
Post-Agricultural Succession in El Petén, Guatemala

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Abstract: *We compared post-agricultural succession across the range of farming activities practiced in Guatemala's northern lowlands: agroforestry, swidden, ranching, and input-intensive monocultures. At 10 sites over 13 to 40 months we assessed the following characteristics of trees and shrubs that were >1 cm diameter at breast height: height, basal-area accumulation, recruitment of all individuals and fleshy-fruited individuals, and accumulation of all species and fleshy-fruited species. Succession, as measured by all these response variables except height, was dramatically faster on agroforestry and swidden sites than on pastures or input-intensive monocultures. Overall recruitment was faster for swiddens than for agroforests, but other response variables did not differ significantly between the two treatments. Regression results suggest that initial ground cover by herbs inhibited recruitment of woody colonists. The significant positive coefficient for initial basal area and the significant negative coefficient for distance from forest for accumulation of both fleshy-fruited individuals and species are probably explained by the behavioral responses of seed-dispersing animals. Our results suggest that the conservation strategy of discouraging swidden agriculture in favor of sedentary, input-intensive agriculture to relieve pressure on old-growth forest may be counterproductive over the long term.*

Key Words: agricultural intensification, agroforestry, El Petén, Guatemala, *Guazuma ulmifolia*, Maya Biosphere Reserve, monocultures, pastures, ranching, shifting agriculture, swidden

Sucesión Post-Agrícola en El Petén, Guatemala

Resumen: *Comparamos la sucesión post-agrícola a lo largo de una serie de actividades de producción practicadas en las tierras bajas del Norte de Guatemala: agroforestería, agricultura migratoria, ganadería, y monocultivos de alto insumo. Durante 13 a 40 meses, en 10 sitios, evaluamos las siguientes características de árboles y arbustos de >1 cm de diámetro a la altura del pecho: altura, acumulación de área basal, reclutamiento de todos los individuos e individuos con frutas carnosas, acumulación de todas las especies y todas las especies con frutas carnosas. La sucesión, medida por todas estas variables de respuesta con excepción de la altura, fue dramáticamente más rápida en agroforestería y en los sitios con agricultura migratoria que en las pasturas o monocultivos con intensos insumos. El reclutamiento fue más rápido en los sitios con agricultura migratoria que en aquellos con agroforestería, pero otras variables de respuestas no difirieron significativamente entre los dos tratamientos. Los resultados de regresiones sugieren que la cobertura inicial del suelo por hierbas inhibió el reclutamiento de colonizadores leñosos. Los coeficientes positivos significativos para el área basal inicial y los coeficientes negativos significativos para la distancia del bosque para la acumulación de ambos individuos y especies con frutos leñosos se explican posiblemente por las respuestas conductuales de animales dispersores de semillas. Nuestros resultados sugieren que las estrategias de conservación para desalentar la agricultura migratoria a favor de la agricultura sedentaria con insumos intensivos para liberar la presión sobre de bosques maduros puede ser contraproducente a largo plazo.*

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Introduction

Agroecosystems can harbor significant associated biodiversity, maintain landscape connectivity, and shield habitat patches from edge effects, but the conservation value of agroecosystems varies dramatically with production strategy (Estrada et al. 1993; Perfecto et al. 1996; Fujisaka et al. 1998; Medellín & Equihua 1998; Griffith 2000). Although little comparative work has been done, successional studies suggest that agroecosystems also vary in the extent to which they preserve forest seeds, seedlings, and rootstocks, and affect the seed dispersal and seedling establishment processes that permit post-agricultural forest regeneration (Uhl et al. 1989). We considered the effects of four broad production strategies that encompass most Neotropical agriculture—swidden, agroforestry, extensive cattle ranching and input-intensive monocultures—on post-abandonment succession.

The rate and composition of fallow development are key to productivity in swidden cultivation (Nations & Nigh 1980; Ewel 1986; Raintree & Warner 1986; Kass et al. 1993), and, not surprisingly, forests generally regenerate swiftly following swidden abandonment. Swiddens are characterized by a cycle of forest/fallow clearing, 2–4 years of cultivation and, 5–15 years of fallow (Montagnini & Mendelsohn 1997). The disturbance caused by clearing and cultivation is brief and light enough to permit substantial tree resprouting (Kammesheidt 1998). Furthermore, swidden fields are small, usually ≤ 1 ha, and surrounded by a mosaic of fallow and secondary forest of varying ages, providing both seed sources and habitat for seed-dispersing animals (Nations & Nigh 1980; Uhl et al. 1990). Some swidden farmers leave old-growth strips between cultivated plots and individual trees within plots, in part to encourage fallow development (Nations & Nigh 1980; E. Ukan Ek', personal communication). Some sow seeds in fallows or otherwise promote useful plants (Nations & Nigh 1980; Kass et al. 1993; Montagnini & Mendelsohn 1997; Levy Tacher 2000). Forest growth on abandoned swiddens reaches tree-species diversity equal to that of mature forest within as few as 20 years (Saldarriaga et al. 1988; Gretzinger 1994) and comparable total basal area within 60 years. Recovery of species composition and size distribution takes considerably longer (Gretzinger 1994; Finegan 1996).

Although forest regeneration following abandonment of agroforestry systems can be quite rapid (Birdsey & Weaver 1983), the process has not been detailed. Unlike swidden systems, agroforestry involves long-term, continuous production on a plot and thus can be expected to eliminate regeneration through resprouting of cut trees (Uhl et al. 1990). Conditions for tree establishment through seed dispersal are close to ideal, however, because the agroforestry canopy can provide seed sources

as well as structural and biological diversity attractive to seed-dispersing animals. Furthermore, agroforestry understory conditions are similar to forest understory or light-gap microenvironments and therefore are suitable for germination and establishment of later successional species. Lessons learned from recent studies of regeneration in plantation forest understories should also be applicable to agroforestry systems. Plantation forests can prevent erosion, contribute to soil formation and nutrient stocks, provide a relatively shady, cool, moist microenvironment, and attract seed dispersers (Parrotta 1992; Lugo 1997; Wunderle 1997). Regeneration in their understories can be diverse and rich in forest species but will vary greatly with the overstory species (Parrotta 1992; Loumeto & Huttel 1997; Lugo 1997).

Cattle ranching and input-intensive monocultures like agroforestry, are sedentary and reduce the potential for regeneration from resprouting trees or seed banks (Garwood 1989; Uhl et al. 1990). Unlike agroforestry, these activities are practiced on vast scales (Uhl et al. 1990) and their managers actively minimize biological diversity (and accompanying structural diversity; Vandermeer & Perfecto 1997). Agronomic services formerly provided by the fallow are replaced by mechanical and chemical inputs, green manures, and, for pastures, frequent burning (Ewel 1986; Serrão & Toledo 1990; Montagnini & Mendelsohn 1997). Together, these practices limit dispersal of woody pioneers and produce ground cover and seed banks dominated by weedy grasses and forbs that further inhibit establishment of pioneers dispersed to the site (Garwood 1989; Aide et al. 1995; Holl 1998).

Few studies have quantified succession following intensive monoculture, but a body of literature is developing on post-pasture succession. Forests grow rapidly on some abandoned pastures, accumulating basal area about one-quarter of that found in mature forests in 8 years or less, with correspondingly high levels of species richness (Uhl et al. 1988; Rivera et al. 2000). Succession on other pasture sites is slower, even arrested (Uhl et al. 1988; Aide et al. 1995; Zahawi & Augspurger 1999). Where details of site conditions are provided, the duration and intensity of usage (Uhl et al. 1988) and the presence or absence of remnant or colonizing trees and shrubs that act as colonization nuclei (Guevara & Laborde 1993; Vieira et al. 1994; da Silva et al. 1996; Zahawi and Augspurger 1999) emerge as key determinants of the pace of succession. Uhl et al. (1990) argue that forest recovery on the most severely disturbed sites will require centuries.

An extensive literature search identified just two studies that compare tropical succession on sites of roughly the same age arising from different types of agriculture. In lowland Costa Rica, Fernandes and Sanford (1995) compared soil and vegetation characteristics after 7 years of succession among a pasture with scattered, remnant trees, an intensively managed *Bactris gasi-*

paes (*pejibaye* palm) monoculture, and a *Theobroma cacao* (cacao) plantation with a moderately diverse overstory. Accumulation of basal area in the palm plantation was less than half as rapid as in the pasture or the cacao plantation. Tree species diversity and similarity to mature forest were greatest in pasture, intermediate in the palm orchard, and least in the cacao plantation. The authors suggest that reduced nutrient levels slowed growth in the palm plantation and that shading reduced colonization in the plots. The second comparative study, an extensive survey of vegetation dynamics in the Amazon basin, also concluded that history of use influenced the pace of succession: average tree height on swidden sites increased at 1.5 m/year, but growth was less than half as fast on pasture sites and less than one-third as fast on mechanized agriculture sites (Moran et al. 2000).

Predicting post-agricultural successional rates and overcoming barriers to regeneration are key to the management of successional sites, whether for production (Birdsey & Weaver 1983; Finegan 1992) or conservation value (Rivera & Aide 1998). The post-abandonment fate of agricultural land is particularly relevant in the humid tropics, where fragile soils, aggressive pests, and volatile social and economic conditions produce sudden changes in land use (e.g., M. Rodríguez Lara, unpublished data cited by Katz 1995). The lack of successional studies that start with agroforestry or input-intensive monocultures, combined with the lack of comparative work, means that only limited conclusions can be drawn about the relative pace of succession across agricultural types. Clearly, further investigation is necessary to permit generalizations about how different agricultural strategies influence the pace of forest regeneration. As a first step, we compare rates of ecological succession on newly abandoned sites in El Petén, Guatemala, representing the gamut of agricultural practices discussed above. Further, we identify site characteristics that explain variation in regeneration rates. Finally, we discuss how differing rates of post-agricultural succession might affect the prospects and strategies for conservation.

Methods

Study Sites

El Petén, Guatemala's northern administrative department, includes one of the largest remaining patches of Central American forest (Santiso 1993). Annual precipitation varies dramatically between 1200 and 1700 mm (CONAP 1992), falling mostly between June and January. The combination of climate and well-drained, karstic soils (Elías et al. 1997) contributes to a tropical semi-deciduous forest type (Pennington & Sarukhán 1998) or a subtropical moist forest type (Holdridge et al. 1979). The ancient Maya and their descendants have oc-

cupied the region for centuries, and their agriculture shaped modern forests (e.g., McSweeney 1993). Traditional agriculture includes sophisticated agroforestry and swiddens (Atran et al. 1999). Beginning in the 1960s, massive immigration from the south, partly a result of government settlement programs, brought rapid changes in land use, including less-efficient swiddens, input-intensive monocultures, and extensive ranching (Schwartz 1995, Shriar 2001).

In February 1997, to permit succession to proceed, we rented and set aside two sites representing each of the four major agricultural strategies. Some sites were "lost" over the course of the study and replaced by new sites (Table 1). Both agroforestry sites and two of the three swidden sites are located near the town of San Andrés, within the Maya Biosphere Reserve buffer zone. The soil here, particularly on the agroforestry sites, appears rich in organic matter, and the terrain is flat to rolling. Land use was a patchwork of swidden, agroforestry, pastures of varying sizes, and selectively logged secondary forest. The pasture and swidden sites on the land of the Comunidades Populares en Resistencia del Petén (CPR-P) occurred in flat valleys between small, steep, limestone hills. The remaining sites were near the Ruta Bethel road between Las Cruces and Josefinos in the La Libertad municipality. Topography here in the Río de la Pasión flood plain is flat, and the reddish-brown soils are among the richest and deepest in El Petén (Shriar 2001). Except for houses and the occasional, small secondary forest reserve, all land within a couple of kilometers of this stretch of road was under permanent cultivation or ranching. The minimum distance between sites of the same type was about 300 m (the agroforestry sites were closest together).

Agricultural Treatments

The agroforestry sites had been worked by the same family since 1930 or longer (Schwartz 1999, personal communication). Farmers plant traditional and introduced crops as well as a variety of timber trees, blending traditional techniques and their own innovations. Most parts of the farms were diverse both taxonomically and structurally. Cultivated areas were surrounded by bush fallow and secondary forest.

The swidden systems included elements of agricultural intensification that characterize the shifting cultivation of immigrants (Schwartz 1987; Shriar 2001). Nevertheless, the three sites were small (0.5–2 ha), hand-worked plots in matrices of fallow and secondary forest.

Both pasture sites were much larger, 20 ha or more. The Montepeque site burned during the 1998 dry season, so we report data from this pasture beginning with the 1998 sampling.

The intensive monoculture sites had all been under

Table 1. Post-agricultural succession study sites; El Petén, Guatemala.

Agriculture type	Owner	Location	Approximate coordinates	Approximate no. years cultivated ^a	Distance from forest (m) ^b	Initial herb cover (%)	Dates studied ^c	Comments
Agroforestry	Zacarías Quixchán	12 km north of San Andrés	17°03'42" N 89°54'19" W	8, 20 (original) 10 (new)	20	22	Oct. 1996– Jun. 2000	one plot lost, replaced in '99
Agroforestry	Nehmías Quixchán	12 km north of San Andrés	17°03'42" N 89°54'19" W	5, 15, 25	10	18	Oct. 1996– May 1999	ownership change
Swidden	Nehmías Quixchán	12 km north of San Andrés	17°03'42" N 89°54'19" W	1.5	10	19	Oct. 1996– May 1999	ownership change
Swidden	Esteban Obando	12 km north of San Andrés	17°02'42" N 89°55'25" W	0.5	20	5	May 1999– Jun. 2000	1 1/3 plots burned in 2000, data excluded
Swidden	CPR-P	Btwn. San Francisco, La Libertad	16°48'28" N 90°01'3" W	0.6	25	4	May 1999– present	
Pasture	CPR-P	Btwn. San Francisco, La Libertad	16°48'29" N 90°01'23" W	9	25	55	May 1999– Jun. 2000	
Pasture	Concepción Montepeque	Las Cruces, La Libertad	16°40' N, 90°22' W	15	2000	18	Oct. 1996– Jun. 2000	data start from after 1998 burn
Monoculture (sesame)	Cruz Galindo	Las Cruces, La Libertad	16°40' N, 90°22'30" W	15	150	36	Oct. 1996– May 1999	repeated cattle intrusion
Monoculture (maize)	Creofi López	Las Cruces, La Libertad	16°39'57" N 90°18'22" W	20	250	47	Oct. 1996– Jun. 2000	
Monoculture (maize)	Leonel Monterroso	Las Cruces, La Libertad	16°40'49" N 90°22'57" W	6	500	56	May 1999– Jun. 2000	

^aLength of time the land was farmed following forest felling or the most recent fallow.

^bMean of the three sampling plots.

^cFirst date represents time of agricultural abandonment. Period under study varies because several plots were lost from the study and later replaced.

mechanized cultivation for several years, with some use of chemical pesticides. Fields ranged from 0.7 to 5 ha and were surrounded by intensively managed cropland and pasture. Sites are described in greater detail elsewhere (Ferguson 2001a).

Data Collection

We collected data from three 10 × 20 m sampling plots at each site. At the swidden, pasture, and intensive-monoculture sites, we rented 0.7-ha parcels (one *manzana*, the local unit of area measurement) and fenced them where necessary. The sampling plots were located randomly within them. Renting such large parcels at the agroforestry sites was not possible, and the sampling plots were embedded within actively managed agroforestry areas. Sampling plots were chosen to represent several different crop combinations of different ages. All had overstories of fruit and/or timber trees. At each agroforestry site, the sampling plots were within 100 m of one another.

Within each sampling plot, all stems that were ≥1 cm diameter at breast height (dbh) were identified and measured. Vegetation was sampled in February–March 1997, October–November 1998, May–June 1999, and June 2000. Groundcover by vegetation was surveyed on the first two sampling dates with a 0.5 × 0.5 m PVC frame at 0.5 m height and classified as shrubs or trees, vines, herbs, or unknown. Botanical voucher specimens are stored at AGUAT (Universidad de San Carlos, Guatemala) and UMICH (University of Michigan, Ann Arbor).

Data Analysis

The proportion of animal-dispersed species in both wet and dry Neotropical forests increases over the course of succession (Opler et al. 1975), and lack of seed-disperser activity can be a significant barrier to regeneration (da Silva et al. 1996, Holl 1999). Thus, we used colonization by fleshy-fruited species as one indicator of successional development. Species that fit the syndrome of plants dispersed by animals that swallow their seeds (showy and/or fleshy fruits, seeds or arils; abbreviated as “animal-dispersed,” “zoochorous,” or “fleshy-fruited”) were identified based on field observations and descriptions in *Flora of Guatemala* (Standley et al. 1946–1975). Species for which sufficient information was lacking were not classified as fleshy-fruited even if they belong to families that usually do have such fruits. We estimated richness of all species and of fleshy-fruited species for each plot by using the SpecRich program (Hines 1998), which is based on the jackknife technique of Burnham and Overton (1979).

Species richness, richness of fleshy-fruited species, total basal area, average height, number of individuals ≥1 cm dbh, and number of fleshy-fruited individuals in that size class were calculated for trees and shrubs in each plot for each sampling event. We excluded individuals that had been present in that size class during the time of active cultivation from this analysis. Comparison of response variables among agricultural treatments was complicated by the loss of sites and individual plots and their replacement. This, in combination with irregular sampling intervals, rendered comparison across all sites

at a particular stage impossible. All of the response variables changed fairly linearly over time for each plot, however, allowing comparison of rates of change (deviations from linearity apparent in Fig. 1 are largely effects of the loss and addition of sites rather than nonlinear change). Comparisons were made among agricultural types with analysis of variance (ANOVA) of sites nested within agricultural types (Zar 1999), which avoids the apparent problems of pseudoreplication. This resulted in 28 degrees of freedom for most response variables but only 18 for height growth because some of the newer plots had no woody recruits the first year they were sampled. Significant contrasts between pairs of treatments were identified with Tukey's tests (Zar 1999).

We performed multiple linear regressions on averaged data for each site to determine which of the independent variables may have influenced the response variables. We selected independent variables using backward elimination to minimize complications from multicollinearity (Zar 1999). Independent variables analyzed were years under cultivation (based on farmer interviews), distance to secondary forest or high fallow, initial basal area, and ground cover by herbs and vines. Where sites had been weeded (by machete) or burned just prior to initial data collection, we used cover data from the next sampling event to define initial conditions so that the seed bank would have time to express itself.

Null hypotheses were rejected at the $p < 0.05$ level. No serious violations of the assumptions of the parametric tests were detected. Analyses were run with SPSS version 9.0 (1998).

Results

By almost any measure, forest regeneration was much faster at the swidden and agroforestry sites than at the pasture and input-intensive monoculture sites, often by an order of magnitude or more (Table 2; Fig. 1). Basal area, for example, increased 36 times faster in swiddens than in pastures. Fleshy-fruited individuals colonized agroforestry sites at 24 times the rate of monoculture sites. Only the average height growth of trees and shrubs did not differ significantly among agricultural treatments. Swidden sites hosted significantly more recruits than agroforestry sites, but other response variables showed no significant differences between the two treatments. Regeneration rates did not differ significantly between pastures and high-input monocultures for any response variable.

Multiple regressions were significant for four of the six response variables, and the results identified three independent variables that influenced community development (Table 3). All four of these response variables declined significantly with increasing initial herb cover.

Competitive suppression of regeneration was particularly evident at the pasture and monoculture sites, where the groundcover was dominated by grasses and a weedy *Bidens* sp. (Asteraceae), respectively, for the duration of the study. Recruitment of fleshy-fruited individuals and species responded positively to initial basal area and negatively to distance from forest. Years under cultivation and initial vine cover were not significant variables in any of the regression equations.

Recruitment at the agroforestry sites, and to a lesser extent the swidden sites, was quite diverse and included many species too rare for inclusion in Table 2. In contrast, almost all species in the pasture and monocultures had importance values of 2 or more. The fleshy-fruited *Hamelia patens* (Rubiaceae) was numerically dominant on the agroforestry plots (53% of all stems on both sites), attaining importance values of 24 at one site and 31 at the other (Table 4). *Spondias mombin* (Anacardiaceae) and *Cecropia obtusifolia* (Cecropiaceae) accounted for 19% and 20%, respectively, of the basal area on the two sites combined. On all three swidden sites, wind-dispersed *Lonchocarpus guatemalensis* (Faboidae), a vigorous resprouter, dominated regeneration (importance values of 17 to 27). This species accounted for 28% of the rapid recruitment of individuals and 26% of the accumulation of basal area observed in the swiddens (Table 2; Fig. 1). The two pastures shared few species in common, perhaps because of their geographic separation, although the wind-dispersed *Cordia alliodora* was of moderate importance at both sites as well as at the López monoculture.

The contrast in species composition and regeneration patterns between the López and Galindo intensive monoculture sites was dramatic and points to differences in seed-dispersal mechanisms between the sites (Table 4). Regeneration on the Galindo site was heavily dominated by *Guazuma ulmifolia* (Sterculiaceae), a species that was of secondary importance on the López site. These fast-growing trees apparently were dispersed by cattle, which occasionally broke through the barbed-wire fence and spread the seeds evenly throughout the site (Ferguson 2001b).

Regeneration at the López site was more heterogeneous. Islands of regeneration forming around large remnant trees stood out in contrast to retarded growth in the rest of the field (Ferguson 2001a). Approximately half of one sampling plot, one-sixth of the area surveyed at the site, fell beneath the crown of an *Attalea cobune* palm. In 2000 this patch included 56% of the woody stems, 64% of the fleshy-fruited individuals, and 86% of the basal area of woody recruits. Seventy percent of recruits in the island were fleshy-fruited, compared with 50% on the rest of the site. Fleshy-fruited species accounted for much of the difference in species richness between the López site and the other monocultures (Table 4).

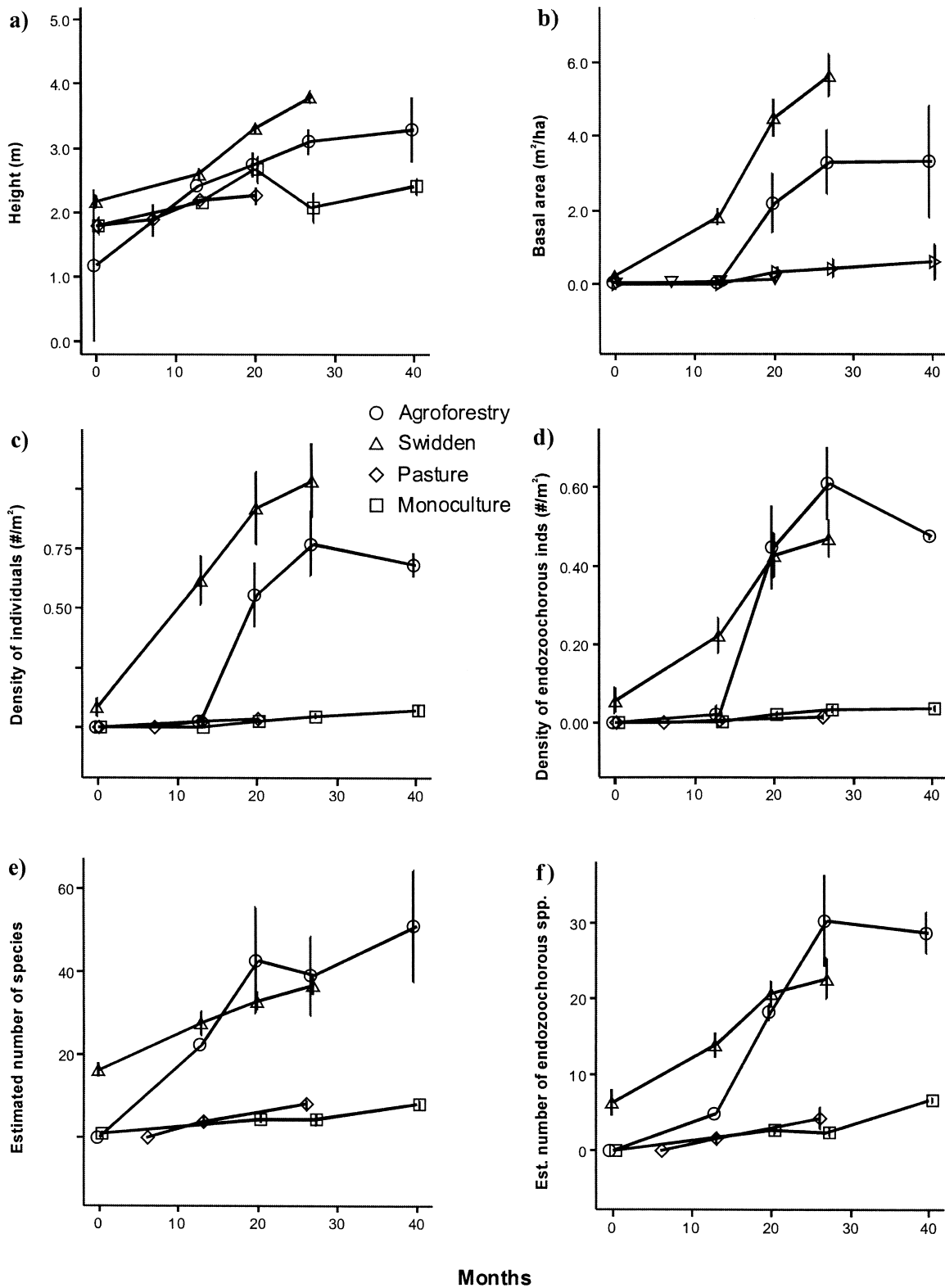


Figure 1. Successional development by agricultural treatment as measured by (a) mean height, (b) basal area, (c) density of stems, (d) density of endozoochorous stems, (e) jackknife estimates of species richness, (f) and jackknife estimate of richness of endozoochorous species. Data are for woody stems that are ≥ 1 cm diameter at breast height. Error bars represent standard errors.

Table 2. Annualized rates of succession as a function of agricultural treatments.*

Variable	Treatment mean \pm 1 SD				Analysis of variance					
					treatment			sites w/in treatment		
	agroforestry	swidden	pasture	monoculture	df	F	p	df	F	p
Height growth (m)	0.28 \pm 0.12	0.75 \pm 0.63	1.3 \pm 1.0	0.34 \pm 0.61	3,18	2.23	0.14	3,18	1.21	0.35
Basal-area accumulation (m ² /ha)	1.3 \pm 0.9 ^b	1.9 \pm 0.5 ^b	0.053 \pm 0.073 ^a	0.11 \pm 0.16 ^a	3,28	30.0	2.0 \times 10 ⁻⁷	6,28	2.36	0.072
Recruitment (individuals/m ²)	0.28 \pm 0.17 ^b	0.53 \pm 0.18 ^c	0.025 \pm 0.023 ^a	0.017 \pm 0.013 ^a	3,28	68.4	5.1 \times 10 ⁻¹⁰	6,28	5.22	2.5 \times 10 ⁻³
Endozoochorous recruitment (individuals/m ²)	0.24 \pm 0.11 ^b	0.19 \pm 0.07 ^b	0.015 \pm 0.018 ^a	0.010 \pm 0.009 ^a	3,28	32.6	1.1 \times 10 ⁻⁷	6,28	2.46	0.063
Estimated species accumulation	17.8 \pm 8.8 ^b	15.5 \pm 11.1 ^b	3.5 \pm 2.8 ^a	1.2 \pm 1.1 ^a	3,28	15.7	2.3 \times 10 ⁻⁵	6,28	3.98	9.6 \times 10 ⁻³
Estimated endozoochorous species accumulation	10.8 \pm 6.5 ^b	9.4 \pm 3.9 ^b	1.6 \pm 1.6 ^a	0.96 \pm 0.90 ^a	3,28	18.7	6.7 \times 10 ⁻⁶	6,28	2.62	0.050

*Columns show the mean rate of succession for each treatment along with results of nested analysis of variance for treatment and sites within treatment for each response variable. Within rows, different superscripts indicate significant differences between treatments as identified by Tukey's tests.

Discussion

Early Successional Patterns, Rates, and Constraints

Although agroforestry and swidden systems may permit rapid forest regeneration, pastures and intensive monocultures diminish regenerative capacity. The marked differences in early successional rates we observed must be

considered conservative. The three intensive monoculture sites and one of the pasture sites were in an area of comparatively rich soils (Shriar 2001), and unusual levels of seed dispersal accelerated regeneration on the López and Galindo sites. Furthermore, whereas agriculture along the Ruta Bethel is as input-intensive as anywhere in El Petén, banana, pineapple, sugar, rice, and cotton plantations elsewhere in Central America are

Table 3. Multiple regression results for relationship between tree recruitment and growth and site factors.^a

Site factors		Dependent variable ^b			
		basal-area accumulation rate	recruitment rate	fleshy-fruited recruitment rate	fleshy-fruited species richness accumulation rate
Distance to forest	β			-0.334	-0.318
	<i>t</i>			-2.79	-2.71
	<i>p</i>			0.027	0.030
Initial basal area	β			0.430	0.457
	<i>t</i>			3.57	3.86
	<i>p</i>			0.0092	0.0062
Herb cover	β	-0.709	-0.765	-0.693	-0.683
	<i>t</i>	-3.02	-3.57	-5.82	-5.84
	<i>p</i>	0.015	0.0061	0.00065	0.00064
Regression	R^2	0.503	0.585	0.902	0.866
	df	1, 9	1, 9	3, 7	3, 7
	<i>F</i>	9.10	12.7	21.6	22.5
	<i>p</i>	0.015	0.0061	0.00065	0.00057

^aFor each dependent variable, coefficients (β), *t* and *p* values are shown for significant site factors selected by backward elimination. Years cultivated and vine cover were also included as site factors but were eliminated from all regressions.

^bThere were no significant site variables for height growth rate or species-accumulation rate.

Table 4. Species dominating post-agricultural succession in El Petén, Guatemala.^a

Species ^b	Agroforestry		Swidden			Pasture		Monoculture		
	ZQ	NQ	NQ	EO	CPR	CPR	CM	CG	CL	LM
<i>Acacia</i> sp.						50				
<i>Acalypha</i> sp.*	4.3									
<i>Aegiphila monstrosa</i> *			15	8.2						
Anacardiaceae 1*					20				21	
Asteraceae 1	1.6		2.3							
Asteraceae 2					0.70				8.6	
<i>Bourreria oxyphylla</i> *	0.71		0.49				4.6			
<i>Bursera simaruba</i> *	1.2	1.0							4.0	
<i>Byttneria aculeata</i>					3.2					
<i>Calliandra confusa</i>		0.76	5.3	3.2	3.8					
<i>Carica mexicanum</i> *	3.3		2.0							
<i>Carica papaya</i> *		0.76	0.57						14	
<i>Cecropia obtusifolia</i> *	2.1	13	5.7	4.5	10					
<i>Cestrum racemosum</i> *	4.4	2.4								
<i>Chromolaena</i> sp.							4.5			
<i>Chrysophyllum mexicanum</i> *	0.76		3.5	2.7	0.70					
<i>Cordia alliodora</i>					0.70	8.8	12		6.8	
<i>Cornutia pyramidata</i> *		1.7	0.69		2.4					
<i>Cupania belizensis</i> *	1.4		0.56				4.3			
<i>Curatella</i> sp.						11				
<i>Ficus</i> sp.*							5.6			
<i>Guazuma ulmifolia</i> *	5.2		1.5		1.9			64	8.9	
<i>Hamelia patens</i> *	24	31	1.8	6.5	2.8					
<i>Lantana camara</i> *		0.78	1.6	2.9						
Lauraceae 1*					2.1		4.4			
<i>Liabum</i> sp.	2.8	1.8	2.7		3.8					
<i>Lonchocarpus guatemalensis</i>	5.1	12	17	27	19					
<i>Phyllanthus brasiliensis</i> *			2.4							
<i>Piper</i> sp.*	1.6	3.3								
<i>Piscidia piscipula</i>			2.8	2.1						
<i>Psidium guajava</i> *							6.8		5.6	
Rubiaceae 1*								5.6	12	41
Sapindaceae 1								6.4		
<i>Senna</i> sp.	0.72	0.68					17			
<i>Solanum</i> sp. 1*									2.9	
<i>Solanum</i> sp. 2*					1.8					59
<i>Solanum</i> sp. 3*	0.72	2.4	3.9	5.9	3.9			7.5		
<i>Spondias mombin</i> *	11	7.4	6		2.8					
<i>Stemmadenia donnell-smithii</i> *	1.6			2.4						
<i>Tabernaemontana</i> sp.*									2.7	
<i>Thevetia</i> sp.*	2.4	2.1	1.4		0.70	8.5	4.4			
Tiliaceae 1			1.2	5.6						
<i>Trema micrantha</i>								9.6		
<i>Trichilia acutanthera</i> *			1.1				11			
<i>Trichilia</i> sp.*				2.9	0.86	8.7				
<i>Triumfetta</i> sp.			0.61		0.70		21		3.1	
<i>Trophis racemosa</i> *	3.4	1.6	1.3		0.87					
Verbenaceae 1*					0.87		4.2		2.8	
<i>Verbesina</i> sp. 1								6.8	4.0	
<i>Verbesina</i> sp. 2			3.9	13	4.2	12			4.6	

^aData are importance values calculated as (relative frequency + relative density + relative basal area) × 100/3. Only species with an importance value of ≥2 for at least one site are listed. Data are from the final round of sampling for each site. Sites are below agricultural treatment and are designated by the initials of each owner (see Table 1).

^bNames with an asterisk denote species classified as fleshy-fruited.

much larger, more heavily treated with chemicals, and generally devoid of trees.

The regression results (Table 3) suggest successional mechanisms and constraints consistent with those described elsewhere and help explain patterns of regener-

ation following the agricultural treatments. The significant negative relationship between regeneration and herb cover concurs with findings that herbs compete strongly with potential woody colonists (Kellman 1980; Aide et al. 1995; Zahawi & Augspurger 1999; Holl et al.

2000; Ferguson 2001a). The lack of significant effects of vine cover may reflect the multiple, conflicting effects these plants have on regeneration (particularly direct competition with woody colonists and indirect facilitation of these same species through competition with herbs; Ferguson 2001a).

The positive effect of initial basal area and the negative effect of distance to forest on recruitment of fleshy-fruited individuals and species (Table 3) likely result from the behavioral response of seed-dispersing animals (MacArthur et al. 1966; da Silva et al. 1996; Wunderle 1997). Few seed-dispersing animals venture far from forests into open habitats (da Silva et al. 1996). When they do, they scatter most seeds around trees and shrubs (Guevara & Laborde 1993). Our results reconfirm the importance of structural diversity to Neotropical forest succession and are congruent with findings of studies of the forest plantation understory (e.g., Loumeto & Huttel 1997; Wunderle 1997). Our observations of regeneration islands around large trees, particularly at the López site, are further evidence of the same relationship. Given time, the islands of regeneration forming on this site will eventually coalesce to form a closed canopy. In contrast, regeneration on the Monterroso monoculture, where remnant trees were all but absent, appears to be arrested.

The significant, negative relationship between distance to forest and two of the response variables (Table 3) highlights an uncontrolled variable in the study design: all of the intensive monoculture sites and one pasture site were much farther from forest than were the agroforestry or swidden sites (Table 1). This situation was largely unavoidable given the nature of the agricultural treatments. Agroforestry and swidden plots tend to be bounded by agroforestry, swidden, and secondary forest, whereas pastures and monocultures are more often surrounded by more pastures and monocultures. Interestingly, distance to forest significantly influenced only regeneration of fleshy-fruited trees and shrubs. The other response variables were unaffected, probably because some weedy shrubs and trees are scattered through fields or clumped along roads and fence lines, providing seed sources even in the largest pastures or monocultures.

Projections

The duration of our study was insufficient to permit predictions of the time it will take mature forest to develop on these sites. Domination of some of the pasture and monoculture sites by weedy herbs seems set to suppress woody growth for years to come. However, given the importance of positive feedback mechanisms in succession (most notably the relationship between structural diversity and seed dispersal by animals), sites with slow initial regeneration may catch up with other sites, at

least in terms of species richness and basal area. As Finegan (1996) cautions, species composition may recover more slowly, complicating comparison of successional sites with each other and with mature forest. Further clouding the issue is the frequency of fire in El Petén. Out-of-control burns are increasingly common (Whitacre 1998; Shriar 2001), and open areas are particularly prone to fire (Uhl & Kauffman 1990). Thus, sites where tree growth is delayed are most likely to remain in a fire disclimax.

Agricultural Intensification and Conservation

In El Petén, as in lowland tropical agricultural frontiers around the globe, swidden farmers take much of the blame for deforestation (Santiso 1993; Nations et al. 1998; Whitacre 1998). Many ecologists and conservationists recognize that swidden farming can be sustainable but rests on a fragile equilibrium between crop production and maintenance of soil conditions, weed control, and other ecological factors (e.g., Kleinman et al. 1995). That equilibrium is threatened as fallow periods shorten in response to increasing population density, and land is soon exhausted and abandoned. Thus, swidden farming becomes extremely inefficient in terms of production per area of forest cleared. This argument, though oversimplified in significant ways (Sundberg 1998), describes one proximate cause of deforestation.

Among the solutions to the swidden problem that have been promoted by conservation organizations in El Petén has been the intensification of agriculture (increasing income generated per land area), in part through elimination of fallowing (Shriar 2001). Intensification has taken two distinct paths: agroforestry and annual cropping in monocultures. Both intensification strategies should help slow the advance of the agricultural frontier in the short run. However, neither the considerable conservation value of active swidden-fallow mosaics and agroforestry systems (Medellín & Gaona 1999; Griffith 2000) nor the effects of agriculture on post-abandonment forest regeneration seem to have been considered. Despite the risks associated with extrapolating from the early, localized patterns of regeneration to the long-term effects of agriculture on forest cover and biological diversity, our results should give pause to those who have advocated sedentary monocultures as a solution to the perceived swidden problem. The long-term effect of low-diversity intensification may be to create extensive wastelands of little agricultural or ecological value (Soulé et al. 1990), where forest recovery is excruciatingly slow. Even environmentally benign inputs, such as green manures, may contribute to land degradation if used to avoid fallowing.

That some of the intensification strategies promoted by conservationists will do more long-term harm than good to both farmers and forests seems highly proba-

ble. Increased research, extension, policy, and marketing efforts in support of high-diversity intensification strategies will likely prove more fruitful for all stakeholders.

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