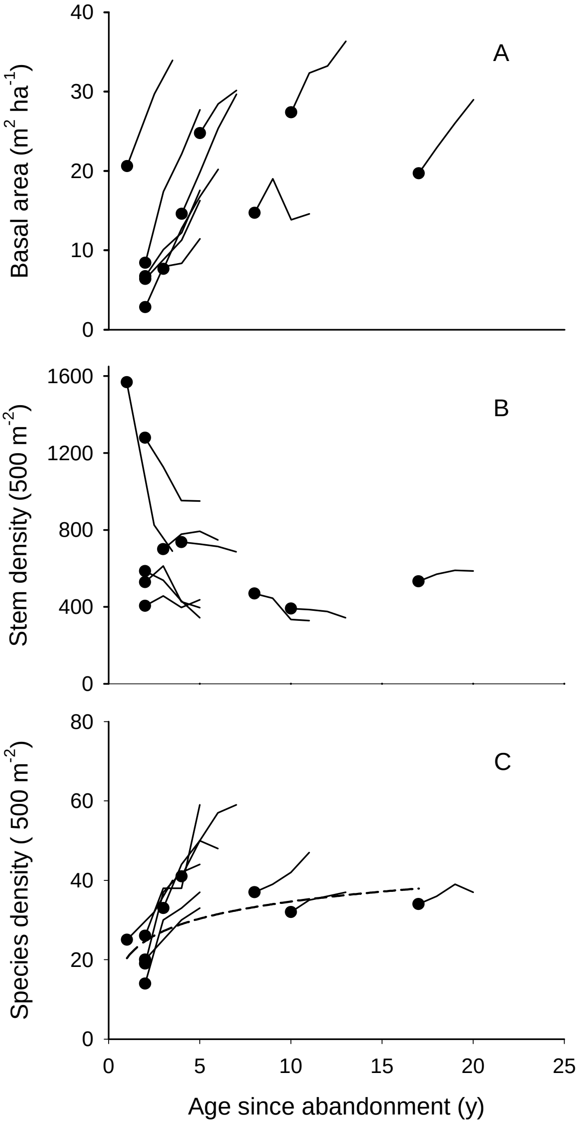

FIGURE 4. Chronosequence data for trees ≥ 1 cm DBH in 10 secondary forest monitoring plots in Chiapas, Mexico (black dots) and successional trajectories within the same set of plots. A) Basal area (m^2 ha^{-1}); B) stem density (number of stems 500 m^{-2}) and C) species density (number of species 500 m^{-2}). Dash line is the regression line on the black dots ($y = 6.2 \, LN(x) + 20.4$, $R^2 = 0.40$, $P = 0.048$).

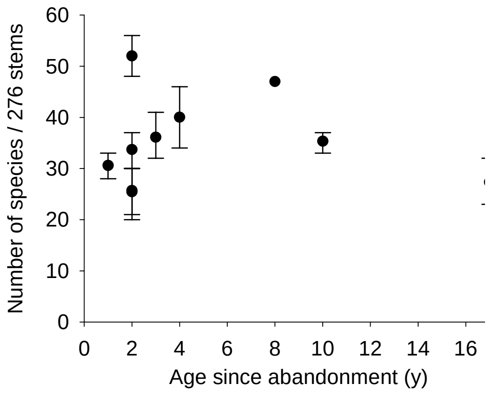

FIGURE 5. Species richness in secondary forest plots in Chiapas, Mexico in year 3 of the study. Species richness was rarefied to the lowest stem density among plots and was not related to plot age for any of the 3

Net changes in basal area sometimes obscured faster dynamics in the constituent processes: growth, mortality and recruitment. Breugel *et al.* (2006, Chapter 4) analyzed rates of change of these parameters as a function of age, and all three declined significantly with stand age. However, diameter increment growth rates exceeded mortality and recruitment in all stands although the margin was widest in the youngest sites. In these sites, large losses in basal area from mortality were offset by larger gains from growth and recruitment.

Initial stem density was not related to stand age, and stem density within plots followed unpredictable trajectories (Fig. 4b). Although density generally decreased within plots over the 3 years, rates of change varied widely among plots. The most dramatic decline in density was shown in the two plots with densities over 1000 trees per plot, suggesting strong density-dependent effects on mortality. Rates of change in the other plots were not related to initial density. An important factor contributing to variation in initial density and the subsequent changes might be variation in species composition, at least in young secondary forests. Variation in stem density of a few very dominant species such as *Trema micrantha, Trichospermum mexicanum* and *Cecropia peltata* reflects to large extent initial differences in stem density inmost plots. Variation in rates of change in stem density is therefore largely explained by the interspecific differences in demographic rates of a few dominant species (Chapters 3, 4).

Species density showed a nonlinear chronosequence trend across the initial age range ($R^2 = 0.40$; Fig. 4c). However, this trend is rather dependent on which census is used, as there was no significant relationship between age and density for the last census. In most individual plots, species density increased dramatically, in most cases much faster than suggested by the chronosequence trend. Especially in the youngest plots (up to 3 years old), changes were very rapid and several plots had a higher species density than in the older plots at the end of the 3-year interval. These trends also applied to species richness. When stands were compared after rarefaction to account for effects of stem density, species richness did not differ significantly with age for any of the censuses (Fig. 5). Within plots, however, species richness (number of trees/276 stems) increased over the 3-year period on average by 81.6% (± 18.4 SE) and this increase was significant in all but the oldest site.

The fact that species richness increases significantly within these stands, but not within the Costa Rican abandoned pasture sites, may reflect the smaller diameter cut-off as well as the younger age of the sites. The probability that a recruit belongs to a new species may be higher in early succession simply because species density is lower, i.e. with succession an increasing proportion of the local species pool would already have arrived at the site. In the first years of succession, fast growing pioneer species still constitute a considerable fraction of new recruits, apparently because high mortality in the early phases of secondary forests opens up new recruitment possibilities (Chapter 3). The lower diameter limit implies that newly established individuals will be included in the tree community more rapidly.

Rates of stem turnover (greater than 1 cm DBH) were very high, with values of stem gains from 13 to 90% and stem losses between 15 and 93% (Fig. 6). Stem loss was negatively related to age ($R^2 = 0.52$), but there was no relationship between stem gain and age (Fig. 6a). Species turnover was very high as well, with species gains up to 75% and species losses up to 50%. Both species loss and gain ($R^2 = 0.48$ and 0.65, respectively; Fig. 6b) were negatively related to age. In contrast to the results presented for an 8-year period for larger stems in the Sarapiquí plots (Fig. 3a), dynamics at the level of stems did translate in species dynamics, as species loss was significantly related to stem loss and species gain to stem gain ($R^2 = 0.58$ and 0.65, respectively).

The rate of successional dynamics, expressed in species and stem turnover rates, thus decreases with plot age in this series of plots. Although dynamics in the older Mexican plots do not seem to be very different from the Sarapiquí light-use plots (Fig. 3b), a robust comparison is difficult owing to the differences in diameter limits, plot size and census period.

Similarity in species composition (Chao Jaccard Abundance Estimator; Chao *et al.* 2005) between pairs of plots ranged from almost total dissimilarity (0.02) to complete similarity (1.00; Table 2). Across plots, only seven species dominated the sites, of which T. *mexicanum*, T. *micrantha* and C. *peltata* were by far the most abundant. Since only a few species were dominant in these plots, variation in their abundance strongly influenced overall similarity between plots. For example, the plots F2 and H2, both dominated by T. *mexicanum*, were highly similar. H17 on the other hand was dominated by Vochysia guatemalensis, a species that was not found in the first two plots and consequently similarity was very low. We also compared pairwise similarities between initial species composition and species composition after 3 years in each plot (Table 2). Only in the three 2-year-old plots did species composition change significantly over the 3-year period. As was observed in the Costa Rican case study, among-plot differences in species composition are not reflected in compositional changes over time within plots; therefore, they seem to be the result of other factors, such as the interaction between site factors (soil, land-use history) and factors related to species colonization (*e.g.* distance to seed sources, regional species pool), rather than being strongly determined by time since agricultural abandonment.

SYNTHESIS

A major finding in our vegetation dynamics studies in successional tropical forests is that trends which appear to reflect age differences across sites (based on statistical analyses of chronosequence data) may actually have relatively little to do with age since abandonment. Studies of vegetation dynamics are a crucial counterpart to chronosequence studies and provide an essential 'reality check' in our understanding of rates of vegetation change and the factors that influence them at local, landscape and regional scales. The potential for misinterpretation of successional trends may be minimized to some extent if chronosequence studies include replicate plots of similar age.

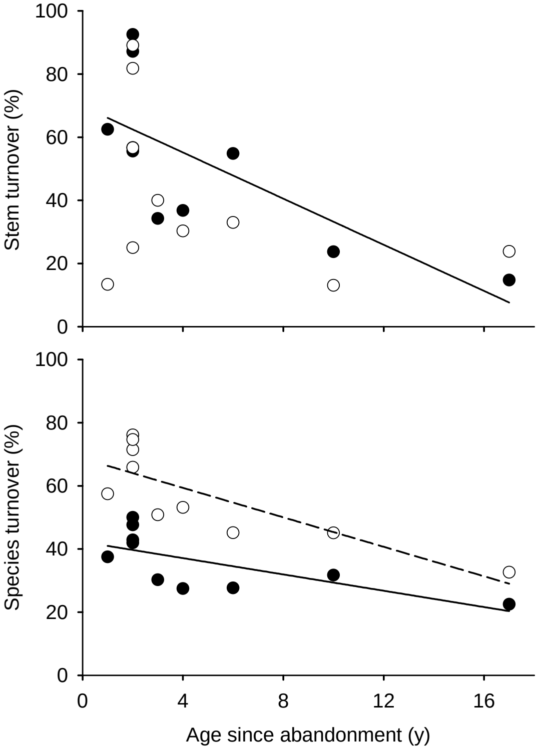

FIGURE 6. Turnover of stems and species in secondary forest plots in Chiapas, Mexico. A) Percent of stems ≥1 cm DBH lost through mortality and gained through recruitment. Stem gain was not significantly related to age, but stem loss decreased significantly with plot age as shown by regression equation; B) percent of species lost and gained; both species loss and gain decreased significantly as a function of plot age.

At least during the first 30 years of secondary regrowth, our case studies show that chronosequence data do not correctly reflect true species dynamics. Clearly, factors other than age since abandonment have influence on species density, species richness and rates of recruitment of new species. For example, none of our studies take landscape context explicitly into account as a source of variation in stand dynamic processes. Availability and proximity of seed sources can vary largely across plots.

Young stands show substantial variation in initial stem density, basal area and species composition, reflecting local patterns of species colonization and effects of remnant vegetation. In the Chiapas sites, species richness was not related to age since abandonment, but showed increases over 3 years within sites. In contrast, species richness increased with age since abandonment across the Costa Rican sites, but remained unchanged over 7 years within four former pasture sites. Our limited data suggest that initial compositional differences often lead to divergence in species composition, at least over time-scales of 5–15 years. Successional forests of different ages within a particular landscape generally differ more in tree species composition than a single site followed over time through the same age range (Tables 1 and 2). This observation reveals the need for more detailed and longer term dynamics studies.

In contrast to species composition, basal area changes are relatively easy to predict from the chronosequence studies. Stand-level basal area and biomass accumulation in secondary forests are more affected by diameter and height growth rates of standing trees than by net changes in density due to tree recruitment and mortality. Stem density, species density and species turnover are far less predictable from a static snapshot of sites of different ages and are more rapid in younger sites and in smaller size classes. Across plots of different ages, stem turnover rates were poor predictors of species turnover rates, especially when evaluated over longer time-intervals (Figsures 2 and 4). Large changes in population size for a small number of species can strongly influence rates of stem turnover at the plot level, but these dynamics will have little or no impact on species turnover rates. Thus, the factors that drive species-level demographic changes appear to be relatively independent of those affecting species loss, gain and accumulation.

The case studies in Costa Rica (sites older than 10 years; all stems ≥ 10 cm DBH) and Chiapas (most sites less than 10 years old; all stems ≥ 1 cm DBH) highlight important effects of plot age and stem size class on rates of vegetation change. Tree communities in the Costa Rican former-pasture plots appear to have stabilized over 7 years in terms of species density, species richness and species composition, whereas the younger and smaller communities in Chiapas are showing significant changes in these attributes over only 3 years. The focus on stems greater than 10 cm DBH ignores much of the dynamic behavior of small stems, including changes in abundance, species richness and growth forms (Capers *et al.* 2005). Particularly in older successional stands that have a closed canopy, new species of trees arriving as seedlings will take many years (perhaps up to several decades) to become evident in tree size classes (above 5 cm

DBH). Long-term vegetation dynamics studies that encompass both small and large size classes will capture these colonization and recruitment events more effectively and will also be more directly comparable across regions.

Our work also highlights gaps in our current understanding of rates of change during forest succession in tropical regions. Although tree dynamics of young and intermediate aged stands are now being characterized, no studies have examined vegetation dynamics in old secondary forests (more than 45 years since abandonment) within a chronosequence context. Moreover, the effects of the surrounding landscape on dynamic processes within individual plots are poorly understood. In particular, the regional species pool and the extent of seed dispersal from neighboring forest fragments are likely to be strong determinants of species accumulation rates and relative abundance patterns within successional forests. Although we know that mature forests have higher species density and species richness of trees compared with second-growth forests in northeastern Costa Rica and Chiapas, Mexico (Guariguata *et al.* 1997; Ibarra-Manríquez & Martínez-Ramos 2002), we have little basis for predicting rates of change in tree community composition during succession, particularly during later phases (Chazdon in press). Tropical forest succession is an idiosyncratic process, driven by many factors; the more we understand about how it operates within sites, the more accurately we will be able to generalize about how this complex process operates at large scales.

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Chapter 6

NEIGHBORHOOD EFFECTS ON SAPLING GROWTH AND SURVIVAL OF TWO PIONEER TREE SPECIES IN SECONDARY TROPICAL MOIST FOREST

Michiel van Breugel, Marco Dekker & Paulo van Breugel

ABSTRACT

The effect of neighbourhood competition on growth and mortality of *Cecropia peltata* and *Trichospermum mexicanum* saplings was examined in two adjacent 1-2 year old secondary tropical humid forests in southern Mexico. The hypothesis was tested whether variation in asymmetric neighbourhood competition accounts for an important part of the within-site variation in diameter growth, height growth, changes in height-diameter ratio (slenderness) and survival.

We selected saplings of 3.5 – 5.5 m high and levels of neighbourhood competition were approximated by the neighbourhood basal area in an area of 25 m^2 around each target tree. We used regression to estimate the neighbourhood basal area of the neighbours larger (NBA_L) and of the neighbours smaller than the target tree (NBA_S) on the response variables.

NBA_L varied between 0 and 30 cm^2 m^2 and accounted for an important part of the variation in all growth variables. Diameter and height growth were strongly negatively related to NBA_L. Results indicate that competition initially reduces diameter growth stronger than height growth, until competition becomes too strong. Mortality of *Cecropia* was very high, and of *Trichospermum* close to zero. Only a small proportion of variation in survival could be accounted for by variation in neighbourhood basal area, suggesting that other factors are more important. The additional effect of NBA_S, on growth and survival was very weak or non-significant.

A simple competition model that only includes size of the larger neighbours could account for much of the observed variation in growth and to a lesser extent for the variation in survival. These results support the prediction that in these young secondary forests asymmetric competition for light predominates and is one of the main mechanisms that govern secondary forest dynamics.

INTRODUCTION

Competition for resources between plants is since long considered to be one of the main steering mechanisms in successional vegetation development and species replacement (Connell & Slatyer 1977; Peet & Christensen 1987; Bazzaz 1990; Begon *et al.* 2006). It starts early in succession when resource spaces of neighboring plants start to overlap, and intensifies with time as plants grow bigger and preempt an increasing proportion of the available resources (Bazzaz 1996; Keddy 2001; Grime 2002). It has been argued that along this successional gradient of increasing plant mass, the importance of aboveground competition for light augments relative to the importance of belowground competition for water and nutrients (Huston & Smith 1987; Belcher *et al.* 1995). In successional communities with vigorously accumulating plant mass, like secondary forests in the humid Tropics (Swaine & Hall 1983; Uhl 1987; Chapters 4, 5), growth of individual plants is thus predicted to become predominantly limited by aboveground competition for light soon after succession started.

In humid tropical (Uhl 1987; Saldarriaga & Luxmoore 1991) and in temperate (Aber 1979) secondary forests, leaf area index (LAI) can reach maximum values within a few (<5) years. A two-year old humid tropical secondary forest stand in Bolivian had a LAI twice that of a 0.5-year old stand (respectively 1.7 and 3.5), which was related to a seven-fold reduction in available light at the forest floor (34% and 5% respectively) (Selaya 2007), indicating very intense light competition at very early age. Yet a dense canopy does not necessarily provide evidence that competition is strictly above-ground as it can coincide with below-ground root competition. In an extensive review of manipulative studies on root competition in forests and woodlands, Coomes & Grubb (2000) found that belowground competition has an important impact on regeneration in many forest communities, especially on soils deficient in nutrient or water supply (see also *e.g.* Denslow *et al.* 1998; Ostertag 1998; Lewis & Tanner 2000; Barberis & Tanner 2005). In the only comparable study in tropical secondary forest that we are aware of, Gerhardt (1996) reported similar results.

Aboveground competition for light is predominantly size asymmetric, i.e. the larger plant takes a larger than size-proportional share of the contested resource, because of the directional and pre-emptable nature of light (Weiner 1990; Berntson & Wayne 2000). In other words, larger plants shade smaller ones and not the other way around. Belowground competition for water and nutrients on the other hand is taken to be size symmetric. Roots generate depletion zones around their surfaces and thus restrict resource availability for other roots relative to plant size (Noordwijk *et al.* 1996; Casper & Jackson 1997; Schwinning & Weiner 1998). These generalizations have been a widely used tool to make inferences about the relative importance of above vs. belowground competition (Schwinning & Weiner 1998). They also imply that the relative importance of below vs. aboveground competition may have large consequences for dynamics and development of population and communities during succession.

The relative importance of competition for light has been poorly studied in the different phases of secondary forest succession. As intensity and balance between below and aboveground competition might change along a successional gradient of increasing plant mass, findings may depend on the scale of a study, i.e. which part of such a gradient is covered (Belcher *et al.* 1995; Keddy 2001). Patterns could differ on rich and poor soils, with respectively shoot and root competition becoming predominant in the course of time (Wilson 1999). Studies in temperate second-growth forests on dry and nutrient-poor soils do not provide unequivocal results. Competition was found to be largely asymmetric by Thomas & Weiner (1989), and partially symmetric by Peterson & Squiers (1995). There are very few studies that examined the degree of competitive asymmetry for different phases of forest succession. Doležal and co-workers (2004) found that weak competition for belowground resources was predominant during the first decades of boreal forest succession on nutrient-poor soils, when stand density was low, while in later stages aboveground competition for light became important.

Neighborhood competition does not only reduce overall growth rate, but also affects allocation patterns. Competition generally results in relatively small crowns and slender (i.e. high height/diameter ratio) stems, as suppressed trees will favor allocation to stem extension over branch and radial stem growth (King 1990; Bongers & Sterck 1998; Sterck 2005). Yet, tree species respond differently to different light conditions with regard to growth allocation (Kohyama & Hotta 1990; King 1991; King 1994; Sterck 1999; Poorter 2001). Hara *et al.* (1991) for example found that neighborhood competition affected height growth in one species, but not diameter growth, while they found the opposite for another species. Typically, early successional species respond strongly by allocating resources to height growth at the expense of diameter growth (Kohyama & Hotta 1990; Hara *et al.* 1991; King 1996). It is, therefore, important to include different aspects of plant growth when examining the importance of competition.

During the first decades of succession secondary forests are thought to be dominated by short and long-lived pioneer species respectively (*cf.* Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1996). Most of these species appear to regenerate successfully only in the beginning of secondary succession (Chapter 3; Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1996; Peña-Claros 2003; Toledo & Salick 2006). Stand dynamics in the first years may thus be determinative for composition and structure of the canopy over the first decades. Moreover, the presence and dominance of long-lived pioneer species in the next successional phase will depend, to a great extent, on the growth and mortality dynamics very early in succession (Finegan 1996), which in turn are presumably governed, or at least modified, by competition (Bazzaz 1996; Pickett & Cadenasso 2005; see also chapter 4). Yet, only very few studies have been done on the

TABLE 1. Species characteristics of *Cecropia peltata* L. and *Trichospermum mexicanum* (DC.) Baill. DS = dispersion syndrome; F = frequency, percentage occurrence in 76 secondary forest plots in the research region; D = dominance, percentage of the 76 plots in which the species held ≥ 10% of the stand basal area; MLS = maximum life span; MH = maximum height.

	DS	F^3 (%)	D^3 (%)	MLS^4 (y)	MH^5 (m)
Cecropia peltata	Animal[1]	75.0	37.5	35	20 (18)
Trichospermum mexicanum	Wind[2]	61.3	33.8	30	15 (18)

1) Burns & Honkala (1990) and Fleming (1990) ; 2) Guevara et al. (1994); 3) Chapter 1; 4) Based on data and observations from long-term studies, conducted at Los Tuxtlas Tropical rain forest (e.g. Ibarra Manriquez *et al.*, 2001; Popma *et al.*, 1992) and in our own study region (M. Martínez-Ramos *et al*. unpublished data); 5) Pennington & Sarukhán (1998), between parentheses the maximum observed height in our study plots

role of competition in secondary forest succession in the Tropics (but see Uriarte *et al.* 2004a; Palomaki *et al.* 2006), and only one that we know of in the first years of secondary forest succession (Selaya 2007).

In this study we examine growth and mortality of *Cecropia peltata* L., and *Trichospermum mexicanum* (DC.) Baill. (henceforth referred to by genus name), two early successional light demanding species with similar traits and characteristics (Table 1) and geographic distributions from Tropical Central America to the northern part of South America (W3TROPICOS; Burns & Honkala 1990). They are the two most abundant and dominant secondary forest species in the region (Table 1; Chapter 1) and thus important components of the early community dynamics of these secondary forests (Chapters 2, 4). As secondary forests are mostly dominated by a very small group of species (Saldarriaga *et al.* 1988; Finegan 1992, Chapter 1), studying the dynamics of such species is crucial for furthering our understanding of secondary forest succession. Specifically, we will test the hypothesis that variation in asymmetric neighborhood competition for light is the main factor that determines within-site variation in radial stem growth, height growth and survival of these species. This means that we expect that patterns of growth and survival are disproportionally determined by the direct neighbors that are larger than a specific target tree (i.e. competitive asymmetry). Secondly, we will test the hypothesis that with increasing neighborhood competition stem slenderness will increase as a consequence of a stronger reduction of radial stem growth as compared to height extension.

METHODS

SITE AND DATA COLLECTION

Research was conducted in the southern-most part of the Selva Lacanda region, between the Montes Azules Biosphere Reserve and the border with Guatemala, near the village of Loma Bonita (approximately 16º04′ N; 90º45′ W), Chiapas, Mexico. The climate is humid tropical, with an average annual temperature of 24 ºC and a mean annual rainfall of ~3000 mm. From February to April there is a dry period with less than 100 mm per month. Since the early 1970s colonization caused large scale clearance of the original lowland tropical rainforests and semi-deciduous forests outside the Biosphere Reserve. Nowadays the landscape consists of a mosaic of small scale slash-and-burn agriculture, pastures, mostly young (<10 yrs) secondary forests and remnants of old-growth forests (de Jong *et al.* 2000). For a description of the original vegetation in the region see Ibarra-Manríquez & Martínez-Ramos (2002).

Data reported in this study is from two study plots that are part of a larger study on the dynamics of early secondary forests in the region (see Chapters 3-5). Distance between both plots was about 500-m. The original old-growth forest on both study sites was cut and burned, farmed for maize cultivation for one harvest period only and then abandoned. This is the usual practice in this region, as a second harvest normally gives a very poor yield on these soils (information based on personal accounts of land-owners and other villagers). The sites were situated in an area with undulating hills with moderate-steep slopes (15°–30°). This is the most common geo-morphological unit in the region and characterized by sandy Humic Acrisols with low pH (4-5), and low total nitrogen and phosphorous content (Siebe *et al.* 1996).

Respectively 1 and 1.5 year after abandonment, a 10 x 50 m plot was established in each site, with a permanently indicated 2 x 2 m grid. All trees with diameter at 1.3 m above ground (dbh) ≥ 1cm were recorded, tagged and their dbh and height to the highest leaf were measured. Within the 2 x 2 m grid the presence of trees was visually estimated in 1x1 m quadrants. A complete re-census was done 12 -16 months (respectively oldest and youngest plot) after the first census.

SELECTION OF TARGET TREES AND THE DEFINITION OF THEIR NEIGHBORHOOD

In this study we evaluated the effect of neighborhood competition on the performance (growth and survival) of selected target trees. Neighborhood basal area was used as a proxy for the level of neighborhood competition, with the neighborhood of an individual tree defined as the area consisting of its own 1x1 m quadrant and the 24 adjacent 1x1 m quadrants, i.e. a 5x5 m area with the target tree's quadrant in the center. At any given location in the forest, a large tree will have more neighbors that are smaller than itself, as compared to a small tree. Hence target tree size and the relative contribution of its smaller neighbors to total neighborhood basal area are expected to be correlated. To minimize this dependency, we selected target trees within a narrow height range of 1 m. Both Cecropia ad Trichospermum saplings with a height around 4.5 m were most abundant in the stands. In two height classes of 3.5-4.5 m and 4.5-5.5 m, abundance and distribution of trees allowed for the selection of ≥ 40 target trees according to our selection procedure (see below). From now on we will refer to them as height class 1 (HC1), and height class 2 (HC2).

For the growth analysis, trees were randomly selected from our database. Trees that had any kind of visible damage in one of the two censuses were excluded. To have independent observations, i.e. to avoid that a tree was both neighbor and target tree, a selected tree was discarded when it was within the neighborhood of a previously selected tree. This procedure went on until no new trees could be included. This resulted in four different sets of data (2 species x 2 height classes) for which all analyses were performed separately. In all four cases the selected trees were well distributed over the plots, thus including most within-plot variation with regard to stand structure and micro-site conditions. For the survival study, all trees were included. For both the growth and survival analyses the trees from both study plots were lumped for further analyses.

The effect of neighborhood competition on target tree growth was analyzed including the basal area of neighbors larger than the target tree (NBA_L) and basal area of neighbors smaller than the target tree (NBA_S) as separate predictor variables. Note that correlation coefficients between NBA_L and NBA_S varied between $r = 0.03$ and $r = 0.23$ and were not significant in all cases. All species were lumped in our measure of neighborhood basal area, i.e. we tested a model that assumed that all competitors had equivalent effects on the target regardless of their taxonomic identity.

DATA ANALYSIS

We analyzed the influence of neighborhood basal area on target tree growth, using different response variables. 1) Absolute height growth (AHG, m y^{-1}), estimated by multiplying initial height with the annual relative growth rate $[(H_{census\ 2} / H_{census\ 1})^{(365/t)}]$ where t = the study period in days. Plant performance is likely to be correlated to plant size, an effect that should be corrected for (Duncan 1995). Since we selected trees within narrow height classes, we did not correct for initial height. 2) The percentage of potential radial stem (diameter) growth rate (PPDG, %). Potential diameter growth is calculated as a function of size (see below), hence in further analyses, the size effects on plant performance (Duncan 1995) is accounted for. To calculate PPDG, we used the Vanclay function (Vanclay 1994) to model potential diameter growth increment (PDG) for each tree as a function of current size, resulting in equations 1a and b:

$$PDG_{Cecropia} = e^{0.52 + 0.93\ \ln(DBH) - 0.14\ (DBH)} \qquad \textit{Equation 1a}$$

$$PDG_{Trichospermum} = e^{1.08 + 0.77\ln(DBH) - 0.13\,(DBH)} \qquad \textit{Equation 1b}$$

where DBH is the initial diameter. This function is realistic for tree growth in that estimates are always positive, allowing some growth even for very large individuals, in contrast to several other common equations that impose a maximum attainable diameter (Vanclay 1994). Parameters of equations 1a and 1b were estimated by using non-linear quantile regression (Scharf *et al.* 1998; Koenker 2005) to fit the Vanclay function through the upper (99%) quantiles of the data. The approach to estimate potential growth from maximum observed growth has been used before, *e.g.* by Clark & Clark (2001) on a study on ontogenetic growth patterns. Data were from nine 1 to 5 year old secondary forest plots, including the present study plots, with similar soil and land-use history. See Appendix I for more detail on this procedure. Next we calculated the annual relative growth rate (ARGR) for each target tree as $(DBH_{census\ 2}/DBH_{census\ 1})^{(365/t)}$ and used this rate to estimate the annual absolute diameter growth rate (ADG, $cm^2\ y^{-1}$) for each target tree. PPDG was then simply calculated as 100 * ADG / PDG (%). Finally we used the response variables (3) Slenderness, calculated as the ratio between height and diameter at the initial census ($m\ cm^{-1}$) and (4) the relative rate of change of slenderness, calculated as $slenderness_{census\ 2}$ / $slenderness_{census\ 1}$.

To obtain linearity in the regression analyses and to achieve normality of the residuals and homogeneity of variances, we applied a Box-Cox transformation on the response variables AHG and PPDG (Sokal & Rohlf 1995). No transformation was needed for the other two response variables. We then applied a multiple linear regression, using the transformed values of the response variables. The null hypothesis employed is that larger trees affect the performance of the target tree, while smaller tree do not have an additional effect (complete asymmetry). Consequently the statistical model first contained the predictor variable NBA_L, then NBA_S and finally the interaction term. If NBA_S and the interaction term were significant (type I sum of squares), we checked the type III sum of squares to examine if the effect of NBA_S on the response variable was additive, an interaction effect, or both. Non-significant factors were left out and we report statistics of the final models only including the significant factors. Assumptions regarding heteroscedasticity and normality were examined with residual plots and QQ plots, and the tolerance and variance inflation factors were used to examine collinearity between the predictor variables (Quinn & Keough 2002).

When NBA_S had a significant additive effect on the response variable, the hypothesis of absolute asymmetric competition is rejected. In that case we examined to what degree asymmetry in the neighborhood accounted for the maximum amount of growth variation. For that, we calculated the neighborhood interference (W), in which the effect of the larger neighbors is proportional to size, but the effect of smaller neighbors is devaluated by a constant factor A (equation 2).

$$W = \sum DBH_i (1-A) + \sum DBH_k \quad \textit{Equation 2}$$

where DBH_i is the diameter of the ith neighbor with $DBH < DBH_f$, DBH_k the diameter of the kth neighbor with $DBH \geq DBH_f$, DBH_f is the diameter of the target tree, and A is the measure of asymmetry representing the proportion by which the effects of smaller neighbors are discounted (adapter after Thomas & Weiner 1989). We evaluated W at values of A ranging from 0 to 1 in steps of 0.2. So when A = 0, the measure is symmetric, and when A = 1, the measure is completely asymmetric. The same regression techniques as described in the former paragraph were applied.

We used Fisher's method randomization (Mitchell-Olds 1987; Thomas & Weiner 1989; Peterson & Squiers 1995) to determine the significance of the relationship between the response variables and W. In this approach, the null hypothesis is that there is no relationship between the response variable and W. All observed response variables were shuffled 10,000 times randomly across the independent variable (W), determining

TABLE 2. Relative importance of neighbor species that constitute ≥ 5% of average neighborhood basal area in at least one of the four species-size class combinations. Numbers give the average proportion of total neighborhood area across all target trees. Standard errors vary between 0.01 and 0.04.

Target species	*C. peltata*		*T. mexicanum*	
Neighbor taxa	3.5-4.5	4.5-5.5	3.5-4.5	4.5-5.5
LARGER NEIGHBORS				
Trichospermum mexicanum	0.21	0.29	0.32	0.47
Cecropia peltata	0.32	0.23	0.28	0.26
Ochromo pyramidale	0.16	0.23	0.19	0.13
Trema micrantha	0.06	0.04	0.09	0.08
Schizolobium parahyba	0.11	0.03	0.08	0.03
SMALLER NEIGHBORS				
Cecropia peltata	0.53	0.54	0.40	0.48
Trichospermum mexicanum	0.15	0.19	0.30	0.34
Solanum spp.	0.07	0.02	0.08	0.01
Trema micrantha	0.06	0.07	0.03	0.05
Schizolobium parahyba	0.06	0.06	0.02	0.05
Vernonia patens	0.06	0.02	0.03	0.01

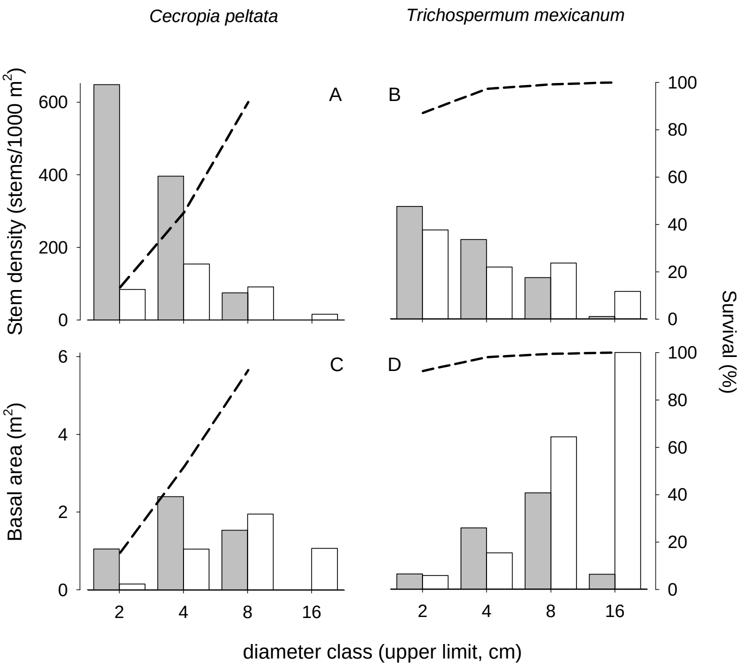

FIGURE 1. Stem density (bars, A-B) and basal area (bars, C-D) distribution over size classes of *Cecropia peltata* and *Trichospermum mexicanum* in two 10x50 m secondary forest plots with initial fallow age of 1-1.5 y. Survival is indicated by the dashed lines, calculated per diameter class as percentage of initial stems (A-B), and initial basal area (C-D). Grey bars: values of the initial census. Open bars: values of the second census.

each time the coefficient of determinations. In this manner an empirical null distribution of coefficients of determination was generated. Percentile confidence intervals (0.99, 0.95, 0.90) were determined by calculating the respective quantiles of the resampling distribution to which the observed coefficient can be compared to determine the level of significance (Venables & Ripley 2002).

To study the influence of neighborhood interference on target tree survival, we calculated W for values of A ranging from 0 to 1 in steps of 0.2 for all trees, as described above. We applied logistic regression of survival (binary response variable) on W (predictor variable). As each individual is treated as both neighbor and target tree, observations are not independent and the significance can not be tested by the typical regression statistics. For that reason, we used the same randomization approach as described before, comparing a random distribution of model R^2s with the observed value. The logistic regression was applied using a generalized linear model with binomial distribution and a logit link function, and report Nagelkerke's R^2 values as an approximation for explained variances of the models (Nagelkerke 1991).

RESULTS

POPULATION STRUCTURE AND DYNAMICS

Dynamics of *Cecropia* and *Trichospermum* differed considerably in this early phase of secondary forest succession. *Cecropia* had a much higher initial stem number (1119) than *Trichospermum* (646), and stems were more concentrated in the smaller size classes compared with the more even diameter frequency distribution of *Trichospermum* (Fig. 1A-B). As a consequence of the latter, total basal area (respectively 5.0 m^2 and 4.8 m^2) and the distribution of basal area over the two size classes did not differ much between the species (Fig. 1C-D). Relative basal area increment of the surviving *Cecropia* trees was 45%. Mortality was very high (69% of stems) and strongly related to size. As a result, total basal area decreased with 15% and the diameter frequency distributions changed drastically (Fig. 1A, C). Mortality of *Trichospermum* was only 5%, and low in all size class (Fig. 1B, D). In this species not mortality but growth was determinative in population dynamics. Relative basal area increment of the surviving trees was 138%, resulting in an overall basal area increment of 134%. Absolute and relative growth was highest in the biggest size classes, resulting in a strong shift of basal area to the higher size classes.

NEIGHBOR SPECIES

Initial across-plot species richness amounted to 44 species, with decreasing species number with increasing size, and increased to 58 species after one year. *Cecropia* and *Trichospermum* were dominant in all size classes but the last, both in terms of stem density (overall 47% and 27% respectively) and basal area (overall 34% and 33% respectively, Fig. 2). The other species in the largest diameter class (DBH ≥ 16 cm) were *Trichospermum mexicanum*, *Trema micrantha* and *Ochroma pyramidale* at the initial census, joined by *Cecropia peltata* and *Schizolobium parahyba* at the second census. The relative importance of *Cecropia* decreased in the two first size classes because of its high mortality, while the relative importance of *Trichospermum* increased in all classes.

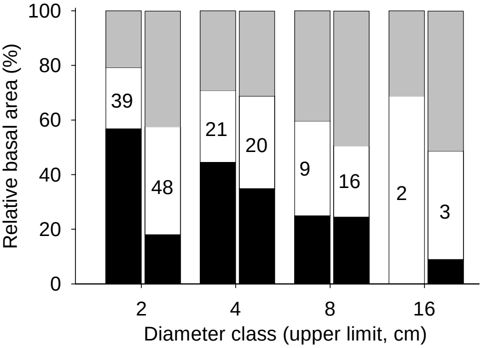

FIGURE 2. Relative basal area of *Cecropia peltata* (black), *Trichospermum mexicanum* (grey) and other species (white). Numbers in the white bars indicate number of species. Left bars: initial census, right bars: second census. Lumped data from two 10x50 m secondary forest plots with fallow age of 1-1.5 y. Patterns of relative density were very similar for both species and both censuses.

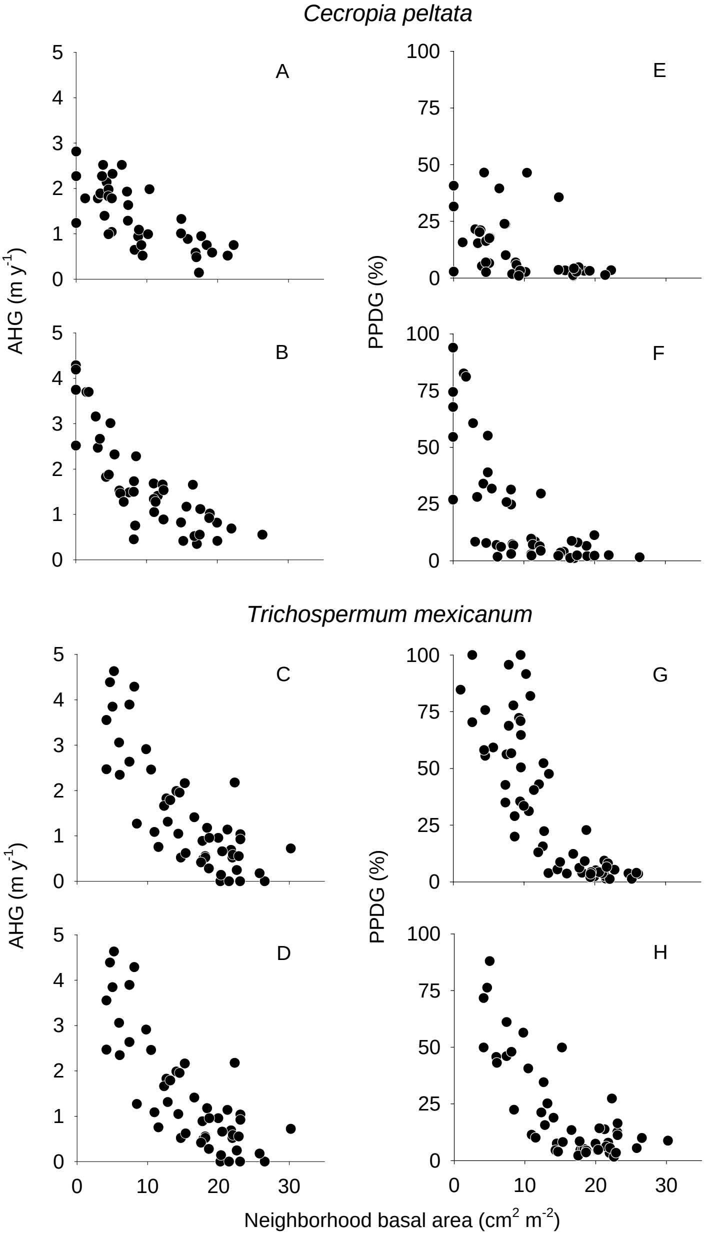

FIGURE 3. The relationship between plant performance and the basal area of larger neighbors. AHG is absolute height growth rate (m y^{-1}). PPDG is percentage of potential diameter growth rate (%). Height class: 3.5 – 4.5 m (A, C, E, G); 4.5 – 5.5 m (B, D, F, H). Regression statistics in Table 1.

The neighborhoods of our target trees for the growth analysis were dominated by very few species. *Cecropia* and *Trichospermum* were by far most abundant, both among the smaller and larger neighbors. *Ochroma pyramidale* was the only other species constituting on average more than 10% of basal area of the larger neighbors, and only two more species constituted on average ≥ 5% (Table 2). The basal area of the smaller neighbors was also dominated by very few species, despite the high species richness in the plot among the smaller trees in the two plots (Fig. 2). Only six species constituted on average ≥ 5% of (Table 2). In both height classes these species together represented around 90% of total neighborhood basal area of both target species.

NEIGHBORHOOD EFFECTS ON GROWTH

Height growth was highly variable as AHGs ranged from 0.14 to 4.30 m y^{-1} in *Cecropia* and 0.00 to 4.60 m y^{-1} in *Trichospermum* (Fig. 3A-D). Annual diameter growth rate ranged from 0.03 to 1.63 cm y^{-1} and 0.03 to 3.70 cm y^{-1} (*Cecropia*, height class 1 (HC1) and height class 2 (HC2) respectively) and from 0.04 to 5.33 cm y^{-1} and 0.06 to 5.94 cm y^{-1} (*Trichospermum*, HC1 and HC2 respectively). This came down to a reduction between 0 and 100% of potential growth in both species (Fig. 3E-H).

The contribution of smaller trees to total neighborhood basal area was highly variable and not correlated to neighborhood basal area of the larger neighbors. The contribution of NBA_S to total neighborhood basal area of *Cecropia* was 40.7% ± 25.4 SD (height class 1) and 50.1% ± 25.4 SD (height class 2), about twice the contribution of smaller trees to the neighborhood basal area of *Trichospermum* (15.7% ± 14.5 SD and 25.2% ± 14.3 SD for height classes 1 and 2 respectively).

Despite the high abundance of smaller neighbors, most of the variation in growth was accounted for by the basal area of the larger neighbors (NBA_L), that had a strong and highly significant negative effect on height growth of both *Cecropia* and *Trichospermum* in both size classes (Fig. 3A-D, Table 3). The basal area of smaller neighbors (NBA_S) on the

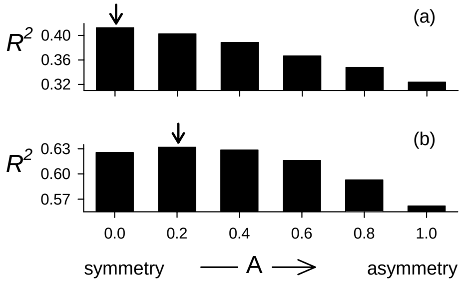

FIGURE 4. Values of the R^2 for the relationships between (i) the PPDG of the target trees and their neighborhood basal area for different levels of competitive asymmetry. A is a measure of asymmetry, representing the proportion by which the effects of the smaller neighbors are discounted. Arrows indicate the model giving the highest R^2 value. Significance levels of all R^2 are < 0.001 and based on randomization tests (see text). (a) Height class 3.5 - 4.5 m; (b) Height class 4.5 – 5.5 m, in both cases species of target tree is *Cecropia peltata*.

TABLE 3. Regression statistics of growth variables (response) *vs.* neighborhood basal area (regressor). AHG = absolute height growth; PPDG = percentage of potential absolute diameter growth; Slenderness = height–diameter ratio; RRC Slenderness = change in slenderness (slenderness in census 2 divided by slenderness in census 1). HC is height class: 1 = 3.5 – 4.5 m; 2 = 4.5 – 5.5 m. NBA$_L$: basal area of larger neighbors, NBA$_S$: basal area of smaller neighbors, NBA$_{LxS}$: interaction term. The table presents the sign of the regression coefficients (i.e. a negative or positive relationship), the partial coefficients of determination (partial R^2) and the significance level of the regressor variables. Coefficients themselves are not presented.

	AHG	PPDG		Slenderness		RRC slenderness	
HC	NBA$_L$	NBA$_L$	NBA$_S$	NBA$_L$	NBA$_{LxS}$	NBA$_L$	NBA$_S$
Cecropia peltata							
1	- 0.58 ***	- 0.32 ***	- 0.10 **	+ 0.70 ***	*ns*	- 0.46 ***	*ns*
2	- 0.70 ***	- 0.56 ***	- 0.07 **	+ 0.73 ***	*ns*	- 0.16 **	*ns*
Trichospermum mexicanum							
1	- 0.79 ***	- 0.80 ***	*ns*	+ 0.68 ***	- 0.14 **	*ns*	+ 0.20 **
2	- 0.65 ***	- 0.59 ***	*ns*	+ 0.66 ***	- 0.05 **	*ns*	*ns*

other hand had no significant additive effect on height growth (Table 3), thus suggesting that height growth is mainly limited by asymmetric competition for light. Diameter growth was also strongly negatively related to NBA$_L$, although a smaller proportion of total variance was explained (Fig. 3E-H, Table 3). NBA$_S$ did not have a significant additional effect on diameter growth of *Trichospermum*, but it did on diameter growth of *Cecropia* (Table 3).

As NBA$_S$ accounted for a part of the variation in diameter growth of *Cecropia*, the hypothesis of complete asymmetry of competition was rejected. The effect of neighborhood interference (W) on PPDG was significant for every value of A that we tested (Fig. 4). The values of A giving the best fit was 0.0 and 0.2 in both size classes, indicating a symmetric competition effect. However, differences were very small, with the increase of the R^2 value over a completely asymmetric model being 0.034 and 0.057 in HC1 and HC2 respectively.

Slenderness at the initial census was linearly and positively related to NBA$_L$ in all cases (Fig. 5, Table 3), indicating that during the earliest phase of stand development higher asymmetric neighborhood competition suppressed radial stem growth more than height growth. Slenderness of *Cecropia* was related to NBA$_L$ only. In *Trichospermum*, smaller trees (NBA$_S$) did not have a significant additive effect, but the interaction term (NBA$_{LxS}$) was significant and opposite to the effect of NBA$_L$ (Table 1). Rather than a

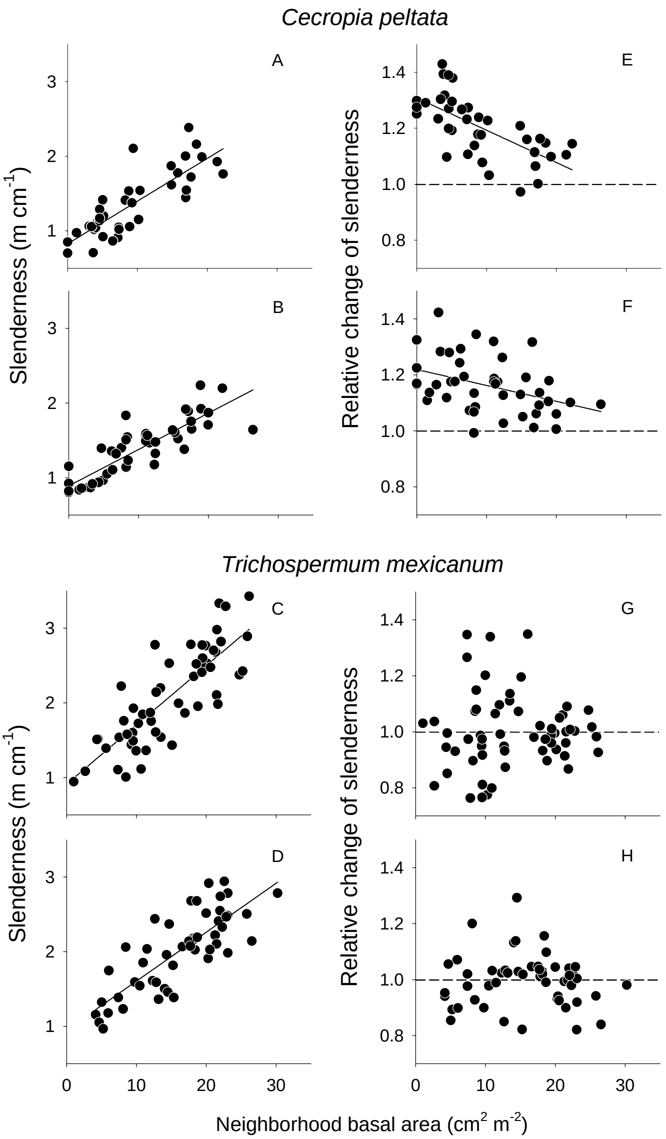

FIGURE 5. The effect of neighborhood competition on stem slenderness. Neighborhood is expressed as the neighborhood area of the larger neighbors. Slenderness is calculated as the ratio between height (m) and diameter (cm). Both variables are from first census data. The relative change of slenderness is calculated as the slenderness of the second census divided by the slenderness of the first census. Above the dashed lines slenderness increased, below this line it decreased. Target tree species: *Cecropia peltata* (A, B, E, F), *Trichospermum mexicanum* (C, D, G, H). Height class: 3.5 – 4.5 m (A, C, E, G); 4.5 – 5.5 m (B, D, F, H). For regression statistics see Table 1.

competitive effect, this likely reflects a co-variation between the past growth of the target tree and its smaller neighbors. All individuals after all, are likely to have been affected by the larger neighbors in a similar fashion.

During the study period, slenderness of *Trichospermum* was found to increase in about 50% of the target trees, and decrease in the other 50%, but without any relationship with neighborhood basal area (Fig. 5G-H). In *Cecropia* trees slenderness increased in nearly all cases. Opposite to the patterns of Figures 5A-B though, the rate of increase was negatively related to NBA_L (Fig. 5E-F, Table 3). That means that the trees that developed highest height-diameter ratio during the first ~1 y of stand development had the slowest increase in this ratio in the following year. This seems to imply a process in which increasing neighborhood competition during the initial phases of vegetation development initially suppresses secondary radial growth stronger than primary height growth (Fig. 5A-D). However, when competition becomes even stronger, height growth becomes increasingly suppressed as well, effectively resulting in a rapprochement between diameter and height growth rates.

In height class 1, the neighborhood basal area of smaller trees had a significant positive effect on RRC of slenderness of *Cecropia* and *Trichospermum*, while the interaction terms were not significant (Table 1). A faster increase in slenderness was thus related to more undergrowth, on first sight in line with the expected positive relationship between competition intensity and slenderness. This effect, however, was opposite to the effect of the larger neighbors in case of *Cecropia*. Hence we did not apply the approach of Thomas & Weiner (1989) for the assessment of the degree of competition asymmetry, as this approach assumes a similar competitive effect (same sign) of both NBA_L and NBA_S when summing them in the of neighborhood interference W. Higher slenderness of the target tree might be the result of more intensive competition from the smaller neighbors but the contrasting effects of larger and smaller neighbors suggest an potential alternatively explanation. There was no significant correlation between NBA_L and NBA_S, the latter, however,

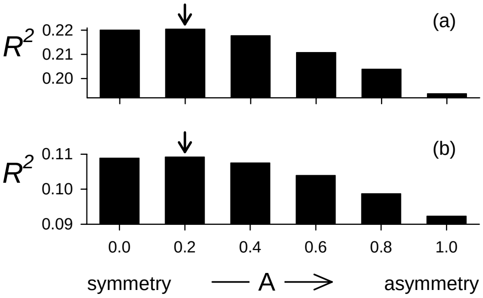

Figure 6. Values of the Nagelkerke R^2 for the relationships between survival of target trees vs. their neighborhood basal area for different levels of competitive asymmetry. Arrows indicate the model with the highest R^2 value. A = proportion of discounting effects of smaller neighbors. Significance levels of all R^2 are < 0.001 and based on randomization tests (see text). A) Height class 3.5 - 4.5 m; B) Height class 4.5 – 5.5 m, in both cases species of target tree is *Cecropia peltata*.

might reflect variation in local light availability that was not captured by NBA_L. A higher NBA_S could accordingly have reflected a lower competition intensity from the larger neighbors as a result of less suppression of height (but not of diameter) growth and hence increasing slenderness.

All regression models resulted in residuals symmetrically distributed around the 1:1 relationship between predicted and observed responses; nonetheless an important part of the scatter remained unaccounted for (Table 2). An important underlying message is that our predictions of the average responses of the trees to competition are estimates of the average population behavior, individual trees may deviate significantly from the average as a consequence of other factors that influence tree growth (*cf.* Canham *et al.* 2004).

NEIGHBORHOOD EFFECTS ON SURVIVAL

Mortality in *Trichospermum* was close to zero except for the smallest trees (Fig. 1B, D). In the height classes 1 and 2 too few individuals died for proper analyses, so we can only conclude that apparently levels of neighborhood competition in our study sites were not high enough to cause significant mortality. Mortality in *Cecropia* was much higher and significantly related to neighborhood basal area (Fig. 6), although the percentages of explained variance were low. The effect of W on survival was significant for every asymmetry value A tested (Fig. 6). The value of A giving the best fit was 0.2 in both size classes, indicating a symmetric competition effect, but again differences in R^2 with the model with only the predictor NBA_L included were small.

DISCUSSION

COMPETITIVE EFFECTS ON GROWTH

Our findings support the hypotheses that variation in the intensity of neighborhood competition is the main factor that determines within-site variation in growth of these early secondary species. Radial stem growth and vertical stem extension of similar sized *Cecropia* and *Trichospermum* trees varied greatly within the study sites and, as predicted, this variation was strongly related to the basal area of its larger neighbors. The contribution of smaller neighbors to total neighborhood basal area varied between 1-100%, and averaged 30% ± 24 SD over all selected target trees. Despite this substantial contribution, the neighborhood basal area of the smaller neighbors did not have a proportional additive effect on height growth, suggesting that variation in height growth was mainly driven by asymmetric competition for light. The same held for diameter growth of *Trichospermum*, but smaller neighbors did account for a part of the variation in radial growth of *Cecropia*. Among a series of regression models in which the effect of the smaller neighbors was devaluated by an increasing factor (A), the most successful model indicated size-symmetric interactions. This could reflect significant symmetric competition for belowground resources between the target tree and its neighbors, but we will discuss a potential alternative explanation below.

Neighborhood competition did not only reduce overall growth rate, but also affected allocation patterns. Tree species have been demonstrated to respond differently with regard to growth allocation under different light conditions (Kohyama & Hotta 1990; King 1991; King 1994; Sterck 1999; Poorter 2001). The general pattern, however, is that allocation of carbohydrates to some functions will have priority over others when carbohydrates become limiting. Suppressed trees first will pay the respiration costs, then allocate to renewal of foliage and fine roots, then to height extension and finally to branching and radial stem growth (Bongers & Sterck 1998; Sterck 2005; Turnbull 2005). So diameter growth will be reduced as soon as a tree starts to get suppressed, and height growth will vary little until competition pressure is much higher. In other words, competition results, typically, in relatively small crowns and slender stems. This relationship between stem shape and competition in fact provides the principle tool in forest management (Oliver & Larson 1996; Smith *et al.* 1997). The strong relationship between slenderness of *Cecropia* and *Trichospermum* and neighborhood basal area at the beginning of this study was thus as expected and in line with what has generally been found for light demanding species (Kohyama & Hotta 1990; Hara *et al.* 1991; King 1996).

The results additionally point to a dynamic link between successional vegetation development and changes in allocation patterns. Although slenderness increased in all *Cecropia* trees during the study period, the relative rate of change was negatively related to neighborhood basal area. While the levels of competition in the beginning of vegetation development primarily suppressed diameter growth, suppression of height growth started to be progressively stronger as competition levels further increased. Lest we understand the dynamic relationship between the coupled development of individual trees and their surroundings during the extremely changeable early phases of succession, static studies do not suffice, and longitudinal studies including the dynamics of both target trees and their direct neighborhood are needed.

COMPETITIVE EFFECTS ON MORTALITY

Mortality among individuals of *Trichospermum* was almost zero, with a survival of > 90% even among the smallest trees. Mortality of *Cecropia* on the other hand was very high among all but the largest individuals, and strongly related to size. Our data suggest that susceptibility to neighborhood competition is important but not sufficient to account for the variation in survival of *Cecropia*. Other mechanisms affecting survival might operate independent of neighborhood crowding, such as water stress during the dry season (Poorter & Hayashida-Oliver 2000) or herbivore and pathogen attacks (Brown & Ewel 1987; Gerhardt 1998). The strong differences in survival rates between *Cecropia* and *Trichospermum*, despite the fact that they have a similar potential life span and pioneer habit, indicate clear differences in their degree of tolerance to neighborhood competition. Although pioneer species are generally considered as a functional group with a narrow range of variation with regard to life history and functional traits, our results are more in line with studies that demonstrated important variation within this group (*e.g.* Pearson *et al.* 2003b; Dalling *et al.* 2004). The range of variation in competition levels that characterized this early successional vegetation might thus represent a selective mechanism, steering patterns of canopy composition among the dominant early successional species.

ASYMMETRIC VS. SYMMETRIC COMPETITION

The contribution to total neighborhood basal area of NBA_S, the variation in this contribution, and its independence from NBA_L are three aspects that are rarely explicitly addressed in comparable studies. However, in our opinion they represent important prerequisites to detect a possible competitive effect of the smaller neighbors; an effect which is, as argued earlier, indicative for the role of belowground competition. The additive effects of the smaller neighbors on radial stem growth and survival of *Cecropia* and their positive effects on the relative rate of change of slenderness of both species appear to suggest a role for belowground competition. The latter result was in fact surprising, since it was opposite to the pattern of a diminishing rate of change of slenderness with increasing competition from larger neighbors. Such contrasting results suggest that a higher basal area from the smaller neighbors and faster rate of change of slenderness co-varied, both reflecting lower competition intensity from the larger neighbors, rather than a more direct competition effect of the smaller neighbors on the target trees.

The composition of the group of trees encompassing the smaller neighbors across all target trees gives additional support for such an interpretation. Between 87% and 95% of the smaller neighbors belonged to 6 pioneer taxa (Table 1), all of them light demanding species; dense undergrowth consisting of these species is thus likely to indicate more elevated levels of light availability. There was not a direct significant correlation between the basal area of smaller and larger neighbors. However, spatial and temporal interactions among trees at different heights in the canopy might cause complex patterns of light availability (see Montgomery & Chazdon 2001) that can be influenced furthermore by species-specific differences in light transmittance characteristics that vary independently from tree size (Kabakoff & Chazdon 1996). The smaller neighbors of the target trees might thus well have reflected variation in local light availability that was not captured by the larger neighbors.

This discourse could also shed another light on the interpretation of the significant effects of the smaller neighbors on radial stem growth and survival of *Cecropia*. In a related study on biomass allocation in saplings of 10 secondary forest species, relative crown depth of both *Cecropia* and *Trichospermum* was strongly related to light availability (Fig. 7, Breugel *et al.* in prep.). If abundant undergrowth is indeed an indication for higher light availability, it would co-vary with the crown depth of the target tree. Then, under favorable light conditions, larger individuals with deeper crowns could be shaded in the lower part of their crowns by their more abundant smaller neighbors. This is in line with findings of Kikuzawa and Umeki (1996) in a temperate forest stand dominated by Picea abies. They found, on the other hand, that the canopy structure in a young Betula spp. stand was more hierarchical and competition therefore more asymmetric. They argued that, even if competition is mediated by light, the degree of asymmetry in competition can be variable depending on canopy structure. Commonly a degree of symmetry in competition is assumed to reflect a significant role of belowground competition (*e.g.* Thomas & Weiner 1989; Peterson & Squiers 1995; but see Schwinning & Weiner 1998). Although the observed effects of trees on their larger neighbors found in this study might indeed reflect some role of belowground competition as suggested by (Thomas & Weiner 1989; *e.g.* Peterson & Squiers 1995; but see Schwinning & Weiner 1998), we believe that it can at least partially be contributed to competition for light between overlapping crowns. An indication for such interaction was only found for *Cecropia* and not for *Trichospermum*. Rather than indicating interspecific differences in their responses to belowground competition, it might thus reflect a more complex interaction between environment and species.

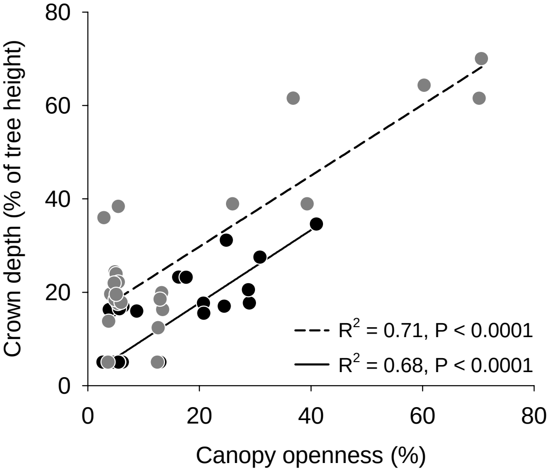

FIGURE 7. Crown depth as function of canopy openness. Trees were selected in the same sites used for this study, around the permanent sample plots. Canopy openness was estimated from a hemispherical photograph, taken directly above each trees. Total tree height was divided in 10% intervals, and leaves were sampled and weighted per interval. Crown depth was calculated as the height (expressed as percentage of total tree height) at which the accumulative leaf area from the top down was 90%. Lines are least square linear regressions. *Trichospermum*: Grey dots / dashed line; *Cecropia*: black dots / solid line. Average height of *Cecropia* was 2.8 m (± 0.07 SE) and of *Trichospermum* 2.8 m (± 0.07 SE). Height and canopy openness were not significantly correlated. Slopes of both lines were not and intercepts were significantly different (slope: F_{55} = 0.57, P=0.45; intercept: F_{56} = 36.7, P<0.0001). Unpublished data M. van Breugel.

Our study sites were characterized by nutrient poor soils and a dry period of three months, so belowground resources can be expected to limit plant growth. Field observations indicated that plant growth was indeed very limited during the dry period. During periods of enough water availability however, light is more likely to be the most limiting resource, i.e. competition for light probably structures interactions between plants. In the same way nutrient deficits may alter rate but not the form of competitive interactions operating at individual plant level (Thomas & Weiner 1989).

SCALE OF COMPETITION

A relevant question is then whether the small area that we defined as neighborhood (25 m^2) represented the appropriate scale, i.e. the scale of interaction between trees. We defined a fixed and small neighborhood area principally because plot size did not allow for larger areas, so we can not examine this question directly. Early secondary forests are often described as having an uniform canopy (*e.g.* Richards *et al.* 1996). Yet, on the scale of individual trees, the plots proved to be far from uniform. The range of variation of the neighborhood values of our target trees indicated high canopy heterogeneity on a very small scale, with total neighborhood basal area ranging from 3 to 30 $cm^2\ m^{-2}$. Along this range of values, and strongly correlated with it, height growth varied over five-fold, and suppression of diameter growth ranged from 0% to 100%. A pragmatic point of view is thus that a scale of 25 m^2 captured a relevant part of the information on the neighborhood of an individual tree.

The relative rate of change of neighbourhood basal area was 1.6 ± 0.07 SE, i.e. neighbourhood density not only varied strongly over short distances but over short periods of time as well (see also Chapter 4). As the size of largest trees increase along a successional gradient, the scale of competition interactions will increase as well (Keddy 2001). Moreover, increasing size differences will result in a divergence of the spatial and temporal scales of the dynamics of juvenile individuals and their larger neighbours. Below- and aboveground interactions may operate on different spatial scales, and these scales may change independently in the course of vegetation development (Peterson & Squiers 1995; Casper *et al.* 2003). Our results suggest that competition in 1-2 year old secondary forests operates on a small spatial scale and is mainly for light. It will be interesting to evaluate how the spatial scales, at which different competitive interactions operate, change during succession.

NEIGHBORHOOD COMPETITION AND SECONDARY FOREST SUCCESSION

A simple competition model, assuming interspecific functional equivalence with regard to competitive effects, accounted for a large part of the variation in growth, so we conclude that neighborhood biomass and size structure are the main variables driving patterns of growth and mortality among individual pioneer trees in these early successional secondary forests. This links the mechanism of competitive plant-plant interactions to a suit of other factors that causes size differences between plants and their non-uniform distribution (Miller & Weiner 1989; Huston 1994), such as micro-habitat heterogeneity (Hartgerink & Bazzaz 1984; Gerhardt 1993; Casper & Jackson 1997; Casper *et al.* 2003; Hutchings *et al.* 2003), variation in colonization and emergence time (Connolly & Wayne 1996), and differences in the genetic makeup (Álvarez-Buylla *et al.* 1996; Atwood 2002). Such initial patterns determine – and will be exacerbated by – the variability in competitive effects and responses we found in this study. Related studies indicated that this within-site variability in asymmetric competitive plant-plant interactions did account for variation in the dynamics of various populations of a species (chapters 5 and 7) and secondary forest stands of various fallow ages (Chapter 4). This study supported the hypothesis that competition of resources is one of the main mechanism steering early successional vegetation development. Studies on the changes in the nature, intensity and relative importance of competition along the successional gradient, and the interactions with other driving factors and mechanisms, are critical for pushing ahead our understanding of secondary forest succession. As yet, both dynamics and competition are poorly studied in the species rich and highly dynamic secondary tropical forests, although recently an increasing amount of permanent plot studies throughout the Tropics (see *e.g.* Chapter 5) promise interesting developments in this field.

ACKNOWLEDGMENTS

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Chapter 7

ASYMMETRIC COMPETITION AND TREE POPULATION DYNAMICS DURING EARLY SECONDARY FOREST SUCCESSION

Michiel van Breugel, Frans Bongers & Miguel Martínez-Ramos

ABSTRACT

Population dynamics of a species can vary much from one secondary forest to another. Asymmetric competition for light is thought to play an important role in the successional dynamics of young secondary forests. Accordingly, between-site differences in demographic behaviour are expected to be related to variation in population size structure and neighbourhood structure. Specifically, differences in growth and mortality between the biggest and smallest trees of a population (growth and survival asymmetry) are predicted to be related to differences in the average level of asymmetric neighbourhood competition in both size groups (competition asymmetry).

We tested these predictions using 24 populations of four pioneer tree species for which growth and mortality data was obtained from permanent sample plots in nine early (1-5 y) secondary forest stands in a humid Neotropical area in southern Mexico. For each population, we compared average neighbourhood basal area, growth and survival of the twenty percent smallest and largest trees.

The between-plot variation in competition asymmetry explained a significant part of the between-plot variation in growth asymmetry, with smallest trees growing faster in populations with low competition asymmetry, and largest trees growing fastest in populations with high competition asymmetry. Survival was size-related, with lowest survival rates among the smallest plants, as expected. However, survival asymmetry was significantly related to competition asymmetry in just one species. The differences in the effects of asymmetric competition on the mortality and survival of the four species show that susceptibility to competition for, presumably, light, varies considerably between early successional pioneer species.

INTRODUCTION

Competition for resources is considered to be an important mechanism regulating plant population dynamics during secondary forest succession (Peet & Christensen 1980; Huston & DeAngelis 1987; Wilson 1999; Keddy 2001). Surprisingly, few studies have directly addressed this topic (see overviews in Rejmanék 1990; Wilson 1999). Competition starts as soon as plants begin to negatively affect each other's resource acquisition, which can be very soon after initiation of succession. As plants grow bigger, community plant mass increases and consequently the ratio of resource demand to supply also increase. Hence, competition intensity is thought to increase as secondary succession proceeds (Wilson 1999; Keddy 2001; Doležal *et al.* 2004).

In forest succession, light is generally assumed to be an important limiting resource as soon as a substantial leaf canopy has been formed. Competition for light has been hypothesized to be asymmetric, since larger plants can shade smaller ones but not visa versa. This asymmetry has important implications for the dynamics of plant populations as bigger individuals are expected to get a proportionally greater amount (per unit size) of shared resources and, therefore, a disproportional share of total population biomass growth. Smaller individuals, on the other hand, will be suppressed and suffer higher mortality (Weiner & Thomas 1986; Weiner 1990; Huston 1994). With increasing size-inequality, the difference in the level of asymmetric competition will increase, which in turn conduce to a higher inequality in growth and mortality between individuals of different size (Huston & DeAngelis 1987; Jobidon 2000; Doležal *et al.* 2004).

Most forests in which such population dynamics have been demonstrated are even-aged, mono-specific stands (Mohler *et al.* 1978; Cannell *et al.* 1984; Kikuzawa & Umeki 1996; Berntson & Wayne 2000). So far, population dynamics of individual species has hardly been studied in mixed-species secondary forests (Hutchings 1997; Watkinson 1997). Stand structure and successional dynamics can vary from the stand to the landscape level (Montgomery & Chazdon 2001; Olano *et al.* 2002) . As a result, the population dynamics can be expected to vary as well across these spatial scales, entangling generalizations regarding the importance of asymmetric competition in the secondary succession process (Peterson & Squiers 1995; Turnbull *et al.* 2007). Within a secondary forest stand, individuals of a population experience a changing and heterogeneous environment due to spatial variation in stand structure and species composition (Alvarez Buylla 1994; Bazzaz 1996) and to fast changes during the early years of succession (Chapter 4, 5). At the landscape level, secondary forest stands may vary widely with respect to stand structure and species composition, depending on factors such as land-use history, soil type, extent and spatial configuration of old-growth forest patches, and the regional species pool (Turner *et al.* 1998; Moran *et al.* 2000; Chazdon 2003; Chinea & Helmer 2003). More complexity might be added by other factors such as the abundance, distribution, identity, and local effect of pollinators, seed dispersal agents, pathogens and herbivores (Augspurger 1984; Castello *et al.* 1995; Renner 1998; Toyohara & Fujihara 1998; Levey *et al.* 2001; Webb *et al.* 2006). Therefore, population dynamics of a species, including size-related distribution of growth and mortality among individuals, is expected to vary between different secondary forest stands.

The importance of competition concerns its result relative to the importance of the other processes and conditions that influence the population dynamics, specially in mixed-species successional plant communities (Welden & Slauson 1986; Keddy 2001). When asymmetric competition is an important mechanism, it will create demographic hierarchies among individuals experiencing different neighbourhood structures. The level of asymmetric competition experienced by plants is expected to decrease with size, simply because a bigger plant is likely to have a lower number of larger neighbours than a smaller plant. The magnitude of such size-related differences will vary between populations differing in size structures and stand characteristics. We tested these predictions using 24 populations of four pioneer tree species for which growth and mortality data was obtained from nine early (1-5 y) secondary forest stands in a humid Neotropical area. Specifically, we examined the degree to which size-related inter-individual variation in growth and mortality was imputable to asymmetric competition. To this end, we examined for each population: (1) differences in growth and mortality between biggest and smallest trees, (2) differences in the average level of asymmetric neighbourhood competition in both size groups. Finally, we examined (3) whether the between-population variation in size-related demographic variability was related to the between-population variation in asymmetric competition levels.

METHODS

DATA COLLECTION

The study was conducted in the Marquéz de Comillas region, South of the Montes Azules Biosphere Reserve (approximately 16º04′ N; 90º45′ W), Chiapas, Mexico. Mean annual temperature is 24 ºC and average annual rainfall is about 3000 mm with less than 100 mm month^{-1} from February to April. The original vegetation consists mainly of lowland tropical rainforests and semi-deciduous forests (Ibarra-Manríquez & Martínez-Ramos 2002). Colonization of the region initiated in the early 1970s and caused large scale deforestation since. Nowadays the landscape consists of a mosaic of small scale agriculture, pastures, mostly young (< 10 yrs) secondary forests and remnants of old-growth forests (de Jong *et al.* 2000). Chapter 2 of this thesis describes patterns of species richness and distribution across a wide range of secondary forest sites in this landscape.

TABLE 1 – Species characteristics. Freq.: Frequency, percentage occurrence in 72 secondary forest plots in the research region; Dom.: dominance, percentage of the 72 plots in which the species held ≥ 10% of the stand basal area. In both cases the rank of the species with regard to its frequency or dominance is also given (see chapter 2). MLS: Maximum life span. MH: Maximum height.

	Freq.[1]		Dom.[1]		MLS[2]	MH[3]
Species	%	rank	%	rank	y	m
Cecropia. peltata L.	75.0	1	37.5	1	35	20 (18)
Schizolobium parahyba (Vell.) S. F. Blake	45.0	5	12.5	5	>50	35 (22)
Trema micrantha (L.) Blume	40.0	9	13.8	4	15	8 (13)
Trichospermum mexicanum (DC.) Baill.	61.3	2	33.8	2	30	15 (18)

1) Chapter 2; 2) Based on data and observations from long-term studies, conducted at Los Tuxtlas Tropical rain forest (e.g. Ibarra Manriquez et al., 2001; Popma et al., 1992) and in our own study region (M. Martínez-Ramos et al. unpublished data); 3) Based on Pennington & Sarukhán (1998), between parentheses the maximum observed height in our study plots.

Nine 1-5 y old secondary-growth stands were selected on abandoned corn fields ("milpas") in areas with undulating hills, at 115-300 m.a.s.l., characterized by complex acidic soils (pH 4-5), derived from sedimentary rocks (sandy and clay) that have low total nitrogen and phosphorous content (Siebe *et al.* 1996; Celedón-Muñiz 2006). Fallow age and land use history was determined based on interviews with the land owners and/or relatives. In each selected stand, one plot of 10 x 50 m was laid out. At the first census, all trees with diameter at breast height (dbh) ≥ 1cm were recorded, tagged and their diameter at 1.3 m above ground (dbh) was measured. Location of each tree was determined using a 1x1 m grid system. One (census 2) and two years (census 3) after plot establishment, dead trees and new recruits were recorded and dbh was measured in all living trees. More information on study sites and stand characteristics is given by in the chapters 1, 3 and 4.

We selected species that (1) occurred with > 30 individuals in each of at least three plots in either the first or second census and (2) occurred with at least 30 surviving individuals in the next census. Four species complied with these criteria: *Cecropia peltata* L., *Schizlobium parahyba* (Vell.) S. F. Blake., *Trema micrantha* (L.) Blume, and *Trichospermum mexicanum* (DC.) Baill. The four species are light demanding pioneers that are amongst the most frequent and dominant species in the young secondary forests of the research region. They differ, however, with respect to longevity and

TABLE 2 – Population statistics summarized per species. Among-population means ± standard errors are given; in case of mortality also the range is given. Pop.= number of populations; SD = stem density; mD = mean diameter; SI = size inequality, the difference between the mean diameters of the 20% smallest and the 20% biggest of all trees alive at the initial census; RRC_{MD} = relative rate of change of mean diameter; RRC_{SI} = relative rate of change of SI.

Species	Pop.	Population structure (initial census)			Population dynamics				
		SD $(500\ m^{-2})$	mD (cm)	SI (cm)	Mortality Range (%)	Mortality Mean (%)	Mean RGR $(cm\ cm^{-1}\ y^{-1})$	RRC_{mD} $(cm\ cm^{-1}\ y^{-1})$	RRC_{SI} $(cm\ cm^{-1}\ y^{-1})$
Cecropia	7	206 ± 116	3.04 ± 0.17	4.08 ± 0.48	12-78	34.7 ± 9.8	0.27 ± 0.06	0.41 ± 0.03	0.5 ± 0.09
Schizolobium	4	113 ± 30	3.09 ± 0.09	3.38± 0.29	8-57	24.7 ± 11.3	0.16 ± 0.03	0.25 ± 0.05	0.4 ± 0.16
Trema	6†	288 ± 170	2.68 ± 0.26	3.20 ± 0.69	34-95	63.3 ± 11.5	0.25 ± 0.12	0.31 ± 0.08†	0.3 ± 0.11†
Trichospermum	7	388 ± 117	2.53 ± 0.26	3.72 ± 0.73	3-16	8.1 ± 2.0	0.43 ± 0.10	0.43 ± 0.10	0.6 ± 0.13

† In two populations only 3 and 8 individuals survived (mortality of respectively 82% and 95%) and hence they were not included in further analyses

stature (Table 1). In total, this selection procedure resulted in twentyfour species-plot combinations (Table 2), distributed over nine plots. Henceforth we will refer to them as 'populations' and we will refer to these species by genus name. For each population we chose the study year with most individuals in the initial census. For two *Trichospermum* and one *Cecropia* populations this was the second census, otherwise it was the first census.

ANALYSIS

Following the approach in chapter 6, we defined the neighborhood of an individual tree as the area encompassing its own 1x1 m quadrant and the 24 adjacent 1x1 m quadrants. For each individual tree, the neighborhood basal area was calculated including only trees that were taller than the focal tree, i.e. assuming completely asymmetric competition. All species in the neighborhood were included; i.e., we dealt with heterospecific competitive interactions. In chapter 6, an important part of the variation in growth, and to a lesser extent survival, of a sample of target trees was accounted for by this proxy of neighborhood competition.

For each population, the 20% biggest and 20% smallest trees were selected (henceforth 'size classes'), and for both size classes the mean diameter (mD, cm); and the average neighborhood basal area (cm^2 m^{-2}) at the first census was calculated. These parameters were used to calculate the following parameters for each population: the difference between the means of the diameters of the two size classes (henceforth 'size inequality', cm); and the difference between the average neighborhood basal areas of the two size classes (henceforth 'competition asymmetry', c^{-1} m^{-2}, see Fig. 1).

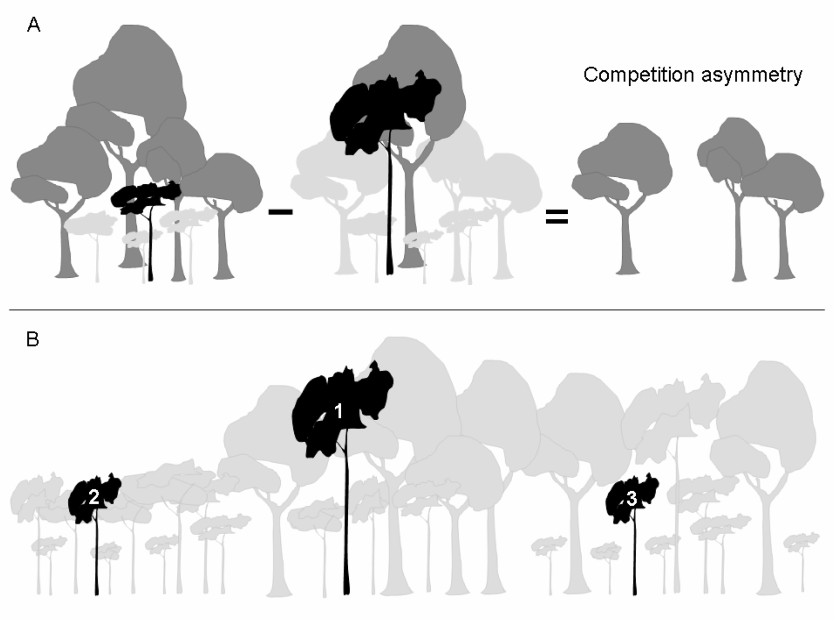

FIGURE 1 – Asymmetric competition and competition asymmetry. In all images the black tree represents the focal tree and the grey trees its neighbors. When competition is totally asymmetric, larger trees exert an influence on smaller trees, but not the other way around. (A) When we (*i*) include only trees larger than the focal tree in our definition of neighborhood (darker grey trees) and (*ii*) assume a homogeneous stand structure, then a small focal tree on average will have more neighbors than a larger focal tree. This difference would then give an approximate measure of difference in competition pressure experienced by the two focal trees. We used stem basal area as a measure of size in this study, and referred to the difference between the average neighborhood basal areas of the 20% largest and the 20% smallest trees as "*competition asymmetry*". (B) When stand structure is homogeneous, size difference would be a good predictor of competition asymmetry. However, when the stand consists of patches with e.g. different canopy height, the same size difference can result in very different competition asymmetry (compare tree 1 vs. 2 and 1 vs. 3). When the trees of a population are not distributed randomly but rather in patches of similar-sized trees (as trees 1 and 2), there might be no relationship between size inequality and competition asymmetry.

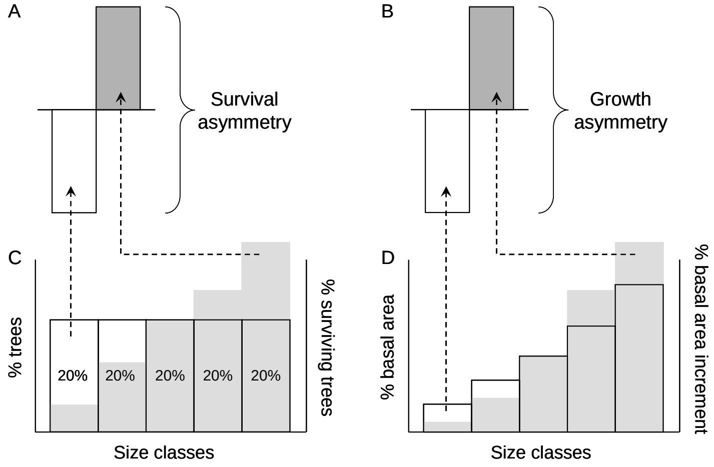

FIGURE 2 – Growth and survival asymmetry. If basal area growth increment would be randomly distributed among the surviving plants of a population (irrespective of size) then the sum of the initial basal area of a size class (D, open bars,) and the sum of their basal area increment (D, shaded bars) would represent approximately equal fractions of their respective total population values. Similarly the fraction of all surviving plants in a given size class (C, shaded bars) would be proportional to the fraction of all plants initially in that size class (C, open bars). In this study we divided the population in equal proportions of 20% of all plants (C) and of the plants that survived the study period (D) and we calculated the deviations of observed percentages from proportional percentages for the size classes of the 20% smallest and 20% biggest trees. We used the deviation of the smallest plants minus the deviation of the largest plants as a measure of survival asymmetry (A) and growth asymmetry in the population (B). So a negative growth or survival asymmetry signifies that small plants grew faster or had a higher survival than the larger plants, and positive values signify the opposite.

Next, for each population, the 20% biggest and 20% smallest trees were selected from the trees that survived at the end of the study period. Again the average stem diameter and neighborhood basal area was calculated for both size classes, and used to calculate size inequality and competition asymmetry. For each tree, we calculated the basal area growth increment (BAG_i) and for both clases we calculated the percentage of absolute population basal area growth rate of each size class (PAGR) as the sum of the BAG_i of the initial trees in the size class divided by the basal area growth of the whole population.

If mortality were randomly distributed within the population, independently of tree size, the percentage of surviving trees in a size-class is expected to be equal to the percentage of the population initially found in that class. For both the large and small size classes, the deviations of the observed survival from that expected by random was calculated. The difference between the deviations of the two size classes is henceforth referred as 'survival asymmetry' (Fig. 2A, C). Similarly, the growth (PAGR) of a size class would be expected to be proportional to the percentage of the initial population basal area in that class. Following the same procedure as for survival, we obtained 'growth asymmetry' values (Fig. 2B, D).

To test if the observed PAGR of the two size classes deviated significantly from the proportional values, we created an empirical sampling distribution for PAGR by shuffling the observed relative growth rates (BAG_i/initial basal area) 10,000 times across all surviving trees, calculating at each shuffling trial the PAGR for both size classes. Likewise, we generated an empirical sampling distribution for the rate of survival by 10,000 times randomly sampling N trees, N being the observed number of surviving trees, from the total population. The 0.05 and 0.95 percentiles of the generated empirical sampling distributions were used as the respectively lower and upper confidence limits for the estimated parameters (Quinn & Keough 2002).

RESULTS

POPULATION STRUCTURE AND DYNAMICS

Initial population structure (stem density, mean diameter, size inequality) differed considerably across and within species (Table 2). Size inequality, based on all trees alive at the initial census, ranged from 1.6 to 7.3 cm for *Trichospermum*, from 1.4 to 5.7 cm for *Trema*, 2.5-5.8 cm for *Cecropia* and from 2.9 to 4.1 cm for *Schizolobium* (Fig. 3). Variation in size inequality was mostly due to variation in mean diameter of the larger trees: the mean diameter of the 20% smallest trees (DS) and of the 20% largest trees (DL) varied between 1.0 and 2.2 cm and 2.5 cm and 8.5 cm respectively, and a rise in DS was accompanied with a faster rise in DL (DL =0.75+3.13* DS; R^2 = 0.34; P = 0.003). The latter entailed a strong correlation between size inequality and mean diameter (*Cecropia*: r = 0.93, P = 0.003; *Schizolobium*: r = 0.85, P = 0.15; *Trema*:

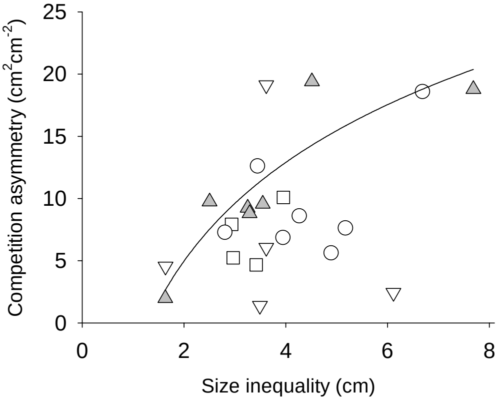

FIGURE 3. The relationship between size inequality (cm) and competition asymmetry (cm^2 m^{-2}). Each symbol represents one population. Circle: *Cecropia*; square: *Schizolobium*; filled triangle and regression line: *Trichospermum*; open triangle: *Trema*. The relationship is only significant for *Trichospermum* (y = 11.45Ln(x) – 2.97, R^2 = 0.81, F = 21.1, P = 0.006).

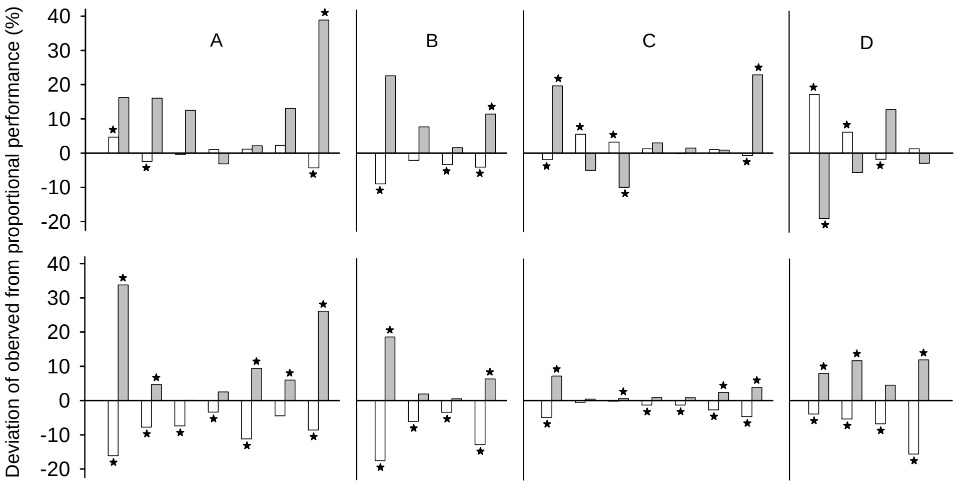

FIGURE 4. Deviation of observed basal area growth from expected random values in classes of the 20% smallest (white bars) and 20% biggest trees (grey bars). When the bars are below the 0-line, basal area growth (upper row) and survival rate (lower row) are lower than randomly expected, while values above the 0-line indicate a more than proportional growth or survival. See Figure 2 for further explanation. Each combination of a white and a grey bar represents one population. A) *Cecropia peltata*; B) *Schizolobium parahyba*; C) *Trema micrantha*; D) *Trichospermum mexicanum*. An asterisk indicates a significant deviation at $p < 0.05$.

r = 0.98, P = 0.001; *Trichospermum*: r = 0.97, P = 0.000). Stem density was not related to any of the other two parameters of population structure.

The species population dynamics (mortality, RRC_{mD} and RRC_{SI}) was generally fast, but varied considerably between the populations of same species. In all cases both mean diameter and size inequality increased during the studied period (Table 2). Most conspicuous inter-specific differences were the relatively high mortality rates of *Trema*, and the relatively high rates of change of mean diameter and size inequality, slow mortality rates, and narrow between-plot variation in mortality rates of *Trichospermum*. The population means of the relative rates of change were not correlated with mortality rates for any of the species.

DISTRIBUTION OF GROWTH AND MORTALITY AMONG SIZE CLASSES

Distribution of population basal area growth among size classes varied greatly between populations. Basal area growth was significantly higher than that expected by random in larger trees, and significantly lower in smaller trees in 16 and 11 of the 22 studied populations, respectively; in the other populations, results were opposite to predictions (Fig. 4). Relative growth rate of individual trees varied considerably and this resulted in large confidence intervals for expected values; because of that, not all differences were significantly different from zero. For bigger trees, differences were significant and according to predicted in four populations, significant and opposite to predicted in two populations, and not significant in six populations. For smaller trees these figures were eight, five and nine, respectively (Fig. 4).

Distribution of survival among size classes showed a more consistent pattern among populations. A higher than proportional percentage (i.e. ≥ 20%) of surviving trees belonged to the 20% biggest trees, while the reverse was true for the 20% smallest trees. Deviations from proportional survival varied widely between populations, but were significantly different from zero in all but few cases (Fig. 4).

RELATING GROWTH AND SURVIVAL ASYMMETRY TO COMPETITION ASYMMETRY

The supposition that increasing size inequality would results in increasing competition asymmetry only held for *Trichospermum*. In the three other species between-stand variation in competition asymmetry was not significantly related to between-stand variation in size inequality. Results were the same whether all trees (not shown) or only surviving trees (Fig. 3) were included in the calculation of size inequality and competition

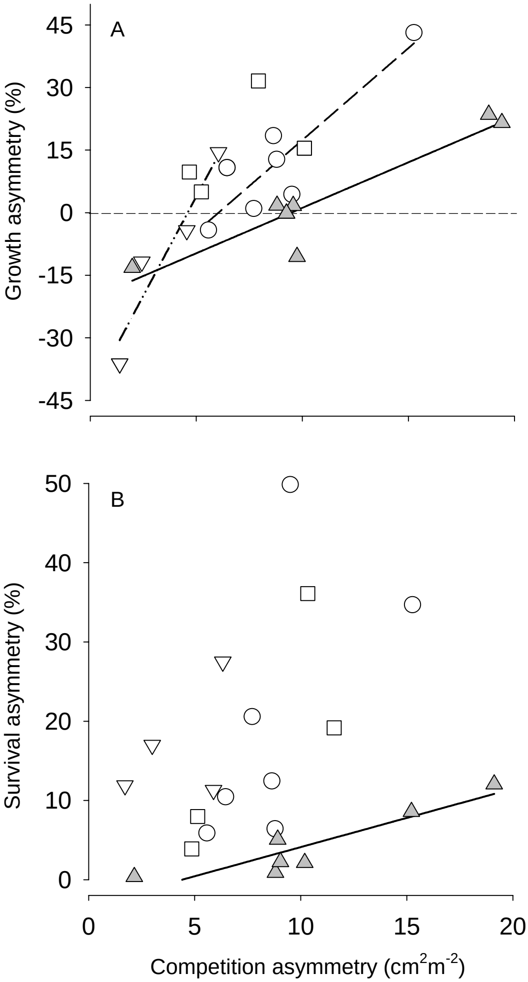

FIGURE 5. Growth asymmetry (A) and survival asymmetry (B) as function of the competition asymmetry (difference between the average neighborhood basal areas of larger and smaller tree classes). See Figure 1 for explanation of the variables growth asymmetry and survival asymmetry. Each symbol represents one population. Species are indicated by (symbol / line): circle / dash: *Cecropia*; square: *Schizolobium*; filled triangle / solid: *Trichospermum*; open triangle / dash-dot: *Trema*. Only regressions significant at P < 0.05 are plotted. Regression statistics are given in table 3.

asymmetry. These results indicate both among-and within-stand variation with regard to the vertical stand structure (Fig. 1). In line with these results, growth asymmetry was related to size inequality only in case of *Trichospermum* ($R^2 = 0.86$, $P = 0.003$; $y = 27.6x - 30.3$). Survival asymmetry was not significantly related to size inequality in any of the species (data not shown).

Growth asymmetry was significantly and positively related to competition asymmetry in three of the four species. The fourth species, *Schizolobium*, showed a similar but non-significant trend (Fig. 5a, Table 3), most probably due to a low number of samples (plots) and a limited range of variation in competition asymmetry. The slopes increased in the order *Trichospermum - Cecropia – Trema*, with significant inter-specific differences (*Trichospermum – Cecropia*: F = 7.39, P = 0.022; *Cecropia – Trema*: F = 6.21, P = 0.041; *Trichospermum – Trema*: F = 16.6, P = 0.005). Regression lines cross the y = 0 line, where the proportion of total population basal area increment is equal in both size classes. Competition asymmetry thus has to reach a minimum threshold value before the competitive advantage of bigger trees compensates for a higher potential relative growth rate of smaller trees. This value varied between 4.6 $cm^2\,cm^{-2}$ (*Trema*) and 9.4 $cm^2\,cm^{-2}$, (*Trichospermum*). The variation in threshold values and slopes indicate a differentiation within the group of early pioneers with respect to the sensitivity of their growth response to neighborhood competition.

Survival probability in these populations was consistently size related (Fig. 4), but the evidence for a dominant role of size asymmetric competition was more ambiguous. Survival asymmetry was relatively low in all *Trichospermum* populations, i.e. mortality rates differed little between the smallest and largest individuals. The regression coefficient (slope) of the positive relationship between survival asymmetry and competition asymmetry was small but significant. (Fig. 5b, Table 3). This means that survival asymmetry of *Trichospermum* augmented only slightly with increasing competition asymmetry. The other species showed much stronger variation in survival

TABLE 3. Regression statistics of least square linear regressions between competition asymmetry (independent variable) and growth and survival asymmetry (dependent variables). See Fig. 1 and text for an explanation of the variables. The regression coefficients *a* (slope) and *b* (intercept) are given only in case of significant results.

	Survival asymmetry				Growth asymmetry			
Species	R^2	P	a	b	R^2	P	*a*	*b*
Cecropia	0.58	0.047	1.56	-12.79	0.79	0.007	4.41	-26.71
Schizolobium	0.65	0.196	-	-	0.29	0.466	-	-
Trema	0.20	0.553	-	-	0.91	0.048	9.53	-43.79
Trichospermum	0.10	0.482	-	-	0.87	0.002	2.18	-20.63

asymmetry. The data suggest that the slopes of the relationships between survival and competition asymmetry of these species were considerably higher, but none of the regression coefficients was significant.

DISCUSSION

We found evidence that indicates that asymmetric competition plays an important role at early stages of tropical secondary forest succession, affecting the population dynamics of pioneer tree species. Population dynamics of a species can differ considerably from one site to another. The between-plot variation in competition asymmetry explained a significant part of the between-plot variation in growth asymmetry. Survival was size-related, with lowest survival rates among the smallest plants, as predicted. However, survival asymmetry was significantly related to competition asymmetry in just one species. The observed inter-specific variation in the demographic effects of asymmetric competition show that susceptibility to competition for, presumably, light, might vary considerably between early successional pioneer species.

ASYMMETRIC COMPETITION AND COMPETITION ASYMMETRY

The concept of competitive asymmetry implies that larger plants obtain a disproportional competitive advantage over small plants (Weiner 1990; Keddy 2001). In an extreme case the (even slightly) larger plant would get all resources (resource pre-emption) while in the opposite site resource acquisition is proportional to plant size. Indeed, the effects of competition interactions have been found to vary between these extremes (Peterson & Squiers 1995; Berntson & Wayne 2000; Kochy & Wilson 2000). The degree of asymmetry depends, to a great extent, on the resources that are considered. During secondary forest succession in the humid tropics light is thought to be the main limiting resource for plant growth and survival (Chave 1999; Hooper *et al.* 2002; Poorter & Arets 2003). As larger plants shade smaller plants, competition for light is largely asymmetric (Schwinning & Weiner 1998). Assuming that competition for light is one of the main mechanisms steering forest succession, the signature of asymmetric competition should be apparent in the species population dynamics, explicitly in their size-specific demographic rates. To examine this we considered the influence of neighbors larger than the focal tree on growth and survival and ignored the competitive influence of smaller plants (Fig. 1A), thus assuming competition was completely asymmetric. In other studies stand structure and crown architecture of competing plants have been shown to influence the degree of asymmetry in light competition (Kikuzawa & Umeki 1996; Doležal *et al.* 2004; Canham *et al.* 2006). In our case, however, this did not play an important role, as we found (chapter 6) that trees smaller than the focal tree did not have a significant additional effect in predicting growth and survival of individual *Trichospermum* and *Cecropia* saplings, when compared to the effects of plants larger than the focal plant. This indicates that competition between plants is strongly asymmetric in our early successional system.

If competition is asymmetric, the smallest plants on average would experience stronger neighborhood competition than the largest plants in a population. This hypothesis implies that: (i) smaller plants have a higher number of larger neighbors (as in Fig. 1A); and (ii) this affects the distribution of growth and survival over size classes in favor of the larger trees. Competition asymmetry and growth and survival asymmetry thus should be related. The alternative hypothesis is that competition in our early secondary forests is symmetric rather than asymmetric, which implies that size-related variation in plant performance is independent of size related differences in asymmetric neighborhood density. In our early secondary forests, competition asymmetry varied considerably between populations of the same species; and increasing competition asymmetry caused increasing growth and survival asymmetry, although the results are equivocal with respect to survival asymmetry. Our data thus supports in general the hypothesis that population level dynamics in these early secondary forests can be linked to asymmetric competition.

PLANT SIZE, COMPETITION, GROWTH AND SURVIVAL

Models of tropical forest succession often assume that growth and mortality during early forest development are regulated by competition for light (Kohler & Huth 1998; Chave 1999; Kohyama *et al.* 2001). However, it has been hardly possible to test this assumption directly as studies about tree population and dynamics in such secondary forests are rare (Chapters 4, 5). Here, we approached this issue by using dynamic data gathered from several permanent plots in young secondary forest stands. Across these stands, different populations of the same species diverged in size structure and dynamics. This enabled us to examine how size-specific growth and survival varied related to asymmetric neighborhood competition. However, another mechanism links growth to plant size as well. RGR is physiologically and morphologically determined to decrease with tree size, as the support mass fraction increases and subsequently the leaf mass fraction decreases during plant development (Veneklaas & Poorter 1998). Therefore, other factors being equal (*e.g.* neighborhood competition), size differences should result in negative growth asymmetry (indicating that relative growth rate of the smaller plants is higher than the RGR of the larger ones). This is exactly what we found. When asymmetric neighborhood competition was relatively similar for both size classes (low competition asymmetry), the smaller plants in a population grew faster than the larger plants (negative growth asymmetry; Fig. 5). The larger plants grew faster (positive growth asymmetry) when differences in neighborhood competition were relatively big.

Smaller trees typically suffer greater mortality rates (Piñero *et al.* 1984; Alvarez Buylla & Martinez Ramos 1992; Condit *et al.* 1995; Zuidema & Boot 2002). Indeed survival of the smaller plants was disproportionately low in all our populations. Theory and field data on how mortality rate relates to size are equivocal though. The main reason is that it is difficult to determine empirically whether higher mortality among the smaller plants results from greater asymmetric competition or from other size-related plant effects (Uriarte *et al.* 2004a). As they grow, trees develop structural support and acquire reserves and consequently physiological buffering capacity to withstand environmental stress (Lieberman *et al.* 1985; Clark & Clark 1992; Condit *et al.* 1995; Blundell & Peart 2001). Moreover the size of the root system is generally positively related to plant size (Niklas & Enquist 2002; Schenk & Jackson 2002). In a study on tree architecture in our secondary forest stands, dry weight, and maximum depth and width of the root system was positively related to total plant dry weight in saplings (18 to 1400 g dry weight) of three of the four studied species (*Trema* was not included, M. van Breugel unpublished data). As a larger root system allows plants to explore larger soil volumes for soil resources, larger plants probably are less affected by water stress during the dry season and better able to profit from nutrient rich patches (Casper & Jackson 1997; Poorter & Hayashida-Oliver 2000; Casper *et al.* 2003; Hutchings *et al.* 2003).

The consistent patterns of disproportional high mortality among the smaller plants in our forests can thus have been caused by alternative size-related processes. Moreover, any factor that affects the plant negatively may be strengthened by another. The significant relationship between survival asymmetry and competition asymmetry that we observed for *Trichospermum* (Fig. 5B) indicate that asymmetric competition influences survival in this species. The small slope of the regression line indicates that the species response is not very strong. This is consistent with the very low mortality figures of this species (Table 1). The slopes of the other species are much steeper but non-significant. These results suggest that these species respond much stronger to competition but also to other factors that affect their survival probabilities.

ABOVE GROUND VS BELOW GROUND COMPETITION

The few community dynamic studies in tropical secondary forests (younger than 5 years) demonstrated that vegetation development can be very fast during the early successional phases, with rapid increasing basal area, canopy height, biomass and/or leaf area index (Chapter 4-5; Swaine & Hall 1983; Uhl 1987). Chronosequence studies (*e.g.* Saldarriaga *et al.* 1988; Uhl *et al.* 1988; Tucker *et al.* 1998; Hughes *et al.* 1999; Steininger 2000) and permanent plot studies (Chapter 4-5; Chazdon *et al.* 2005) suggest that these trends continue later in succession, although at decreasing rate.

Plants compete for above ground (light) and below ground (nutrients, water) resources (Grime 2002). Along both spatial and temporal (succession) gradients, below ground root competition is expected to be greater in sites with low availability of soil water and/or nutrients (*e.g.*, sites with low above ground plant mass and relatively open canopies), and above ground shoot competition in sites where light resources are limited (*e.g.*, places with high above ground plant mass (Keddy 2001). Based upon this premise and observations of rapid vegetation development during secondary forest succession, it has been argued that above ground competition for light becomes predominant very soon after disturbance (Holl 1998; Wilson 1999). Yet there seem to be few studies that tested this presupposition directly (Bazzaz 1996). A dense canopy is not necessarily an indication that competition is dominated by above-ground interactions, as they can coincide with strong belowground root competition (Coomes & Grubb 2000). The rate of vegetation development has been shown to vary with soil type and duration and intensity of the former land-use (*e.g.* Buschbacher *et al.* 1988; Uhl *et al.* 1988; Hughes *et al.* 1999), suggesting that soil resources may constitute a limiting factor during succession on poor soils.

It is rather hard to come to generalizations about the relative importance of above ground as opposed to belowground competition in forest environments with the scarcity of studies approaching this issue. Putz (1992) conducted one such study and reviewed other 16 studies that compared experimentally above and below ground effects of competition exerted by dominant trees on tree regeneration. He found that in about half of the studies (10/17) belowground competition was stronger. Comparisons of experimental studies in tropical rain forests suggest that both above and below ground competition limits plant performance on oligotrophic soils (*e.g.*Burslem *et al.* 1996; Coomes & Grubb 1998; Lewis & Tanner 2000; Barberis & Tanner 2005; Schnitzer *et al.* 2005). The relative importance of above and below ground competition for tree fitness will depend to a large extent on the species (target species as well as neighbours) and site conditions, in particular on the resource (light, nutrients or water) that is most limiting (Wilson 1988; Putz & Canham 1992; Coomes & Grubb 1998, 2000; Grime 2002).

The studies mentioned above correspond to old growth forest systems, and dealt mostly with adult-juvenile (seedlings, small saplings) competition. Our study, on the other hand, dealt with competition between saplings and young adult trees in early secondary forest, a scenario with both low community plant mass and much lower size inequality of competing individuals. Belcher *et al.* (1995) argued that the relative importance between below and above ground competition will change along a gradient of increasing plant mass (and decreasing stress). Wilson (1999) proposed that root competition becomes predominant on poor soils, whereas shoot competition becomes predominant on rich soils. The balance between below and above ground competition depends on which part of such a gradient is covered by the study system (Belcher *et al.* 1995; Keddy 2001).

Our research region is characterized by a dry period of about 3 months with less than 100 mm month^{-1} rainfall and sand and clay poor soils (Celedón-Muñiz 2006), and as a consequence competition for below ground resources may well have had a limiting effect on plant growth. Yet basal area was very high in all sites (6.7-24.7 m^2 ha^{-1}) which suggest strong above-ground competition. Stand dynamics were characterized by very high growth and mortality rates (Chapter 4). Most trees appear to experience strongly reduced growth rates (Chapter 8, Fig 1). The present study suggests a predominant role for above ground competition for light. Competition for water and nutrients is presumed to be size symmetric, while competition for light is size asymmetric (Berntson & Wayne 2000; Coomes & Grubb 2000). As we argued above, the size-related patterns of growth and survival along the gradient of competition asymmetry in our studied populations provide evidence for a predominant role of asymmetric competition.

ASYMMETRIC COMPETITION AND POPULATION STRUCTURE AND DYNAMICS

The present study relates demographic differences between populations to differences in population size structure through the process of asymmetric competition. In consequence, the population size structure at a starting time is expected to steer further population development. A large size inequality in a population results in higher asymmetric competition, hence the larger trees may seize a disproportional share of the available resources. As a result, larger trees improve their competitive position, amplifying the size-related differences in growth and mortality rates among interacting trees (Huston 1994; Schwinning & Weiner 1998). Growth asymmetry enlarges size inequality, while a positive survival asymmetry has the opposite effect. Size inequality increased in all populations (Table 2) indicating that the effect of growth asymmetry prevailed in these young populations.

The present size structure of a population also reflects past population dynamics. In early phases of secondary succession, plants are predicted to compete size-symmetrically since most trees are similarly small and occupy similar positions in a low canopy (Schwinning & Weiner 1998). However, size differences will develop rapidly due to factors such as within-location variability in arrival and emergence time (Connolly & Wayne 1996), spatial soil resource variability (Hartgerink & Bazzaz 1984), and variation in spatial levels of competition intensity due to non-uniform spatial distribution of trees (Huston 1986; Miller & Weiner 1989).

Such patterns are demonstrated for even-aged stands of one single species, and are likely to be much stronger for populations in the context of uneven-aged mixed-species stands of naturally regenerating secondary forests. Species may differ with respect to their impact on other species, for example because of differences with regard to light interception by tree canopies (Canham *et al.* 1994), and as well in their response to competing neighbors. Spatial variation in canopy composition thus could add to within-population variability in growth and survival (Uriarte *et al.* 2004a; Canham *et al.* 2006). However it has also been suggested that competitive effects are more or less equivalent for species rich tree communities, i.e. species identity is not important

(Hubbell 2005; Hubbell 2006). As large populations are needed to be able to test equivalence of neighboring species we could not analyze this and we treated all neighboring species as identical.

Pioneers have been considered as the only clearly defined group of tropical wet-forest trees sharing a common life history (Swaine & Whitmore 1988; Clark & Clark 1992). Recent studies have demonstrated that life history traits of pioneer species vary considerably (Pearson *et al.* 2003a; Dalling *et al.* 2004) challenging the general treatment of early pioneers as a well defined and uniform ecological group. Survival asymmetries of three out of four studied species were not significantly related to competition asymmetry; hence it is difficult to relate the large interspecific differences in average mortality rates to differences in tolerance to asymmetric competition. The very low overall mortality rate of *Trichospermum* (Table 2) however does suggest that this species is relatively tolerant to the levels of asymmetric competition predominant in our young secondary forest stands. This interpretation is consistent with the small regression coefficient (slope) of the growth-competition asymmetry relationships found for this species. The differences in these regression coefficients do indicate interspecific differences in the growth response to levels of (asymmetric) competition. Thus, the present study show that pioneer species differ considerably in their population dynamics and in the extent to which neighborhood competition affects such dynamics.

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Chapter 8

GENERAL SUMMARY AND DISCUSSION

INTRODUCTION

The objective of this thesis was to study the dynamics – the direction and rate of change of community structure and composition – of secondary forests and some of the processes that direct this dynamics (Chapter 1, p. 19). A long tradition of secondary forest research has given us much insight in the general patterns of succession and in conditions and constraints that affect the course of succession. In chapters 1 and 5 these patterns and factors are already discussed to some length. A hierarchical framework to organize (i) general causes, (ii) aggregated processes and (iii) specific interactions, constraints and conditions that govern the dynamics of succession was proposed by Picket and co-workers (1987). In order for succession to occur, first disturbance has to create a new site for establishment (site availability), then species have to colonize the site or have survived on-site (species availability) and further on succession will be directed by the differential performance of these species (Fig. 4, chapter 1). At the base of most models and hypotheses on vegetation succession are (i) the differences in functional traits and life histories of species and (ii) how these differences affect the outcome of competition for resources along a successional gradient, i.e. differential species performance. The main limiting resource during forest succession is generally thought to be light and competition for light is thought to fashion a sequential replacement of increasingly shade tolerant species with time (*e.g.* Huston & Smith 1987).

Assuming a predominant role of competition for light during secondary forest development is possible to put forward some predictions regarding stand structure development as well. With accumulating biomass in the course of succession, competition for light is predicted to intensify (Keddy 2001). Competition for light is inherently asymmetric, that means that larger trees shade smaller trees, and not the other way around. Bigger trees would thus have an advantage and grow disproportionably fast compared with smaller individuals, while the smallest individuals would suffer highest mortality rates. During the successional development of a secondary forest stand, a growing basal area and average tree size is thus expected to be accompanied by a declining stem density and increasing size-inequality.

Long-term chronosequences in a wide variety of tropical forest types confirm expected patterns of compositional and structural change, *e.g.* in humid lowland forests (*e.g.* Saldarriaga *et al.* 1988), upper montane forest (*e.g.* Kappelle *et al.* 1995; Kappelle *et al.* 1996) or dry tropical forests (Kennard 2002; Lebrija-Trejos *et al.* submitted). Successional dynamics, however, are inferred rather than directly monitored in such studies; and this goes all the way to the level of underlying processes such as competition. Long-term permanent-plot studies in the temperate zone demonstrated that actual developments may diverge considerably form patterns predicted from chronosequences (*e.g.* Hibbs 1983; Pickett *et al.* 2001). From the few published time studies on tropical forest succession a similar picture emerges. During the first five years of succession in plots in Ghana (Swaine & Hall 1983) and in the Venezuelan Amazon (Uhl 1987), high stand dynamics resulted from complex patterns of species and stem turnover. In a long-term chronosequence originally set up by Eggeling (1947), stand dynamics were monitored from the 1930-40s to the early 1990s; Sheil *et al.* (2000) found that changes over this period were less consistent than predicted from the original chronosequence. In a sixty-year old secondary forest in Panama, intra- and interspecific growth and mortality rates were highly variable, and presumably related to differing resource conditions and life-history traits (Milton *et al.* 1994). In four secondary forests in Costa Rica with initial age ranging from 12-25 years, mortality and recruitment rates varied between sites, size-classes, and census years (Chazdon *et al.* 2005).

These observations support the notion that the complexity of interrelated factors and ecological processes that influence the course of succession, on any particular place and at any particular moment along the successional time-axis, as well as the probabilistic nature of many of them, can not be captured by evaluating their net effects only. For a better understanding of the variation in rates and directions of secondary forest succession, detailed studies are needed that monitor vegetation dynamics over time. The present study focuses on community dynamics in the first years of secondary forest succession on abandoned agricultural fields, and on the role of competition on the level of individuals, populations and communities. Its main aims are: 1) To evaluate the dynamics of young secondary forests on abandoned agricultural fields in terms of community changes and to asses how these dynamics change with time since abandonment; 2) To evaluate the dynamics of young secondary forests in terms of growth, mortality and recruitment, and how community changes are related to these processes; and 3) To examine the degree to which competition for light can account for variation in growth and mortality of saplings within a population and for variation in population dynamics across distinct sites.

The following summary goes from local interactions (neighborhood competition), between-site variation in population dynamics of the same species, to community dynamics. The paragraphs describe how variability in growth and survival of saplings in a young secondary forest environment is related to small-scale heterogeneity in neighborhood crowding and especially to variation in the basal area of the larger neighbors. They further evaluate how population dynamics of a species can differ from one secondary forest patch to another, and how this can be related to the concept of asymmetric competition. Then rates of change of stand structure of young secondary forests are assessed in terms of growth, mortality and recruitment and related to initial stand structure. Finally patterns and short-term dynamics of species richness and dominance are evaluated.

COMPETITION AFFECTS GROWTH AND SURVIVAL OF INDIVIDUAL TREES

Competition is a mechanism that operates on the level of individual trees. A tree competes with its neighbors for resources, not with the whole community (*e.g.* Peterson & Squiers 1995; Uriarte *et al.* 2005b). Growth of trees within populations varied considerably (Chapter 5 and 6), and was strongly suppressed in most of them (Fig. 1). Potential maximum growth rates of *Cecropia peltata* and *Trichospermum mexicanum* (henceforth referred to by their genus name) were estimated from three years growth increment data from 11 permanent plots (Appendix A). The two species are the most frequent and abundant species in the secondary forests of the study region (Chapter 2). Across populations in various young secondary forests plots, an average of over 60% of trees obtained less than 10% of its potential growth, while less than 3% obtained 25% or more of its potential growth (Fig. 1). This thesis addresses the hypothesis that competition for light can account for (an important part of) such patterns of growth reduction and variation in growth.

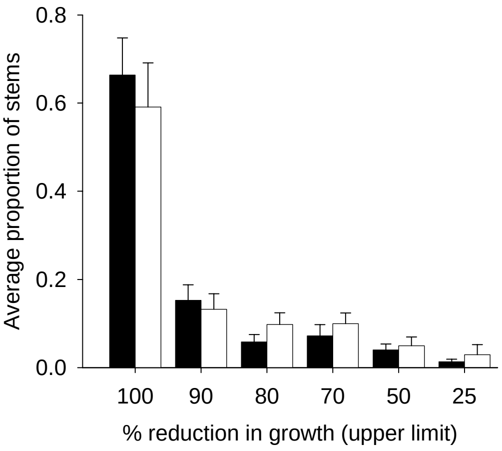


FIGURE 1. The among-population means (n = 7) of the fractions of stems within each growth reduction class. Growth reduction is computed for each tree as percentage of its potential growth, and potential growth was approximated by fitting a non-linear quantile regression through the upper 0.99-quantiles of diameter increment data of *Cecropia* (black bars) and *Trichospermum* (white bars). Whiskers give standard error. See Appendix A for approximated growth functions.

Both below-ground competition for water and nutrients and above-ground competition for light can affect growth and survival of trees. While competition for light is largely asymmetric, competition for soil resources appears to be size-symmetric, i.e. plants take a share of the contested resources proportional to their size (Schwinning & Weiner 1998; Casper *et al.* 2003). So when competition is important, variation in growth and survival will be related to some measure of competition intensity, *e.g.* the basal area of its neighbors. If light is more limiting than soil resources, growth and survival will thus be largely affected by the taller neighbors. If not, the influence of smaller neighbors will be proportional to their size.

Within a population, variation in radial stem growth and vertical stem extension of similar sized *Cecropia* and *Trichospermum* trees strongly decreased with increasing basal area of larger neighbors. Competition also affected allocation patterns. In the first year of succession, the height-diameter ratio (slenderness) of *Cecropia* and *Trichospermum* was strongly and positively related to basal area of taller neighbors. This is typically found for pioneer species in crowded conditions (Kohyama & Hotta 1990; Hara *et al.* 1991; King 1994; Sterck 1999; Poorter 2001; Dekker *et al.* 2007). Results indicate that as succession proceeds and competition becomes more intensive, the rate of change in slenderness decreases, i.e. height and diameter become both equally suppressed. These results fit to the general order of priorities with which trees allocate limited carbohydrates to different functions. When suppressed, a tree will first cut back on allocation to branching and diameter growth, then on height growth, and finally on renewal of foliage and fine roots (Sterck 2005; Turnbull 2005). Height growth will have priority over diameter growth, because it allows plants to acquire better light conditions (King 1990).

Mortality among individuals of *Trichospermum* was close to zero, and mainly confined to the smallest trees. Mortality of *Cecropia*, on the other hand, was very high and strongly related to size. Variation in neighborhood competition accounted only for a small proportion of the variation in survival (Chapter 6 and 7). Strong competition will not result directly in the death of a tree. Such an event will be preceded by a period of reduced growth and shedding of leaves, before the tree will fail to pay for respiration costs (Sterck 2005; Turnbull 2005). Other mechanisms affect survival as well, for example water stress during periods of drought (Poorter & Hayashida-Oliver 2000) or herbivore and pathogen attacks (Brown & Ewel 1987). These factors may interact with – or operate independently of neighborhood crowding (Howlett & Davidson 2001; Pearson *et al.* 2003a). Growth thus represents a more direct response to competition than mortality and, consequently, is easier to relate to neighborhood competition (Poorter 1998).

A significant relationship between basal area of smaller neighbors and diameter growth (*Cecropia*) and slenderness (both species) suggest a role for belowground competition. However, smaller neighbors had a negative effect on slenderness, opposite to the effect of the taller neighbors and to what would be expected from competition. Across all target trees, over 87% of smaller neighbors belonged to 6 pioneer taxa. A negative relationship between slenderness and basal area of smaller neighbors might, thus, also reflect a co-varying response to elevated light availability. Following this line of reasoning, the negative effect of smaller neighbors on diameter growth of *Cecropia* could be explained as the result of competition for light between overlapping crowns. Crown depth of *Cecropia* is strongly related to light availability and neighborhood crowding was on average much higher below *Cecropia* than below *Trichospermum* (Chapter 6).

A large part of the variation in growth and survival of early pioneer species, such as *Cecropia* and *Trichospermum*, can thus be related to small-scale spatial patterns in intensity of neighborhood competition. Results suggest that competition for light may, indeed, be an important mechanism directing population dynamics of such species in the first years of secondary forest succession. Population dynamics of a species may differ considerably between different secondary forest patches. The next question is if asymmetric competition – that operates on individual plant level – can account for this variation.

ASYMMETRIC COMPETITION AND VARIATION IN POPULATION DYNAMICS

Population structure and dynamics of a species can differ very much across secondary forests (Chapter 7, Table 2). Within study sites, growth was size related, but in different and contrasting ways: the smaller individuals of a population grew on average faster or slower than the larger individuals, had a higher or lower survival, or there were no significant difference. Survival rates of the smallest individuals, on the other hand, were consistently lower across all populations (Chapter 7, Fig. 4). This is generally found in studies on the demography of tree species (*e.g.* Piñero *et al.* 1984; Alvarez Buylla & Martinez Ramos 1992; Condit *et al.* 1995; Zuidema & Boot 2002). The smaller individuals of a population are expected to have a higher number of taller neighbors than the larger individuals of that population, i.e. they are expected to experience stronger asymmetric competition. Results of chapter 6 indicate that asymmetric competition for light is one of the main mechanisms regulating tree growth and mortality of the dominant pioneer species. Consequently growth and survival rates of the smaller individuals are expected to be, on average, lower than the population mean, while for the largest individuals the opposite is expected. How does that relate to the diverging patterns of the different populations that were observed?

To answer this question, measures of growth asymmetry and survival asymmetry were related to competition asymmetry. The three variables approximate how much the smaller trees in a population differ from the larger trees with regard to, respectively, their average growth, their survival probability and the degree of asymmetric competition they experience (Chapter 7). Survival asymmetry was related to competition asymmetry only in *Trichospermum*. Many factors and processes that affect survival may be size-dependent, and it is difficult to disentangle them from the effects of asymmetric competition for light. More structural support and reserves may allow larger plants to better endure environmental stress (Lieberman *et al.* 1985; Clark & Clark 1992; Condit *et al.* 1995; Blundell & Peart 2001). A larger root system may give plants better access to deeper soil water resources during dry periods (Caspersen & Kobe 2001; Casper *et al.* 2003; Hutchings *et al.* 2003). Soil water and nutrient availability and herbivore or pathogen outbreaks may be a very local phenomena and account for the large between-population variation in survival asymmetry. High survival, low average survival asymmetry, and the shallow slope of its relationship between survival asymmetry and competition asymmetry indicates that *Trichospermum* not only tolerates higher levels of competition than other pioneer species, but is also less affected by other (size-related) mortality agents.

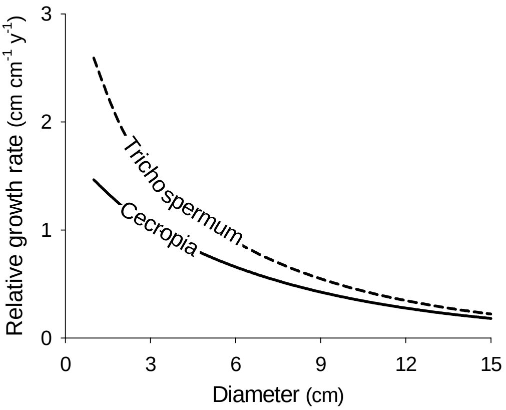


FIGURE 2. Estimated relative growth rate curves, computed from equations 1 and 2, Appendix I

Growth asymmetry of three out of four early pioneer species increased linearly with increasing competition asymmetry, from negative values (smaller trees grow faster than larger trees) to positive values (larger trees grow faster than smaller trees). These results suggest that the diversity in size-related growth variability among different populations reflects a successional pathway that is related to tree size and asymmetric competition. The potential relative growth rate of a plant will decrease because the mass fraction of productive tissues (leaves, fine roots) will decrease as the plant accumulates more support mass during growth (Vanclay 1994; Veneklaas & Poorter 1998). Potential relative growth rate for *Cecropia* or *Trichospermum* was estimated to decrease from respectively 1.5-2.6 cm cm^{-1} y^{-1} at 1 cm DBH, to only 0.4-0.5 cm cm^{-1} y^{-1} at 10 cm DBH (Fig. 2). Competition asymmetry can be low because of low population size inequality or because the distribution of smaller trees is biased towards more open places. Either way, it results in negative growth asymmetry. When competition asymmetry increases, growth of the smaller individuals becomes more strongly suppressed than growth of the larger individuals. Consequently growth asymmetry will become increasingly positive as the competitive advantage related to larger size compensates for an inherently lower RGR.

STRUCTURE AND DYNAMICS ON THE SCALE OF INDIVIDUAL TREES

The canopy position of a tree depends on its neighbors as much as on its own size. Stand structure of young secondary forests may differ very much, even when successional age is similar (Chapters 2, 4, 5). For example, basal area varied between 3 and 21 m^2 ha^{-1}; stem density between 370 and 1570 stems/500 m^2; and average canopy height between 3.2 and 4.5 m among five plots of two years old. Ultimately, within- and between-site variation in growth and mortality rates relate to within-site variation in stand structure, and to the degree to which stands differ in that respect, rather than to average plot values. Young secondary forests are often described as having an uniform canopy (*e.g.* Oldeman 1990; Richards *et al.* 1996). Nonetheless, on the small spatial scale on which competitive interactions operate, these forests can be very heterogeneous. Neighborhood basal area of individual trees, even when of similar height, was found to be very variable (Chapter 6). Figure 3 gives an impression of the degree of spatial heterogeneity in eight study sites in the vertical (white vs. grey box-plots) as well as horizontal plane (variation indicated by a box-plot).

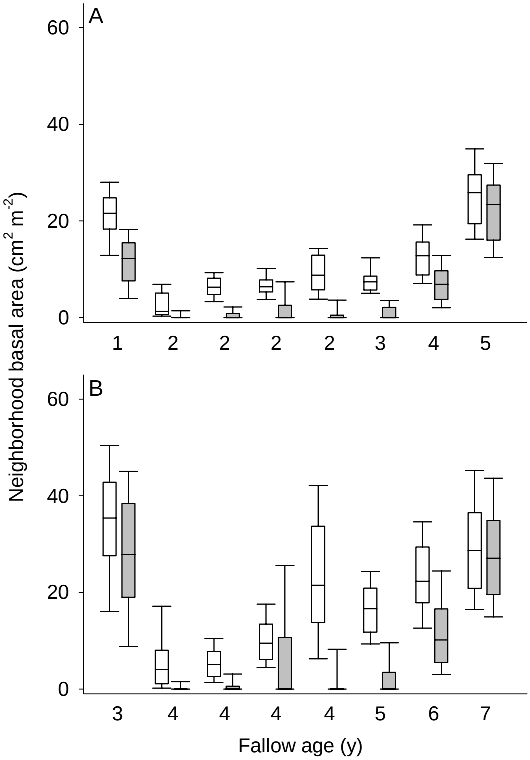


FIGURE 3. Spatial-temporal variability in neighborhood basal area. For fifty randomly selected 1x1 m quadrants, the sum of the basal area of all trees that were rooted in the same quadrant or one of the 24 adjacent quadrants was computed. *White box plots*: All trees with height ≥ 1.5 m included. *Grey box plots*: All trees with height ≥ 4.5 m (second and third plot) or ≥ 6.0 m (other plots) included. A) Initial census. B) A census two year later. Approach was similar as in chapter 5.

Both average and variation in neighborhood basal area increased in most plots (compare Fig, 3A and B), indicating that competition pressure not only varied strongly over short distances but over time as well (see also chapter 4). A tree is growing in a dynamic context, and whether growth results in an improvement of its canopy position depends on how fast it grows relative to its neighbours. When competition is asymmetric, the growth increment of a tree will stay behind the growth of its larger neighbors. Moreover, this effect will be stronger according as the initial difference is larger, i.e. as the neighborhood basal area of taller neighbors is bigger. This patterns was found among the target trees of Chapter 4 (see Fig. 4A), providing additional evidence that competition was asymmetric.

AND THE IDENTITY OF NEIGHBORS?

In this study, we used a simple competition model assuming that all competitors had equivalent effects on the target trees, regardless of their identity. An ongoing debate in ecological research is questioning this assumption of species equivalence (Hubbell 2005; Uriarte *et al.* 2005b). Recently several studies in temperate forests (*e.g.* Peterson & Squiers 1995; Canham *et al.* 2004; Doležal *et al.* 2004; Canham *et al.* 2006) and in tropical forests (Hubbell *et al.* 1990; Peters 2003; Uriarte *et al.* 2004a; Uriarte *et al.* 2004b) demonstrated that species may have a different effect upon growth of target trees, although about half of the target species did not respond to the identity of neighbors in some of these studies (Hubbell *et al.* 1990; Peters 2003; Uriarte *et al.* 2004b).

When competition is mainly for light, interspecific differences in crown light transmittance represent the most relevant aspect of neighborhood identity. In temperate and tropical secondary forests long-lived pioneers are found to caste a deeper shade below their crowns than short-lived pioneers, mainly due to a higher unit leaf area per unit aboveground mass and LAI (Canham *et al.* 1994; Kitajima *et al.* 2005). Selaya *et al.* (2007), on the other hand, found that differences between these two groups with regard to biomass allocation and crown structure resulted in the similar a light capture per unit mass. Differences among early secondary species, such as dominated our stands (Chapters 2-4), appear to be relatively small (Canham *et*

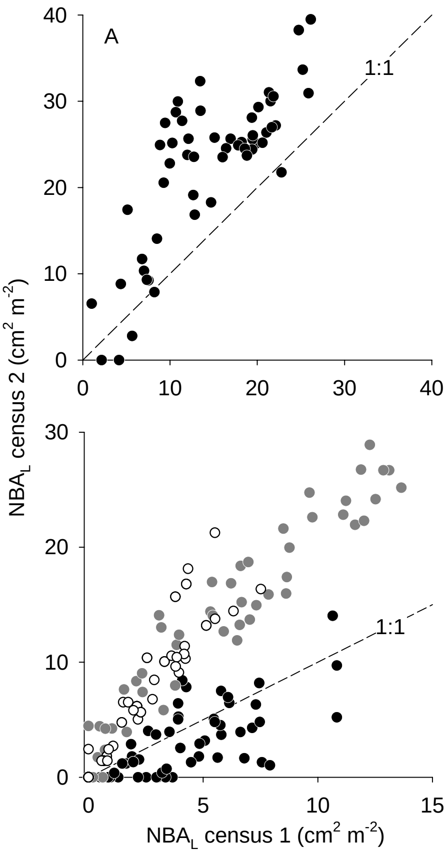


FIGURE 4. Change of neighborhood basal area over 1 year. In each census, only neighbors that were taller than the target trees were included. Target trees were *Trichospermum mexicanum* saplings, height 3.5 m - 4.5 m). A) All species. Correlation coefficient (*r*) = 0.81. The slope of the regression line deviates significantly from the 1:1 line. B) Neighborhood basal area including only specific species: *Cecropia peltata* (black dots, *r* = 0.69), *Trichospermum mexicanum* (grey dots, *r* = 0.96) and *Ochroma pyramidale* (white circles, *r* = 0.94). Slopes deviate significantly from the 1:1 line in case of *Trichospermum* and *Ochroma*. See chapter 6 for methods.

al. 1994; Kitajima *et al.* 2005; Selaya *et al.* 2007).

Spatial or compositional variation of vegetation below the main canopy may further reduce the relationship between identity of larger neighbors and light availability (Kabakoff & Chazdon 1996; Nicotra *et al.* 1999; Denslow & Guzman 2000; Montgomery & Chazdon 2001; Kitajima *et al.* 2005). A tree generally has to deal with different species in its neighborhood. Across all the sites of Fig. 3, an average of 40.7 (± 3.8 SE) neighbors taller than 1.5 m, representing an average of 7.4 (± 3.8 SE) species, were present in the 25 m^2 neighborhood areas around the randomly selected points. Taken neighbors taller than 4.5 m, these figures were 10.6 (± 1.6 SE) trees and 3.5 (± 0.3 SE) species.

Moreover, species dynamics in youngest stands is very high (Chapter 3, 5). Patterns of growth and mortality can diverge strongly among the dominant species in early secondary forest, which might result in drastically changing dominance patterns over short periods of time (Chapter 3). Composition of the tallest neighbors of a target trees may thus change rapidly (Fig. 4B). Neighborhood basal area at a particular moment may predict both basal area in a following census (Fig. 4A) and growth reduction of the target tree (Chapter 6), despite strong shifts in the species that dominates the neighborhood basal area (Fig. 4B). These results suggest that the size of a neighbor matters much more than identity.

TRENDS AND RATES OF CHANGE OF COMMUNITY STRUCTURE

The chronosequence based on data from the initial census of the permanent plots (Chapters 3-5) indicated successional trajectories similar to findings of most chronosequence studies (see review in chapter 1). The trajectories predicted an increasing basal area, canopy height and average diameter increase, and decreasing slope of the stem size distribution as succession advances, and no predictable trend with age of stem density (Chapter 4). Many of the real changes over time followed these predictions, but with completely different rates of change. Variation between plots was very substantial, by that indicating the unpredictability of successional patterns. As a result, the initial relationship between sites, assumingly reflecting differences in age, changed or completely disappeared. The statistical analyses of chronosequences suggest the existence of age-related successional trends, assuming that different sites represent points on the same successional pathway. The findings of this study, on the contrary, demonstrate that they represent different successional pathways that are results of different local histories (*e.g.* colonization patterns) and local dynamics.

Although the relative rate of change in community structural attributes varied considerably among plots, a general pattern was found of very high rate values early in succession followed by a rapidly decline in these rates with age of succession (Chapter

4). The disentanglement of community dynamics in tree mortality, growth, and recruitment demonstrated that the decline in the rate of change of community attributes, such as basal area, is a consequence of reduction in recruitment, mortality, and growth rates. Very early in succession (< 5 y), relative mortality, recruitment, and growth rates were very high with highest relative annual growth rates even exceeding 100%. At 20 years, dynamics were much lower. Net rate of change may, however, sometimes conceal the true dynamic nature of a stand. In three plots, sudden massive mortality among the dominant species resulted in high recruitment and high growth rates among the remaining trees. The resulting net change in basal area was very modest, suggesting low dynamics in plots that, in fact, underwent very dramatic changes.

The findings of this study indicate that successional patterns of size-related attributes (canopy height, mean diameter, basal area) are governed by different processes than patterns related to numbers (stem density). All size-related community attributes were mutually correlated, and so were their relative rates of change. Stem density, however, was unrelated to all of them, contrary to successional models that predict a negative relation between stem density and statistics of tree size distribution (Niklas *et al.* 2003b). A decreasing slope of diameter frequency distributions (α) is the result of trees growing in larger size classes and/or relative high mortality in the smaller size classes. Across sites, α was correlated with stand basal area but not with stem density, and this holds for the rates of change of these variables (Chapter 4). So it appears that stand structure development, in the sense of biomass and size structure, is determined largely by continuous growth increments of persisting trees, while highly variable patterns of recruitment and mortality result in independently changing stem densities.

In line with this conclusion, relative growth rates of basal area were much higher than relative basal-area-based mortality and recruitment rates, and drove patterns of basal area increment. Recruitment of trees was mostly in the smallest size classes and had consequently little impact on basal area increment in most sites. Basal area removal due to mortality was generally much lower than basal area growth increments because mortality was concentrated in the lower stem size classes. These patterns suggest that asymmetric competition played a role in community dynamics. Competition-mediated variation in growth and mortality is expected to affect mainly the smaller individuals of a community, resulting in their suppressed growth and higher mortality, while the taller remain unaffected (Midgley *et al.* 2002; Coomes *et al.* 2003). Indeed, basal area growth was concentrated into a relatively small proportion of the trees, and this proportion declined with increasing initial stand basal area.

Patterns as discussed above did not occur consistently across all plots. As mentioned before, episodic events of mass mortality occurred in three sites, apparently due to a pathogen outbreak (Chapter 3-4). Two of these sites were 2-year old stands dominated by *Trema micrantha* (H2 and F2 in chapter 4, the second and third plot in Fig, 3) and the other site was a 9-year old stand dominated by Ochroma pyramidale (S8 in chapter 4). In all cases, mortality occurred irrespective of size, and eliminated most of the dominant canopy trees. Adjacent older secondary forest dominated by *Trichospermum mexicanum* facilitated the subsequent abundant regeneration of this species in the two youngest sites, resulting in relatively little change in all stand structure attributes over a 2-years period. The death of large canopy trees in older stands imply stronger changes and growth of other trees will take longer to replace basal area loss (Chapter 4). In the 9-year old stand, it appears that absence of nearby seed sources impeded enhanced recruitment, hence stem density declined. However a time study over the first 17 years of succession in Costa Rica, with a similar drastic decline in the dominant canopy species (see Chapter 5), indicate that such patterns reflect fluctuations rather than long-term trends. The relationship between short-term observations and processes and longer-term trends seem difficult to assess and may require up to several decades of monitoring forest dynamics (Sheil & May 1996; Sheil *et al.* 2000).

The discussion of some very site-specific events and developments may appear to have little generality to other sites. However, they further emphasize the complexity of forest change. Results of this thesis indicate that short-term successional forest development is driven by size-related growth, recruitment and mortality, mediated by the process of asymmetric competition for light. On the other hand, the significance of a range of influences upon vegetation dynamics and the role of more stochastic elements, such as disturbance and landscape configuration, imply that every site is a product of local history (Chazdon 2003). Defining the particular may be necessary to elucidate the role and generality of specific processes across sites (Sheil *et al.* 2000), such as size and competition-related dynamics that were the focus of this thesis.

SHORT TERM TREE SPECIES DYNAMICS

PIONEER SPECIES AND PATTERNS OF DOMINANCE

Most secondary forests are dominated by few species in terms of numbers and basal area (Chapters 2-4); and across sites these tend to come from a very small subset of the regional species pool (Chapter 2; *cf.* Finegan 1992). Patterns and dynamics of canopy dominance appear to be driven partly by the differential response of the major canopy species to variation in competition levels that characterize early successional vegetation (Chapter 3-7). Four of the most abundance species across the secondary forests of the study region (*Cecropia*, *Trichospermum*, *Trema micrantha* and *Schizolobium parahyba*; Chapter 2) are classical examples of pioneer species: highly light demanding, fast growing and with an efficient dispersal mechanism (as judged from their frequencies across the region). Yet, they differed considerably in potential growth rates, overall mortality rates, and the strength of their response to the variation in levels of

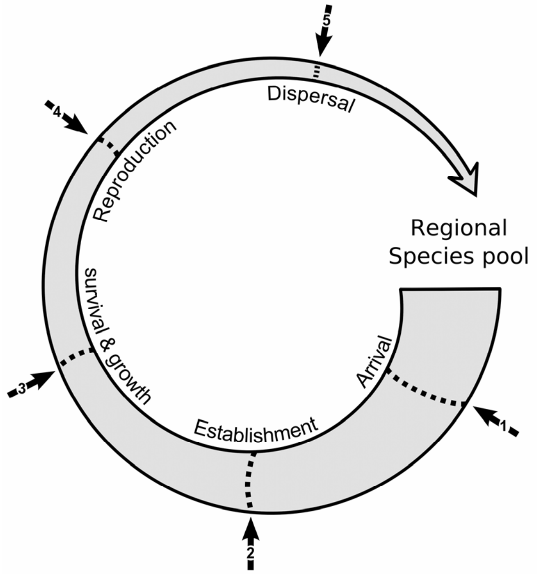


FIGURE 5. The contribution of a secondary forest to the maintenance of regional tree diversity depends on a cyclic chain of events that include arrival; establishment; growth to maturity; reproduction; and dispersal to new suitable sites of species from the regional species pool. These events are governed by assembly rules that may de defined as a hierarchical set of filters (1-5) that operate along this chain of events and determine the probability of a species to pass all life stages, and to contribute again to the regional species pool, under a particular set of circumstances, given their particular set of functional traits (*cf.* Fig. 1.4). See text for further discussion on this figure.

neighborhood competition (Chapters 6-7). Pioneer species are often compared with mid- and late successional species and are found to have a relative narrow range of variation with regard to life history and functional traits compared with the other groups (*e.g.* Clark & Clark 1992; Kammesheidt 2000). In a study on secondary forest dynamics, it might be more relevant to compare the behavior of dominant pioneer species against the range of variation typical for their habitats (see *e.g.* Pearson *et al.* 2003b; Dalling *et al.* 2002, 2004; Poorter *et al.* 2006).

Elements of the trade-off thought to be typical for pioneer species, such as a wide ecological range, efficient seed dispersal, and a seed bank (Whitmore 1990), would enhance the probability of a wide distribution across a landscape dominated by secondary forests. Yet, the distribution patterns of trees across secondary forests in our region demonstrate that the frequency of occurrence varies widely among pioneer species (Chapter 2). While a large group occurred at a high frequency relative to the distribution of shade tolerant species, about 50% of the pioneer occurred in < 5% of all sites. On the other hand, only 3 species occurred in > 40% of all sites. Different assembly rules may determine patterns of frequency and dominance (Fig. 5), ranging from aspects that directly affect dispersal (*e.g.* landscape configuration and local species pools), to local site factors and biotic interactions (*e.g.* competition). While it may be clear that dispersal limitations constitute the main selective filter for many shade tolerant species, this might be less clear in case of pioneer species.

The prediction of different phases during the first decades of forest succession, dominated by respectively early pioneers and long-lived pioneers for time-periods according to their longevity (Gomez-Pompa & Vazquez-Yanes 1981; Finegan 1984), finds support in several chronosequence studies (*e.g.* Saldarriaga *et al.* 1988; Aide *et al.* 2000). However from this and earlier time-series studies (Swaine & Hall 1983; Uhl 1987) it is clear that a decline in a dominant species may occur long before the end of its lifespan. The results of this study indicate that competitive replacement of one dominant canopy species by another may be the responsible mechanism in some cases. Incidental, stochastically occurring events such as an outbreak of pathogens may result in very drastic changes, similar to what has been found in temperate young successional forests (Toyohara & Fujihara 1998). These observations accentuate that very high dynamics during the early years of succession can complicate the interpretation of dominance patterns across a range of secondary forests, and highlight the necessity for detailed time-series studies.

PATTERNS OF RECRUITMENT, SPECIES DENSITY AND SHADE-TOLERANT SPECIES

Initial species density varied considerably across all permanent monitoring plots, but was still significantly related to fallow age. Among the youngest plots (initial age ≤ 5 y), the rates of species gain diverged less than the differences in initial diversity (see Chapters 3 and 5) and were reasonably in line with the chronosequence prediction. In the three older sites, species density increased slower. Including these sites in the chronosequence data resulted concordantly in a prediction of a decreasing rate of species accumulation with fallow age. The prediction of decreasing rates of loss and gain of species with initial age was actually observed over a three-year period (Chapter 4-5), although the quantitative predictions of this chronosequence model strongly underestimated the rates of gain in the youngest plots. The actual mechanisms behind these observations remain poorly understood. With increasing resident species density, the probability that a recruit belongs to a new species decreases and this could account for the age effect. There was, however, no significant relationship between initial species density and the rate of species gain ($R^2=0.18$, $P=0.19$). The sites differed in the degree of isolation from old-growth fragments, but there was no clear link with number of newly recruited species. Changes in the surrounding landscape matrix (*e.g.* Table 1) may imply that the present species composition reflect past conditions, which complicates the picture.

TABLE 1. Dynamics of secondary forest landscapes. Adjacent vegetation types of 11 permanent sample plots and changes therein over a three years period (see chapter 4). A = agriculture (including pastures); SF = secondary forest; OGF = old growth forest patches. Clearance indicates that (part of the) adjacent secondary forest was cleared for maize cultivation followed by fallow (3 cases) and maize cultivation followed by conversion to pasture (2 cases). Two of the study plots were cleared themselves at the end of the third year.

	A	SF	A+SF	A+OGF + SF
Clearance		1	2	2
No change	1		2	3

As in other mixed-species secondary forest communities (*e.g.* Guariguata *et al.* 1997; Peña-Claros 2003; Capers *et al.* 2005; Toledo & Salick 2006), shade-tolerant species were relatively abundant amongst smaller trees in our study sites. Moreover, a large proportion of newly recruited species were shade tolerant species (Note that recruitment was defined as entering the height class of ≥ 1.5 m). Perhaps more surprisingly, pioneer species continued recruiting in these secondary forest sites and often in large numbers. As most shade tolerant species recruited in very low numbers, pioneer species dominated recruitment in number of stems. Recruitment rates of number of trees were correlated with stand-level mortality, but recruitment rates in number of species were not. This suggests that high mortality rates during the first years of forest succession may open up the canopy and create new recruitment opportunities for more light demanding species. Mortality among the shade tolerant fraction was very low, opposite to the high mortality among the pioneer species. Overall, these results demonstrate that stand-level dynamics in terms of stem density fluctuations reflect mainly patterns of competition-mediated growth, mortality and recruitment among the most abundant pioneer species. The process of continuously accumulating species density or richness is, on the other hand, probably related to the availability and proximity of seed sources, and is relatively independent of site factors and processes in the first years of succession.

AND THE LONG TERM CONTRIBUTION TO THE REGIONAL SPECIES POOL?

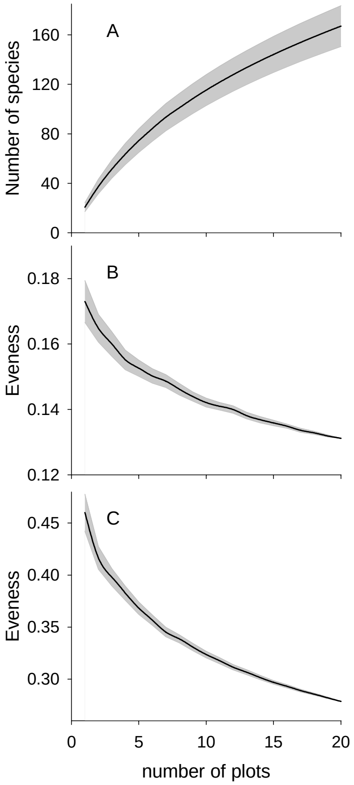
The concurrent decline in old-growth forest cover and increase of secondary forest cover in large parts of the Tropics have caused a growing interest for the role of secondary forests in biodiversity conservation (Finegan & Nasi 2004). A large number of studies have demonstrated that species diversity can increase rapidly in secondary forests, but that it takes much longer (> 100 y) for species composition to converge with the species composition of old-growth forests. Given the current developments in our research area, similar to developments in many other tropical regions (see Chapter 1), most secondary forests will just not become that old. In order to understand the role that those young secondary forests can play in the maintenance of tree biodiversity on landscape scale, we need information on how many and which species are able to arrive, establish, grow to maturity, reproduce and disperse to new sites in these secondary forests (Fig. 5). In other words, which species are able to persist in the secondary forests of an agricultural landscape, and what attributes allow them to do so are important research questions.

High species richness in most of our study sites indicate that still many species are able to reach the sites and establish successfully, although mostly at low numbers. In our study region, species richness increases rapidly with increasing number of sites (Fig. 6A), indicating that species recruitment may come from different local source communities and/or is very stochastic (Capers *et al.* 2005). Of these species, however, only early reproductive pioneer species will contribute from these sites to the local species pool when fallow periods are short. Pioneer species shape structure and dynamics of early secondary forests and create the conditions for establishment and growth of other species. Under the current land-use dynamics in many regions, their importance and dominance can be expected to increase even further and understanding their dynamics is thus of particular importance.

Few pioneer species are widely distributed across the secondary forests of our region and are abundant in many of the forest where they occur, while most pioneer species appear to have a relatively limited distribution (Chapter 2). Complex interactions between landscape configuration, local site factors, biotic interactions and species life history attributes may determine frequency, abundance and dominance of a species. For example, in this thesis drastic changes in abundance and dominance of pioneer trees and saplings were related to factors such as competition for resources or pathogen outbreaks (Chapters 3-7), demonstrating that one-time inventories have to be interpreted cuatiously. Wide dispersal is often considered to be typical for pioneer species (Swaine & Whitmore 1988). Nonetheless, several studies on the seed rain, the soil seed bank, and seedlings of pioneer species in 53 recently formed gaps in the BCI forest, Panama, found dispersal limitation, next to seedling emergence probabilities and species-specific establishment requirements, to be an important determinant of local abundance (Dalling *et al.* 1998a; 1998b).

From a local species pool, only a proportion will arrive at a new site, depending on factors such as distance to the new site and dispersal mechanisms of the species. Several studies evaluated specific aspects of landscape configuration, most commonly

FIGURE 6. Sample-based accumulation curve of species density and evenness. A) The sample-based species rarefaction curve (Mao Tau) and 95% confidence intervals (shaded area), computed using the EstimateS version 7.5 (Colwell, 2005). B+C) Evenness was calculated as the E_{var} index of Smith & Wilson (1996; see equation 1 in chapter 3). Accumulation curves were calculated by computing E_{var} for one sample, then for the pooled data of two samples and so on until all 20 samples were included. This was repeated 100 times with randomized sample order and average and confidence intervals were computed. B) E_{var} calculated based on species basal area. C) E_{var} computed based on species abundance. Chronosequence data from twenty 150 m^2 plots, collected in 1995. See chapter 2 for details.



distance to old-growth forest and the influence of remnant trees (Galindo-Gonzalez *et al.* 2000; Wijdeven & Kuzee 2000; Benitez-Malvido *et al.* 2001). However, species density or richness at any particular moment will be determined by present and past availability and proximity of seed sources. Clearance of vegetation, or successional vegetation development, in surrounding patches implies a continuous change of the surrounding landscape matrix. Exemplary are the fast changes in the surroundings of the permanent study plots (Table 1) and that 18 of the 20 secondary forests that were samples in 1995 were already cleared in 2000, and mostly converted to pastures. Such changes are difficult to include in a chronosequence approach. A site of, for example, 10 years old might not have adjacent old-growth forest at the moment of sampling, just because it was cleared one year before. Moreover, the spatial and temporal dynamics of patches in the surrounding landscape matrix where seeds have different probabilities to reach the seedling stage not only determines the probability of successful dispersal to, but also from a site (Martinez Ramos & Alvarez Buylla Elena 1995). An important next step is therefore to include both the dynamics of secondary forests as well as their surroundings in time-series studies.

Species richness increased with increasing number of sample plots in our research area, but evenness decreased (Fig. 6B, C). Decreasing evenness curves or steep rank-frequency curves (Chapter 2) describe similar aspects of the landscape-scale patterns of species diversity and composition. Low evenness values indicate that plots are dominated by a few species and the decline of evenness values indicates that these few species are largely the same across different plots. Species dominance increases thus with larger spatial scale, i.e. from individual plots to landscape scale. Because dispersal may be a limiting factor even for pioneer species, the distribution and abundance of seed sources is extremely important (Dalling *et al.* 2002). Dispersal to suitable sites for establishment is a stochastic process. An abundant and widespread distribution may thus be an important species attribute in itself because it enhances the probability to be in the proximity of a suitable recruitment opportunity. The landscape-level diversity pattern of existing young secondary forests may thus contribute to a further decline in species evenness in new secondary forest sites (see *e.g.*, Lawrence 2004).

Expectations, as discussed above, imply a limited value of secondary forests for tree biodiversity conservation. However, other indirect functions, such as providing resources for native animals, and buffering and protecting old-growth forest may still imply an important role for secondary forests (Turner *et al.* 1997). Moreover, secondary forests are able to restore rapidly different structural and functional aspects of old-growth forests (Guariguata & Ostertag 2001; Lugo 2002) and can thus be very important for ecosystem functioning and environmental services (*e.g.*, Grau *et al.* 2003), although the relationship between species diversity (i.e. species richness and evenness) and ecosystem resiliency is an important point for further studies (Silver *et al.* 1996).

APPENDIX I

GESTIMATING POTENTIAL GROWTH OF *CECROPIA PELTATA* AND *TRICHOSPERMUM MEXICANUM* IN EARLY SECONDARY FORESTS

Michiel van Breugel & Patrick Jansen

OBJECTIVE

Estimation of the potential growth of the early pioneer species *Cecropia peltata* L. and *Trichospermum mexicanum* (DC.) Baill. in young secondary forests, using data from a permanent plot study.

METHODS

Research was conducted in the southern-most part of Marquéz de Comillas region, between the border of Guatemala and the Montes Azules Biosphere Reserve, within the surroundings of the village of Loma Bonita (approximately 16º04′ N; 90º45′ W), Chiapas, Mexico. The climate is humid tropical, with an average annual temperature of 24 ºC and a mean annual rainfall of ~3000 mm. From February to April there is a dry period with less than 100 mm month^{-1}. For a description of the original vegetation in the region see (Ibarra-Manríquez & Martínez-Ramos (2002).

Twelve secondary forest sites with fallow age varied between 1 and 17 y were selected on abandoned corn fields. All sites were characterized by undulating hills with moderate-steep slopes (15°–30°). Soils of these low hill areas have been described as sandy Humic Acrisols with low pH (4-5), and low total nitrogen and phosphorous content (Siebe *et al.* 1996; Celedón-Muñiz 2006). In each site, the original forest was cut and burned, farmed for maize cultivation for one harvest period only and then abandoned according to the usual practice in this region. In four sites the previous vegetation was respectively 8, 13 and 16 y (2) old secondary forest, in the other sites original vegetation was old-growth forest (i.e. > 100 y). Information on land-use history was obtained from land-owners and other villagers. Both land-use type and geo-morphological unit are very common in the region. More information on the stand structure and dynamics of these sites can be found in Chapters 3-5.

In each site, a 10 x 50 m plot was established. In the first census all trees with diameter at 1.3 m above ground (dbh) ≥ 1cm were recorded, tagged and their dbh and height to the highest leaf were measured. Annually a complete re-census was done, including all trees with height ≥ 1.5 m from the second census onwards.

We used this data to assess effects of limiting factors by comparing realized growth with potential growth (Vanclay 1994 p159: Ek & Monserud 1974, Leary 1979, Arney 1985, Pretzsch 1992) as Δd = Δdmax × f, where the realized diameter increment Δd, the potential diameter increment Δdmax and the limiting factor f are all functions of tree diameter (not including the increment). We estimated Δdmax by fitting a function on the growth increments of the fastest growing individuals across the full range of diameters for which we had large sample sizes (i.e., excluding the smallest and largest individuals). Here we report data of two species (*Cecropia peltata* and *Trichospermum mexicanum*) from 3 censuses. To ensure independence of data and to minimize measurement error (Vanclay 1994 p 160), we used a single annual growth rate value per tree, averaged over the first two years of monitoring for each tree, rather than multiple measurements of annual growth per individual.

We used non-linear quantile regression (Koenker & Bassett 1978; Scharf *et al.* 1998; Koenker 2005) to obtain a diameter increment function through the upper (>99%) quantiles of the data. Quantile regression is a conditional regression technique that allows estimating rates of change for different quantiles of the distribution of responses (Cade *et al.* 1999). For example, Qy(0.75|x), the regression quantile at τ = 0.75, is the 75th percentile of the distribution of y conditional on the values of x. This function minimizes the sum of absolute deviations of the fit from the observed values in such a way that 75% of the values of y are equal or smaller than the regression estimate and 25% of the values are equal or greater. High (>95%) regression quantiles – describing the "envelope" of distributions as – are commonly used to model the upper limit of the response, where limitation by other factors than the explanatory variable is supposedly minimal (Cade *et al.* 1999; Cade & Guo 2000).

Many functions have been proposed to model expected growth increment as a function of current size (reviewed in Vanclay 1994). The function that we used to model

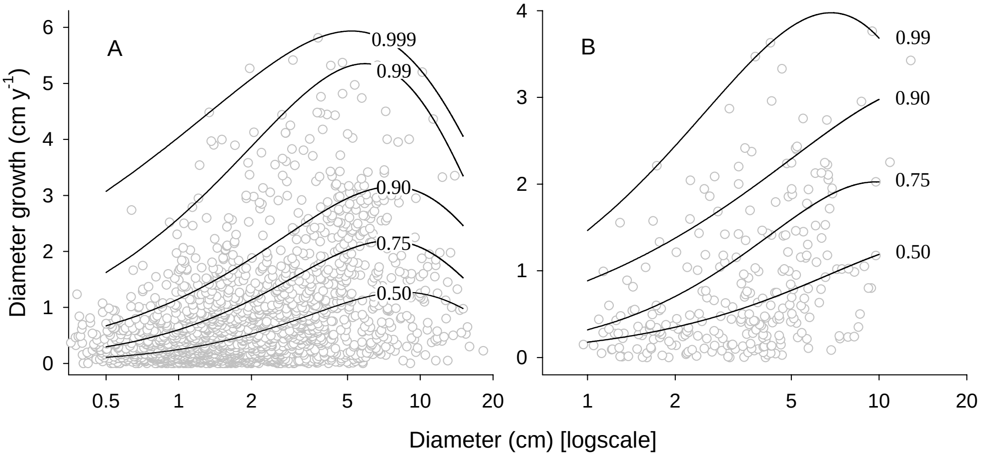


FIGURE 1. Size dependent absolute diameter growth rates in two early successional tree species. Effects of initial size on estimated potential diameter increments. Lines are best non-linear quantile regressions for absolute growth rate. Numbers in graphs give the regression quantiles. Dots are observed diameter increment values for individual trees, averaged over the first two years of monitoring. A) *Trichospermum mexicanum*; B) *Cecropia peltata*.

diameter increment was $\ln\Delta d = \alpha + \beta\cdot\ln d - \gamma\cdot d$ (Vanclay 1994), where d is the original diameter, Δd is the diameter increment and α, β and γ are the estimated coefficients. This equation is realistic for tree growth in that estimates are always positive, allowing some growth even for very large individuals, in contrast to several other common equations that impose a maximum attainable diameter. Zeide (1993) examined many equations for predicting tree growth and found this equation the best alternative for estimating individual tree diameter increment. We fitted the increment function with the "nlrq" routine for nonlinear quantile regression in the R-package "quantreg", which uses likelihood maximization to optimize the fit. We approximated Δdmax for a species as the 99% regression quantile, that gave ≥10 individuals above the regression estimates.

RESULTS

For *Trichospermum* (Fig. 1a), Δdmax was approximated by the 0.99-quantile for individuals $0.5 \le d \le 15$ cm ($n = 2960$) as $\ln\Delta d = 1.08 + 0.77\cdot\ln d - 0.13\cdot d$. For *Cecropia* (Fig. 1b), Δdmax was approximated by the 0.99-quantile for individuals $1 \le d \le 10$ cm ($n = 553$) as $\ln\Delta d = 0.09 + 0.75\cdot\ln d - 0.10\cdot d$. Regression lines for lower quantiles are plotted as well.

REFERENCES

Aber, J. D. 1979. Foliage-Height Profiles and Succession in Northern Hardwood Forests. Ecology 60: 18-23.

Achard, F., H. D. Eva, H.-J. Stibig, P. Mayaux, J. Gallego, T. Richards & J.-P. Malingreau 2002. Determination of Deforestation Rates of the World's Humid Tropical Forests. Science 297: 999-1002.

Aide, T. M. & J. Cavelier 1994. Barriers to Lowland Tropical Forest Restoration in the Sierra Nevada De Santa Marta, Colombia. Restoration Ecology 2: 219-229.

Aide, T. M., J. K. Zimmerman, L. Herrera, M. Rosario & M. Serrano 1995. Forest Recovery in Abandoned Tropical Pastures in Puerto Rico. Forest Ecology and Management 77: 77-86.

Aide, T. M., J. K. Zimmerman, M. Rosario & H. Marcano 1996. Forest Recovery in Abandoned Cattle Pastures Along an Elevational Gradient in Northeastern Puerto Rico. Biotropica 28: 537-548.

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

Aide, T. M. & H. R. Grau 2004. Globalization, Migration, and Latin American Ecosystems. Science 305: 1915-1916.

Álvarez-Buylla, E. R., A. Chaos, D. Piñero & A. A. Garay 1996. Demographic Genetics of a Pioneer Tropical Tree Species: Patch Dynamics, Seed Dispersal, and Seed Banks. Evolution 50: 1155-1166.

Alvarez Buylla, E., R. 1994. Density Dependence and Patch Dynamics in Tropical Rain Forests: Matrix Models and Applications to a Tree Species. American Naturalist 143: 155-191.

Alvarez Buylla, E. R. & M. Martinez Ramos 1992. Demography and Allometry of Cecropia-Obtusifolia, a Neotropical Pioneer Tree. An Evaluation of the Climax-Pioneer Paradigm for Tropical Rain Forests. Journal of Ecology 80: 275-290.

Alves, D. I., J. V. Soares, S. Amaral, E. M. K. Mello, S. A. S. Almeida, O. Fernandes Da Silva & A. M. Silveira 1997. Biomass of Primary and Secondary Vegetation in Rondonia, Western Brazilian Amazon. Global Change Biology 3: 451-461.

Andel, T. v. 2001. Floristic Composition and Diversity of Mixed Primary and Secondary Forests in Northwest Guyana. Biodiversity and Conservation 10: 1645-1682.

Atwood, R. A. 2002. Genetic Parameters and Gains for Growth and Wood Properties in Florida Source Loblolly Pine in the Southeastern United States. Canadian Journal of Forest Research 32: 1025-1038.

Aubréville, A. 1938. La Forêt Coloniale: Les Forêts De L'afrique Occidentale Française. Annales de l'Académie des Sciences Coloniales 9: 1-245.

Augspurger, C. K. 1984. Seedling Survival of Tropical Tree Species: Interactions of Dispersal Distance, Light-Gaps and Pathogens. Ecology 65: 1705-1712.

Augspurger, C. K. & C. K. Kelly 1984. Pathogen Mortality of Tropical Tree Seedlings. Experimental Studies of the Effects of Dispersal Distance, Seedling Density and Light Conditions. Oecologia 61: 211-217.

Bakker, J. P., H. Olff, J. H. Willems & M. Zobel 1996. Why Do We Need Permanent Plots in the Study of Long-Term Vegetation Dynamics? Journal of Vegetation Science 7: 147-156.

Balvanera, P., C. Kremen & M. Martínez-Ramos 2005. Applying Community Structure Analysis to Ecosystem Function: Examples from Pollination and Carbon Storage. Ecological Applications 15: 360-375.

Barberis, I. M. & E. V. J. Tanner 2005. Gaps and Root Trenching Increase Tree Seedling Growth in Panamanian Semi-Evergreen Forest. Ecology 86: 667-674.

Bazzaz, F. A. 1990. Plant-Plant Interactions in Successional Environments. In J. B. Grace and D. Tilman (Eds.). Prespectives on Plant Competition, pp. 240-263. Academic Press, San Diego, USA.

--- 1996. Plant in Changing Environments. Linking Physiological, Population, and Community Ecology. Cambridge University Press, Cambridge, UK.

Begon, M., C. R. Townsend & J. L. Harper 2006. Ecology: From Individuals to Ecosystems. Blackwell Science, Oxford, UK.

Belcher, J. E. S., P. A. Keddy & L. Twolan-Strutt 1995. Root and Shoot Competition Intensity Along a Soil Depth Gradient. Journal of Ecology 83: 673-682.

Bellingham, P. J., E. V. J. Tanner & J. R. Healey 1994. Sprouting of Trees in Jamaican Montane Forests, after a Hurricane. Journal of Ecology 82: 747-758.

--- 1995. Damage and Responsiveness of Jamaican Montane Tree Species after Disturbance by a Hurricane. Ecology 76: 2562-2580.

Benitez-Malvido, J., M. Martínez-Ramos & E. Ceccon 2001. Seed Rain Vs. Seed Bank, and the Effect of Vegetation Cover on the Recruitment of Tree Seedlings in Tropical Successional Vegetation. In G. Gottsberger and S. Liede (Eds.). Life Forms and Dynamics in Tropical Forests, pp. 1-18. Cramer, Stuttgart.

Berntson, G. M. & P. M. Wayne 2000. Characterizing the Size Dependence of Resource Acquisition within Crowded Plant Populations. Ecology 81: 1072-1085.

Blay, D. 2003. Tropical Secondary Forest Management in Humid Africa: Reality and Perspectives. In C. Geldenhuys, F. Castañeda, H. Savenije and M. Kuzee (Eds.). Proceedings of the Workshop on Tropical Secondary Forest Management in Africa: Reality and Perspectives, Kenya, 9-13 December 2002, FAO, Nairobi, Kenya.

Blundell, A. G. & D. R. Peart 2001. Growth Strategies of a Shade-Tolerant Tropical Tree: The Interactive Effects of Canopy Gaps and Simulated Herbivory. Journal of Ecology 89: 608-615.

Bond, W. J. & J. J. Midgley 2001. Ecology of Sprouting in Woody Plants: The Persistence Niche. Trends in Ecology and Evolution 16: 45-51.

--- 2003. The Evolutionary Ecology of Sprouting in Woody Plants. International Journal of Plant Sciences 164: S103-S114.

Bongers, F., J. Popma, J. M. Del Castillo & J. Carabias 1988. Structure and Floristic Composition of the Lowland Rain Forest of Los Tuxtlas Mexico. Vegetatio . 1988; 74: 55-80.

Bongers, F. & F. J. Sterck 1998. Architecture and Development of Rainforest Trees: Responses to Light Variation. In D. M. Newberry and H. H. T. Prins (Eds.). Dynamics of Tropical Communities, pp. 125-162, London, UK.

Bongers, F. & E. Blokland 2003. Forêts Secondaires: Stades De Succession Écologique Et Multiples Chemins. In M. Kuzee, H. Savenije and F. Castañeda (Eds.). Actes de l'atelier régional sur la gestion des forêts tropicales secondaires en Afrique francophone: Réalité et perspectives, pp. 19-34. FAO/IUCN, Douala, Cameroon, 17-21 Novembre 2003.

Boucher, D. H., J. H. Vandermeer, I. G. de la Cerda, M. A. Mallona, I. Perfecto & N. Zamora 2001. Post-Agriculture versus Post-Hurricane Succession in Southeastern Nicaraguan Rain Forest. Plant Ecology 156: 131-137.

Box, G. E. P. & D. R. Cox 1964. An Analysis of Transformation. Journal of the Royal Statistical Society B 26: 211-243.

Brearley, F. Q., S. Prajadinata, P. S. Kidd, J. Proctor & Suriantata 2004. Structure and Floristics of an Old Secondary Rain Forest in Central Kalimantan, Indonesia, and a Comparison with Adjacent Primary Forest. Forest Ecology and Management 195: 385-397.

Breugel, M. v., M. Martínez-Ramos & F. Bongers 2006. Community Dynamics During Early Secondary Succession in Mexican Tropical Rain Forests. Journal of Tropical Ecology 22: 663-674.

Breugel, M. v., F. Bongers & M. Martínez-Ramos in press. Species Dynamics During Early Secondary Forest Succession: Recruitment, Mortality and Species Turnover. Biotropica.

Brown, B. J. & J. J. Ewel 1987. Herbivory in Complex and Simple Tropical Successional Ecosystems. Ecology 68: 108-116.

Brown, D. & K. Schreckenberg 1998. Shifting Cultivators as Agents of Deforestation: Assessing the Evidence. ODI, London.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. Cid Ferreira & R. A. Victoria 1995. Uncertainty in the Biomass of Amazonian Forests: An Example from Rondonia, Brazil. Forest Ecology and Management 75: 175-189.

Brown, S. & A. E. Lugo 1982. The Storage and Production of Organic Matter in Tropical Forests and Their Role in the Global Carbon Cycle. Biotropica 14: 161-187.

Brown, S., A. J. R. Gillespie & A. E. Lugo 1989. Biomass Estimation Methods for Tropical Forests with Applications to Forest Inventory Data. Forest Science 35: 881-902.

Brown, S. & A. E. Lugo 1990. Tropical Secondary Forests. Journal of tropical ecology 6: 1-32.

Brown, S. 1997. Estimating Biomass and Biomass Change of Tropical Forests: A Primer, Forestry Paper 134. FAO, Rome.

Budowski, G. 1965. Distribution of Tropical American Rain Forest Species in the Light of Successional Processes. Turrialba 15: 40-42.

--- 1970. The Distinction between Old Secondary and Climax Species in Tropical Central American Lowland Forests. Tropical Ecology 11: 44-48.

Bullock, S. H. 1995. Plant Reproduction in Neotropical Dry Forests. In S. H. Bullock, H. A. Mooney and E. Medina (Eds.). Seasonally Dry Tropical Forests, pp. 277-303. Cambridge University Press, Cambridge, UK.

Burns, R. M. & B. H. Honkala 1990. Silvics of North America: Hardwoods, Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington DC, USA.

Burslem, D., P. J. Grubb & I. M. Turner 1996. Responses to Simulated Drought and Elevated Nutrient Supply among Shade-Tolerant Tree Seedlings of Lowland Tropical Forest in Singapore. Biotropica 28: 636-648.

Burslem, D. F. R. P., T. C. Whitmore & G. C. Brown 2000. Short-Term Effects of Cyclone Impact and Long-Term Recovery of Tropical Rain Forest on Kolombangara, Solomon Islands. Journal of Ecology 88: 1063-1078.

Buschbacher, R., C. Uhl & E. A. S. Serrao 1988. Abandoned Pastures in Eastern Amazonia, Brazil Ii. Nutrient Stocks in the Soil and Vegetation. Journal of Ecology 76: 682-699.

Cade, B. S., J. W. Terrell & R. L. Schroeder 1999. Estimating Effects of Limiting Factors with Regression Quantiles. Ecology 80: 311-323.

Cade, B. S. & Q. Guo 2000. Estimating Effects of Constraints on Plant Performance with Regression Quantiles. Oikos 91: 245-254.

Cairns, M. & D. P. Garrity 1999. Improving Shifting Cultivation in Southeast Asia by Building on Indigenous Fallow Management Strategies. Agroforestry Systems 47: 37-48.

Cairns, M. A., P. K. Haggerty, R. Alvarez, B. H. J. de Jong & I. Olmsted 2000. Tropical Mexico's Recent Land-Use Change: A Region's Contribution to the Global Carbon Cycle. Ecological Applications 10: 1426-1441.

Canham, C. D., C. Finzi Adrien, S. W. Pacala & D. H. Burbank 1994. Causes and Consequences of Resource Heterogeneity in Forests: Interspecific Variation in Light Transmission by Canopy Trees. Canadian Journal of Forest Research 24: 337-349.

Canham, C. D., P. T. LePage & K. D. Coates 2004. A Neighborhood Analysis of Canopy Tree Competition: Effects of Shading versus Crowding. Canadian Journal of Forest Research 34: 778-787.

Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins & M. J. Twery 2006. Neighborhood Analyses of Canopy Tree Competition along Environmental Gradients in New England Forests. Ecological Applications 16: 540-554.

Cannell, M. G. R., P. Rothery & E. D. Ford 1984. Competition within Stands of *Picea-Sitchensis* and *Pinus-Contorta*. Annals of Botany London 53: 349-362.

Capers, R. S., R. L. Chazdon, A. R. Brenes & B. V. Alvarado 2005. Successional Dynamics of Woody Seedling Communities in Wet Tropical Secondary Forests. Journal of Ecology 93: 1071-1084.

Casper, B. B. & R. B. Jackson 1997. Plant Competition Underground. Annual Review of Ecology and Systematics 28: 545-570.

Casper, B. B., H. J. Schenk & R. R. B. Jackson 2003. Defining a Plant's Belowground Zone of Influence. Ecology 84: 2313-2321.

Caspersen, J. P. & R. K. Kobe 2001. Interspecific Variation in Sapling Mortality in Relation to Growth and Soil Moisture. Oikos 92: 160-168.

Castello, J. D., D. J. Leopold & P. J. Samallidge 1995. Pathogens, Patterns, and Processes in Forest Ecosystems. BioScience 45: 16-24.

Ceccon, E., I. Olmsted, C. Vázquez-Yanes & J. Campo-Alves 2002. Vegetation and Soil Properties in Two Tropical Dry Forests of Differing Regeneration Status in Yucatan. Agrociencia 36: 621-631.

Ceccon, E., P. Huante & J. Campo 2003. Effects of Nitrogen and Phosphorus Fertilization on the Survival and Recruitment of Seedlings of Dominant Tree Species in Two Abandoned Tropical Dry Forests in Yucatan, Mexico. Forest ecology and management 182: 387-402.

Ceccon, E., S. Sánchez & J. Campo 2004. Tree Seedling Dynamics in Two Abandoned Tropical Dry Forests of Differing Successional Status in Yucatán, Mexico: A Field Experiment with N and P Fertilization. Plant Ecology 170: 277-285.

Ceccon, E., P. HuanteII & E. Rincón 2006. Abiotic Factors Influencing Tropical Dry Forests Regeneration. Brazilian Archives of Biology and Technology 49: 305-312.

Celedón-Muñiz, H. 2006. Impacto Del Sistema Agrícola De Roza, Tumba Y Quema Sobre Las Características De Tres Unidades De Suelo En La Selva Lacandona De Chiapas., Facultad de Ciencias, Universidad Nacional Autónoma de México, México.

Challenger, A. 1998. Utilizatión Y Conservación De Los Ecosistemas Terrestres De México. Pasado, Presente Y Futuro. Comisión Nacional para el conocimiento y uso de la biodiversidad, México, México.

Chao, A., R. L. Chazdon, R. K. Colwell & T. J. Shen 2005. A New Statistical Approach for Assessing Similarity of Species Composition with Incidence and Abundance Data. Ecology Letters 8: 148-159.

Chave, J. 1999. Study of Structural, Successional and Spatial Patterns in Tropical Rain Forests Using Troll, a Spatially Explicit Forest Model. Ecological modelling 124: 233-254.

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao & R. Perez 2004. Error Propagation and Scaling for Tropical Forest Biomass Estimates. Philosophical Transactions of the Royal Society B 359: 409-420.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera & T. Yamakura 2005. Tree Allometry and Improved Estimation of Carbon Stocks and Balance in Tropical Forests. Oecologia 145: 87-99.

Chazdon, R. L. 1998. Tropical Forests - Log 'Em or Leave 'Em? Science 281: 1295-1296.

Chazdon, R. L., R. K. Colwell, J. S. Denslow & M. R. Guariguata 1998. Statistical Methods for Estimating Species Richness of Woody Regeneration in Primary and Secondary Rain Forests of Ne Costa Rica. In F. Dallmeier and J. Comiskey (Eds.). Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies, pp. 285-309. Parthenon Publishing, Paris, France.

Chazdon, R. L. & F. G. Coe 1999. Ethnobotany of Woody Species in Second-Growth, Old-Growth, and Selectively Logged Forests of Northeastern Costa Rica. Conservation Biology 13: 1312-1322.

Chazdon, R. L. 2003. Tropical Forest Recovery: Legacies of Human Impact and Natural Disturbances. Perspectives in Plant Ecology Evolution and Systematics 6: 51-71.

Chazdon, R. L., S. Careaga, C. Webb & O. Vargas 2003. Community and Phylogenetic Structure of Reproductive Traits of Woody Species in Wet Tropical Forests. Ecological Monographs 73: 331-348.

Chazdon, R. L., A. Redondo Brenes & B. Vilchez Alvarado 2005. Effects of Climate and Stand Age on Annual Tree Dynamics in Tropical Second-Growth Rain Forests. Ecology 86: 1808-1815.

Chazdon, R. L., S. Letcher, M. van Breugel, M. Martínez-Ramos, F. Bongers & B. Finegan 2007. Rates of Change in Tree Communities of Secondary Neotropical Forests Following Major Disturbances. Philosophical Transactions of the Royal Society B 362: 273-289.

Chazdon, R. L. in press. Successional Vegetation Dynamics of Tropical Forests. In W. P. Carson and S. A. Schnitzer (Eds.). Tropical Plant Community Ecology. Blackwell Publishing, Oxford, UK.

--- in press. Successional Vegetation Dynamics of Tropical Forests. In W. P. Carson and S. A. Schnitzer (Eds.). Tropical Plant Community Ecology. Blackwell Publishing, Oxford.

Chinea, J. D. 2002. Tropical Forest Succession on Abandoned Farms in the Humacao Municipality of Eastern Puerto Rico. Forest Ecology and Management 167: 195-207.

Chinea, J. D. & E. H. Helmer 2003. Diversity and Composition of Tropical Secondary Forests Recovering from Large-Scale Clearing: Results from the 1990 Inventory in Puerto Rico. Forest Ecology and Management 180: 227-240.

Chokkalingam, U. & W. d. Jong 2001. Secondary Forest: A Working Definition and Typology. International Forestry Review. 2001; 3: 19-26.

Chokkalingam, U., J. Smith, W. de Jong & C. Sabogal 2001. A Conceptual Framework for the Assessment of Tropical Secondary Forest Dynamics and Sustainable Development Potential in Asia. Kuala Lumpur, Malaysia: Forest Research Institute Malaysia.

Choudhury, D. & R. C. Sundriyal 2003. Factors Contributing to the Marginalization of Shifting Cultivation in North-East India: Micro-Scale Issues. Outlook on Agriculture 32: 17-28.

Clark, D. A. & D. B. Clark 1992. Life History Diversity of Canopy and Emergent Trees in a Neotropical Rain Forest. Ecological Monographs 62: 315-344.

--- 2001. Getting to the Canopy: Tree Height Growth in a Neotropical Rain Forest. Ecology 82: 1460-1472.

Clark, D. B. 1996. Abolishing Virginity. Journal of Tropical Ecology 12: 735.

Clark, D. B., M. W. Palmer & D. A. Clark 1999. Edaphic Factors and the Landscape-Scale Distributions of Tropical Rain Forest Trees. Ecology 80: 2662-2675.

Clark, D. B. & D. A. Clark 2000. Landscape-Scale Variation in Forest Structure and Biomass in a Tropical Rain Forest. Forest Ecology and Management 137: 185-198.

Clark, J. S. 1992. Density-Independent Mortality, Density Compensation, Gap Formation, and Self-Thinning in Plant Populations. Theoretical Population Biology 42: 172-198.

Colón, S. M. & A. E. Lugo 2006. Recovery of a Subtropical Dry Forest after Abandonment of Different Land Uses. Biotropica 38: 354-364.

Colwell, R. K. & J. A. Coddington 1994. Estimating Terrestrial Biodiversity through Extrapolation. Philosophical Transactions of the Royal Society B 345: 101-118.

Condit, R., P. Hubbell Stephen & B. Foster Robin 1995. Mortality Rates of 205 Neotropical Tree and Shrub Species and the Impact of a Severe Drought. Ecological monographs 65: 419-439.

Condit, R., P. Hubbell Stephen, V. Lafrankie James, R. Sukumar, N. Manokaran, B. Foster Robin & S. Ashton Peter 1996. Species-Area and Species-Individual Relationships for Tropical Trees: A Comparison of Three 50-Ha Plots. Journal of Ecology 84: 549-562.

Condit, R., R. Sukumar, P. Hubbell Stephen & B. Foster Robin 1998. Predicting Population Trends from Size Distributions: A Direct Test in a Tropical Tree Community. American Naturalist 152: 495-509.

Connell, J. H. 1971. On the Role of Natural Enemies in Preventing Competitive Exclusion in Some Marine Animals and in Rain Forest Trees. In P. J. Den Bier and G. Gradwell (Eds.). Dynamics of Numbers in Populations, Proc. Advanced Study Institute, pp. 298-3121. Center for Agricultural Publication and Documentation, Wageningen.

Connell, J. H. & R. O. Slatyer 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. American Naturalist 111: 1119-1144.

Connell, J. H., I. R. Noble & R. O. Slatyer 1987. On the Mechanisms Producing Successional Change. Oikos 50: 136-137.

Connolly, J. & P. Wayne 1996. Asymmetric Competition between Plant Species. Oecologia Berlin 108: 311-320.

Coomes, D. A. & P. J. Grubb 1998. Responses of Juvenile Trees to above- and Belowground Competition in Nutrient-Starved Amazonian Rain Forest. Ecology 79: 768-782.

--- 2000. Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. Ecological Monographs 70: 171-207.

Coomes, D. A., R. P. Duncan, R. B. Allen & J. Truscott 2003. Disturbances Prevent Stem Size-Density Distributions in Natural Forests from Following Scaling Relationships. Ecology Letters 6: 980-989.

Coomes, O. T., F. Grimard & G. J. Burt 2000. Tropical Forests and Shifting Cultivation: Secondary Forest Fallow Dynamics among Traditional Farmers of the Peruvian Amazon. Ecological Economics 32: 109-124.

Corlett, R. T. 1991. Plant Succession on Degraded Land in Singapore. Journal of tropical forest science 4: 151-161.

--- 1992. The Ecological Transformation of Singapore, 1819-1990. Journal of Biogeography 19: 411-420.

--- 1995. Tropical Secondary Forests. Progress in Physical Geography 19: 159-172.

Cubina, A. & T. M. Aide 2001. The Effect of Distance from Forest Edge on Seed Rain and Soil Seed Bank in a Tropical Pasture. Biotropica 33: 260-267.

Dalling, J. W., S. P. Hubbell & K. Silvera 1998a. Seed Dispersal, Seedling Establishment and Gap Partitioning among Tropical Pioneer Trees. Journal of Ecology 86: 674-689.

Dalling, J. W., M. D. Swaine & N. C. Garwood 1998b. Dispersal Patterns and Seed Bank Dynamics of Pioneer Trees in Moist Tropical Forest. Ecology 79: 564-578.

Dalling, J. W., K. Winter, J. D. Nason, S. P. Hubbell, D. A. Murawski & J. L. Hamrick 2001. The Unusual Life History of Alseis Blackiana: A Shade-Persistent Pioneer Tree? Ecology 82: 933-945.

Dalling, J. W., H. C. Muller-Landau, S. J. Wright & S. P. Hubbell 2002. Role of Dispersal in the Recruitment Limitation of Neotropical Pioneer Species. Journal of Ecology 90: 714-727.

Dalling, J. W., K. Winter & S. P. Hubbell 2004. Variation in Growth Responses of Neotropical Pioneers to Simulated Forest Gaps. Functional ecology 18: 725-736.

Davies, S. J. 2001. Tree Mortality and Growth in 11 Sympatric Macaranga Species in Borneo. Ecology 82: 920-932.

de Gouvenain, R. C. & J. A. Silander 2003. Do Tropical Storm Regimes Influence the Structure of Tropical Lowland Rain Forests? Biotropica 35: 166-180.

de Jong, B. H. J., S. Ochoa-Gaona, M. A. Castillo-Santiago, N. Ramírez-Marcial & M. A. Cairns 2000. Carbon Flux and Patterns of Land-Use/Land-Cover Change in the Selva Lacandona, Mexico. Ambio 29: 504-511.

de Jong, W. & U. Chokkalingam 2001. The Evolution of Swidden Fallow Secondary Forests in Asia. Journal of Tropical Forest Science 13: 800-815.

de Jong, W., U. Chokkalingam, J. Smith & C. Sabogal 2001. Tropical Secondary Forests in Asia: Introduction and Synthesis. Journal of Tropical Forest Science 13: 563-576.

DeFries, R. S., J. A. Foley & G. P. Asner 2005. Land-Use Choices: Balancing Human Needs and Ecosystem Function. Frontiers in Ecology and the Environment 2: 249.

Dekker, M., M. v. Breugel & F. J. Sterck 2007. Effective Height Development of Four Co-Occurring Species in the Gap-Phase Regeneration of Douglas Fir Monocultures under Nature-Oriented Conversion. Forest Ecology and Management 238: 189-198.

Denslow, J., S., A. M. Ellison & R. E. Sanford 1998. Treefall Gap Size Effects on above- and Below-Ground Processes in a Tropical Wet Forest. Journal of Ecology 86: 597-609.

Denslow, J. S. 1995. Disturbance and Diversity in Tropical Rain Forests. The Density Effect. Ecological Applications 5: 962-968.

Denslow, J. S. & G. S. Guzman 2000. Variation in Stand Structure, Light and Seedling Abundance across a Tropical Moist Forest Chronosequence, Panama. Journal of Vegetation Science 11: 201-212.

Dewalt, S., J., K. Maliakal Satya & S. Denslow Julie 2003. Changes in Vegetation Structure and Composition Along a Tropical Forest Chronosequence: Implications for Wildlife. Forest Ecology and Management 182: 139-151.

DeWalt, S. J. & J. Chave 2004. Structure and Biomass of Four Lowland Neotropical Forests. Biotropica 36: 7-19.

Dichtl, S. 1988. Cae Una Estrella. Desarrollo Y Destrucción De La Selva Lacandona. Secretaría de Educacíon Publica, Ciudad de México, México.

Dittus, W. P. J. 1985. The Influence of Cyclones on the Dry Evergreen Forest of Sri Lanka. Biotropica 17: 1-14.

Doležal, J., H. Ishii, V. P. Vetrova, A. Sumida & T. Hara 2004. Tree Growth and Competition in a *Betula Platyphylla-Larix Cajanderi* Post-Fire Forest in Central Kamchatka. Annals of Botany 94: 333-343.

Donfack, P., C. Floret & R. Pontanier 1995. Secondary Succession in Abandoned Fields of Dry Tropical Northern Cameroon. Journal of Vegetation Science 6: 499-508.

Dourojeanni, R. M. 1987. Aprovechamiento Del Barbecho Forestal En Areas De Agricultura Migratoria En La Amazonia Peruana. Revista Forestal del Peru 14: 15-61.

Duivenvoorden, J. E. 1995. Tree Species Composition and Rain Forest-Environment Relationships in the Middle Caquetá Area, Colombia, Nw Amazonia. Plant Ecology 120: 91-113.

Duncan, R. P. 1995. A Correction for Including Competitive Asymmetry in Measures of Local Interference in Plant Populations. Oecologia 103: 393-396.

Duncan, R. S. & C. A. Chapman 1999. Seed Dispersal and Potential Forest Succession in Abandoned Agriculture in Tropical Africa. Ecological Applications 9: 998-1008.

Eggeling, W. J. 1947. Observations on the Ecology of the Budongo Rain Forest, Uganda. The Journal of Ecology 34: 20-87.

Egler, F. E. 1954. Vegetation Science Concepts I. Initial Floristic Composition, a Factor in Old-Field Vegetation Development. Vegetatio 4: 412-417.

Elmqvist, T., M. Wall, A. L. Berggren, L. Blix, Å. Fritioff & U. Rinman 2001. Tropical Forest Reorganization after Cyclone and Fire Disturbance in Samoa: Remnant Trees as Biological Legacies. Conservation Ecology 5: URL: http://www.consecol.org/vol5/iss2/art10/.

Enquist, B. J. & K. J. Niklas 2001. Invariant Scaling Relations across Tree-Dominated Communities. Nature 410: 655-660.

Ewel, J. 1980. Tropical Succession: Manifold Routes to Maturity. Biotropica 12: 2-7.

Ewel, J. J. 1977. Differences between Wet and Dry Tropical Successional Tropical Ecosystems. Geo-Eco-Trop 1: 103-117.

Fanshawe, D. B. 1952. The Vegetation of British Guiana: A Preliminary Review. Imperial Forestry Institute, University of Oxford, Oxford, UK.

FAO 2006. Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management, FAO Forestry Paper 147. United Nations Food and Agricultural Organization, Rome.

Fearnside, P. M. 2000. Global Warming and Tropical Land-Use Change: Greenhouse Gas Emissions from Biomass Burning, Decomposition and Soils in Forest Conversion, Shifting Cultivation and Secondary Vegetation. Climatic Change 46: 115-158.

Fehse, J., R. Hofstede, N. Aguirre, C. Paladines, A. Kooijman & J. Sevink 2002. High Altitude Tropical Secondary Forests: A Competitive Carbon Sink? Forest Ecology and Management 163: 9-25.

Feldpausch, T. R. 2004. Carbon and Nutrient Accumulation in Secondary Forests Regenerating on Pastures in Central Amazonia. Ecological Applications 14: S164.

Feldpausch, T. R., S. J. Rihab, E. C. M. Fernandesc & E. V. Wandellid 2005. Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia. Earth Iteractions 9: 1-22.

Ferguson, B. G., J. Vandermeer, H. Morales & D. M. Griffith 2003. Post-Agricultural Succession in El Peten, Guatemala. Conservation Biology 17: 818-828.

Fetcher, N., B. L. Haines, R. A. Cordero, D. J. Lodge, L. R. Walker, D. S. Fernandez & W. T. Lawrence 1996. Responses of Tropical Plants to Nutrients and Light on a Landslide in Puerto Rico. Journal of Ecology 84: 331-341.

Fine, P. V. A. 2002. The Invasibility of Tropical Forests by Exotic Plants. Journal of Tropical Ecology 18: 687.

Finegan, B. 1984. Forest Succession. Nature 312: 109-114.

--- 1992. The Management Potential of Neotropical Secondary Lowland Rain Forest. Forest Ecology and Management 47: 295-322.

--- 1996. Pattern and Process in Neotropical Secondary Rain Forests: The First 100 Years of Succession. Trends in Ecology & Evolution 11: 119-124.

Finegan, B. & D. Delgado 2000. Structural and Floristic Heterogeneity in a 30-Year-Old Costa Rican Rain Forest Restored on Pasture through Natural Secondary Succession. Restoration Ecology 8: 380-393.

Finegan, B. & R. Nasi 2004. The Biodiversity and Conservation Potential of Shifting Cultivation Landscapes. In G. Schroth, G. A. B. da Fonseca, C. A. Harvey, C. Gason, H. L. Vasconcelos and A. N. Isaac (Eds.). Agroforestry and Biodiversity Conservation in Tropical Landscapes, pp. 153-197. Island Press, Washington DC.

Flinn, K. M. & M. Vellend 2005. Recovery of Forest Plant Communities in Post-Agricultural Landscapes. Frontiers in Ecology and the Environment 3: 243–250.

Floret, C. & R. Pontanier (Eds.) 2000. Fallows in Tropical Africa: Roles, Management, Alternatives. Proceedings of the International Seminary, Dakar, April 13-16 1999. John Libbey Eurotext, Paris.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty & P. K. Snyder 2005. Global Consequences of Land Use. Science 309: 570-574.

Foley, J. A., G. P. Asner, M. H. Costa, M. T. Coe, R. DeFries, H. K. Gibbs, E. A. Howard, S. Olson, J. Patz, N. Ramankutty & P. Snyder 2007. Amazonia Revealed: Forest Degradation and Loss of Ecosystem Goods and Services in the Amazon Basin. Frontiers in Ecology and the Environment 5: 25-32.

Foster, B. L. & D. Tilman 2000. Dynamic and Static Views of Succession: Testing the Descriptive Power of the Chronosequence Approach. Plant Ecology 146: 1-10.

Foster, D. R., M. Fluet & E. R. Boose 1999. Human or Natural Disturbance: Landscape-Scale Dynamics of the Tropical Forests of Puerto Rico. Ecological applications 9: 555-572.

Fox, J., M. Truong Dao, A. T. Rambo, P. Tuyen Nghiem, T. Cuc Le & S. Leisz 2000. Shifting Cultivation: A New Old Paradigm for Managing Tropical Forests. BioScience 50: 521-528.

Franklin, J., R. Drake Donald, A. Bolick Leslie, S. Smith Darren & J. Motley Timothy 1999. Rain Forest Composition and Patterns of Secondary Succession in the Vava'u Island Group, Tonga. Journal of Vegetation Science 10: 51-64.

Freckleton, R. P. & A. R. Watkinson 2001. Asymmetric Competition between Plant Species. Functional Ecology 15: 615-623.

Fujihara, M. 1996. Development of Secondary Pine Forests after Pine Wilt Disease in Western Japan. Journal of Vegetation Science. 1996; 75: 729-738.

Fuller, J. L., D. R. Foster, J. S. McLachlan & N. Drake 1998. Impact of Human Activities on Regional Forest Compositon and Dynamics in Central New England. Ecosystems 1: 76-98.

Galindo-Gonzalez, J., S. Guevara & J. Sosa Vinicio 2000. Bat- and Bird-Generated Seed Rains at Isolated Trees in Pastures in a Tropical Rainforest. Conservation Biology 14: 1693-1703.

Garcia Queila, S., L. P. Rezende Juliana & M. S. Aguiar Ludmila 2000. Seed Dispersal by Bats in a Disturbed Area of Southeastern Brazil. Revista de Biologia Tropical 48: 125-128.

Gehring, C., S. Park & M. Denich 2004. Liana Allometric Biomass Equations for Amazonian Primary and Secondary Forest. Forest Ecology and Management 195: 69-83.

Gehring, C., M. Denich & P. L. G. Vlek 2005. Resilience of Secondary Forest Regrowth after Slash-and-Burn Agriculture in Central Amazonia. Journal of Tropical Ecology 21: 519-527.

Geist, H. J. & E. F. Lambin 2002. Proximate Causes and Underlying Driving Forces of Tropical Deforestation. BioScience 52: 143-150.

Geldenhuys, C., F. Castañeda, H. Savenije & M. Kuzee (Eds.) 2003. Proceedings of the Workshop on Tropical Secondary Forest Management in Africa: Reality and Perspectives, Kenya, 9-13 December 2002. FAO, United Nations, Nairobi, Kenya.

Gemerden, B. S. v., H. Olff, M. P. E. Parren & F. Bongers 2003a. The Pristine Rain Forest? Remnants of Historical Human Impacts on Current Tree Species Composition and Diversity. Journal of Biogeography 30: 1381-1390.

Gemerden, B. S. v., N. Shu Gideon & H. Olff 2003b. Recovery of Conservation Values in Central African Rain Forest after Logging and Shifting Cultivation. Biodiversity and Conservation 12: 1553-1570.

Gentry, A. H. 1995. Diversity and Floristic Composition of Neotropical Dry Forests. In S. H. Bullock, H. A. Mooney and E. Medina (Eds.). Seasonally Dry Tropical Forests, pp. 146-194. Cambridge University Press, Cambridge, UK.

Gerhardt, K. & H. Hytteborn 1992. Natural Dynamics and Regeneration Methods in Tropical Dry Forests: An Introduction. Journal of vegetation science 3: 361-364.

Gerhardt, K. 1993. Tree Seedling Development in Tropical Dry Abandoned Pasture and Secondary Forest in Costa Rica. Journal of vegetation science 4: 95-102.

--- 1996. Effects of Root Competition and Canopy Openness on Survival and Growth of Tree Seedlings in a Tropical Seasonal Dry Forest. Forest ecology and management 82: 33-48.

--- 1998. Leaf Defoliation of Tropical Dry Forest Tree Seedlings - Implications for Survival and Growth. Trees 13: 88-95.

Gillespie, T., W. 1999. Life History Characteristics and Rarity of Woody Plants in Tropical Dry Forest Fragments of Central America. Journal of tropical ecology 15: 637-649.

Gleason, H. A. 1926. The Individualistic Concept of of the Plant Association. Bulletin of the Torrey Botanical Club 53: 7-26.

--- 1939. The Individualistic Concept of Plant Association. American Midland Naturalist 21: 92-110.

Gomez-Pompa, A. & C. Vazquez-Yanes 1981. Successional Studies of a Rain Forest in Mexico. In D. C. West, H. H. Shugart and D. B. Botkin (Eds.). Forest Succession, Concepts and Application, pp. 246-266. Springer-Verlag, New York.

Gómez-Pompa, A. 1991. Learning from Traditional Ecological Knowledge: Insights from Mayan Silviculture. In A. Gómez-Pompa, T. C. Whitmore and M. Hadley (Eds.). Rain Forest Regeneration and Management, pp. 335-341. UNESCO-MAB, Paris.

González-Iturbe, J. A., I. Olmsted & F. Tun-Dzul 2002. Tropical Dry Forest Recovery after Long Term Henequen (Sisal, *Agave Fourcroydes* Lem.) Plantation in Northern Yucatan, Mexico. Forest Ecology and Management 167: 67-82.

González-Soriano, E., R. Dirzo & R. C. Vogt (Eds.) 1997. Historia Natural De Los Tuxtlas. Universidad Nacional Autónoma de México, Mexico, Mexico.

Gotelli, N. J. & R. K. Colwell 2001. Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness. Ecology letters 4: 379-391.

Gotelli, N. J. & G. L. Entsminger 2001. Ecosim: Null Models Software for Ecology. Acquired Intelligence Inc. & Kesey-Bear.

Grau, H. R., M. F. Arturi, A. D. Brown & P. G. Acenolaza 1997. Floristic and Structural Patterns Along a Chronosequence of Secondary Forest Succession in Argentinean Subtropical Montane Forests. Forest ecology and management 95: 161-171.

Grau, H. R., T. M. Aide, J. K. Zimmerman, J. R. Thomlinson, E. Helmer & X. M. Zou 2003. The Ecological Consequences of Socioeconomic and Land-Use Changes in Postagriculture Puerto Rico. BioScience 53: 1159-1168.

Green, R. V. 2005. Farming and the Fate of Wild Nature. Science 307: 550.

Grime, J. P. 2002. Plant Strategies, Vegetation Processes, and Ecosystem Properties. John Wiley & Sons Ltd., West Sussex, UK.

Guariguata, M., R., R. Rheingans & F. Montagnini 1995. Early Woody Invasion under Tree Plantations in Costa Rica: Implications for Forest Restoration. Restoration Ecology 3: 252-260.

Guariguata, M. R., R. L. Chazdon, J. S. Denslow, J. M. Dupuy & L. Anderson 1997. Structure and Floristics of Secondary and Old-Growth Forest Stands in Lowland Costa Rica. Plant Ecology 132: 107-120.

Guariguata, M. R. & R. Ostertag 2001. Neotropical Secondary Forest Succession: Changes in Structural and Functional Characteristics. Forest ecology and management 148: 185-206.

Guevara, S., S. E. Purata & E. V. d. Maarel 1986. The Role of Remnant Forest Trees in Tropical Secondary Succession. Vegetatio 66: 77-84.

Guevara, S., J. Meave, P. Moreno-Casasola & J. Laborde 1992. Floristic Composition and Structure of Vegetation under Isolated Trees in Neotropical Pastures. Journal of vegetation science 3: 655-664.

Guevara, S., J. A. Meave, P. Moreno-Casasola, J. Laborde & S. Castillo 1994. Vegetacion Y Flora De Potreros En La Sierra De Los Tuxtlas, Mexico. Acta Botánica Mexicana 28: 1-27.

Hammond, D. S. 1995. Post-Dispersal Seed and Seedling Mortality of Tropical Dry Forest Trees after Shifting Agriculture, Chiapas, Mexico. Journal of tropical ecology 11: 295-313.

Hansen, M. C. & R. S. DeFries 2004. Detecting Long-Term Global Forest Change Using Continuous Fields of Tree-Cover Maps from 8-Km Advanced Very High Resolution Radiometer (Avhrr) Data for the Years 1982–99. Ecosystems 7: 695-716.

Hara, T., M. Kimura & K. Kikuzawa 1991. Growth Patterns of Tree Height and Stem Diameter in Populations of *Abies Veitchii*, *A. Mariesii* and *Betula Ermanii*. Journal of Ecology 79: 1085-1098.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez & E. A. Herre 2000. Pervasive Density-Dependent Recruitment Enhances Seedling Diversity in a Tropical Forest. Nature 404: 493-495.

Harms, K. E., R. Condit, S. P. Hubbell & R. B. Foster 2001. Habitat Associations of Trees and Shrubs in a 50-Ha Neotropical Forest Plot. Journal of Ecology 89: 947-959.

Hartgerink, A. P. & F. A. Bazzaz 1984. Seedling Scale Environmental Heterogeneity Influences Individual Fitness and Population Structure. Ecology 65: 198-206.

Harvey, C. A. & W. A. Haber 1998. Remnant Trees and the Conservation of Biodiversity in Costa Rican Pastures. Agroforestry Systems 44: 37-68.

Hashimotio, T., K. Kojima, T. Tange & S. Sasaki 2000. Changes in Carbon Storage in Fallow Forests in the Tropical Lowlands of Borneo. Forest Ecology and Management 126: 331-337.

Hassan, R., R. Scholes & N. Ash (Eds.) 2005. Ecosystems and Human Well-Being: Current State and Trends. Findings of the Conditions and Trends Working Group of the Millennium Ecosystem Assessment. Island Press, Washington.

He, F., P. Legendre & J. V. LaFrankie 1996. Spatial Pattern of Diversity in a Tropical Rain Forest of Malaysia. Journal of biogeography 23: 240-539.

He, X. S. & L. Orlóci 1993. Comparative Diversity Analysis of Vegetation. Abstracta botanica 17: 79-86.

Helmer, E. H. 2000. The Landscape Ecology of Tropical Secondary Forest in Montane Costa Rica. Ecosystems 3: 98-114.

Helmer, E. H., S. Brown & W. B. Cohen 2000. Mapping Montane Tropical Forest Successional Stage and Land Use with Multi-Date Landsat Imagery. International journal of remote sensing 21: 2163-2183.

Herben, T. 1996. Permanent Plots as Tools for Plant Community Ecology. Journal of Vegetation Science 7: 195-202.

Herrera, B. & B. Finegan 1997. Substrate Conditions, Foliar Nutrients and the Distributions of Two Canopy Tree Species in a Costa Rican Secondary Rain Forest. Plant and Soil 191: 259-267.

Hibbs, D. E. 1983. 40 Years of Forest Succession in Central New-England USA. Ecology 64: 1394-1401.

Hill, J. L. & P. J. Curran 2003. Area, Shape and Isolation of Tropical Forest Fragments: Effects on Tree Species Diversity and Implications for Conservation. Journal of Biogeography 30: 1391-1403.

Hill, M. O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54: 427-431.

Hjerpe, J., H. Hedenås & T. Elmqvist 2001. Tropical Rain Forest Recovery from Cyclone Damage and Fire in Samoa. Biotropica 33: 249.

Holdridge, L. R., W. G. Grenke, W. H. Haheway, T. Liang & J. J. A. Tosi 1975. Forest Environments in Tropical Life Zones. Pergamon Press, New York, USA.

Holl, K., D. 1998. Effects of above- and Below-Ground Competition of Shrubs and Grass on *Calophyllum Brasiliense* (Camb.) Seedling Growth in Abandoned Tropical Pasture. Forest Ecology and Management. 10: 187-195.

Holl, K. D. 1999. Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil. Biotropica 31: 229-242.

Holl, K. D., M. E. Loik, E. H. V. Lin & I. A. Samuels 2000. Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment. Restoration Ecology 8: 339-349.

Holl, K. D. 2002. Effect of Shrubs on Tree Seedling Establishment in an Abandoned Tropical Pasture. Journal of Ecology 90: 179-187.

--- in press. Old Field Succession in the Neotropics. In V. A. Cramer and R. J. Hobbs (Eds.). Old Fields: Dynamics and Restoration of Abandoned Farmland. Island Press, Washinton D.C., USA.

Holmgren, M., L. Poorter & A. Siepel 2004. What Explains the Distribution of Rare and Endemic West African Plants? In L. Poorter, F. Bongers, F. N. Kouamé and W. D. Hawthorne (Eds.). Biodiversity of West African Forests. An Ecological Atlas of Woody Plant Species, pp. 73-85. CABI Publishing, Oxon, U.K.

Holmgren, M. & L. Poorter in press. Does a Ruderal Strategy Dominate the Endemic Flora of West African Forests? Journal of Biogeography.

Hooper, E., R. Condit & P. Legendre 2002. Responses of 20 Native Tree Species to Reforestation Strategies for Abandoned Farmland in Panama. Ecological Applications 12: 1626-1641.

Hooper, E. R., P. Legendre & R. Condit 2004. Factors Affecting Community Composition of Forest Regeneration in Deforested, Abandoned Land in Panama. Ecology 85: 3313-3326

Houle, G. 1995. Seed Dispersal and Seedling Recruitment: The Missing Link(S). Ecoscience 2: 238-244.

Howlett, B. E. & D. W. Davidson 2001. Herbivory on Planted Dipterocarp Seedlings in Secondary Logged Forests and Primary Forests of Sabah, Malaysia. Journal of Tropical Ecology 17: 285-302.

Huante, P., E. Rincon & I. Acosta 1995a. Nutrient Availability and Growth Rate of 34 Woody Species from a Tropical Deciduous Forest in Mexico. Functional Ecology 9: 849-858.

Huante, P., E. Rincon & F. S. C. Iii 1995b. Responses to Phosphorus of Contrasting Successional Tree-Seedling Species from the Tropical Deciduous Forest of Mexico. Functional Ecology 9: 760-766.

Huante, P. & E. Rincón 1997. Responses to Light Changes in Tropical Deciduous Woody Seedlings with Contrasting Growth Rates. Oecologia 113: 53-66.

Hubbell, S. H. 2005. Neutral Theory in Community Ecology and the Hypothesis of Functional Equivalence. Functional Ecology 19: 166.

Hubbell, S. P., R. Condit & R. B. Foster 1990. Presence and Absence of Density Dependence in a Neotropical Tree Community. Philosophical Transactions of the Royal Society of London B 330: 269-282.

Hubbell, S. P. 2006. Neutral Theory and the Evolution of Ecological Equivalence. Ecology 87: 1387-1398.

Hughes, R. F., J. B. Kauffman & V. J. Jaramillo 1999. Biomass, Carbon, and Nutrient Dynamics of Secondary Forests in a Humid Tropical Region of Mexico. Ecology 80: 1892-1907.

Hughes, R. F., J. B. Kauffman & D. L. Cummings 2000a. Fire in the Brazilian Amazon: 3. Dynamics of Biomass, C, and Nutrient Pools in Regenerating Forests. Oecologia 124: 574-588.

Hughes, R. F., J. B. Kauffman & V. J. Jaramillo 2000b. Ecosystem-Scale Impacts of Deforestation and Land Use in a Humid Tropical Region of Mexico. Ecological Applications 10: 515-527.

Hughes, R. F., J. B. Kauffman & D. L. Cummings 2002. Dynamics of Aboveground and Soil Carbon and Nitrogen Stocks and Cycling of Available Nitrogen Along a Land-Use Gradient in Rondonia, Brazil. Ecosystems 5: 244-259.

Huston, M. A. 1986. Size Bimodality in Plant Populations an Alternative Hypothesis. Ecology 67: 265-269.

Huston, M. A. & D. L. DeAngelis 1987. Size Bimodality in Monospecific Populations: A Critical Review of Potential Mechanisms. The American naturalist 129: 678-707.

Huston, M. A. & T. Smith 1987. Plant Succession: Life History and Competition. The American Naturalist 130: 168-198.

Huston, M. A. 1994. Biological Diversity. The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.

Hutchings, M. J. 1997. The Structure of Plant Populations. In M. J. Crawley (Ed.). Plant Ecology, pp. 325-358. Blackwell Science Ltd, Oxford.

Hutchings, M. J., E. A. John & D. K. Wijesinghe 2003. Toward Understanding the Consequences of Soil Heterogeneity for Plant Populations and Communities. Ecology 84: 2322-2334.

Ibarra-Manríquez, G., M. Martínez-Ramos & K. Oyama 2001. Seedling Functional Types in a Lowland Rain Forest in Mexico. American Journal of Botany 88: 1801-1812.

Ibarra-Manríquez, G. & M. Martínez-Ramos 2002. Landscape Variation of Liana Communities in a Neotropical Rain Forest. Plant Ecology 160: 91-112.

Iida, S. & T. Nakashizuka 1995. Forest Fragmentation and Its Effect on Species Diversity in Sub-Urban Coppice Forests in Japan. Forest Ecology and Management 73: 197-210.

Iriarte Vivar Balderrama, S. & R. L. Chazdon 2005. Light-Dependent Seedling Survival and Growth of Four Tree Species in Costa Rican Second-Growth Rain Forests. Journal of Tropical Ecology 21: 383-395.

Janzen, D. H. 1971. Escape of Juvenile *Dioclea Megacarpa* (Leguminosae) Vines from Predators in a Deciduous Tropical Forest. The American naturalist 105: 97-112.

--- 1988. Management of Habitat Fragments in a Tropical Dry Forest: Growth. Annals of the Missouri Botanical Garden 75: 105-116.

Jepsen, M. R. 2006. Above-Ground Carbon Stocks in Tropical Fallows, Sarawak, Malaysia. Forest Ecology and Management 225: 287-295.

Jobidon, R. 2000. Density-Dependent Effects of Northern Hardwood Competition on Selected Environmental Resources and Young White Spruce (*Picea Glauca*) Plantation Growth, Mineral Nutrition, and Stand Structural Development - a 5-Year Study. Forest Ecology and Management 130: 77-97.

Johnson, C. M., D. J. Zarin & A. H. Johnson 2000. Post-Disturbance Aboveground Biomass Accumulation in Global Secondary Forests. Ecology 81: 1395-1401.

Justiniano, M. J. & T. S. Fredericksen 2000. Phenology of Tree Species in Bolivian Dry Forests. Biotropica 32: 276-281.

Kabakoff, R. P. & R. L. Chazdon 1996. Effects of Canopy Species Dominance on Understorey Light Availability in Low-Elevation Secondary Forest Stands in Costa Rica. Journal of Tropical Ecology 12: 779-788.

Kammesheidt, L. 1998. The Role of Tree Sprouts in the Restoration of Stand Structures and Species Diversity in Tropical Moist Forest after Slash-and-Burn Agriculture in Eastern Paraguay. Plant Ecology 139: 155-165.

--- 1999. Forest Recovery by Root Suckers and above-Ground Sprouts after Slash-and-Burn Agriculture, Fire and Logging in Paraguay and Venezuela. Journal of Tropical Ecology 15: 143-157.

--- 2000. Some Autecological Characteristics of Early to Late Successional Tree Species in Venezuela. Acta Oecologica 21: 37-48.

--- 2002. Perspectives on Secondary Forest Management in Tropical Humid Lowland America. Ambio 31: 243-250.

Kappelle, M., P. A. F. Kennis & R. A. J. de Vries 1995. Changes in Diversity Along a Successional Gradient in a Costa Rica Upper Montane Quercus Forest. Biodiversity and Conservation 4: 10-34.

Kappelle, M., T. Geuze, M. E. Leal & A. M. Cleef 1996. Successional Age and Forest Structure in a Costa Rican Upper Montane Quercus Forest. Journal of tropical ecology 12: 681-698.

Keddy, P. A. 1992. Assembly and Response Rules: Two Goals for Predictive Community Ecology. Journal of Vegetation Science 3: 157.

--- 2001. Competition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Kennard, D. K. 2002. Secondary Forest Succession in a Tropical Dry Forest: Patterns of Development across a 50-Year Chronosequence in Lowland Bolivia. Journal of Tropical Ecology 18: 53-66.

Ketterings, Q. M., R. Coe, M. v. Noordwijk, Y. Ambagau & C. A. Palm 2001. Reducing Uncertainty in the Use of Allometric Biomass Equations for Predicting above-Ground Tree Biomass in Mixed Secondary Forests. Forest Ecology and Management 146: 199-209.

Kikuzawa, K. & K. Umeki 1996. Effect of Canopy Structure on Degree of Asymmetry of Competition in Two Forest Stands in Northern Japan. Annals of botany 77: 565-571.

Kindt, R. 2002. Methodology for Tree Species Diversification Planning for African Agroecosystems. PhD thesis, Universiteit van Gent, Gent, Belgium.

Kindt, R., P. V. Damme & A. J. Simons 2006. Tree Diversity in Western Kenya: Using Profiles to Characterise Richness and Evenness. Biodiversity and Conservation 15: 1253-1270.

King, D. A. 1990. The Adaptive Significance of Tree Height. American Naturalist 135: 809-828.

--- 1991. Correlations between Biomass Allocation, Relative Growth Rate and Light Environment in Tropical Forest Saplings. Functional Ecology 5: 485-492.

--- 1994. Influence of Light Level on the Growth and Morphology of Saplings in a Panamanian Forest. American Journal of Botany 81: 948-957.

--- 1996. Allometry and Life History of Tropical Trees. Journal of Tropical Ecology 12: 25-44.

Kitajima, K., S. S. Mulkey & S. J. Wright 2005. Variation in Crown Light Utilization Characteristics among Tropical Canopy Trees. Annals of Botany 95: 535-547.

Kochy, M. & S. D. Wilson 2000. Competitive Effects of Shrubs and Grasses in Prairie. Oikos 91: 385-395.

Koenker, R. & G. Bassett 1978. Regression Quantiles. Econometrica 46: 33-50.

Koenker, R. 2005. Quantile Regression. Cambridge University Press, Cambridge, UK.

Kohler, P. & A. Huth 1998. The Effects of Tree Species Grouping in Tropical Rainforest Modelling: Simulations with the Individual-Based Model Formind. Ecological Modelling 109: 301-321.

Kohyama, T. & M. Hotta 1990. Significance of Allometry in Tropical Saplings. Functional Ecology 4: 515-522.

Kohyama, T., E. Suzuki, T. Partomihardjo & T. Yamada 2001. Dynamic Steady State of Patch-Mosaic Tree Size Structure of a Mixed Dipterocarp Forest Regulated by Local Crowding. Ecological research 16: 85-98.

Krebs, C. J. 1999. Ecological Methodology. Addison Wesley Longman, Menlo Park, California, USA.

Kuntz, S. & F. Siegert 1999. Monitoring of Deforestation and Land Use in Indonesia with Multitemporal Ers Data. International Journal of Remote Sensing 20: 2835-2853.

Lambin, E. F., B. L. Turner, H. J. Geist, S. B. Agbola, A. Angelsen, J. W. Bruce, O. T. Coomes, R. Dirzo, G. Fischer, C. Folke, P. S. George, K. Homewood, J. Imbernon, R. Leemans, X. Li, E. F. Moran, M. Mortimore, P. S. Ramakrishnan, J. F. Richards, H. Skanes, W. Steffen, G. D. Stone, U. Svedin, T. A. Veldkamp, C. Vogel & J. Xu 2001. The Causes of Land-Use and Land-Cover Change: Moving Beyond the Myths. Global Environmental Change 11: 261.

Lang, G. E. & D. H. Knight 1983. Tree Growth, Mortality, Recruitment, and Canopy Gap Formation during a 10-Year Period in a Tropical Moist Forest. Ecology 64: 1075-1080.

Lawrence, D., D. R. Peart & M. Leighton 1998. The Impact of Shifting Cultivation on a Rainforest Landscape in West Kalimantan: Spatial and Temporal Dynamics. Landscape Ecology 13: 135-148.

Lawrence, D. 2001. Nitrogen and Phosphorus Enhance Growth and Luxury Consumption of Four Secondary Forest Tree Species in Borneo. Journal of Tropical Ecology 17: 859-869.

Lawrence, D. & W. H. Schlesinger 2001. Changes in Soil Phosphorus during 200 Years of Shifting Cultivation in Indonesia. Ecology 82: 2769-2780.

Lawrence, D. 2004. Erosion of Tree Diversity During 200 Years of Shifting Cultivation in Bornean Rain Forest. Ecological Applications 14: 1855-1869.

Lebrija-Trejos, E., F. Bongers, P.-G. E.A. & J. A. Meave submitted. Successional Change and Recovery Rates in a Tropical Dry Forest: Contrasts between Dry and Wet Forests.

Legendre, P. & L. Legendre 1998. Numerical Ecology. Elsevier, Amsterdam, The Netherlands.

Levey, D. J., W. R. Silva & M. Galetti (Eds.) 2001. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, Oxon, UK.

Lewis, S. L. & E. V. J. Tanner 2000. Effects of above- and Belowground Competition on Growth and Survival of Rain Forest Tree Seedlings. Ecology 81: 2525-2538.

Lieberman, D., M. Lieberman, R. Peralta & G. S. Hartshorn 1985. Mortality Patterns and Stand Turnover Rates in a Wet Tropical Forest in Costa Rica. Journal of Ecology 73: 915-924.

Lövei, G. L. 2005. Generalised Entropy Indices Have a Long History in Ecology -a Comment. Community Ecology 6: 245-247.

Lu, D., E. Moran & P. Mausel 2002. Linking Amazonian Secondary Succession Forest Growth to Soil Properties. Land Degradation and Development 13: 331-343.

Lucas, R. M., M. Honzak, P. J. Curran, G. M. Foody & D. T. Nguele 2000. Characterizing Tropical Forest Regeneration in Cameroon Using Noaa Avhrr Data. International Journal of Remote Sensing 21: 2831-2854.

Lucas, R. M., M. Honzak, I. D. Amaral, P. J. Curran & G. M. Foody 2002. Forest Regeneration on Abandoned Clearances in Central Amazonia. International Journal of Remote Sensing 23: 965-988.

Lugo, A. E. 2002. Can We Manage Tropical Landscapes? An Answer from the Caribbean Perspective. Landscape Ecology 17: 601-615.

Lugo, A. E. & E. Helmer 2004. Emerging Forests on Abandoned Land: Puerto Rico's New Forests. Forest Ecology and Management 190: 145-161.

Lussier, J. M., H. Morin & R. Gagnon 2002. Mortality in Black Spruce Stands of Fire or Clear-Cut Origin. Canadian Journal of Forest Research. 2002; 32: 539-547.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing, Malden, MA, USA.

Marcano Vega, H., T. M. Aide & D. Baez 2002. Forest Regeneration in Abandoned Coffee Plantations and Pastures in the Cordillera Central of Puerto Rico. Plant Ecology 161: 75-87.

Marod, D., U. Kutintara, H. Tanaka & T. Nakashizuka 2002. The Effects of Drought and Fire on Seed and Seedling Dynamics in a Tropical Seasonal Forest in Thailand. Plant Ecology 161: 41-57.

Martínez-Ramos, M., E. Álvarez-Buylla & J. Sarukhán 1989. Tree Demography and Gap Dynamics in a Tropical Rain Forest. Ecology 70: 555-558.

Martínez-Ramos, M. & E. Álvarez-Buylla 1995a. Population Ecology of Plants in a Tropical Rainforest of Mexico. Boletin de la Sociedad Botanica de Mexico 0: 121-153.

Martínez-Ramos, M. & E. R. Álvarez-Buylla 1995b. Seed Dispersal and Patch Dynamics in Tropical Rain Forests: A Demographic Approach. Ecoscience 2: 223-229.

Martínez-Ramos, M. & E. Álvarez-Buylla 1998. How Old Are Tropical Rain Forest Trees? Trends in Plant Science 3: 400-405.

Martínez, E., A. C. H. Ramos & F. Chiang 1994. Floristic List of the Lacandona, Chiapas. Boletin de la Sociedad Botanica de Mexico 0: 99-177.

Martinez Ramos, M. & R. Alvarez Buylla Elena 1995. Seed Dispersal and Patch Dynamics in Tropical Rain Forests: A Demographic Approach. Ecoscience 2: 223-229.

Maury-Lechon, G. 1991. Comparative Dynamics of Tropical Rain Forest Regeneration in French Guyana. In A. Gómez-Pompa, T. C. Whitmore and M. Hadley (Eds.). Rain Forest Regeneration and Management, pp. 285-293. UNESCO-MAB, Paris, France.

McCook, L. J. 1994. Understanding Ecological Community Succession: Causal Models and Theories, a Review. Plant Ecology 110: 115-147.

McLaren, K. P. & M. A. McDonald 2003. Coppice Regrowth in a Disturbed Tropical Dry Limestone Forest in Jamaica. Forest ecology and management 180: 99-111.

Méndez-Bahena, A. 1999. Sucesión Secundaria De La Selva Húmeda Y Conservación De Recursos Naturales En Marquuéz De Comillas, Chiapas. MSc thesis, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.

Mendoza, E. & R. Dirzo 1999. Deforestation in Lacandonia (Southeast Mexico): Evidence for the Declaration of the Northernmost Tropical Hot-Spot. Biodiversity and Conservation 8: 1621-1641.

Mesquita, R., C. G., K. Ickes, G. Ganade & G. B. Williamson 2001. Alternative Successional Pathways in the Amazon Basin. Journal of Ecology 89: 528-537.

Metzger, J. P. 2002. Landscape Dynamics and Equilibrium in Areas of Slash-and-Burn Agriculture with Short and Long Fallow Period (Bragantina Region, Ne Brazilian Amazon). Landscape Ecology 17: 419-431.

Midgley, J. J., R. Parker, H. Laurie & A. Seydack 2002. Competition among Canopy Trees in Indigenous Forests: An Analysis of the 'Additive Basal Area' Phenomenon. Australian Ecology 27: 269-272.

Miller, P. M. & J. B. Kauffman 1998. Effects of Slash and Burn Agriculture on Species Abundance and Composition of a Tropical Deciduous Forest. Forest Ecology and Management 103: 191-201.

Miller, P. M. 1999. Effects of Deforestation on Seed Banks in a Tropical Deciduous Forest of Western Mexico. Journal of Tropical Ecology 15: 179-188.

Miller, T. E. & J. Weiner 1989. Local Density Variation May Mimic Effects of Asymmetric Competition on Plant Size Variability. Ecology 70: 1188-1191.

Milton, K., E. A. Laca & M. W. Demment 1994. Successional Patterns of Mortality and Growth of Large Trees in a Panamanian Lowland Forest. Journal of Ecology 82: 79-87.

Mitchell-Olds, T. 1987. Analysis of Local Variation in Plant Size. Ecology 68: 82-87.

Mohler, C. L., P. L. Marks & D. G. Sprugel 1978. Stand Structure and Allometry of Trees During Self-Thinning of Pure Stands. Journal of Ecology 66: 599-614.

Montgomery, R. A. & R. L. Chazdon 2001. Forest Structure, Canopy Architecture, and Light Transmittance in Tropical Wet Forests. Ecology 82: 2707-2718.

Mooney, H. A., S. H. Bullock & E. Medina 1995. Introduction. In S. H. Bullock, H. A. Mooney and E. Medina (Eds.). Seasonally Dry Tropical Forests, pp. 1-8. Cambridge University Press, Cambridge, UK.

Moran, E. F., E. Brondizio, P. Mausel & Y. Wu 1994. Integrating Amazonian Vegetation, Land-Use, and Satellite Data. BioScience 44: 329.

Moran, E. F., A. Packer, E. Brondizio & J. Tucker 1996. Restoration of Vegetation Cover in the Eastern Amazon. Ecological Economics 18: 41-54.

Moran, E. F., E. S. Brondizio, J. M. Tucker, M. C. da Silva Forsberg, S. McCracken & I. Falesi 2000. Effects of Soil Fertility and Land-Use on Forest Succession in Amazonia. Forest Ecology and Management 139: 93-108.

Murphy, P. G. & A. E. Lugo 1986. Ecology of Tropical Dry Forest. Annual Review of Ecology and Systematics 17: 67-88.

--- 1987. Structure and Biomass of a Subtropical Dry Forest in Puerto Rico USA. Biotropica 18: 89-96.

Myers, N. D. 1993. Tropical Forests: The Main Deforestation Fronts. Environmental Conservation 20: 9.

Myster, R. W. 2003. Seed Regeneration Mechanisms over Fine Spatial Scales on Recovering Coffee Plantation and Pasture in Puerto Rico. Plant Ecology 166: 199-205.

Nagelkerke, N. J. D. 1991. A Note on a General Definition of the Coefficient of Determination. Biometrika 78: 691-692.

Nelson, B. W., R. Mesquita, J. L. G. Pereira, S. Garcia Aquino de Souza, T. Batista Getulio & B. Couto Luciana 1999. Allometric Regressions for Improved Estimate of Secondary Forest Biomass in the Central Amazon. Forest ecology and management 117: 149-167.

Nepstad, D. C., C. Uhl & E. A. S. Serrao 1991. Recuperation of a Degraded Amazonian Landscape Forest Recovery and Agricultural Restoration. Ambio 20: 248-255.

Nepstad, D. C., C. A. Klink, C. Uhl, I. C. Vieira, P. Lefebvre, M. Pedlowski, E. Matricardi, G. Negreiros, I. F. Brown, E. Amaral, A. Homma & R. Walker 1997. Land-Use in Amazonia and the Cerrado of Brazil. Ciencia e Cultura Sao Paulo 49: 73-86.

Nepstad, D. C., A. Verssimo, A. Alencar, C. Nobre, E. Lima, P. Lefebvre, P. Schlesinger, C. Potter, P. Moutinho, E. Mendoza, M. Cochrane & V. Brooks 1999. Large-Scale Impoverishment of Amazonian Forests by Logging and Fire. Nature 398: 505-508.

Nicotra, A. B., R. L. Chazdon & S. V. B. Iriarte 1999. Spatial Heterogeneity of Light and Woody Seedling Regeneration in Tropical Wet Forests. Ecology 80: 1908-1926.

Niklas, K. J. & B. J. Enquist 2002. On the Vegetative Biomass Partitioning of Seed Plant Leaves, Stems, and Roots. American Naturalist 159: 482-497.

Niklas, K. J., J. J. Midgley & B. J. Enquist 2003a. A General Model for Mass-Growth-Density Relations across Tree-Dominated Communities. Evolutionary Ecology Research 5: 459-468.

Niklas, K. J., J. J. Midgley & R. H. Rand 2003b. Tree Size Frequency Distributions, Plant Density, Age and Community Disturbance. Ecology Letters 6: 405-411.

Noordwijk, M. v., G. Lawson, A. Soumaré, J. J. R. Groot & K. Hairiah 1996. Root Distribution of Trees and Crops: Competition and/or Complementarity. In C. K. Ong and P. Huxley (Eds.). Tree-Crop Interactions, pp. 319-364. CAB International, Wallingford, UK.

Okimori, Y. & P. Matius 2000. Tropical Secondary Forest and Its Succession Following Traditional Slash-and-Burn Agriculture in Mencimai, East Kalimantan. In E. Guhardia (Ed.). Rainforest Ecosystems of East Kalimantan: El Niño, Drought, Fire, and Human Impacts, pp. 185-197. Springer-Verlag, New York.

Oksanen, J., R. Kindt, P. Legendre & R. B. O'Hara 2007. Vegan: Community Ecology Package Version 1.8-5. R Development Core Team.

Olano, J. M., I. Caballero, N. A. Laskurain, J. Loidi & A. Escudero 2002. Seed Bank Spatial Pattern in a Temperate Secondary Forest. Journal of vegetation science 13: 775-784.

Oldeman, R. A. A. 1990. Forests: Elements of Silvology. Springer-Verlag, Berlin, Germany.

Oliver, C. D. & B. C. Larson 1996. Forest Stand Dynamics. John Wiley & Sons, New York, USA.

Orlóci, L. 1991. Entropy and Information. SPB Academic Publishing, The Hague, The Netherlands.

Ostertag, R. 1998. Belowground Effects of Canopy Gaps in a Tropical Wet Forest. Ecology 79: 1294-1304.

Overman, J. P. M., H. J. L. Witte & J. G. Saldarriaga 1994. Evaluation of Regression Models for above-Ground Biomass Determination in Amazon Rainforest. Journal of Tropical Ecology 10: 207-218.

Palomaki, M. B., R. L. Chazdon, J. P. Arroyo & S. G. Letcher 2006. Juvenile Tree Growth in Relation to Light Availability in Second-Growth Tropical Rain Forests. Journal of Tropical Ecology 22: 223-226.

Parren, M. P. E. 2003. Lianas and Logging in West Affrica. PhD thesis, Center for Ecosystem Studies, Wageningen University, Wageningen, The Netherlands.

Parrotta, J. A. 1995. Influence of Overstory Composition on Understory Colonization by Native Species in Plantations on a Degraded Tropical Site. Journal of Vegetation Science 6: 627-636.

Parrotta, J. A., O. H. Knowles & J. M. Wunderle 1997. Development of Floristic Diversity in 10-Year-Old Restoration Forests on a Bauxite Mined Site in Amazonia. Forest Ecology and Management 99: 21-42.

Pascarella, J. B., T. M. Aide, M. I. Serrano & J. K. Zimmerman 2000. Land-Use History and Forest Regeneration in the Cayey Mountains, Puerto Rico. Ecosystems 3: 217-228.

Pascarella, J. B., T. M. Aide & J. K. Zimmerman 2004. Short-Term Response of Secondary Forests to Hurricane Disturbance in Puerto Rico, USA. Forest Ecology and Management 199: 379-393.

Pavlis, J. 2000. Succession of Rain Forest in Colombian Amazonia, Araracuara Region. Journal of Forest Science 46: 369-387.

Pearson, T. R. H., D. Burslem, R. E. Goeriz & J. W. Dalling 2003a. Interactions of Gap Size and Herbivory on Establishment, Growth and Survival of Three Species of Neotropical Pioneer Trees. Journal of Ecology 91: 785-796.

--- 2003b. Regeneration Niche Partitioning in Neotropical Pioneers: Effects of Gap Size, Seasonal Drought and Herbivory on Growth and Survival. Oecologia 137: 456-465.

Peet, R. K. & N. L. Christensen 1980. Succession: A Population Process. Plant Ecology 43: 131-140.

--- 1987. Competition and Tree Death. BioScience 37: 586.

Peña-Claros, M. 2003. Changes in Forest Structure and Species Composition During Secondary Forest Succession in the Bolivian Amazon. Biotropica 35: 450-461.

Pennington, T. D. & J. Sarukhán 2005. Árboles Tropicales De México. Manual Para La Identificación De Las Principales Especies. Universidad Nacional Autónoma de México, Fondo de cultura Económica, México.

Pereira, C. A. & I. C. G. Vieira 2001. A Importancia Das Florestas Secundarias E Os Impactos De Sua Substituicao Por Plantios Mecanizados De Graos Na Amazonia. Interciencia 26: 337-341; 362.

Perz, S. G., C. Aramburú & J. Bremner 2005. Population, Land Use and Deforestation in the Pan Amazon Basin: A Comparison of Brazil, Bolivia, Colombia, Ecuador, Perú and Venezuela. Environment, Development and Sustainability 7: 23-49.

Peters, H. A. 2003. Neighbour-Regulated Mortality: The Influence of Positive and Negative Density Dependence on Tree Populations in Species-Rich Tropical Forests. Ecology Letters 6: 757-765.

Peterson, C., J. & E. Squiers, R. 1995. Competition and Succession in an Aspen-White-Pine Forest. Journal of Ecology 83: 449-457.

Pickett, S. T. A. 1976. Succession: An Evolutionary Interpretation. The American Naturalist 110: 107-119.

Pickett, S. T. A., S. L. Collins & J. J. Armesto 1987. A Hierarchical Consideration of Causes and Mechanisms of Succession. Plant Ecology 69: 109-114.

Pickett, S. T. A. 1989. Space for Time Substitution as an Alternative to Long-Term Studies. In G. E. Likens (Ed.). Long-Term Studies in Ecology : Approaches and Alternatives, pp. 110-135. Springer, New York.

Pickett, S. T. A., M. L. Cadenasso & S. Bartha 2001. Implications from the Buell-Small Succession Study for Vegetation Restoration. Applied Vegetation Science 4: 41-52.

Pickett, S. T. A. & M. L. Cadenasso 2005. Vegetation Dynamics. In E. v. d. Maarel (Ed.). Vegetation Ecology, pp. 172-198. Blackwell Science Ltd, Oxford.

Piñero, D., M. Martinez Ramos & J. Sarukhan 1984. A Population Model of Astrocaryum-Mexicanum and a Sensitivity Analysis of Its Finite Rate of Increase. Journal of Ecology 72: 977-992.

Poorter, L. 1998. Seedling Growth of Bolivian Rain Forest Tree Species in Relation to Light and Water Availability. PhD thesis, Faculteit Biologie, Universiteit Utrecht, Utrecht, The Netherlands.

Poorter, L. & Y. Hayashida-Oliver 2000. Effects of Seasonal Drought on Gap and Understorey Seedlings in a Bolivian Moist Forest. Journal of Tropical Ecology 16: 481-498

Poorter, L. 2001. Light-Dependent Changes in Biomass Allocation and Their Importance for Growth of Rain Forest Tree Species. Functional Ecology 15: 113-123.

Poorter, L. & E. Arets 2003. Light Environment and Tree Strategies in a Bolivian Tropical Moist Forest: An Evaluation of the Light Partitioning Hypothesis. Plant Ecology 166: 295-306.

Poorter, L. L., L. L. Bongers & F. F. Bongers 2006. Architecture of 54 Moist-Forest Tree Species: Traits, Trade-Offs, and Functional Groups. Ecology 87: 1289-1301.

Potts, M. D., P. S. Ashton, L. S. Kaufman & J. B. Plotkin 2002. Habitat Patterns in Tropical Rain Forests: A Comparison of 105 Plots in Northwest Borneo. Ecology 83: 2782-2797.

Powers, J. S., J. P. Haggar & R. F. Fisher 1997. The Effect of Overstory Composition on Understory Woody Regeneration and Species Richness in 7-Year-Old Plantations in Costa Rica. Forest Ecology and Management 99: 43-54.

Pringle, C. M. 1991. Geothermally Modified Waters Surface at La Selva Biological Station, Costa Rica: Volcanic Processes Introduce Chemical Discontinuities into Lowland Tropical Streams. Biotropica 23: 523-529.

Purata, S. E. 1986. Floristic and Structural Changes During Old-Field Succession in the Mexican Tropics in Relation to Site History and Species Availability. Journal of Tropical Ecology 2: 257-276.

Purvis, A. & A. Hector 2000. Getting the Measure of Biodiversity. Nature 405: 212-219.

Putz, F. E. 1992. Reduction of Root Competition Increases Growth of Slash Pine Seedlings on a Cutover Site in Florida. Southern Journal of Applied Forestry 16: 193-197.

Putz, F. E. & C. D. Canham 1992. Mechanisms of Arrested Succession in Shrublands: Root and Shoot Competition between Shrubs and Tree Seedlings. Forest Ecology and Management 49: 267-275.

Quinn, G. P. & M. J. Keough 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Ramírez León, R. H. & M. Carrera Pola 2004. Población En Chiapas. Universidad Autónoma de Chiapas.

Ray, G. J. & B. J. Brown 1994. Seed Ecology of Woody Species in a Caribbean Dry Forest. Restoration Ecology 2: 156-163.

Read, L. & D. Lawrence 2003. Recovery of Biomass Following Shifting Cultivation in Dry Tropical Forests of the Yucatan. Ecological Applications 13: 85-97.

Reiners, W. A., A. F. Bouwman, W. F. J. Parsons & M. Keller 1994. Tropical Rain Forest Conversion to Pasture: Changes in Vegetation and Soil Properties. Ecological Applications 4: 363-377.

Rejmanék, M. 1990. Old and New Fields of Old-Field Ecology. In J. Osbornov, M. Kovarova, J. Leps and K. Pracj (Eds.). Succession in Abandoned Fields, pp. ix-xiii. Kluwer Academic Press, Dordrecht, The Netherlands.

Remmers, G. G. A. & H. Koeijer 1992. The T'olche', a Maya System of Communally Managed Forest Belts: The Causes and Consequences of Its Disappearance. Agroforestry Systems 18: 149-177.

Renner, S. S. 1998. Effects of Habitat Fragmentation on Plant-Pollinator Interactions in the Tropics. In D. M. Newberry, H. H. T. Prins and N. D. Brown (Eds.). Dynamics of Tropical Communities, pp. 339-360. Blackwell Science, Oxford, UK.

Rényi, A. 1961. On Measures of Entropy and Information. In J. Neyman (Ed.). Proceedings of the fourth Berkeley symposium on mathematical statistics and probability, p. 239. University of California Press, Berkeley, Berkeley, USA.

Richards, K. R. & C. Stokes 2004. A Review of Forest Carbon Sequestration Cost Studies: A Dozen Years of Research. Climate Change 63: 1-48.

Richards, P. W., R. P. D. Walsh, I. C. Baillie & P. Greig-Smith 1996. The Tropical Rain Forest : An Ecological Study. Cambridge University Press, Cambridge.

Rico-Gray, V. & J. García-Franco 1992. Vegetation and Soil Seed Bank of Successional Stages in Tropical Lowland Deciduous Forest. Journal of Vegetation Science 3: 617.

Ricotta, C. & G. Avena 2000. A Parametric Index of Community Evenness. Ecoscience 7: 511-515.

Ricotta, C. & G. C. Avena 2002. On the Information-Theoretical Meaning of Hill's Parametric Evenness. Acta Biotheoretica 50: 63-71.

Ricotta, C. 2003. On Parametric Evenness Measures. Journal of Theoretical Biology 222: 189-197.

--- 2005. On Parametric Diversity Indices in Ecology: A Historical Note. Community Ecology 6: 241-244.

Rincón, E. & P. Huante 1993. Growth Responses of Tropical Deciduous Tree Seedlings to Contrasting Light Conditions. Trees 7: 202-207.

Rivera, L. W. & T. M. Aide 1998. Forest Recovery in the Karst Region of Puerto Rico. Forest Ecology and Management 108: 63-75.

Rivera, L. W., J. K. Zimmerman & T. M. Aide 2000. Forest Recovery in Abandoned Agricultural Lands in a Karst Region of the Dominican Republic. Plant Ecology 148: 115-125.

Robinson, J. G. & E. L. Bennett (Eds.) 2000. Hunting for Sustainability in Tropical Forests. Colombia University Press, New York, USA.

Román-Cuesta, R. M., M. Gracia & J. Retana 2003. Environmental and Human Factors Influencing Fire Trends in Enso and Non-Enso Years in Tropical Mexico. Ecological Applications 13: 1177-1192.

Román-Cuesta, R. M., J. Retana & M. Gracia 2004. Fire Trends in Tropical Mexico: A Case Study of Chiapas. Journal of Forestry 102: 26-32.

Rudel, T. K., D. Bates & R. Machinguiashi 2002. A Tropical Forest Transition? Agricultural Change, out-Migration, and Secondary Forests in the Ecuadorian Amazon. Annals of the Association of American Geographers 92: 87-102.

Ruiz, J., M. C. Fandino & R. L. Chazdon 2005. Vegetation Structure, Composition, and Species Richness across a 56-Year Chronosequence of Dry Tropical Forest on Providencia Island, Colombia. Biotropica 37: 520-530.

Sabogal, C. 1992. Regeneration of Tropical Dry Forests in Central America, with Examples from Nicaragua. Journal of Vegetation Science 3: 407-416.

Saldarriaga, J. G., D. C. West, M. L. Tharp & C. Uhl 1988. Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76: 938-958.

Saldarriaga, J. G. & R. J. Luxmoore 1991. Solar Energy Conversion Efficiencies During Succession of a Tropical Rainforest in Amazonia. Journal of tropical ecology 7: 233-242.

Salimon, C. I. & I. F. Brown 2000. Secondary Forests in Western Amazonia: Significant Sinks for Carbon Released from Deforestation? Interciencia 25: 198-202.

Sampson, R. N., N. Bystriakova, S. Brown, P. Gonzales, L. C. Irland, P. Kauppi, R. Sedjo, I. D. Thompson, C. V. Barber & R. Offrell 2005. Timber, Fuel, and Fiber. In R. Hassan, R. Scholes and N. Ash (Eds.). Ecosystems and Human Well-Being: Current State and Trends. Findings of the Conditions and Trends Working Group of the Millennium Ecosystem Assessment, pp. 243-269. Island Press, Washington.

Sanchez-Azofeifa, G. A., M. Quesada, J. P. Rodriguez, J. M. Nassar, K. E. Stoner, A. Castillo, T. Garvin, E. L. Zent, J. C. Calvo-Alvarado, M. E. R. Kalacska, L. Fajardo, J. A. Gamon & P. Cuevas-Reyes 2005. Research Priorities for Neotropical Dry Forests. Biotropica 37: 477-485.

Sanders, H. 1968. Marine Benthic Diversity: A Comparative Study. The American Naturalist 102: 243-282.

Sanford Jr., R. L. P., P., J. C. Luvall & E. Phillips 1994. Climate, Geomorphology, and Aquatic Systems. In L. A. McDade, K. S. Bawa and H. A. Hespenheide (Eds.). La Selva: Ecology and Natural History of a Neotropical Rain Forest, pp. 19-33. University of Chicago Press, Chicago, USA.

Sarukhán, J., D. Piñero & M. Martínez-Ramos 1985. Plant Demogrpahy: A Community Level Interpretation. In J. White (Ed.). Plant Population Ecology, pp. 17-31. Blackwell, Oxford, UK.

Scharf, F. S., F. Juanes & M. Sutherland 1998. Inferring Ecological Relationships from the Edges of Scatter Diagrams: Comparison of Regression Techniques. Ecology 79: 448-460.

Schenk, H. J. & R. B. Jackson 2002. Rooting Depths, Lateral Root Spreads and Below-Ground/above-Ground Allometries of Plants in Water-Limited Ecosystems. Journal of Ecology 90: 480-494.

Schmidt-Vogt, D. 1999. Swidden Farming and Fallow Vegetation in Northen Thailand. Franz Steiner Verlag, Stuttgart, Germany.

Schnitzer, S. A., M. E. Kuzee & F. Bongers 2005. Disentangling above- and Below-Ground Competition between Lianas and Trees in a Tropical Forest. Journal of Ecology 93: 1115-1125.

Schwinning, S. & J. Weiner 1998. Mechanisms Determining the Degree of Size Asymmetry in Competition among Plants. Oecologia 113: 447-455.

Selaya, N. G. 2007. Sprinting, Climbing and Presisting: Light Interception and Carbon Gain in a Secondary Tropical Forest Succession. Promab Scientific Series 11. PhD thesis, Institute of environmental Biology, Utrecht University, Utrecht.

Selaya, N. G., N. P. R. Anten, R. J. Oomen, M. Matthies & M. J. A. Werger 2007. Above-Ground Biomass Investments and Light Interception of Tropical Forest Trees and Lianas Early in Succession. Annals of Botany 99: 141-151.

Sheil, D. & R. M. May 1996. Mortality and Recruitment Rate Evaluations in Heterogeneous Tropical Forests. Journal of Ecology 84: 91-100.

Sheil, D. 1998. A Half-Century of Permanent Plot Observations in Budongo Forest, Uganda: Histories, Highlights, and Hypotheses. In F. Dallmeier and J. Comiskey (Eds.). Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies, pp. 399-428. Parthenon Publishing, Paris, France.

--- 1999a. Tropical Forest Diversity, Environmental Change and Species Augmentation: After the Intermediate Disturbance Hypothesis. Journal of Vegetation Science 10: 851-860.

--- 1999b. Developing Tests of Successional Hypotheses with Size-Structured Populations, and an Assessment Using Long-Term Data from a Ugandan Rain Forest. Plant Ecology 140: 117-127.

Sheil, D., S. Jennings & P. Savill 2000. Long-Term Permanent Plot Observations of Vegetation Dynamics in Budongo, a Ugandan Rain Forest. Journal of Tropical Ecology 16: 765-800.

Sheil, D. 2001. Long-Term Observations of Rain Forest Succession, Tree Diversity and Responses to Disturbance. Plant Ecology 155: 183-199.

Shriar, A. J. 2002. Food Security and Land Use Deforestation in Northern Guatemala. Food Policy 27: 395-414.

Shvidenko, A., C. V. Barber, R. Persson, P. Gonzales, R. Hassan, P. Lakyda, I. McCallum, S. Nilsson, J. Pulhin, B. v. Rosenburg & B. Scholes 2005. Forest and Woodland Systems. In R. Hassan, R. Scholes and N. Ash (Eds.). Ecosystems and Human Well-Being: Current State and Trends. Findings of the Conditions and Trends Working Group of the Millennium Ecosystem Assessment, pp. 585-621. Island Press, Washington.

Siebe, C., M. Martínez-Ramos, G. Segura-Warnholtz, J. Rodríguez-Velázquez & S. Sánchez-Beltran 1996. Soil and Vegetation Patterns in the Tropical Rainforest at Chajul, Chiapas, Southeast Mexico. In D. Simmorangkir (Ed.). Proceedings of the International Congress on Soils of Tropical Forest Ecosystems. 3rd Conference on Forest Soils, ISSS-AISS-IBG, pp. 40-58. Mulawarman University Press, Samarinda, Indonesia.

Silver, W. L., S. Brown & A. E. Lugo 1996. Effects of Changes in Biodiversity on Ecosystem Function in Tropical Forests. Conservation Biology 10: 17-24.

Silver, W. L., R. Ostertag & A. E. Lugo 2000. The Potential for Carbon Sequestration through Reforestation of Abandoned Tropical Agricultural and Pasture Lands. Restoration Ecology 8: 394-407.

Sist, P., C. Sabogal & Y. Byron (Eds.) 1999. Management of Secondary and Logged-over Forests in Indonesia. Selected Proceedings of an International Workshop 17-19 November 1997. Center for International Forestry Research, Bogor, Indonesia.

Slocum, M., G. 2001. How Tree Species Differ as Recruitment Foci in a Tropical Pasture. Ecology 82: 2547-2559.

Slocum, M. G. & C. C. Horvitz 2000. Seed Arrival under Different Genera of Trees in a Neotropical Pasture. Plant Ecology 149: 51-62.

Slocum, M. G., T. M. Aide, J. K. Zimmerman & L. Navarro 2004. Natural Regeneration of Subtropical Montane Forest after Clearing Fern Thickets in the Dominican Republic. Journal of Tropical Ecology 20: 483-486.

Smith, B. & J. B. Wilson 1996. A Consumer's Guide to Evenness Indices. Oikos 76: 70-82.

Smith, D. M., B. C. Larson, M. J. Kelty & P. M. S. Ashton 1997. The Practice of Silviculture: Applied Forest Ecology. John Wiley & Sons, Inc., New York, USA.

Smith, T. M. & M. A. Huston 1989. A Theory of the Spatial and Temporal Dynamics of Plant Communities. Vegetatio 83: 49-69.

Sokal, R. R. & F. J. Rohlf 1995. Biometry, the Principles and Practice of Statistics in Biological Research. W. H. Frreman and Company, New York, USA.

Sollins, P., R. M. Sancho & R. L. Sanford Jr. 1994. Soils and Soil Process Research. In L. A. McDade, K. S. Bawa and H. A. Hespenheide (Eds.). La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, USA.

Steininger, M., K. 2000. Secondary Forest Structure and Biomass Following Short and Extended Land-Use in Central and Southern Amazonia. Journal of Tropical Ecology 16: 689-708.

Sterck, F. J. 1999. Crown Development in Tropical Rain Forest Trees in Gaps and Understorey. Plant Ecology 143: 89-98.

--- 2005. Woody Tree Architecture. In C. G. N. Turnbull (Ed.). Plant Architecture and Its Manipulation, pp. 210-237. Blackwell Publishing Ltd, Oxford, UK.

Suazo-Ortuño, I. 1998. Aspectos Ecologicos De La Especies Invasora Pteridium Aquilinum (L.) Kuhn (Polypodiaceae) En Una Selva Húmeda De La Región De Chajul, Chiapas, Mexico. MSc thesis, Univ. Michoacana de San Nicolas de Hidalgo, Morelia, Michoacán, México.

Sunderlin, W. D. 1997. Shifting Cultivation and Deforestation in Indonesia: Steps toward Overcoming Confusion in the Debate. Network Paper 21b, Rural Development Forestry Network. ODI.

Swaine, M. D. & J. B. Hall 1983. Early Succession on Cleared Forest Land in Ghana. Journal of Ecology 71: 601-628.

Swaine, M. D. & T. C. Whitmore 1988. On the Definition of Ecological Species Groups in Tropical Rain Forests. Vegetatio 75: 81-86.

Swaine, M. D. 1992. Characteristics of Dry Forest in West Africa and the Influence of Fire. Journal of Vegetation Science 3: 365-374.

Ter Braak, C. J. F. & P. Smilauer 1998. Canoco Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4). p. 352. Centre for Biometry, CPRO-DLO, Wageningen, The Netherlands.

Terborgh, J., C. Flores, P. Mueller & L. Davenport 1997. Estimating the Ages of Successional Stands of Tropical Trees from Growth Increments. Journal of tropical ecology 13: 833-856.

Thomas, S. C. & J. Weiner 1989. Including Competitive Asymmetry in Measures of Local Interference in Plant Populations. Oecologia 80: 349-355.

Thomlinson, J. R., M. I. Serrano, T. D. M. Lopez, T. M. Aide & J. K. Zimmerman 1996. Land-Use Dynamics in a Post-Agricultural Puerto Rican Landscape (1936-1988). Biotropica 28: 525-536.

Toledo, M. & J. Salick 2006. Secondary Succession and Indigenous Management in Semideciduous Forest Fallows of the Amazon Basin. Biotropica 38: 161-170.

Toledo, V. M., B. Ortiz-Espejel, L. Cortés, P. Moguel & M. d. J. Ordoñez 2003. The Multiple Use of Tropical Forests by Indigenuous People in Mexico: A Case of Adaptive Management. Conservation Ecology 7: http:/www.consecol.org/vol7/iss3/art9.

Tóthméresz, B. 1995. Comparison of Different Methods for Diversity Ordering. Journal of Vegetation Science 6: 283-290.

Toyohara, G. & M. Fujihara 1998. Succession of Secondary Forests Affected by Pine Wilt Disease in Western Japan Followed on Vegetation Maps.

Tucker, J. M., E. S. Brondizio & E. E. Moran 1998. Rates of Forest Regrowth in Eastern Amazonia: A Comparison of Altamira and Bragantina Regions, Para State, Brazil. Interciencia 23: 64-73.

Turnbull, C. G. N. 2005. Shoot Architecture Ii Control of Branching. In C. G. N. Turnbull (Ed.). Plant Architecture and Its Manipulation, pp. 92-120. Blackwell Publishing Ltd, Oxford, UK.

Turnbull, L. A., D. A. Coomes, D. W. Purves & M. Rees 2007. How Spatial Structure Alters Population and Community Dynamics in a Natural Plant Community. Journal of Ecology 95: 79-89.

Turner, I. M., Y. K. Wong, P. T. Chew & I. Ali 1997. Tree Species Richness in Primary and Old Secondary Tropical Forest in Singapore. Biodiversity and Conservation 6: 537-543.

Turner, M., G., L. Baker William, J. Peterson Christopher & K. Peet Robert 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. Ecosystems 1: 511-523.

Uhl, C., K. Clark, H. Clark & P. Murphy 1981. Early Plant Succession after Cutting and Burning in the Upper Rio-Negro Region of the Amazon Basin Venezuela. Journal of Ecology 69: 631-650.

Uhl, C., C. Jordan, K. Clark, H. Clark & R. Herrera 1982. Ecosystem Recovery in Amazon Caatinga Forest after Cutting, Cutting and Burning and Bulldozer Clearing Treatments. Oikos 38: 313-320.

Uhl, C. & C. F. Jordan 1984. Succession and Nutrient Dynamics Following Forest Cutting and Burning in Amazonia Brazil. Ecology 65: 1476-1490.

Uhl, C. 1987. Factors Controlling Succession Following Slash-and-Burn Agriculture in Amazonia. Journal of Ecology 75: 377-408.

Uhl, C., R. Buschbacher & E. A. S. Serrao 1988. Abandoned Pastures in Eastern Amazonia Brazil I. Patterns of Plant Succession. Journal of Ecology 76: 663-681.

Uriarte, M., C. D. Canham, J. Thompson & J. K. Zimmerman 2004a. A Neighborhood Analysis of Tree Growth and Survival in a Hurricane-Driven Tropical Forest. Ecological Monographs 74: 591-614.

Uriarte, M., R. Condit, C. D. Canham & S. P. Hubbell 2004b. A Spatially Explicit Model of Sapling Growth in a Tropical Forest: Does the Identity of Neighbours Matter? Journal of Ecology 92: 348-360.

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman & N. Brokaw 2005a. Seedling Recruitment in a Hurricane-Driven Tropical Forest: Light Limitation, Density-Dependence and the Spatial Distribution of Parent Trees. Journal of Ecology 93: 291-304.

Uriarte, M., S. P. Hubbell, R. Condit & C. D. Canham 2005b. Neighborhood Effects on Sapling Growth and Survival in a Neotropical Forest and the Ecological Equivalence Hypothesis. In D. Burslem (Ed.). Biological Interactions in the Tropics, pp. 89-106. Blackwell Publishing, Oxford, UK.

Valencia, R., R. B. Foster, G. Villa, R. Condit, J.-C. Svenning, C. Hernandez, K. Romoleroux, E. Losos, E. Magard & H. Balslev 2004. Tree Species Distributions and Local Habitat Variation in the Amazon: Large Forest Plot in Eastern Ecuador. Journal of Ecology 92: 214-229.

van Gemerden, B. S., H. Olff, P. E. Parren Marc & F. Bongers 2003. The Pristine Rain Forest? Remnants of Historical Human Impacts on Current Tree Species Composition and Diversity. Journal of Biogeography 30: 1381-1390.

Vanclay, J. K. 1994. Modelling Forest Growth and Yield. Applications to Mixed Tropical Forests. CAB International, Wallingford, UK.

Vandermeer, J., I. G. d. l. Cerda, D. Boucher, I. Perfecto & J. Ruiz 2000. Hurricane Disturbance and Tropical Tree Species Diversity. Science 290: 788-791.

Venables, W. N. & B. D. Ripley 2002. Modern Applied Statistics with S. Springer, New York, USA.

Veneklaas, E. J. & L. Poorter 1998. Growth and Carbon Partitioning of Tropical Tree Seedlings in Contrasting Light Environments. In H. Lambers, H. Poorter and M. M. I. Vuuren Van (Eds.). Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences., pp. 337-361. Backhuys Publishers, Leiden, the Netherlands.

Vester, H. 1997. The Trees and the Forest. The Role of Tree Architecture in Canopy Development; a Case Study in Secondary Forests (Araracuara, Colombia). PhD thesis, The Hugo de Vries Laboratory, University of Amsterdam, Amsterdam, The Netherlands.

Vieira, D. L. M. & A. Scariot 2006. Principles of Natural Regeneration of Tropical Dry Forests for Restoration. Restoration Ecology 14: 11-20.

Vieira, D. L. M., A. Scariot, A. B. Sampaio & K. D. Holl 2006. Tropical Dry-Forest Regeneration from Root Suckers in Central Brazil. Journal of tropical ecology 22: 353-357.

W3tropicos: Access to Missouri Botanical Garden's Vast Nomenclatural Database and Associated Authority Files. http://mobot.mobot.org/W3T/Search/vast.html. accessed on 05-03-2007.

Wal, H. v. d. 1998. Chinantec Shifting Cultivation and Secondary Vegetation. A Case Study on Secondary Vegetation Resulting from Indigenous Shifting Cultivation in the Chinantla, Mexico. PhD thesis, Wageningen University, Wageningen, The Netherlands.

Walker, L. R. 1991. Tree Damage and Recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 379-385.

Walker, L. R., D. J. Lodge, S. M. Guzman Grajales & N. Fetcher 2003. Species-Specific Seedling Responses to Hurricane Disturbance in a Puerto Rican Rain Forest. Biotropica 35: 472-485.

Walker, R. & A. K. O. Homma 1996. Land Use and Land Cover Dynamics in the Brazilian Amazon: An Overview. Ecological Economics 18: 67-80.

Walker, R., E. Moran & L. Anselin 2000. Deforestation and Cattle Ranching in the Brazilian Amazon: External Capital and Household Processes World Development 28: 683-699.

Watkinson, A. R. 1997. Plant Population Dynamics. In M. J. Crawley (Ed.). Plant Ecology, pp. 359-400. Blackwell Science Ltd, Oxford.

Webb, C. O., G. S. Gilbert & M. J. Donoghue 2006. Phylodiversity-Dependent Seedling Mortality, Size Structure, and Disease in a Bornean Rain Forest Ecology 87: 123-131.

Weiner, J. & S. C. Thomas 1986. Size Variability and Competition in Plant Monocultures. Oikos 47: 211-222.

Weiner, J. 1988. Variation in the Performance of Individuals in Plant Populations. In A. J. Davy, M. J. Hutchings and A. R. Watkinson (Eds.). Plant Population Ecology, pp. 59-81. Blackwell Scientific Publications, Oxford, UK.

--- 1990. Asymmetric Competition in Plant Populations. Trends in Ecology and Evolution 5: 360-364.

Welden, C. W. & W. L. Slauson 1986. The Intensity of Competition Versus Its Importance: An Overlooked Distinction and Some Implications. The Quarterly Review of Biology 61: 23-44.

Westoby, M. 1984. The Self-Thinning Rule. Advances in Ecological Research 14: 167-225.

White, J. & J. L. Harper 1970. Correlated Changes in Plant Size and Number in Plant Populations. Journal of Ecology 58: 467-485.

White, J. 1980. Demographic Factors in Populations of Plants. In O. T. Solbrig (Ed.). Demography and Evolution, pp. 21-48. Blackwell Scientific Publications, Oxford, UK.

--- 1981. The Allometric Interpretation of the Self-Thinning Rule. Journal of Theoretical Biology 89: 475-500.

Whitmore, T. C. 1974. Change with Time and the Role of Cyclones in Tropical Rain Forest on Kolombangara, Solomon Islands, Commonwealth Forestry Institute Paper 46. Commonwealth Forestry Institute, Oxford, UK.

--- 1990. An Introduction to Tropical Rain Forests. Clarendon Press, Oxford, UK.

Whitmore, T. C. & D. Burslem 1998. Major Disturbances in Tropical Rainforests. In D. M. Newberry, H. H. T. Prins and N. D. Brown (Eds.). Dynamics of Tropical Communities, pp. 549-565. Blackwell Science, Oxford, UK.

Whitmore, T. M. & B. L. Turner 1992. Landscapes of Cultivation in Mesoamerica on the Eve of the Conquest. Annals of the Association of American Geographers 82: 402-425.

Whittaker, R. H. 1972. Recent Evolution of Ecological Concepts in Relation to the Eastern Forests of North America. In F. Egerton (Ed.). History of American Ecology. Arno Press, New York, NY, USA.

Wijdeven, S. M. J. & M. E. Kuzee 2000. Seed Availability as a Limiting Factor in Forest Recovery Processes in Costa Rica. Restoration Ecology 8: 414-424.

Wills, C., R. Condit, B. Foster Robin & P. Hubbell Stephen 1997. Strong Density- and Diversity-Related Effects Help to Maintain Tree Species Diversity in a Neotropical Forest. Proceedings of the National Academy of Sciences of the United States of America 94: 1252-1257.

Wills, C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, H. C. Muller-Landau, P. Ashton, E. Losos, L. Comita, S. Hubbell, J. LaFrankie, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, R. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, A. Itoh, R. John, S. Kiratiprayoon, S. L. de Lao, M. Massa, C. Nath, M. N. S. Noor, A. R. Kassim, R. Sukumar, H. S. Suresh, I. F. Sun, S. Tan, T. Yamakura & J. Zimmerman 2006. Nonrandom Processes Maintain Diversity in Tropical Forests. Science 311: 527-531.

Wilson, J. B. 1988. Shoot Competition and Root Competition. Journal of Applied Ecology 25: 279-296.

Wilson, J. B., H. Gitay, S. H. Roxburgh, W. M. King & R. S. Tangney 1992. Egler's Concept of 'Initial Floristic Composition' in Succession - Ecologists Citing It Don't Agree What It Means. Oikos 64: 591-593.

Wilson, S. D. 1999. Plant Interactions During Secondary Succession. In L. R. Walker (Ed.). Ecosystems of Disturbed Ground, pp. 611-632. Elsevier, Amsterdam.

Wright, S. J. 2005. Tropical Forests in a Changing Environment. Trends in Ecology and Evolution 20: 553-560.

Wright, S. J. & H. C. Muller-Landau 2006. The Future of Tropical Forest Species. Biotropica 38: 287-301.

Wunderle, J. M. 1997. The Role of Animal Seed Dispersal in Accelerating Native Forest Regeneration on Degraded Tropical Lands. Forest Ecology and Management 99: 223-235.

Yih, K., D. H. Boucher, J. H. Vandermeer & N. Zamora 1991. Recovery of the Rain Forest of Southeastern Nicaragua after Destruction by Hurricane Joan. Biotropica 23: 106-113.

Yoda, K., T. Kira, H. Ogawa & K. Hozumi 1963. Self Thinning in Overcrowded Pure Stands under Cultivated and Natural Conditions. Journal of Biology 14: 107-129.

Zarin, D. J., M. J. Ducey, J. M. Tucker & W. A. Salas 2001. Potential Biomass Accumulation in Amazonian Regrowth Forests. Ecosystems 4: 658-668.

Zarin, D. J., E. A. Davidson, E. Brondizio, I. C. G. Vieira, T. Sá, T. Feldpausch, E. A. G. Schuur, R. Mesquita, E. Moran, P. Delamonica, M. J. Ducey, G. C. Hurtt, C. Salimon & M. Denich 2005. Legacy of Fire Slows Carbon Accumulation in Amazonian Forest Regrowth. Frontiers in Ecology and the Environment 3: 365-369.

Zeide, B. 1993. Analysis of Growth Equations. Forest Science 39: 594-616.

Zimmerman, J., K., T. M. Aide, M. Rosario, M. Serrano & L. Herrera 1995. Effects of Land Management and a Recent Hurricane on Forest Structure and Composition in the Luquillo Experimental Forest, Puerto Rico. Forest Ecology and Management 77: 65-76.

Zimmerman, J., K., B. Pascarella John & T. M. Aide 2000. Barriers to Forest Regeneration in an Abandoned Pasture in Puerto Rico. Restoration Ecology 8: 350-360.

Zuidema, P. A. & R. G. A. Boot 2002. Demography of the Brazil Nut Tree (*Bertholletia Excelsa*) in the Bolivian Amazon: Impact of Seed Extraction on Recruitment and Population Dynamics. Journal of Tropical Ecology 18: 1-31.

SUMMARY

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RESUMEN

SUMMARY

The succession of tropical secondary forests on abandoned agricultural fields has been studied since long, most often by comparing stands of different age since abandonment. These so-called chronosequence studies have yielded much insight in general patterns of succession and the constraints and conditions that affect the course of succession (shortly reviewed in chapter 1). Successional dynamics, however, are inferred rather than directly monitored in such studies; i.e. direction and rates of change of community structure and composition are deduced indirectly on the assumption that similar successional processes take place in any one stand. Only very few studies followed successional dynamics through repeated measurements in permanent sample plots, hence our current understanding of the variation in successional dynamics across secondary forest stands, the underlying processes of growth, mortality and recruitment, and the processes and mechanism that steer them, is still poor.

This thesis presents data from one of the very few studies on secondary tropical forest succession in multiple permanent sample plots. The focus of this work is on the first years of secondary forest succession, and on the role of competition on the level of individuals, populations and communities. The main aims of this work were: 1) To evaluate the dynamics of young secondary forests on abandoned agricultural fields in terms of rates and direction of community changes, how these dynamics vary across sites and how they change with time since abandonment; 2) To evaluate the dynamics of young secondary forests in terms of growth, mortality and recruitment, and how community changes are related to these processes; and 3) To examine the degree to which competition for light can account for variation in growth and mortality of saplings within a population and for variation in population dynamics across distinct sites.

The study was carried out in three villages in the Marqués de Comillas (MdC) region, part of the Selva Lacandona in eastern Chiapas, Mexico. The climate of the MdC region is humid tropical, with an average annual temperature of 24 ºC, mean annual rainfall of ~3000 mm and a short dry period in February-April. The original vegetation consists mainly of tropical evergreen and semi-deciduous forests. Colonization of the region started in the late 1960s, and since then a large part of the landscape has been converted to a mosaic of temporary and permanent grazing pastures, cultivated land, young secondary forest and old-growth remnants. The prevailing land use types in the three villages are slash-and-burn shifting cultivation practices (mainly maize) with short fallow periods and semi-permanent cattle ranging.

Data for this study were collected in secondary forests on abandoned agricultural fields and pastures with time since abandonment (age) ranging from 0.5 to 18 years. A first dataset consisted of a chronosequence of 72 stands, widely distributed over an area of roughly 60 km^2 and encompassing different geomorphological units (low hills vs. alluvial planes) and former land-use types (abandoned agricultural fields vs. pastures). In each stand, three 2 x 25 m transects were randomly located in which all woody stems with diameter at 1.3-m above ground (dbh) ≥ 1 cm identified to lowest possible taxon and their dbh and height were measured. A second dataset consists of permanent sample plots in twelve secondary forests with similar former land-use (maize fields) and geomorphology (low hills with sandy acidic and unfertile soils). Initial stand age ranged from 1-17 y. In each stand a 10 x 50-m permanent sample plot is established, and all trees with height ≥ 1.5-m are recorded, and tagged. Location of each tree was determined using a 1 x 1-m grid system. Every year dead trees and new recruits are recorded and dbh and height of all living trees is (re-)measured. The first dataset is used in chapter 2, and in chapters 3-7 data are used from the first three years of permanent plot study.

Chapter 2 demonstrates that patterns of species diversity, frequency and dominance are highly variable across secondary forests of an agricultural landscape, even when they are of similar age. Diversity varied widely between the plots, which could only partly be explained by differences in time since abandonment and geomorphology while the influence of former land use was even more ambiguous. Species richness changed with age, but dominance levels remained similar over the first 18 year of succession. Similarly, species richness, but not dominance, differed between secondary forests on low hills and alluvial plains. Across-stand frequency and abundance patterns varied strongly among tree species, and most among pioneer species. Despite the high species richness (almost 200 species identified across all plots), only a very small subset of the regional species pool dominated secondary forests in terms of frequency of occurrence and abundance, all of them pioneer species. Most pioneer species, however, and nearly all shade tolerant species, occurred in less than 15% of the plots and always in low densities. Only two species (*Cecropia peltat*a and *Trichospermum mexicanum*) occurred in ≥ 50% of the plots and they were also the only species that were relatively dominant (> 10 stems / > 10% of stand basal area) in ≥ 20% of the plots. Other species were dominant (> 10% basal area) in the plots were they occurred, but never abundant (e.g. *Ochroma pyramidale*); frequent but never abundant (e.g. *Vernonia patens*); or locally abundant but with low relative basal area (e.g. *Acalypha diversifolia*).

The "Initial Floristic Composition" hypothesis predicts that, on abandoned agricultural fields with light previous land-use and close to seed sources, both pioneer and shade-tolerant species colonize a site directly after abandonment and that the recruitment of pioneers sharply declines while the recruitment of shade-tolerant species continues as soon as the canopy closes. It also predicts higher mortality among pioneers. Consequently, recruited and dead trees are expected to differ in species composition, with highest species richness for the recruits. To evaluate these predictions, recruitment and mortality was examined in eight permanent sample plots with initial fallow age of 1 to 5 y (chapter 3). Shade-tolerant species established in the first years of succession, albeit in low numbers. As predicted, recruited and dead trees differed in species richness and composition, and in shade-tolerant frequency. In contrast to expected, over 50% of recruits were from pioneer species. Results suggested that high stand-level mortality opened new opportunities for continued pioneer colonization. Results demonstrate that species turnover starts very early in succession but is not always a gradual and continuous process, complicating prevailing succession models.

In chapter 4, stand structure dynamics (i.e, rate and direction of stand structure changes) were related to mortality, growth, and recruitment rates over a two-year period, and the dependence of these demographic processes on fallow age and initial stand structure attributes was evaluated. Changes in stand structure were especially fast in the first 5 y of succession, and decreased rapidly afterwards, which resulted from similar stand-level changes in relative mortality, growth, and recruitment rates. Changes in most stand structure attributes (e.g. basal area, canopy height) were closely correlated, and more linked with tree growth rates than with net changes in tree density due to recruitment and mortality. Demographic processes were negatively related with initial stand basal area, but independent of initial tree density. Results suggest that asymmetric competition and resulting patterns of size and density dependent mortality and growth are major driving forces determining secondary forest successional pathways. Sudden mass mortality among dominant species in some stands showed that early secondary forest succession is not always a gradual and unidirectional process.

The strong spatial and temporal variability of successional dynamics emphasizes the need to monitor these dynamics in permanent plots across a range of initial stand ages, with multiple plots in a given age class. In chapter 5, case studies in Costa Rica and

Mexico show that the actual rates of change in tree communities often deviate from chronosequence trends. With respect to tree species composition, sites of different ages differ more than a single site followed over time through the same age range. While changes in stem density have little to do with chronosequence trends, changes in basal area within stands generally followed chronosequence trends. Stem turnover rates were poor predictors of species turnover rates, particularly at longer time-intervals. Effects of the surrounding landscape on tree community dynamics within individual plots were not specifically included in this or in any of the other chapters, but results suggest that they are likely to be important determinants of species accumulation rates and relative abundance patterns.

Competition for light is often considered to be one of the main mechanisms that regulate successional vegetation dynamics. Competition for light is largely asymmetric, as larger trees shade smaller trees and not the other way around. Consequently, within-site variation in growth and survival of tree saplings can be expected to relate to variation in the degree of neighborhood competition, especially from the larger neighbors. In chapter 6, these hypotheses were tested for *Cecropia peltata* and *Trichospermum mexicanum* saplings in two adjacent 1-2 year old secondary forest stands. The degree of competition was estimated by neighborhood basal area (NBA). Both diameter and height growth were strongly negatively related to NBA of the larger neighbors. Only a small proportion of variation in survival, on the other hand, could be accounted for by variation in NBA, suggesting that other factors are more important. The effect of NBA of smaller neighbors on growth and survival was very weak or non-significant, indicating that competition between neighbors, indeed, is largely asymmetric.

Population dynamics of a species vary much from one secondary forest to another. In chapter 7 we examined if such between-site differences in demographic behavior can be related to variation in asymmetric competition that result from differences in stand and population size structures. Specifically, we tested if differences in mean growth and mortality of the biggest and of the smallest trees of a population (growth and survival asymmetry) were related to differences in the average level of asymmetric neighborhood competition in both size groups (competition asymmetry). We used 24 populations of four pioneer tree species in nine early (1-5 y) secondary forest stands. For each population, we compared average neighborhood basal area, growth and survival of the twenty percent smallest and twenty percent largest trees. The between-plot variation in competition asymmetry explained a significant part of the between-plot variation in growth asymmetry, with smallest trees growing faster in populations with low competition asymmetry, and largest trees growing fastest in populations with high competition asymmetry. Survival was size-related, with lowest survival rates among the smallest plants, as expected. However, survival asymmetry was significantly related to competition asymmetry in just one species. The differences in the effects of asymmetric competition on the mortality and survival of the four species show that susceptibility to competition for, presumably, light, varies considerably between early successional pioneer species. Results of chapter 6 and 7 support the prediction that in young secondary forests, asymmetric competition for light is one of the main mechanisms that govern secondary forest dynamics.

SAMENVATTING

De vegetatiesuccessie van secundaire tropische bossen op verlaten en/of braakliggende landbouwgronden wordt sinds lange tijd bestudeerd, meestal door het vergelijken van opstanden met verschillende leeftijd sinds braaklegging. Deze zogenoemde chronosequentiestudies hebben veel inzicht opgeleverd in algemene successiepatronen en in de voorwaarden en factoren die deze patronen bepalen (zie kort overzicht in hoofdstuk 1). Successiedynamiek, d.w.z. de richting waarin - en de snelheid waarmee opstandstructuur en soortensamenstelling verandert, wordt in dergelijke studies niet gevolgd in tijd en kan dus slechts op indirecte wijze worden afgeleid uit de gevonden patronen. Impliciete aanname in een dergelijke afleiding is dat vergelijkbare processen plaatsvinden in alle opstanden, en dat gevonden patronen de dynamiek in elk van de individuele opstanden weerspiegelt. Tot nu toe hebben slechts zeer weinig studies tropische secundaire bossuccessie bestudeerd door herhaalde metingen in permanente onderzoekpercelen. Hierdoor hebben we geen goed idee van de mate waarin successiedynamiek verschilt tussen secundaire bosopstanden, en een beperkt begrip van de ecologische processen en mechanismen die deze dynamiek beïnvloeden.

Dit proefschrift presenteert de resultaten van een van de weinige studies die secundaire tropische bossuccessie op verlaten landbouwgronden gevolgd hebben in meerdere permanente onderzoekspercelen. The focus van dit werk is op de eerste jaren van de bossuccessie en op de rol die concurrentie speelt in de dynamiek van secundaire bosgemeenschappen en van populaties van enkele boomsoorten. De belangrijkste doelstellingen van dit proefschrift zijn: 1) Evaluatie van de snelheid en richting waarin jonge secundaire bossen op verlaten landbouwgronden veranderen, van de mate waarin deze dynamiek verschilt tussen opstanden van dezelfde leeftijd, en hoe dit verandert met toenemende leeftijd. 2) Analyse van de patronen van groei, mortaliteit en vestiging van nieuwe planten die deze dynamiek bepalen. 3) Evaluatie van het belang van concurrentie om licht tussen individuele bomen voor de variatie in groei en mortaliteit van jonge staken in een populatie en voor de verschillen in de dynamiek van populaties (van dezelfde soorten) in verschillende bosopstanden.

Veldwerk voor deze studie heeft plaatsgevonden in drie dorpen in de Marqués de Comillas (MdC) regio, dat deel is van de 'Selva Lacandona' in oostelijk Chiapas, Mexico. De MdC regio heeft een gemiddelde jaartemperatuur van 24 °C, een jaarlijkse regenval van ongeveer 3000 mm en een korte drogere periode van februari tot april. De oorspronkelijke vegetatie bestaat uit immergroen en deels bladverliezend tropisch loofbos. Kolonisatie van de regio is begonnen in de vroege jaren zestig, en sindsdien zijn grote delen van het oorspronkelijke landschap omgevormd naar een mozaïek van landbouwgronden, veeweiden, jong secundair bos en restanten van het oorspronkelijke bos. De belangrijkste vormen van landgebruik in het onderzoeksgebied zijn zwerflandbouw (vooral maïs) met korte rotaties en semipermanente veeweiden.

Gegevens voor deze studie zijn verzameld in secundaire bossen op verlaten landbouwgronden en veeweiden, met leeftijden (vanaf het moment waarop ze verlaten zijn) die variëren van een half tot 18 jaar. Voor hoofdstuk 2 zijn gegevens verzameld in een chronosequence van 72 secundaire bosopstanden. Deze opstanden waren verspreid over een gebied van ruwweg 60 km^2 en werden gekenmerkt door een grote variatie in geomorfologie en voormalig landgebruik. In elke opstand is een inventarisatie van alle bomen met een diameter van tenminste 1 cm uitgevoerd in drie 2 x 25 m transekten. Alle bomen werden zover als mogelijk geïdentificeerd en hun diameter en hoogte werden gemeten. In de andere hoofdstukken zijn de gegevens gebruikt van permanente studiepercelen in twaalf secundaire bossen. Deze opstanden hebben hetzelfde voormalige landgebruik (maïs), dezelfde geomorphologie (lage heuvels met arme zanderige bodems), en hun leeftijd aan het begin van de studie varieerde van 1 tot 17 jaar. In elke opstand is een 10 x 50 m perceel uitgelegd, waarin alle bomen met een hoogte van ≥ 1.5 m zijn geïdentificeerd en gemerkt. Positie van alle bomen is bepaald met behulp van een 1 x 1 m grid. Elk jaar wordt mortaliteit en rekrutering van nieuwe bomen (in de ≥ 1.5 m hoogteklasse) gevolgd en worden diameters en hoogtes van alle levende bomen (opnieuw) gemeten.

Hoofdstuk twee laat zien dat diversiteit sterk varieert tussen secundaire bosopstanden, ook als ze dezelfde leeftijd hebben. Opstandsleeftijd en verschillen in geomorfologie verklaarden een beperkt deel van deze variatie, en de invloed van voormalig landgebruik was zelfs minder duidelijk. Soortenrijkdom veranderde met leeftijd, maar de mate waarin de opstanden werden gedomineerd door een of enkele soorten was niet gerelateerd aan leeftijd. Op dezelfde manier verschilde soortenrijkdom wel, maar soortendominantie niet tussen verschillende geomorfologische landschapseenheden. De frequentie waarmee soorten voorkwamen in de 72 plots – een benadering van hoe wijdverspreid deze soorten zijn – en de aantallen waarmee ze voorkwamen in de individuele plots, verschilde sterk tussen soorten. De grootste variatie werd gevonden in de groep van pioniersoorten. Ondanks de hoge soortenrijkdom in de secundaire bossen (bijna 200 soorten geïdentificeerd), kwamen maar slechts enkele (pionier)soorten wijdverspreid en in grote aantallen voor. Toch werden ook de meeste pioniersoorten, net als bijna alle schaduwtolerante boomsoorten, in minder dan 15% van de opstanden gevonden en in lage dichtheden (meestal met slechts een individu).

Slechts twee pioniersoorten (*Cecropia peltat*a and *Trichospermum mexicanum*) kwamen in ≥ 50% van de plots voor en dit waren ook de enige twee soorten die relatief dominant waren (> 10 bomen / > 10% van grondvlak) in ≥ 20% van de opstanden. Andere soorten waren dominant (> 10% van grondvlak) in de opstanden waar ze voorkwamen, maar nooit abundant (bijv. *Ochroma pyramidale*); kwamen frequent voor waren nooit abundant in de opstanden waar ze gevonden werden (bijv. *Vernonia patens*); of lokaal heel erg abundant maar met een relatief laag grondvlak (e.g. *Acalypha diversifolia*).

De "Initial Floristic Composition" hypothese voorspelt dat, op verlaten landbouwgronden met licht voormalig landgebruik en dichtbij potentiële zaadbronnen (overblijvende bomen of stukken ouder bos), zowel pioneer als schaduwtolerante soorten een stuk grond koloniseren direct nadat dit verlaten is. Verder voorspelt de IFC hypothese dat, na sluiting van het kronendak, rekrutering van de pioniersoorten sterk afneemt en mortaliteit sterk toeneemt, terwijl rekrutering van de schaduw tolerante groep gewoon doorgaat. Als een gevolg hiervan zou de soortensamenstelling van de groep van nieuw gevestigde bomen sterk moeten verschillen van de bomen die dood zijn gegaan over een zelfde periode, waarbij verwacht kan worden dat de soortenrijkdom van de eerste groep veel hoger is. Om deze voorspellingen te evalueren hebben we rekrutering en mortaliteit gevolgd in acht opstanden van 1 tot 5 jaar oud gedurende anderhalf jaar (hoofdstuk 3). Schaduwtolerante en pioneersoorten vestigden zich in het begin van vegetatiesuccessie, hoewel de schaduw tolerante soorten in heel lage aantallen. Zoals voorspeld verschilden de nieuw gerekruteerde bomen van de bomen die doodgingen in soortenrijkdom en -samenstelling en het percentage van schaduwtolerante soorten. In tegenstelling tot wat we verwachtten was meer dan 50% van de gerekruteerde bomen pionier. De resultaten suggereren dat de hoge mortaliteit in deze jonge secundaire bossen het kronendak opent en zo doorlopend nieuwe mogelijkheden genereert voor de vestiging van pioniers. Deze studie toont aan dat succesionele veranderingen in soortensamenstelling vroeg in vegetatiesuccessie niet altijd een gradueel en continu proces is, wat de ontwikkeling van successietheorieën compliceert.

In hoofdstuk 4 wordt opstanddynamiek over een periode van twee jaar (d.w.z. snelheid en richting waarin opstand structuur verandert) gerelateerd aan de dynamiek van groei, mortaliteit en rekrutering, en de mate waarin deze demografische processen zijn gerelateerd aan opstandleeftijd en initiële opstandstructuur wordt geëvalueerd. Mortaliteit, groei en rekrutering en de resulterende veranderingen in bosstructuur waren heel erg hoog en variabel in de eerste vijf jaar van successie, en namen daarna snel af. Veranderingen in de meeste variabelen die waren gebruikt om bosstructuur te beschrijven (zoals grondvlak, hoogte van het kronendak) waren sterk gecorreleerd en sterker beïnvloed door boomgroeisnelheden dan door veranderingen in stamdichtheid door mortaliteit en rekrutering. Demografische processen waren negatief gerelateerd met initiële opstandgrondvlak, maar onafhankelijk van initiële stamdichtheid.

Resultaten van deze studie suggereren dat asymmetrische concurrentie en de resulterende patronen van grootte- en dichtheidafhankelijke groei en mortaliteit belangrijke mechanismen zijn die grote invloed hebben op de successie van secundaire bossen. In de hoofdstukken 6 en 7 wordt hier verder op ingegaan. Plotseling optredende en massale mortaliteit die in sommige plots een dominante soort zwaar trof, illustreerden dat vroege bossuccessie niet altijd een geleidelijk en unidirectioneel proces is.

Studies in Costa Rica and Mexico laten zien dat de werkelijke veranderingen en snelheid van verandering in bosstructuur en samenstelling sterk kan afwijken van voorspellingen die gebasseerd zijn op chronosequenties (hoofdstuk 5). De sterke variatie van successie dynamiek in ruimte (verschillen tussen opstanden) en tijd (in een opstand) die we gevonden hebben benadrukken dat permanente plotstudies nodig zijn. De resultaten van de hoofdstukken 3 en 4 van dit proefschift geven al aan dat een benadering waarin een reeks van plots met verschillende leeftijden worden gevolgd in tijd zeer nuttig kan zijn, vooral wanneer er meerdere plots in elke leeftijdsklasse worden genomen. Verschillen in soortensamenstelling waren groter tussen opstanden van verschillende leeftijd dan de veranderingen in een enkele opstand over dezelfde leeftijdsperiode. Veranderingen in stamdichtheid had weinig van doen met chonosequentie trends, maar veranderingen in grondvlak volgde over het algemeen min of meer de trens zoals voorspeld bij chronosequenties. De ratio tussen mortaliteit en rekrutering van individuele bomen en van soorten waren niet of nauwelijks gerelateerd. Het effect van de omliggende vegetatie was niet meegenomen in deze studies, maar de resultaten van deze studies suggereren wel dat de aard van de omliggende vegetatie een grote invloed heeft op de soortendynamiek in individuele opstanden.

Concurrentie om licht wordt vaak beschouwd als een van de belangrijkste mechanismen die vegetatiesuccessie beïnvloeden. Concurrentie om licht is grotendeels asymmetrisch, dat wil zeggen dat grotere bomen kleinere bomen beschaduwen, maar niet andersom. Een gevolgtrekking zou kunnen zijn dat de variatie in groei en mortaliteit van jonge bomen voor een belangrijk deel wordt bepaald door variatie in de dichtheid van buurbomen en vooral van grotere buurbomen. In hoofdstuk 6 testten we deze hypothese voor geselecteerde *Cecropia peltata* en *Trichospermum mexicanum* staken (doelbomen) in twee 1-2 jaar oude secundaire bosopstanden. De sterkte van concurrentie door de buurbomen werd benaderd door het gecombineerde grondvlak van alle buurbomen (BGV). Zowel hoogte als diameter groei waren sterk gerelateerd aan het BGV van de buurbomen die hoger waren dan de doelbomen. Aan de andere kant werd slechts een klein deel van de variatie in mortaliteit verklaard door het BGV van de grotere bomen wat aangeeft dat andere factoren een belangrijke(re) rol spelen. Kleinere buurbomen hadden geen of een verwaarloosbaar kleine invloed op groei en mortaliteit van de doelbomen. Dit geeft aan dat onderlinge concurrentie in deze jonge secundaire bossen inderdaad grotendeels asymmetrisch is.

De dynamiek van populaties van dezelfde soort kan sterk verschillen tussen opstanden. In hoofdstuk 7 bekijken we of deze verschillen in demografie gerelateerd kunnen worden aan variatie in asymmetrische concurrentie die voortkomen uit verschillen in populatie - en opstandstructuur. Meer specifiek bekijken we of de verschillen tussen de gemiddelde groei en mortaliteit van de 20% kleinste en van de 20% grootste bomen van een populatie (groei- en mortaliteit-asymmetrie) gerelateerd waren aan verschillen tussen deze twee groepen in de gemiddelde sterkte van de concurrentie van grotere buurbomen (concurrentie-asymmetrie). Zoals in hoofdstuk 6 was concurrentiedruk benaderd door het gecombineerde grondvlak van de (grotere) buurbomen. We analyseerden deze relaties voor 24 populaties van vier verschillende pioneersoorten in negen 1-5 jaar oude secundaire bosopstanden. De verschillen in concurrentie-asymmetrie tussen populaties verklaarden een significant deel van de variatie in groei-asymmetrie: de kleinste bomen groeiden sneller dan de grootste bomen in populaties met lage concurrentie-asymmetrie, en de grootste bomen groeiden sneller wanneer de concurrentie-asymmetrie groot was. Mortaliteit was gerelateerd aan boomgrootte, met zoals verwacht de hoogste mortaliteit onder de kleinere bomen. Mortaliteit was echter slecht in één soort gerelateerd aan concurrrentie-asymmetrie. De verschillen tussen de vier sooreten met betrekking tot deze relaties laten zien dat gevoeligheid voor concurrentie behoorlijk kan verschillen tussen soorten die tot dezelfde groep van vroege pioneersoorten behoren. De resultaten van de hoofdstukken 6 en 7 ondersteunen de hypothese dat concurrentie om licht een belangrijk mechanisme is gedurende de eerste jaren van secundaire bossuccessie

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RESUMEN

La sucesión secundaria de bosques tropicales en campos agrícolas abandonados ha sido estudiada desde hace mucho tiempo, la mayoría de las veces mediante la comparación de parcelas con distintas edades de abandono. Estos estudios, conocidos como cronosequencias, han permitido elucidar tanto patrones generales de sucesión, como las limitantes y condiciones que afectan el curso de la sucesión (brevemente revisados en el capítulo 1). No obstante, la dinámica sucesional ha sido inferida más que monitoreada de forma directa en dichos estudios; i.e. la dirección y las tasas de cambio en la estructura y la composición de la comunidad han sido deducidas indirectamente bajo el supuesto de que procesos sucesionales similares se desarrollan en cualquier parcela. Son muy pocos los estudios que han seguido la dinámica sucesional a través de mediciones repetitivas en parcelas permanentes; por ello, todavía es muy pobre el conocimiento actual cacerca de la variación en la dinámica sucesional en los bosques tropicales, los procesos subyacentes de crecimiento, mortalidad y reclutamiento, y los procesos y mecanismos que los gobiernan.

Esta tesis presenta datos de uno de los pocos estudios de sucesión secundaria en bosques tropicales realizado en múltiples parcelas permanentes de muestreo. El estudio se enfoca en los primeros años de sucesión y en el papel que juega la competencia a nivel de individuos, poblacional y de comunidades. Los principales objetivos de esta investigación fueron: 1) evaluar la dinámica de bosques secundarios jóvenes en campos agrícolas abandonados en términos de las tasas y la dirección de los cambios en la comunidad vegetal; 2) evaluar como esta dinámica varía entre sitios y cómo cambian con el tiempo de abandono; 3) evaluar la dinámica en los bosques secundarios jovenes en términos de crecimiento, mortalidad y reclutamiento, y cómo los cambios en la comunidad vegetal estan relacionados a estos procesos; y 4) y cómo la competencia por la luz puede explicar la variación en el crecimiento y la mortalidad de los brinzales de una población, y la variación en la dinámica poblacional entre sitios.

El estudio se llevo a cabo en tres pueblos de la región del Marqués de Comillas (MdC), en la selva Lacandona del este de Chiapas, México. El clima de la región del MdC es tropical húmedo, con una temperatura media anual de 24 °C, precipitación media anual de ~3000 mm y un breve periodo de sequía entre Febrero y Abril. La vegetación original consiste principalmente de selva perenifolia y selva semi-decidua. La colonización de la región inicio a finales de la decada de los 60 y desde entonces una gran parte del paisaje ha sido convertida a potreros temporales y permanentes, parcelas de cultivo y bosque secundarios jóvenes. El tipo de uso de suelo dominante en los tres poblados son: cultivos (principalmente de maíz) por roza tumba y quema con periodos cortos de barbecho y ganadería semi-permanente.

Los datos de este estudio se colectaron en bosques secundarios en campos agrícolas y pastizales abandonados, con un tiempo de abandono (edad) entre 0.5 a 18 años. Una primera base de datos consistió en una cronosecuencia de 72 parcelas ampliamente distribuidas en un área de alrededor de 60 km2 que abarcó unidades geomorfológicas (cerros bajos vs. planicies aluviales) y usos del suelo distintos (campos agrícolas vs. pastizales, abandonados). En cada parcela se eligieron aleatoreamente tres transectos de 2 × 25 m en los cuales se identificaron taxonomicamente todos los individuos leñosos con un diámetro a la altura del pecho de 1.3 m(>1cm), asimismo su dap y y altura fueron medidos. Una segunda base de datos consintió en parcelas permanentes de muestreo ubicadas en doce bosques secundarios con una historia de uso (maizales abandonados) y geomorfología semejantes (cerros bajos con suelos arenosos ácidicos e infértiles). La edad de las parcelas varió entre 1 y 17 años. En cada parcela se estableció un cuadro de muestreo de 10 × 50 m en donde se marcó y se registró la altura y el dap de todos los árboles ≥1.5 m. La localización de cada árbol se determino con una cuadrícula de 1 × 1 m. Cada año se registraron los árboles muertos y reclutados, y se rehicieron las mediciones de altura y dap. La primera base de datos se utilizó en el capítulo 2 y en los capítulos 3-7 la de los 3 primeros años de seguimiento de las parcelas permanentes.

El capítulo 2 demuestra que en los patrones de diversidad, la frecuencia y dominancia de especies son altamente variables entre los boques secundarios del paisaje agrícola. La amplia variación de la diversidad entre las parcelas pudo explicarse en parte por las diferencias en el tiempo de abandono y el tipo de sustrato, mientras que la influencia del uso de suelo previo fue más ambigua. La riqueza de especies cambió con la edad pero los niveles de dominancia se mantuvieron similares a lo largo de los primeros 18 años de sucesión. Similarmente la riqueza de especies, pero no la dominancia, difirió entre los bosques secundarios de los cerros bajos y las planicies aluviales. Los patrones de frecuencia y abundancia entre parcelas variaron fuertemente entre las especies de árboles, fundamentalmente las pioneras. A pesar de la alta riqueza de especies (casi 200 especies fueron identificadas en todas las parcelas), solo un pequeño grupo del pool de especies regionales, todas ellas pioneras, dominó los bosques secundarios en términos de frecuencia y abundancia. No obstante, la mayoría de las pioneras, y casi todas las especies tolerantes a la sombra, estuvieron presentes en menos del 15% de las parcelas y siempre en bajas densidades. Solamente dos especies (Cecropia peltata y Trichospermum mexicanum) estuvieron presentes en ≥ 50% de las parcelas y fueron las únicas especies relativamente dominantes (> 10 tallos / > 10% del área basal de la parcela) en ≥ 20% de las parcelas. Otras especies fueron dominantes (> 10% área basal) en las parcelas en las que estuvieron presentes, pero nunca abundantes (e.g. Ochroma pyramidale); frecuentes pero nunca abundantes (e.g. Vernonia patens); o localmente abundantes pero con un área basal relativa baja (e.g. Acalypha diversifolia).

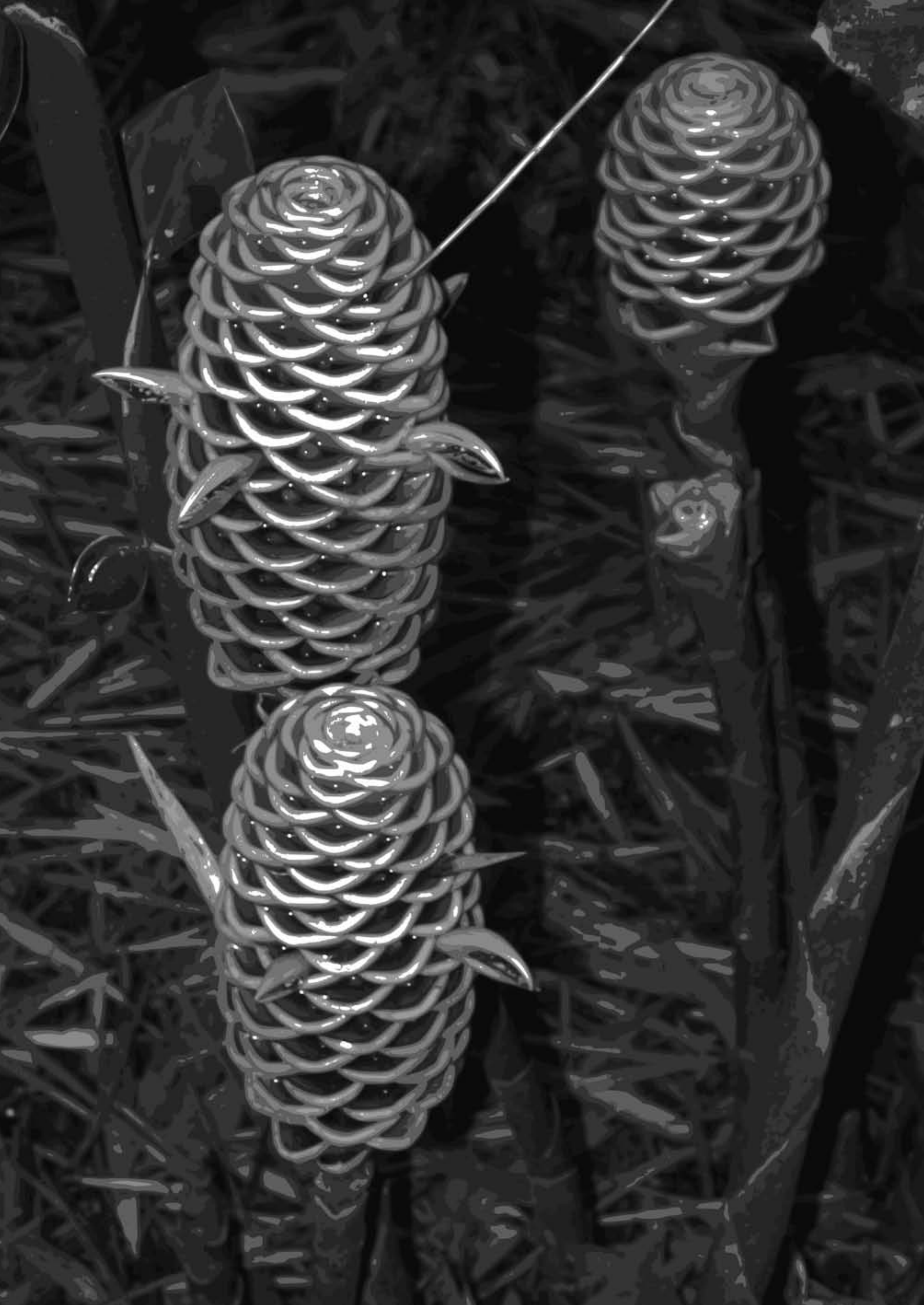
La hipótesis de la “Composición florística inicial” predice que en campos agrícolas abandonados que previamente tuvieron un uso “ligero” y cercanos a fuentes de semillas, 1) tanto las especies pioneras, como las tolerantes a la sombra, colonizan el sitio directamente después del abandono y 2) el reclutamiento de especies pioneras declina rápidamente mientras que el reclutamiento de especies tolerantes a la sombra continúa con el cierre del dosel. Así mismo predice una alta mortalidad de las especies pioneras. Consecuentemente, se espera que los grupos de árboles reclutados y los muertos difieran en su composición específica, con una riqueza específica mayor en los reclutas. Para evaluar estas predicciones, se examinó el reclutamiento y la mortalidad de ocho parcelas permanentes de muestreo con una edad inicial de 1-5 años (capítulo 1). Las especies tolerantes a la sombra se establecieron en los primeros anos de sucesión, aunque en bajas densidades. De acuerdo con las predicciones, los grupos de árboles reclutas y muertos difirieron en su composición y riqueza de especies, así como en la frecuencia de especies tolerantes a la sombra. En contraste con lo esperado, más del 50% de los reclutas fueron especies pioneras, toda vez que la gran mortalidad registrada a nivel de la parcela abrió nuevas posibilidades para el reclutamiento continuo de las pioneras. Los resultados demuestran que el recambio de especies inicia muy temprano en la sucesión, pero no siempre es un proceso gradual y continuo, lo que complica los modelos de sucesión prevalecientes.

En el capítulo 4 se relacionó la dinámica estructural (i.e. la tasa y dirección de los cambios en la estructura de la comunidad) con las tasas de mortalidad, crecimiento y reclutamiento durante un periodo de dos años; también se evaluó la dependencia de estos procesos demográficos a la edad y a la estructura inicial de la parcela en barbecho. Los cambios en la estructura del barbecho fueron especialmente rápidos durante los primeros 5 años de sucesión y con una desaceleración rápida después de este período, la cual fue el resultado de cambios similares entre las tasas relativas de mortalidad, crecimiento y reclutamiento a nivel de la parcela. Los cambios en la mayoría de los atributos de la comunidad (e.g. área basal y altura del dosel) estuvieron fuertemente correlacionados y más ligados a las tasas de crecimiento de árboles que a los cambios netos en la densidad debidos al reclutamiento y la mortalidad. Los procesos demográficos estuvieron negativamente correlacionados con el área basal inicial y fueron independientes de la densidad inicial de árboles. Los resultados sugieren que la competencia asimétrica y los patrones de aclareo resultantes, son fuerzas gobernantes fundamentales en la determinación de las vías de sucesión de los bosques secundarios. La mortalidad masiva y repentina de las especies dominantes en algunas de las parcelas mostró que la sucesión secundaria temprana no siempre es un proceso unidireccional ni gradual.

La fuerte variación temporal y espacial de la sucesión secundaria enfatiza la necesidad del seguimiento de su dinámica en varias parcelas permanentes con un mismo tiempo de abandono y a lo largo de un intervalo amplio de edades de abandono. En el capítulo 5 se muestra, con estudios de caso de Costa Rica y México, que las tasas de cambio reales de la comunidad de árboles frecuentemente se desvía de los patrones establecidos mediante cronosecuencias. Con respecto a la composición de especies de árboles, los sitios con edades distintas fueron más diferentes entre sí que con un mismo sitio seguido en el tiempo por un lapso equivalente al intervalo de edades entre los sitios en cuestión. Mientras que los cambios en la densidad de tallos tuvieron poca relación con los patrones establecidos en la cronosequencia, los cambios en el área basal generalmente siguieron dichos patrones. Las tasas de recambio de tallos fueron pobres predictores de las tasas de recambio de especies, particularmente a intervalos de tiempo prologados. Los efectos del paisaje adyacente en la dinámica de las comunidades de árboles de las parcelas no fueron incluidos de forma específica ni en este ni en ningún otro capítulo, pero los resultados sugieren que probablemente sean factores importantes que determinan de las tasas de acumulación de especies y los patrones de abundancia relativa.

La competencia por la luz se considera, frecuentemente, como uno de los principales mecanismos reguladores de la dinámica sucesional vegetal. La competencia por la luz es ampliamente asimétrica, toda vez que son los árboles grandes los que sombrean a los pequeños y no a la inversa. Consecuentemente, se puede esperar que la variación en el crecimiento y la sobrevivencia de brinzales en un sitio este relacionada a la variación en el grado de competencia en su vecindario y, en especial, con respecto a los vecinos más grandes. En el capítulo 6 se ponen a prueba estas hipótesis estudiando brinzales de Cecropia peltata y Trichospermum mexicanum en dos parcelas adyacentes de bosque secundario con 1-2 años de edad. El grado de competencia fue estimado según el área basal del vecindario (ABV). Tanto el crecimiento en altura como en el diámetro del tallo de los brinzales estuvieron negativamente correlacionados con el ABV de los vecinos más grandes. En contraparte, sólo una pequeña proporción de la variación en la sobrevivencia pudo relacionarse con la variación en el ABV, lo cual sugiere que otros factores son más importantes en este aspecto. El efecto adicional del ABV de vecinos más pequeños en el creciemiento y la sobrevivencia de los brinzales fue muy débil o no significativo.

La dinámica poblacional de especies varía mucho de un bosque secundario a otro. En el capítulo 7 examinamos si las diferencias en el comportamiento demográfico entre sitios pueden estar relacionandas a la competencia asimétrica que resulta de las diferencias en la estructura de tamaños de las poblaciones y las parcelas. Específicamente probamos si las diferencias en crecimiento y mortalidad entre los árboles más grandes y más pequeños de una población (asimetría en crecimiento y sobrevivencia) estaban relacionadas con las diferencias en el nivel promedio de competencia asimétrica del vecindario en ambos grupos (competencia simétrica). Para ello utilizamos 24 poblaciones de cuatro especies de árboles pioneros en nueve parcelas de bosque secundario joven (1-5 años). Para cada población comparamos el área basal del vecindario con el crecimiento y la sobrevivencia de los árboles dentro del 20% más pequeño y el 20% más grande. La variación en la competencia asimétrica entre parcelas explicó una parte siginificativa de la variación en el crecimiento asimétrico entre parcelas, con los árboles pequeños creciendo más rápido en poblaciones con baja competencia asimétrica y los árboles más grandes creciendo más rápido en poblaciones con gran competencia asimétrica. Como se esperaba, la sobrevivencia también estuvo relacionada al tamaño, con menores tasas de sobrevivencia entre las plantas más pequeñas. No obstante, la sobrevivencia asimétrica estuvo relacionada con la competencia asimétrica en tan sólo una especie. Las diferencias en los efectos de la competencia asimétrica en la mortalidad y la sobrevivencia de las cuatro especies muestra que la susceptibilidad a la competencia por (presumiblemente) la luz varía considerablemente entre las especies pioneras de la sucesión temprana. Los resultados de los capítulos 6 y 7 apoyan la predicción de que en los bosques sucesionales jóvenes la competencia asimétrica por la luz es uno de los principales mecanismos que gobiernan la dinámica sucesional de los bosques secundarios.



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After finishing my masters in 1997, I went for one year to Mexico, to join the Laboratorio de Ecología de Poblaciones y Comunidades Tropicales of Miguel Martínez-Ramos, part of the Centro en Investigaciones en Ecosistemas, of the Universidad Nacional Autónoma de México (CIEco-UNAM). It was the beginning of an adventure, which resulted in this dissertation and, at least as important, some great friendships. I went without knowing anyone, without speaking Spanish, without a very good idea of what to expect. It turned out to be great. I learned to love Mexico, its diversity in nature and culture, its food of course, and above all its people. I was received in a wonderful way by Miguel, Paty Balvanera and their family. The people that are/were part of the laboratory: Horacio Paz Hernández, mi hermanito Mike Salinas Melgoza, Jorge Rodríguez Velazquez, Leonel López Toledo, Julieta Benitez Malvido, Charly Ramos Guerrero, Ireri Suazo Ortuño, Carmen Gonzáles Soberanis, Lucy, Alfredo Mendez Bahena, Juan Dupuy, have been like another family from the first day I arrived. Les agradezco tantos momentos compartidos, no solo de trabajo, sino también de convivencia, a todos ellos muchísimos gracias por su amistad. Many more people from CIEco were there as well, forming an extended group of colleagues and friends, and a great professional and social environment: Guillermo Ibarra, Janik, Rolo, Omar, Diana, Ana Maria, Ana Bertha, Gabi, Vicente, Erna y Manuel, Gaby, Irene, Rene, Paloma, Miguel, Toño, Mariana, Tamara, Mery Santos, Andres, Paty, Fer y Damar, Beto y Alma, Raul, Alejandro, Chucho, Leo Solis, Araceli, Gabriela, Heberto, Laura Barraza and Alfredo Cuaron and many other students, researchers and other members the CIEco community. Gracias a todos por los pachangas, por los discusiones, por muchos momentos muy especiales. One of the best things of this PhD project was the opportunity to be part of this group of wonderful people for many years.

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The last 4 years I have been a lecturer tropical forestry at Hogeschool Larenstein. Thanks to Marc Parren for introducing me at Larenstein. Teaching about ecology, forest and nature management, plantation forestry and related issues proved to be a very interesting experience, from which I probably learned as much as my students. My focus on completing my dissertation during the last year has only been possible due to the enormous support and patience of my collegues from the tropical forestry group: Arjen Hettema, Alex van der Meer and Jaap de Vletter. I am especially and heavily indebted to Jaap for creating a lot of space for me to work on my dissertation, at the expense of his own time.

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CURRICULUM VITAE

Michiel van Breugel was born in Haarlem, the Netherlands, on the 25th of Octobre 1971. In 1991 he obtained his high school degree from College Hageveld in Heemstede. In the same year he began his MSc study Forestry at Wageningen University.

During his study he worked on spatial patterns of canopy structure and light climate of tropical rain forest, and did a comparative study on natural gap dynamics and logging induced gap formation, both in the tropical rain forest of southern Cameroon. He was also part of an interdisciplinary study group that, on request of the Foundation Information & Documentation Papua People, collected and evaluated published and non-published information on the environmental and social impacts of a copper and gold mine in Indonesia. He spent his practical period in Equatorial Guinea where he visited various governmental institutions, companies and NGO's to collected information on the state of affairs of the forestry sector in that country. He graduated in 1997.

After graduating he went for one year to Mexico, where he participated in different research projects of the laboratory of Dr. Martínez-Ramos of the Centro de investigaciones en ecosistemas, de la Universidad Nacional Autónoma de México (CIEco-UNAM). In the following year he went to French Guyana and to Mexico where he did fieldwork for a comparative study on forest structure and light climate of tropical rain forests.

In October 1999 he got a position as a PhD student at the Forest Ecology and Forest Management group (FEM) of the Centre for Ecosystem Studies of Wageningen University. As PhD student he did research on the dynamics of secondary forests in a collaborative project of his promoters Prof. Dr. Frans Bongers (FEM) and Dr. M. Martínez-Ramos (CIEco-UNAM), which resulted in this thesis.

Since September 2003 he works as a lecturer Tropical Forestry at Hogeschool Larenstein, Velp, the Netherlands, where he teaches forest ecology, tropical forest and nature management, plantation forestry, agroforestry and research methods, and supervises thesis projects.

PUBLICATIONS

PUBLISHED IN REFEREED JOURNALS

Breugel, M. v., M. Martínez-Ramos & F. Bongers (2006) Community Dynamics during Early Secondary Succession in Mexican Tropical Rain Forests. Journal of Tropical Ecology 22: 663-674.

Breugel, M. v., F. Bongers & M. Martínez-Ramos (in press) Species Dynamics During Early Secondary Forest Succession: Recruitment, Mortality and Species Turnover. Biotropica, to be publisher in the November 2007 issue.

Chazdon, R. L., S. Letcher, M. van Breugel, M. Martínez-Ramos, F. Bongers & B. Finegan (2007) Rates of Change in Tree Communities of Secondary Neotropical Forests Following Major Disturbances. Philosophical Transactions of the Royal Society B 362: 273-289.

Dekker, M., M. v. Breugel & F. J. Sterck (2007). Effective Height Development of Four Co-Occurring Species in the Gap-Phase Regeneration of Douglas Fir Monocultures under Nature-Oriented Conversion. Forest Ecology and Management 238: 189-198.

SUBMITTED TO REFEREED JOURNALS

López-Toledo, L., F. Sterck & M. van Breugel. Soil and light effects on the performance of saplings of a shade tolerant species

OTHER PUBLICATIONS

Breugel, M. van, & M. Parren (1997). Forestry in Equatorial Guinea. In: The Congo Basin - Recent developments and alternatives for sustainable management. Bos Nieuwsletter 16: 76-83.