Community dynamics during early secondary 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.

Key Words: asymmetric competition, community dynamics, density-dependent mortality, growth, recruitment, secondary succession, tropical rain forest

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 (Guariguata *et al.* 1997, Saldarriaga *et al.* 1988, Tucker *et al.* 1998, Uhl *et al.* 1988), while species composition takes over a century to recover (Aide *et al.* 1996, 2000; DeWalt

et al. 2003, Finegan 1996). 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 (Aide *et al.* 1996, Chinea & Helmer 2003, Ferguson *et al.* 2003, Mesquita *et al.* 2001, Pascarella *et al.* 2000, Purata 1986, Uhl *et al.* 1988).

Considering the asymptotic behaviour 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. 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. $\Delta BA = \Delta BA_{growth} + \Delta BA_{recruitment} - \Delta BA_{mortality}$). 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 (Gerhard 1993, Guariguata 1999, Iriarte & Chazdon 2005, Pearson et al. 2003, Walker et al. 2003). 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. Earlier 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, Coomes et al. 2003, Enquist & Niklas 2001, Midgley et al. 2002). These concepts have been studied extensively in even-aged monocultures (Begon et al. 1990, Westoby 1984, White 1980, 1981; Yoda et al. 1963), 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 (Condit et al. 1995, Davies 2001, Martínez-Ramos & Alvarez-Buylla 1995, 1998; Sarukhán et al. 1985), 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. 2003). 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 chrono-sequence 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 behaviour 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 16°04′N; 90°45′W), within the Lacandona rain-forest area, Chiapas, Mexico. Average annual rainfall is about 3000 mm, and mean annual temperature about 24 °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 research area consists mainly of three geomorphologic units defined on soil and topographic criteria (Ibarra-Manríquez & Martínez-Ramos 2002, 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 asl with small hills and valleys with sandy and limestone soils of low pH (< 5.5). The original vegetation consists mainly of lowland tropical rain forests and semi-deciduous forests. For a more extensive description of the natural vegetation in the region, see Ibarra-Manríquez & Martínez-Ramos (2002).

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. An earlier study demonstrated clear differences in secondary vegetation among the three geomorphological units present in the region (Méndez-Bahena 1999). The same study demonstrated that former land use, more specifically abandoned pastures vs. abandoned cornfields ('milpas'), exerted a strong influence on vegetation

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

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), 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 quadrats. Plots and quadrats 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 1×1-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 ($\bar{D}$, cm), and mean canopy height ($\bar{H}$, the mean of the tallest trees of the 2×2-m quadrats, 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.* 2003). 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 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):

$$\text{RRC}(X) = (X_f / X_i)^{365/t} - 1 \qquad (1)$$

Net change of community basal area (BA) over the 2 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).

$$R_X = [(X_0 + R)/X_0]^{365/CP} - 1 \qquad (2)$$

$$M_X = 1 - [1 - (M/X_0)]^{365/t} \qquad (3)$$

$$G_{BA} = [(BA_{S(0)} + G)/BA_{S(0)}]^{365/t} - 1 \qquad (4)$$

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*, $\bar{D}$, $\bar{H}$, α and species density (S) at census 0 vs. fallow age. (2) Annual rates of change of *BA*, *NT*, $\bar{D}$, $\bar{H}$, 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: $y = a + b \times x$; Logarithmic: $y = a + (b \times \ln(x))$; Inverse: $y = a + {}^b/_x$; Power: $y = a \times x^b$; Compound: $y = a \times b^x$; S: $y = e^{(a + b/x)}$; Growth: $y = e^{(a + b \times x)}$; Exponential: $y = a \times e^{(b \times x)}$. 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 (Aide *et al.* 2000, Denslow & Guzman 2000, Guariguata & Ostertag 2001, Saldarriaga *et al.* 1988). 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 (Figure 1a). Among plots, basal area ranged from 2.8 to 27.4 m^2 ha^{-1} (Figure 1b), average canopy height from 3.2 to 9.9 m (Figure 1c), and average diameter from 1.6 to 5.0 cm (Figure 1d). All these variables showed a positive and asymptotic trajectory with fallow age. The slope of the log-log size-frequency 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 (Figure 1e). Tree density ranged from 7320 to 24240 trees ha^{-1}, showed quite a large variation among youngest stands, and was not related to fallow age (Figure 1f). $\bar{H}$, $\bar{D}$, 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 (Figure 1). Overall, the general trend was an increase of
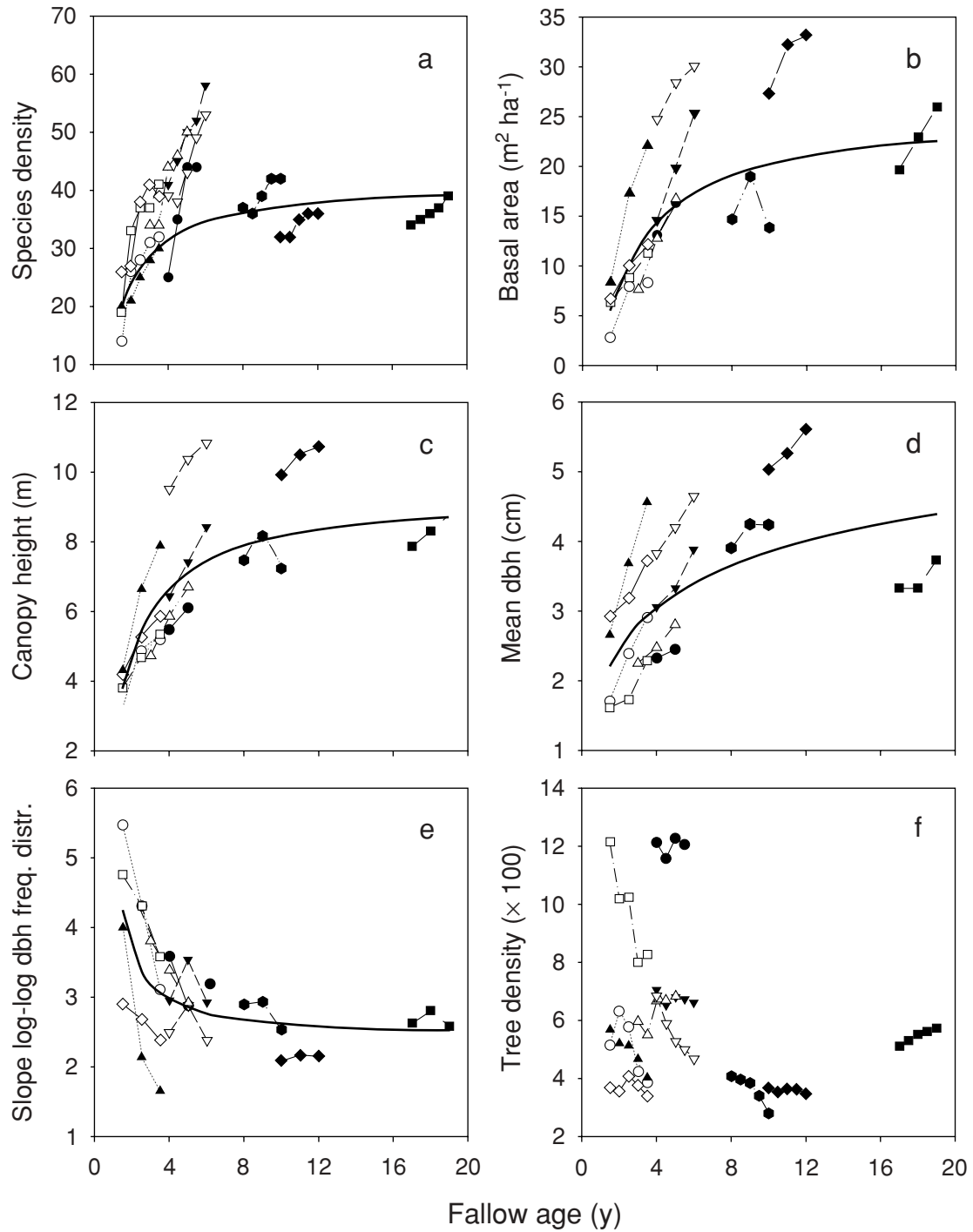
Figure 1. Successional trends of tree community structural attributes with fallow age in abandoned milpa fields in south-east Mexico. (a–f) For each one of 11 secondary forest 10 × 50-m plots, attribute values in three consecutive annual censuses (tree density, five 6-monthly censuses) are plotted against fallow age (lines connecting same symbols). (a) Basal area, expressed as m^2 ha^{-1}. (b) Tree density in number of trees per 500 m^2. (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). 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.

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; $\bar{H}$ = mean canopy height; $\bar{D}$ = mean dbh; α = slope of the log-log dbh frequency distribution.

	NT	BA	$\bar{H}$	$\bar{D}$
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, ns, not significant.

species density, BA, $\bar{H}$, $\bar{D}$ 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; Figure 1a). Mean canopy height and basal area increased in all but one plot (Figure 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%), $\bar{H}$ of 36.7% (3.1–82.7%), and $\bar{D}$ 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 (Figure 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 (Figure 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 (Figure 2a).

RRC of BA, $\bar{D}$, α and $\bar{H}$ 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
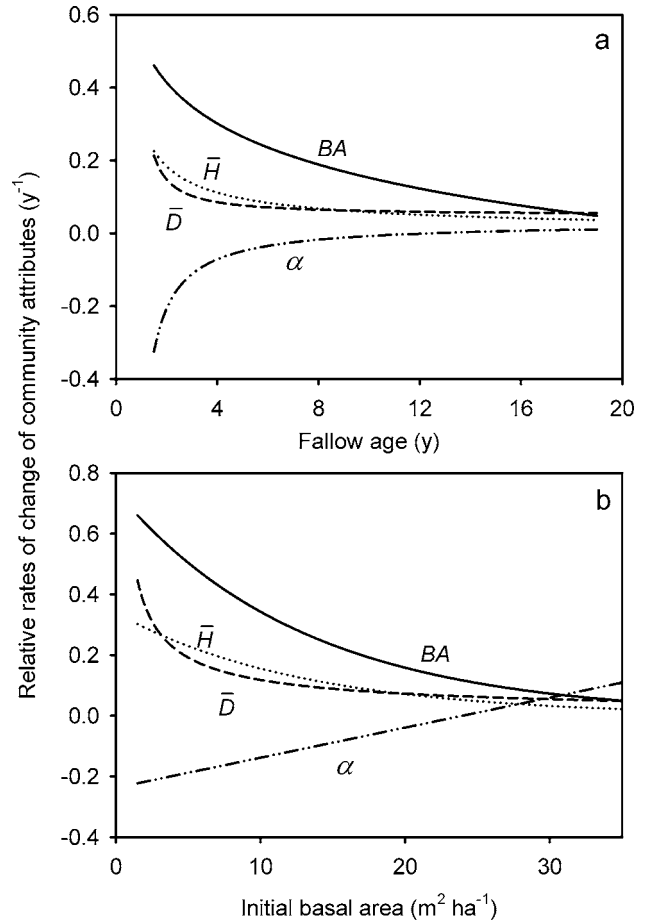

Figure 2. Relationships of annual relative rates of change (RRC) of tree community attributes with fallow age (a), and initial basal area (b) obtained for secondary forests in south-east Mexico. BA = basal area; $\bar{H}$ = mean canopy height; $\bar{D}$ = mean dbh; $-\alpha$ = slope of the log-log diameter 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; $RRC_{\bar{H}}$: Power, $R^2 = 0.78$, P < 0.0001; $RRC_{\bar{D}}$: 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; $RRC_{\bar{H}}$: Exponential, $R^2 = 0.81$, P < 0.0001; $RRC_{\bar{D}}$: Power, $R^2 = 0.54$, P < 0.01; $RRC_{-\alpha}$: Linear, $R^2 = 0.44$, P < 0.05.

weakly but significantly negatively related with the RRC of $\bar{D}$ (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 (Figure 3a, Table 4). Relative growth rates were higher than relative mortality and recruitment rates in all stands, more markedly so in the youngest ones (Figure 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
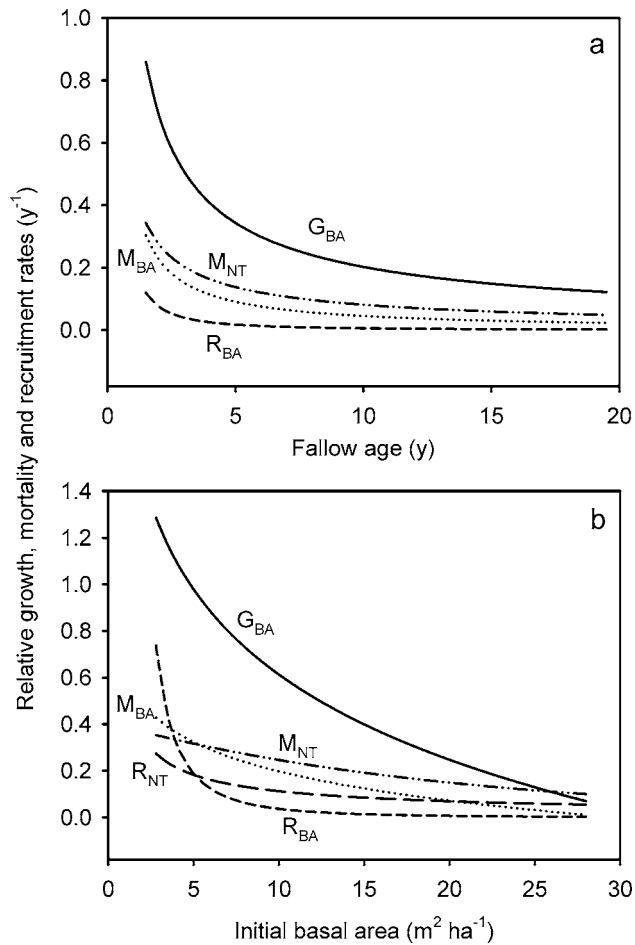
Table 3. Pair-wise relationships among annual relative rates of change (RRC) of community attributes obtained for secondary forests in south-east Mexico. R^2 and significance level of least square linear regressions are shown. NT = tree density; BA = basal area; $\bar{H}$ = mean canopy height; $\bar{D}$ = mean dbh; α = slope of the log-log dbh frequency distribution.

	RRC_{BA}	$RRC_{\bar{H}}$	$RRC_{\bar{D}}$	RRC_{α}
RRC_{NT}	ns	ns	−0.44*	ns
RRC_{BA}		0.87***	0.78***	−0.66*
$RRC_{\bar{H}}$		–	0.86***	−0.79***
$RRC_{\bar{D}}$			–	−0.66*

*P < 0.01, **P < 0.001, ***P < 0.0001, ns, not significant.

Figure 3. Relationships between annual relative rates of growth (G), mortality (M) and recruitment (R) on the one hand 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.

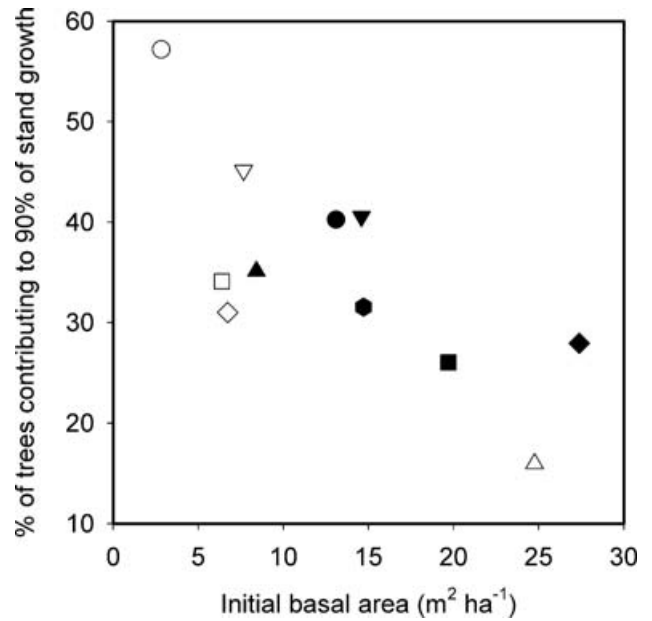**Figure 4.** Relationship between percentage of fastest growing trees accounting for 90% of stand basal area growth and the initial basal area (BA_o) in 11 secondary forests sites in south-east Mexico. Each point represents one study plot, symbols as in Table 1. Pearson correlation coefficient (r) =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

(Figure 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

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.

of this time indicator (Figure 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 (Figure 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) (Wilcoxon 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 (Figure 2b), except for the RRC of tree density (not shown). A similar analysis of the relation between the RRC of BA, $\bar{H}$, $\bar{D}$ and α 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).

Relative growth, mortality and recruitment rates were not related to initial tree density but were quite sensitive to changes in BA_0 (Figure 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 (Figure 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 $c.$ 4 m^2 ha^{-1} (Figure 3b). However at any point, loss of basal area resulting from mortality was overcompensated by the basal area gains due to growth (Figure 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. Figure 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 Figure 1f).

DISCUSSION

Secondary vs. old-growth forest

The degree and rate of structural convergence of secondary forests with old-growth forests strongly depended on the parameter considered, as has been demon-strated 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 $\geq$ 1, M. Martínez-Ramos, unpubl. 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 $\geq$ 1 cm, M. Martínez-Ramos, unpubl. data) within the same Low-Hill area. Such rapid and early successional increase of basal area has been observed in other studies (Denslow & Guzman 2000, Saldarriaga et al. 1988, 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, unpubl. 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 $\pm$ SD = 6.1 $\pm$ 2.3 m) still remained well behind the old-growth forest average in the Low-Hill area (16.8 $\pm$ 8.9 m, five 20 $\times$ 250-m plots, M. van Breugel, unpubl. 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 ($\leq$ 10 cm dbh) to larger trees is a key indicator of early successional stage in the Amazon. Niklas et al. (2003) similarly suggested that a high α reflects a relatively short time since disturbance. Such observation implies that when trees with dbh $\leq$ 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 (Denslow & Guzman 2000, Guariguata *et al.* 1997, Peña-Claros 2003, Saldarriaga *et al.* 1988, Tucker *et al.* 1998). 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 rapid 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 (Enquist & Niklas 2001, Freckleton & Watkinson 2001, Huston 1994, Schwinning & Weiner 1998). 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, 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.* (2003).

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. Figure 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 (Condit *et al.* 1995, Davies 2001, Martínez-Ramos & Alvarez-Buylla 1995, 1998; Sarukhán *et al.* 1985). 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, unpubl. 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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