

# Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia

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**ABSTRACT.** Stand structure, species richness and population structures of tree species were characterized in 12 stands representing 50 y of succession following slash-and-burn agriculture in a tropical dry forest in lowland Bolivia. Estimates of tree species richness, canopy cover and basal area reached or surpassed 75% of mature forest levels in the 5-, 8-, and 23-y-old stands respectively. Total stem density of the 50-y-old stand was almost twice that of the mature forest stand. This rapid recovery may be due to a high percentage of sprouting tree species, potentially high seed fall into abandoned fields, or the disturbance history of the mature stand. The even-aged size-class structures, dominance of long-lived pioneers, and presence of charcoal and pottery shards in soils of the mature forest stand suggest it formed after a severe disturbance, possibly fire of anthropogenic origin.

**KEY WORDS:** disturbance history, forest management, forest structure, secondary forests, species richness, succession, tropical dry forests

## INTRODUCTION

Patterns of tropical forest succession on abandoned agricultural fields have been documented by many studies in the past several decades (reviews by Brown & Lugo 1990, Finegan 1996, Guariguata & Ostertag 2001). Most of these studies, however, were conducted in humid or wet tropical forests. Comparatively few studies have focused on tropical dry forests, despite the fact that dry forests occupy a larger area of tropical forest land than wet or humid forests, and their rate of conversion to secondary forests has been higher historically (Mooney *et al.* 1995).

Seasonal variation in rainfall creates fundamental differences in patterns of

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succession characteristic of dry and humid tropical forests. For example, vegetative regeneration is more common in the dry tropics (Ewel 1980), due to the susceptibility of seedlings to drought and the greater proportion of biomass invested in root systems. Succession in dry forests is also reported to be floristically simpler and the number of seral stages fewer than in the wet tropics (Ewel 1980). Growth rates are slower in dry forests than wet, but because dry forests are lower in height and their structure is simpler than wet forests, they have the potential to recover to a mature state more quickly than wet forests, and therefore are considered more resilient (Ewel 1980, Murphy & Lugo 1986).

Forest dynamics in late successional stages are also expected to differ between the dry and more humid tropics. Researchers who have worked in tropical dry forests realize that gap phase dynamics, the paradigm of forest dynamics in humid and wet forests, does not adequately describe the dominant disturbance and regeneration patterns characteristic of dry forests. Certainly tree falls are a common feature of dry forests, but many of the tree species appear to be dependent on larger, more intense disturbances (Dickinson 1998, Snook 1996).

This paper describes patterns of forest succession across a 50-y chronosequence of abandoned agricultural fields in a dry forest in the lowlands of Bolivia. Changes in stand structure, species richness, and population structures of selected tree species are documented. Historic disturbance regimes and their implications for the sustainable management of dry forests in this region of Bolivia are also discussed.

#### STUDY SITE

This study was conducted in the dry forests of Chiquitanía, a geographic region in the eastern lowlands of Bolivia located in the Province of Nuflo de Chavez, Department of Santa Cruz (16°45'S, 61°45'W). Chiquitanía is situated in a transition zone between the humid forests on the southern rim of the Amazon basin and the thorn scrub formations of the Gran Chaco. The natural vegetation is classified as tropical dry forest (*sensu* Holdridge 1967). The regional climate is characterized by pronounced seasonality with a strong dry season that corresponds to the austral winter. Most of the canopy trees are seasonally deciduous, shedding their leaves from June to September. The mean annual temperature at Concépcion (~ 70 km from the study site) is 24.3 °C; mean annual precipitation at Concépcion is 1129 mm (Killeen *et al.* 1990). The landscape is dominated by low hills composed of granite, gneiss and metamorphic rocks of Precambrian origin (Geobold 1981) punctuated by exposed granitic outcrops (inselbergs). Elevation varies between 400 and 600 m asl. The soils of the area are classified as Inceptisols (group: Ustropepts) and Oxisols (group: Eutrusox; Iporre 1996). Although these soils are mildly acidic (pH = 5.8 to 6.8 in the A horizon; Iporre 1996) with a low to moderate cation exchange capacity (1.4–73 me 100 g<sup>-1</sup>; Iporre 1996), they are relatively fertile compared to the

more highly weathered soils found in savannas and humid forests in lowland Bolivia (Killeen *et al.* 1990).

Canopies of mature forest are dominated by trees of the Leguminosae (60% of total basal area of trees > 10 cm dbh); trees in the families Bignoniaceae, Anacardiaceae and Bombacaceae are also abundant (Killeen *et al.* 1998). Understorey trees are mostly represented by the families Sapindaceae and Myrtaceae. A spiny ground bromeliad, *Pseudananas sagenarius* (Arruda) Camargo, is very abundant and occurs in clumps of up to 2000 m<sup>2</sup>.

Chiquitanía is so named for the Chiquitano indigenous people, the largest of the lowland indigenous groups in Bolivia, with a population of around 72 500. Lomerio, where this study was conducted, is a political region within Chiquitania made up of 27 Chiquitano communities with a total population of around 5000. The Chiquitanos of Lomerio have been managing their forests for timber since 1982 with technical and financial support from several international institutions. Shifting agriculture is the principal occupation of the Chiquitanos and there is an abundance of fallow agricultural fields abandoned at various times in the past. Agriculture in Lomerio is traditional slash-and-burn. At the beginning of the dry season (May–June), understoreys of selected forest land are slashed with machetes and then trees are felled by axe. Slash is allowed to dry for at least 2 mo until the end of the dry season (August–September), when fields are burned. Fields are not ploughed. Crops are planted after the start of the rainy season (October–November). Each field, or *chaco*, that is opened can be used for 3–5 y. The general sequence of crop rotation for fields on more soils is rice, corn and occasionally beans the first year, manioc and plantains the second year, corn and rice again in the third year, and manioc or sugar cane the fourth year. While the site is being actively farmed it must be weeded 2–3 times a year to prevent second growth vegetation from taking over. Abandoned fields are sometimes cultivated again after 15–20 y, although many fields are left for much longer periods as fallows, or *barbechos*. The size of agricultural fields varies from 1–7 ha, although most fields are 2 ha (McDaniel 2000). Most fields are surrounded by mature forest or older fallows, and therefore seed sources are locally available.

#### METHODS

The forest fallows chosen for this study were located in lands communally owned by the town of San Lorenzo. Fourteen fallows representing 12 different ages from 1 to 50 y were located with the help of local Chiquitano farmers. Each age had one replicate except for the 1-y-old fallow, which had three replicates. The replicates for the 1-y-old fallow were used to show variation among fallows of same age, but were averaged for analyses. Fallow ages were estimated by interviewing the owners of the original fields. Ages of fallows are only estimates and confidence of age decreases with fallow age. The mature forest stand used for comparison is owned by the community of Las Trancas, located

roughly 20 km from the town of San Lorenzo. This site was chosen because it is the focus of a number of studies conducted jointly by BOLFOR and the Museo de Historia Natural Noel Kempff Mercado, including an intensive floristic inventory (Killeen *et al.* 1998).

### Data collection

Tree inventories in fallows were conducted during the wet season (February and March) of 1998. Within each fallow, six 50-m  $\times$  20-m plots were randomly located along transects, with plots separated by 50–100 m. Each plot was composed of nested quadrats, with smaller quadrats situated within larger ones (Figure 1). This sampling design follows that of Killeen *et al.* (1998). In each quadrat, all trees within the targeted size class were identified to species, their diameter at breast height measured (1.3 m, dbh), and total height estimated visually. Sprouts were counted as individuals. Due to abundant seed production of *Anadenanthera colubrina* several months before this field study, newly germinated seedlings of this species were distinguished from seedlings  $> 1$  y old. Mature forest values of basal area, stem density and canopy height were obtained from a 1995 inventory of 100 plots in a 300-ha area (Killeen *et al.* 1998). Tree species richness of the mature forest was estimated from a subsample of six plots randomly selected from the 1995 data set.

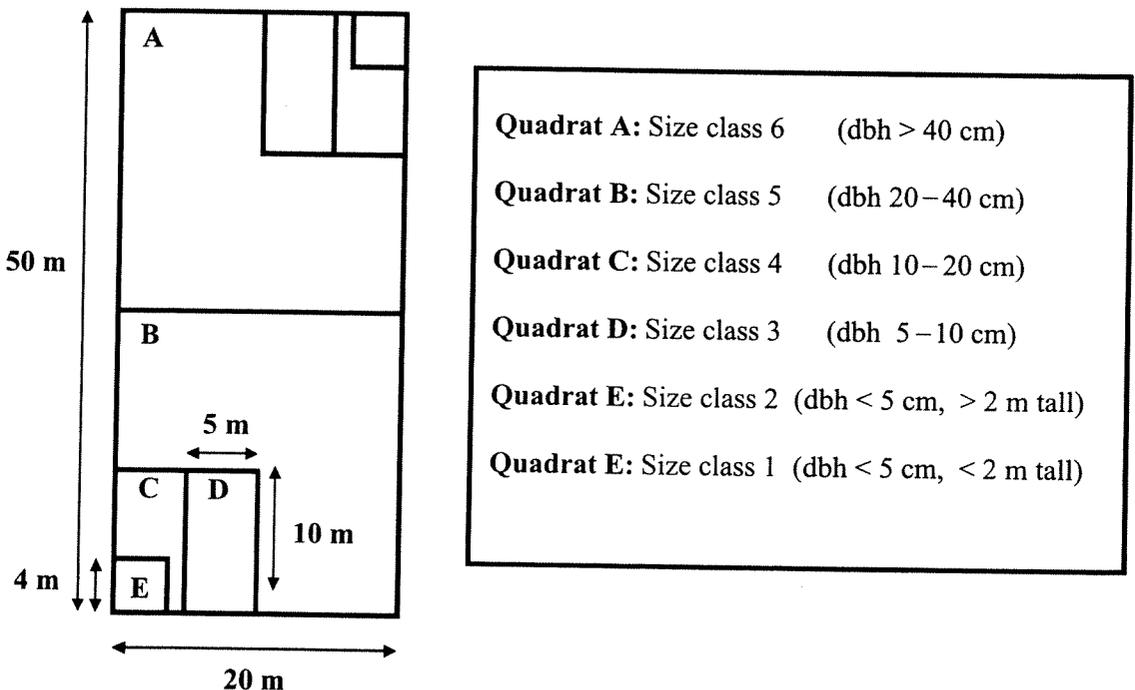


Figure 1. Layout of sample plot used to measure tree structure and richness in abandoned shifting agricultural fields. Each plot had nested quadrats of five sizes (A–E) with a different tree size class (1–6) targeted for each quadrat. The smallest quadrat (E) had two targeted size classes (1 and 2).

In forest fallows, total plant cover < 2 m tall and per cent cover < 2 m tall by life form was estimated visually for four 1-m<sup>2</sup> subplots per plot. Life form categories were: graminoids (grasses, sedges, rushes), herbs (non-woody plants excluding graminoids, bromeliads and herbaceous vines), ground bromeliads (*Pseudananas sagenarius*), shrubs (woody, multiple-stemmed), herbaceous and woody vines, and trees. Canopy cover was estimated with a spherical densiometer at one corner of each plot. For the mature forest, total plant cover < 2 m tall, per cent cover < 2 m tall by life form (graminoids, herbs, bromeliads, shrubs, lianas and trees), and canopy cover were determined in March 1998 in 32 4-m<sup>2</sup> subplots randomly distributed throughout the mature forest (Kennard 2000). Voucher specimens were collected and identified at the Museo de Historia Natural de Noel Kempff Mercado, Santa Cruz.

## RESULTS

### *Species richness and forest structure*

Tree species richness (stems > 2 m height) reached 75% of mature forest richness within 5 y after agricultural abandonment (Figure 2a). Basal area (stems > 2 m height) was slower to recover, reaching 75% of the mature forest values in the 23-y-old stand (Figure 2b, c). Based on visual estimates, canopy height also appeared to reach 75% of mature forest values at 20–40 y. Total stem density (stems > 2 m height) was highly variable in stands up to the 30-y-old stand (Figure 2d); total stem density of the 50-y-old stand was almost twice that of the mature forest stand.

Changes in stem density and basal area by size class revealed important developments in forest structure (Figure 3). Most of the variation in total stem density between the 50-y-old stand and mature forest was largely due to the greater abundance of these small stems in the younger stand. In contrast, the variation in total basal area along the chronosequence was due more to large stems > 20 cm dbh, reflecting the contribution of large trees. Basal areas of the five size classes were similar in the 50-y-old and mature forest stand, although the mature forest stand had comparatively more basal area in the > 20-cm size classes and less in the < 20-cm size classes.

### *Canopy cover and understorey cover*

Canopy cover was low in the 1-, 2-, and 3-y-old stands (10–22%), but increased to 56% in the > 5-y-old stand. Canopy cover of the mature stand was 78%. Total cover < 2 m was high in the 1-y-old stand (100%) and declined to 50% in the 8-y-old stand (Figure 4). More variation was detected in the per cent cover of individual life forms, which revealed changes in cover of different plant groups with successional age. Grasses and herbs were a dominant part of plant cover in the young stands, but their cover declined in older stands. Shrubs were absent in young stands but more abundant in stands older than 8 y. The same pattern emerged for a very common ground bromeliad,

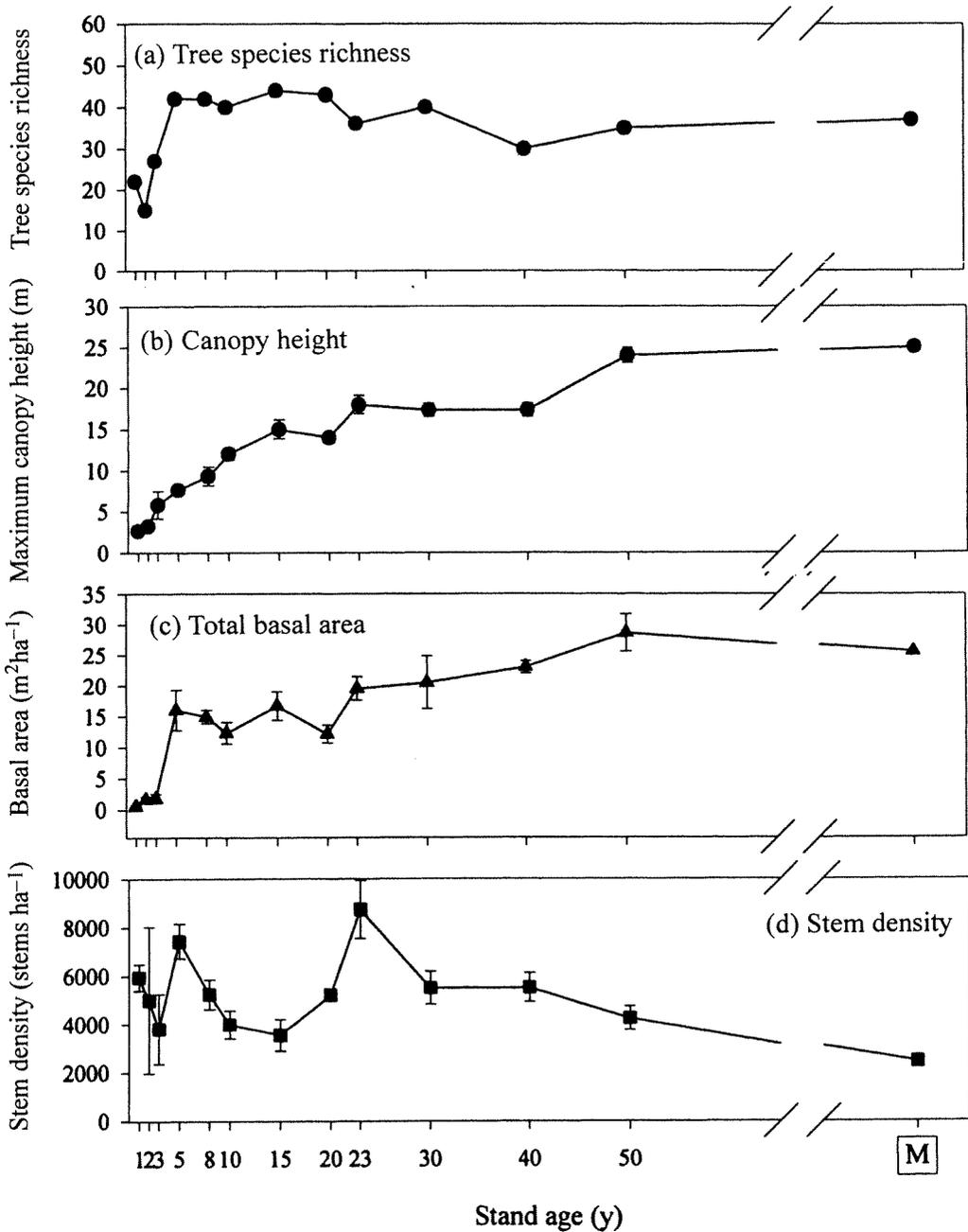


Figure 2. Tree species richness (stems > 2 m tall), canopy height, total basal area (stems > 2 m tall) and total stem density (stems > 2 m tall) of agricultural fallows 1–50 y after abandonment. Dotted lines represent 75% of mature forest values for each index. Tree species richness is the total number of tree species found in each fallow. Canopy height, total basal area, and total stem density are averages (with standard errors) of the six sampling plots used in each fallow. Mature forest values are designated on the x-axis by an 'M'.

*Pseudananas*, which covers about 15% of mature forest understoreys, but was only present in large quantities after 20 y of post-agricultural succession. Tree regeneration lost dominance in the understorey in stands > 15 y old, likely due to saplings recruiting into larger size classes combined with reduced

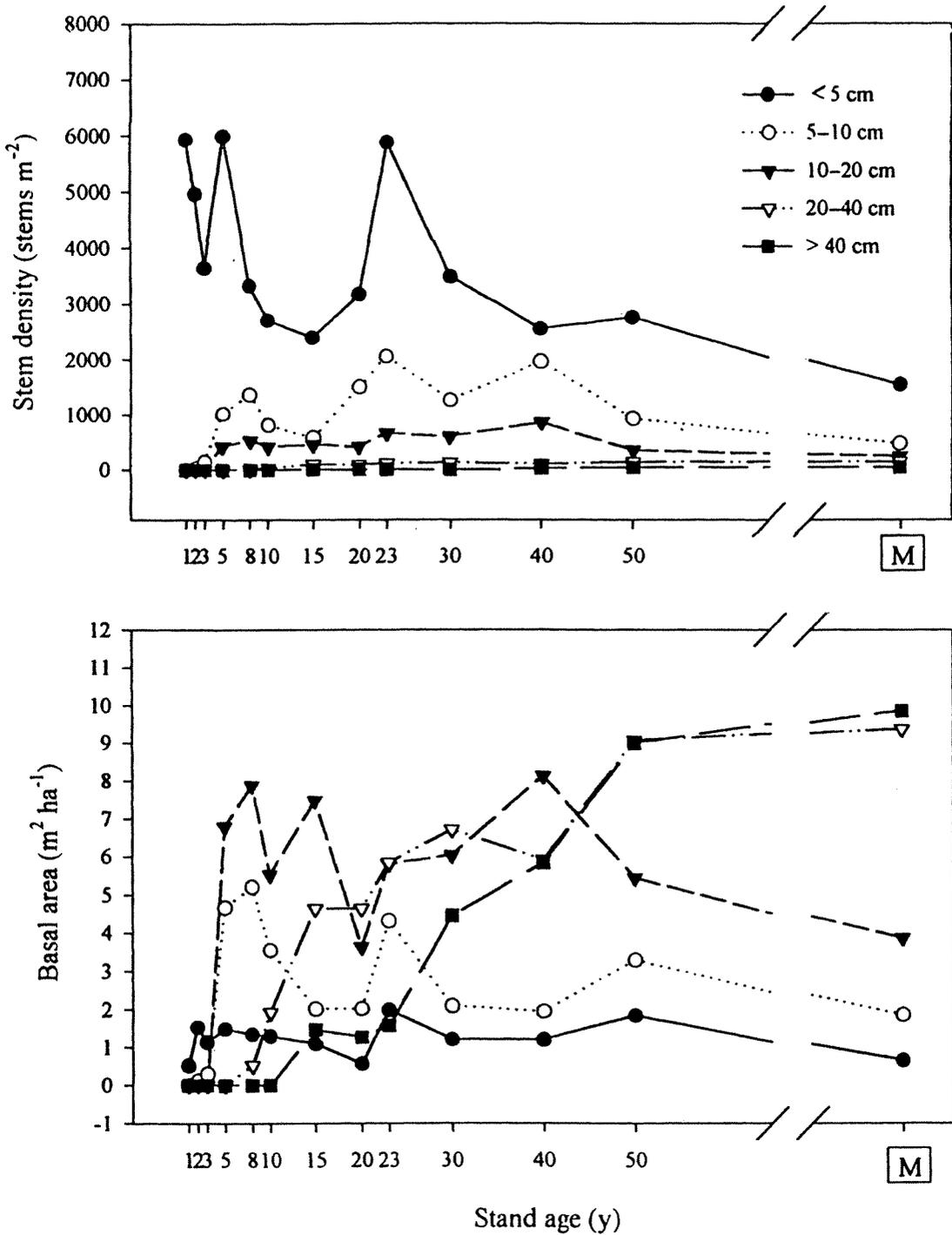


Figure 3. Stem density (stems > 2 m tall) and basal area (stems > 2 m tall) by diameter size class of agricultural fallows 1–50 y after abandonment. The mature forest stand is designated on the x-axis by an 'M'.

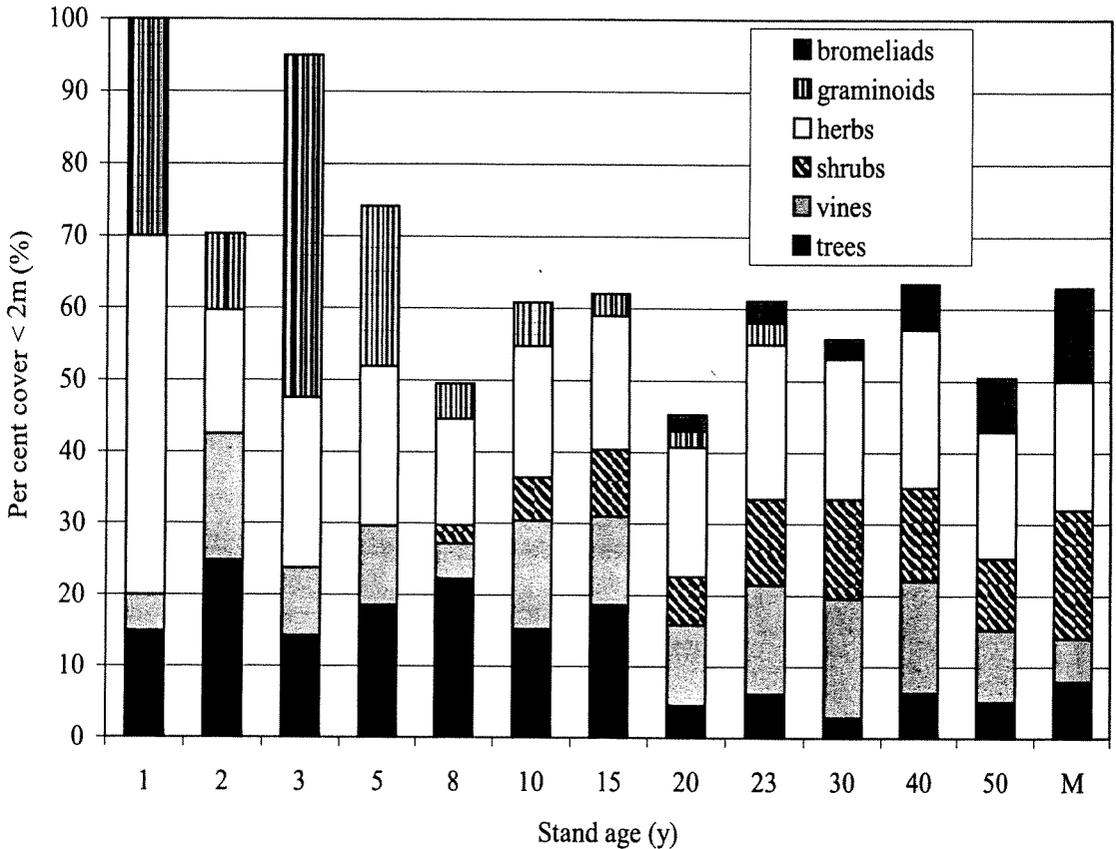


Figure 4. Per cent understorey cover < 2 m by life form. The mature forest stand is designated on the x-axis by an 'M'.

recruitment into seedling and sapling classes. Vine cover varied from 5 to 18% throughout the stands of the chronosequence with no distinct pattern in cover with stand age.

#### *Importance values and dominance throughout the chronosequence*

Importance values for 36 species are displayed in Table 1 in descending order. The combined importance values of commercial tree species (bottom line of Table 1) tended to decline with increasing fallow age. Figure 5 depicts the dominance of four regeneration guilds (short-lived pioneers, long-lived pioneers, partially shade-tolerant and shade-tolerant) throughout the 50-y chronosequence. Classifications are based on shade tolerance of species obtained from Pinard *et al.* (1999). Long-lived pioneers dominated all stands throughout the chronosequence. Shade-tolerant species became more dominant in older stands, but did not dominate long-lived pioneers even in the mature stand. Short-lived pioneers and partially shade-tolerant species did not dominate the successional stands at any point in the chronosequence.

Table 1. Importance values ((relative abundance + relative dominance + relative frequency)/3) of individual tree species in each of 12 differently aged stands in a 50-y chronosequence of abandoned agricultural fields (stems > 2 m tall). Only species with total importance values for all stand ages greater than 5% are reported. Species are listed in descending order of summed importance values.

Species	Stand age													
	1	2	3	5	7	9	10	15	20	23	30	40	50	M
<i>Centrobium microchaete</i> (C. Martius ex Benth.)	27	10	32	2	2	9	1	5	15	24	13	7	4	1
H.C. de Lima														
<i>Anadenanthera colubrina</i> (Vell.) Brenan	9	8	11	13	11	11	15	11	7	15	11	11	9	13
<i>Astronium urundeuva</i> (Allemão) Engl.	9	22	6	18	10	10	10	8	5	2	1	5	7	2
<i>Acosmium cardenasii</i> H. S. Irwin & Arroyo	9	1	4	1	5				3	4	6	14	13	30
<i>Phyllostylon rhamnoides</i> (Poisson) Taub.	2	2	2	2	9			2	9	6	6	14	14	1
<i>Casearia gossypiosperma</i> Briq.	6	5	2	4	5	3	3	4	5	4	4	4	3	2
<i>Caesalpinia floribunda</i> Tul.	9	4	3	4	4	4	5	4	3	3	2	4	6	3
<i>Cordia alliodora</i> (Ruis & Pavon) Oken	8	5	7	6	0.4	0.4	4	2	3	4	0.5	1	2	0.3
<i>Aspidosperma rigidum</i> Rusby	7	2	3	3	1	1	2	1	2	1	1	1	3	5
<i>Chorisia speciosa</i> St. Hilaire	1						1	3	3	3	8	4	4	2
<i>Machaerium acutifolium</i> J. Vogel	1	2	0.4	2	3		2	1	1	3	4	4	2	3
<i>Galipea trifoliata</i> Aubl.	0.4	1		4	2	3	1	4	2	2	3	5	4	3
<i>Rhamnidium elaeocarpum</i> Reissek	1		4	3	3	3	1	4	3	5	1			
<i>Simira rubescens</i> (Benth.) Bremek. ex Steyerf.	0.4	1	1	2	1	2	2	2	2	1	5	1	4	1
<i>Allophylus pauciflorus</i> Radlk.			1	1	7	1	1	1	4	1	1	3	2	1
<i>Spondias mombin</i> L.	6	5	2	1	1	1	1	3	1	1	1	1	2	1
<i>Guazuma ulmifolia</i> Lam.		4	1	4	1	1	7	2	1	1	1	1	2	1
<i>Combretum leprosum</i> Mart.				5	2	4	1	1	4	0.4	2		0	1
<i>Acacia loretensis</i> J.F. Macbr.	1			1	2	10	2	1	1	1	1	1	1	3
<i>Machaerium scleroxylon</i> Tul.	0.4		5	1	3	2	2	1	1	1	1	1	1	2
<i>Cecropia concolor</i> Willd.				2	3	3	5	5	3	1	1	4	2	0.0
<i>Bougainvillea modesta</i> Heimerl				1				2	2	5	2	4	2	
<i>Cariniana estrellensis</i> (Raddi) Kuntze			0.4	1				4	4	1	6			1
<i>Sterculia apetala</i> (Jacq.) Karsten			3	1	1		2	3	1	2	2	1	1	
<i>Pterogyne nitens</i> Tul.			3					1	1	2	1	2	2	1
<i>Cedrela fissilis</i> Vell.				6			4	1	1	2	1	2	2	1
<i>Talisia esculenta</i> (Camb.) Radlk.				1	2		2	3	1	1	1	1	1	0.1
<i>Neea hermaphrodita</i> S. Moore								0.3	0.3	1	0.4	1	2	5
<i>Cybistax antiphyllitica</i> (C. Martius) C. Martius ex DC.	0.3	1	1	2	2	2	0.4	1	1	1	1	0.2	1	
<i>Rollinia herzogii</i> R.E. Fries			2	1	1	1	1	2	1	1	1	1	1	0.2
<i>Celtis pubescens</i> (Humb. & Bonpl.) Spreng.			1	1	2	1	1	0.5	1	1	1	1	1	

Table 1. Continued

Species	Family/Subfamily	Stand age											M				
		1	2	3	5	7	10	15	20	23	30	40		50			
<i>Pogonopus tubulosus</i> K. Schum.	Rubiaceae			0.4		1		5	1		1						
<i>Eugenia flavescens</i> O. Berg	Myrtaceae					0.3		1	2		1		3				0.3
<i>Samanea saman</i> (Jacq.) Merr.	Mimosoideae				1	1	1	2	1		1		1				0.02
<i>Enterolobium contortisiliquum</i> (Vell.) Morong	Mimosoideae					1	1	2	3								0.01
Unknown sp.	Combretaceae			1									0.3	2	1	1	
<i>Trema micrantha</i> (L.) Blume	Ulmaceae			5													
Commercial species		71	52	67	55	47	44	35	44	56	42	44	46	28			
Total species		98	72	97	88	88	88	83	90	91	91	94	93	80			

Table 2. Comparison of rates of recovery of basal area, tree species richness and canopy height reported by other studies of forest succession in the tropics and subtropics. For each index, the age by which secondary stands reach 75% of the mature forest stand and the mature stand values are reported.

Forest type	Basal area ( $\text{m}^2 \text{ha}^{-1}$ )		Canopy height		Tree species richness		Source
	Age at 75% (y)	Mature ( $\text{m}^2 \text{ha}^{-1}$ )	Age at 75% (y)	Mature (m)	Age at 75% (y)	Mature (no.)	
montane	>>30	60.3	>>30	36	15	20	Kappelle <i>et al.</i> 1996
lower montane	>35	62.8	11	21	>35	105 <sup>1</sup>	Kuzee <i>et al.</i> 1994
subtropical wet	20	33.8	20	24	>21	37	Brown & Lugo 1990
subtropical wet					25	20	Aide <i>et al.</i> 1995
tropical moist	>80	34.8	>35	25–35	60	67	Saldarriaga <i>et al.</i> 1986
tropical moist	>80	35.6			5	66	Saldarriaga <i>et al.</i> 1988
tropical wet	17	33			>17	70	Guariguata <i>et al.</i> 1997
tropical dry			>10	10.4	10	25	Aweto 1981 a, b
tropical dry	23	25	23–40	25	5	37	This study

>> signifies that the mature stand value was more than twice that of the oldest secondary stand reported.

<sup>1</sup> Total species richness.

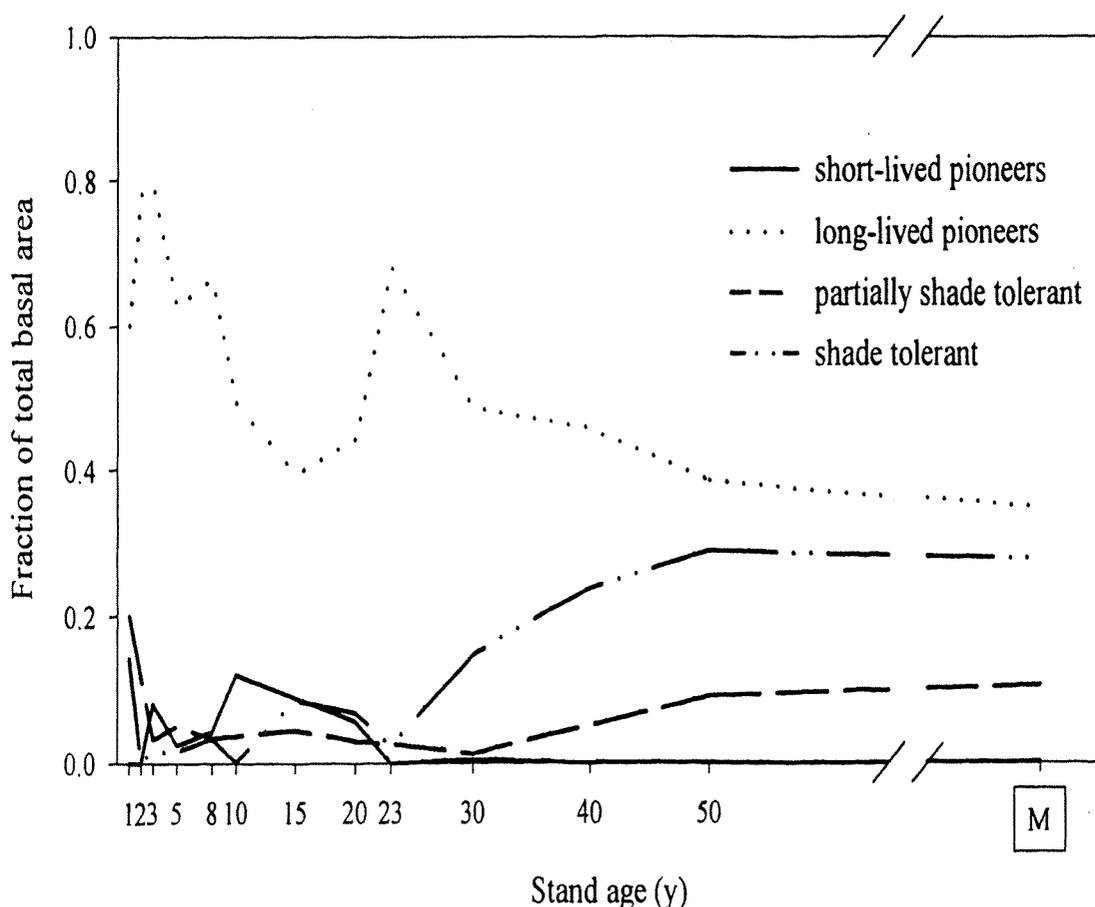


Figure 5. Dominance (proportion of total basal area) of four different regeneration guilds (short-lived pioneers, long-lived pioneers, partially shade-tolerant and shade-tolerant) over the 50-y chronosequence of forest falls following agricultural abandonment. Classification of species into regeneration guilds follows Pinard *et al.* (1999). The mature forest is represented by an 'M'.

## DISCUSSION

Although a distinct pattern emerged from the chronosequence, there was notable variation in structural traits among the different stands not explained by differences in age. For example, the 23-y-old stand had higher stem densities and canopy height than expected. This may be due to a number of factors that likely varied between fields formed at different times and in different locations, including differences in the length of cultivation, soil type, size of clearing, availability of propagules, and rainfall during the first years of development; or, disturbance by fire, cattle grazing, or fuel wood collection in the years after abandonment. Substantial differences among the three stands formed in the same year suggest that variation among factors operating very early in succession, such as initial site conditions, seed dispersal, germination, and predation, could also account for much of the variation among stands. The three 1-y-old stands had ranges of tree species richness of 11–18 species, basal area 0.84–2.28 m<sup>2</sup> ha<sup>-1</sup> and stem density of 9880–42 800 stems (all stems < 5 cm) ha<sup>-1</sup> dbh. The lack of replication within stands aged 2–50 y therefore limits the interpretation of results to general trends.

The patterns of change in forest structure observed among the abandoned agricultural fields in this study follow descriptions of tropical secondary forest dynamics reviewed by Brown & Lugo (1990), specifically, total stem density decreases during stand development as tree density > 10 cm, canopy height and basal area increase. These changes occurred relatively quickly in this chronosequence: tree species richness recovered to 75% of mature forest richness in the 5-y-old stand; basal area and canopy height reached 75% that of mature forest values in the 23-y-old stand. It is important to note, however, that although species richness was high in young successional stands in Lomerio, species composition is almost always slower to recover than species richness (Finegan 1996).

These relative rates of recovery are among the higher rates documented in other studies of tropical forest regeneration, particularly for species richness (Table 2). The fast relative recovery of the Bolivian site may be due to several factors. First, a high percentage of tree species in these forests regenerate by sprouting (Kennard 2000). Forests with a high percentage of sprouting species are thought to be more resilient to disturbance (Corlett 1981, Ewel 1980, Janzen 1975, Nyerges 1989), as growth rates of sprouts are generally higher than those of seedlings, allowing sprouts to form taller and larger crowns soon after disturbance (Miller & Kauffmann 1998). Secondly, although not quantified in this study, seed fall of tree species into abandoned fields was potentially high due to the large percentage of wind-dispersed tree species in this forest (Justiniano 1997) and the relatively small size of forest clearings (usually ~ 2 ha).

A discussion of the disturbance history of the mature stand may also help to explain the apparently rapid rate of forest recovery at this site, as the mature

forest was used as the reference stand. Several lines of evidence suggest the mature forest formed after a severe disturbance; this evidence includes the dominance of long-lived pioneers and their even-aged size class structures and soil charcoal fragments found at various locations and depths (Kennard 2000). If the mature stand is, in fact, a very old successional stand, then general estimates of stand recovery to mature forest values are likely to be overestimates. However, disturbance also appears to have been a pervasive influence on forests in this region, and therefore, this mature stand may be representative of mature forests in Lomerio. For example, dendrochronology of *Cedrela fisilis*, one of the few species that creates annual rings, indicated that intense fires have occurred roughly every 30–60 y in Lomerio (J. Huffman, *pers. comm.*). Although the exact causes of these past fires are unknown, pottery shards found at six different locations within the mature forest (Kennard 2000) suggest that at least some fires were anthropogenic in origin. Denevan (1976) estimated that the pre-European contact population density of the region that includes Chiquitania was nine times higher than other Amazonian lowland forests. In fact, present population densities in Lomerio ( $\sim 2.0$  people  $\text{km}^{-2}$ ) are only slightly higher than the pre-contact density estimated by Denevan (0.6–1.8 people  $\text{km}^{-2}$ ). The even-aged population structures and dominance of long-lived pioneers may, in fact, be the legacy of centuries of slash-and-burn cultivation by indigenous peoples in this region. Although some may argue that a stand that has escaped human disturbance is the only appropriate yardstick against which to measure forest recovery, in Lomerio, an undisturbed stand may not be a relevant reference.

The results of this study also have important implications for forest management in Lomerio, where approximately half of the commercial timber tree species are long-lived pioneers and found in abundance in forest fallows. Using forest fallows as a source of shade-tolerant timber species may be a viable alternative to regenerating these species in mature forests.

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