

Effects of pasture management on the natural regeneration of neotropical trees

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Summary

1. Natural regeneration of forest trees in grazed pastures could potentially contribute to the conservation of tree diversity within the fragmented and agricultural landscapes that dominate much of the tropics. To understand this potential, we evaluated the effects of several widely used pasture management practices on tree regeneration in pastures in a tropical dry forest (subhumid) region of central Nicaragua.
2. Species richness, density, diversity and composition of seedlings, saplings and adult trees were compared in 46 pastures under different management conditions. The management conditions included three different types of grasses (*Brachiaria* spp., *Cynodon* spp. and naturalized pastures) and two categories of fire history (recently burnt and not recently burnt).
3. Thirty-seven of the 85 tree species present in the pastures were regenerated under the current management conditions. The remaining 48 species may have had reduced natural regeneration because of limitations in either germination, dispersal, establishment or growth, as well as because of negative effects of pasture management practices.
4. The richness, density and species composition of tree seedlings within pastures were explained by grass species composition, the density and richness of adult trees, cattle management and the distance of the pasture to forest. In contrast, no clear effect of fire history was found.
5. *Synthesis and applications.* Current management practices allow the regeneration of almost half of the tree species in grazed pastures. However, to enhance the regeneration of species that show limited regeneration, management strategies, such as the retention of adult trees, protection of saplings and seedlings from weeding and grazing and use of enrichment plantings, may be necessary. These changes in pasture management would help contribute to the long-term conservation of tree diversity within agricultural landscapes across the tropics.

Key-words: *Brachiaria* spp., *Cynodon* spp., fire history, saplings, seedlings, species composition, species diversity, tropical dry forest, tropical pastures

Introduction

Across the tropics, large areas of forest have been destroyed, fragmented and converted to pasture for cattle production, resulting in the loss of plant and animal diversity and the disruption of ecosystem processes (Kaimowitz 1996; Houghton 2003). As a consequence, vast areas of the tropics are now

characterized by agricultural mosaics of pastures and fields interrupted by the occasional forest remnant, a scenario that presents significant new challenges to conservation (Tilman *et al.* 2002). If global initiatives to conserve biodiversity are to succeed, it will be critical to find ways of designing and managing agricultural landscapes that maintain native habitats and intact species assemblages (Fischer, Lindenmayer & Manning 2005).

One potential approach to maintaining biodiversity within pasture-dominated landscapes is to retain a diverse and dense tree component within pastures and to encourage natural tree

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regeneration (Mayfield & Daily 2005). Isolated trees within pastures can contribute to the conservation of plant and animal diversity by providing habitats and resources, increasing the structural and floristic complexity of the landscape, and enhancing connectivity (Harvey, Tucker & Estrada 2004). In addition, the trees can serve as important sources of seeds for reforestation efforts and foci for natural regeneration (Harvey & Haber 1999; Harvey 2000; Esquivel, Calle & Silverstone 2001; Gordon *et al.* 2003). However, such an approach will only contribute to the long-term conservation of biodiversity if the trees are able to maintain viable populations within managed pastures; consequently, there is a critical need to understand the dynamics of natural regeneration of tropical trees within grazed pastures and how management practices influence their regeneration patterns.

There is currently some debate regarding tree species regeneration in pastures. Several studies have suggested that many tree species are unable to reproduce successfully and maintain populations in pastures over the long-term (Janzen 1986; Wilson 1990). The limited seed rain (Radford *et al.* 2001) and unfavourable microsites and microclimatic conditions in open pastures (Nepstad *et al.* 1996; Holl 1999) are known to reduce tree colonization. Grass competition (Camargo *et al.* 1999; Schaller *et al.* 2003), cattle grazing (Hall *et al.* 1992; Archer 1995) and pasture management (Teague & Dowhower 2003) may also limit regeneration. Trees in pastures could therefore be alive yet unable to reproduce successfully within these habitats, i.e. 'living dead' (Janzen 1986). If this is the case, the density, diversity and conservation value of tree cover will quickly diminish over time.

Few studies, however, have examined the colonization dynamics of different tree species in active tropical pastures (Arnaiz *et al.* 1999; Esquivel, Calle & Silverstone 2001). Even less is known about the way in which pasture management practices, such as the grass species planted and their competitive effects (Camargo *et al.* 1999; Fairfax & Fensham 2000) and the use of fire to maintain herbaceous cover and its effect on tree seed viability and seedling mortality (Koonce & Gonzales-Caban 1990; Conrado, Chavelas & Camacho 1993; Setterfield 2002; Dokrak *et al.* 2004), influence regeneration processes.

The aim of this study was to contribute to the understanding of the dynamics of natural regeneration of tropical trees in grazed pastures under different management practices. The specific objectives were to (i) determine the density, species richness and composition of seedlings, saplings and adult trees in pastures, (ii) identify species with either active or limited natural regeneration, (iii) compare the density, species richness and composition of tree seedlings in pastures with different grass species (*Cynodon* spp., *Brachiaria* spp. and native species such as *Paspalum* spp.) and different fire histories and (iv) evaluate the effects of weed management, cattle type and the surrounding tree cover on tree regeneration. This study provides the first information on the ability of native tropical tree species to maintain their populations in actively managed pastures, and also highlights the potential

contribution of natural regeneration to the conservation of tree diversity within tropical agricultural landscapes.

Materials and methods

STUDY SITE

The study was conducted in the Rio Grande watershed (municipality of Muy Muy, department of Matagalpa) in central Nicaragua (12°31'–13°20'N, 84°45'–86°15'W). The annual temperature is 24.5 °C and mean annual precipitation is 1576 mm, with rains between May and September (Holdridge 1984). The ecosystem is tropical dry forest (subhumid) with semi-deciduous vegetation (Meyrat 2000). The landscape consists of plains and undulating areas between 100 and 450 m a.s.l. and the soils consist mainly of vertisols, inceptisols and alfisols.

The region is dedicated to cattle production, with 53% of the land under natural (i.e. not sown) grasses such as *Paspalum* spp., 22% planted with improved exotic grasses such as *Brachiaria* spp. and *Cynodon* spp., 10% under early secondary succession (tacotales) and only 5% under forest. The cattle farms have an average of 40 heads of dual-purpose cattle (meat and milk production). Farms average 40 ha and are divided into 6–10 paddocks of 3–6 ha each. Livestock production is generally of low intensity (with an average stocking rate of 1 livestock unit ha⁻¹) and range management consists primarily of weeding, either manually (with machetes) or through the use of fire and herbicides (Koonce & Gonzales-Caban 1990). Just one type of cattle is bred, and grazing is divided into three groups: (i) lactating cows (currently producing milk), (ii) non-lactating cows (outside milk production) and (iii) heifers or calves.

SAMPLING SCHEME

Study plots were established in 46 actively used pastures on 17 cattle farms. These plots were selected to ensure a non-grouped spatial arrangement that covered the different conditions of pastures present in the region. The pastures were selected on the basis of grass composition and history of fire use, and were representative of pastures in the region. The selected pastures were dominated (i.e. cover = 70%) by one of three grass types: (i) *Brachiaria* spp. [*Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf and *Brachiaria decumbens* Stapf, synonymous with *Urochloa decumbens* (Stapf) R.D. Webster and *Urochloa brizantha* (Hochst. ex A. Rich.) R.D. Webster, respectively] (B, $n = 15$); (ii) mixtures of *Cynodon nlemfuensis* Vanderyst and *Cynodon dactylon* (L.) Pers. (C, $n = 13$); or (iii) naturalized grasses (i.e. not planted or seeded) such as *Paspalum* spp. (N, $n = 18$). Pastures were categorized into two fire histories: (i) burnt in the last 5 years (Br, $n = 16$) and (ii) not burnt during the last 5 years (nBr, $n = 30$). Pastures fell into six categories, depending on the combination of pasture type and fire history: BBr ($n = 5$), BnBr ($n = 10$), CBr ($n = 5$), CnBr ($n = 8$), NBr ($n = 6$), and NnBr ($n = 12$). The total area of each pasture varied from 1 to 22 ha (mean 5.82 ± 1.34 ha).

SAMPLING DESIGN

The tree cover in pastures was characterized by sampling three size classes: seedlings, saplings and adult trees. Seedlings were defined as woody plants with a height between 10 and 30 cm, saplings as woody plants with heights > 30 cm and diameters at breast height (d.b.h.) ≤ 10 cm, and adult trees as plants with d.b.h. > 10 cm. Although all the size classes included both trees and shrubs, for simplicity we refer to them all as trees.

Total sampling effort varied between pastures because of differences in paddock area and shape. The basic sampling scheme for regularly shaped (square) pastures greater than 1 ha in size was as follows: (i) adults were sampled within a 1-ha area (100 × 100 m) located in the centre of each pasture; (ii) saplings were sampled in 12 quadrats (each 20 × 20 m) arranged in a rectangle in the centre of the 1-ha plot and forming a grid of 60 × 80 m; and (iii) seedlings were sampled within circular plots (with a radius of 1.5 m, i.e. an area of 7 m²), with one plot positioned at each of the 20 corners or intersections of the grid for sampling saplings, for a total of 20 circular plots per pasture. In pastures with irregular shapes, the same arrangement of quadrats and circular plots was used but the number of quadrats and plots that could be accommodated was lower. As a result, saplings were sampled in a mean of 10 quadrat plots per pasture (minimum 3 and maximum 12) while seedlings were sampled in a mean of 18 circular plots (minimum 7 and maximum 20) per pasture. Because total sampling effort varied between pastures, all analyses were conducted on the average number of individuals and species found in each plot within a pasture, with pastures as replicates.

NATURAL REGENERATION OF TREES

Seedlings, saplings and adult trees were sampled in the 46 pastures from May to late July 2004. Each individual was identified to species and its height, d.b.h. and crown sizes (two diameters along perpendicular axes) were measured. The relative abundance (Ar_i) and relative frequencies (Fr_i) were calculated for all size classes, whereas the relative dominance (Dr_i) was only calculated for adults. These values were summed to calculate the importance value index (IVI) for each species with adult trees, and the simplified importance value index (IVI_s, calculated with Ar_i and Fr_i) for species with only saplings and seedlings (Magurran 1988). The expected species richness for seedlings, saplings and adults was obtained using the non-parametric richness estimator Chao 1 in EstimateS Version 7 (Colwell 2004). The Shannon's diversity and Pielou's evenness indices were calculated for each plant size class in each pasture using Species Diversity and Richness Version 3.0 (Henderson & Seaby 2002).

MANAGEMENT CONDITIONS

Information on management practices (additional to pasture type and fire history) was gathered through interviews with farmers. The annual frequency of manual weed control, the annual use of herbicides, cattle type (lactating cows, non-lactating cows, heifers or calves) and grazing management (density of animals, rotational system and resting periods) were identified for each paddock. The tree cover (% area under tree canopy), tree density and tree species richness of each pasture were calculated using the 1-ha plots for adult trees (d.b.h. > 10 cm). In addition, the type of land use in neighbouring areas of each pasture was recorded (secondary forest, riparian forest, taceuticals or farmyards).

STATISTICAL ANALYSIS

Comparisons among seedlings, saplings and adult trees in density, species richness and diversity were used to determine the structure of tree regeneration in active pasturelands. Diversity and evenness indices were compared among the three size classes using ANOVA, followed by Tukey comparisons (InfoStat 2004). Accumulation and rarefaction curves, with individuals as sample units, were calculated

in EcoSim Version 7.5 (Gotelli & Entsminger 2005) and compared across size classes.

The presence of individuals in each size class was used to identify species' natural regeneration capacity (regeneration categories). The presence of individuals of a given species in all three size classes (seedlings, saplings and adults) was assumed to indicate the ability of the species to maintain its population in grazed pastures through natural regeneration. Conversely, the lack of individuals in one or two size classes was used as an indicator of potential limitations in the species' ability to maintain its population through natural regeneration. The most important species in each size class and in each regeneration category were identified using IVI and IVI_s.

The density, species richness and species composition of tree seedlings were compared across pastures with different grass species (*Cynodon* spp., *Brachiaria* spp. and *Paspalum* spp.) and different fire histories (recently burnt vs. not recently burnt). Pasture composition (B, C, N) and fire history (Br, nBr) effects on density and species richness of tree seedlings per m² were evaluated using ANOVA, followed by Tukey comparison tests. Seedling and adult tree species composition in different pasture types (BBr, BnBr, CBr, CnBr, NBr, NnBr) were compared using cluster analysis, with Euclidean distances calculated by the Ward method in Infostat (2004).

The effects of management on tree seedlings in active pastures were evaluated using multivariate analyses. The contribution of management variables, such as pasture composition and fire-use history, to explain the variability observed in the composition and abundance of tree seedlings in the pastures was determined using canonical correspondence analysis (CCA) and Monte Carlo permutation tests, using 499 permutations in the program CANOCO (ter Braak & Smilauer 1998). The correlations between pasture composition (B, C, N) and management conditions were evaluated using correlation indices of CA in CANOCO (ter Braak & Smilauer 1998) and contingency tables with chi-square tests in InfoStat (2004). Correlations between seedling species richness and adult tree species richness, and between seedling density and density of adult trees in pastures with different grass composition, were conducted using linear regressions in Infostat (2004).

Results

TREE COVER IN PASTURES

A diverse array of seedlings, saplings and adult trees was found in the active pasturelands (Table 1). A total of 85 species (36 families) and 13 845 tree individuals were registered in the 46 pastures sampled (total area of 46 ha). Adult trees represented a larger number of species but had fewer individuals than either saplings or seedlings (Fig. 1). Evenness was significantly higher among adults than among either saplings or seedlings (ANOVA, $F_{2,135} = 8.97$, $P = 0.002$; Table 1).

Pioneer species, typical of disturbed areas and tolerant of the conditions within pastures, had the ten greatest IVI in all size classes. Six of these species were dispersed by cattle, two species by wind and two by wild animals (Table 2). All these species have potential value as fruit, timber and/or forage (Stevens *et al.* 2001; Cordero & Boshier 2003).

Two groups of species were identified based on their presence or absence and their importance values in each size class: (i) species with adequate natural regeneration in

Table 1. Community characteristics of different tree size classes in 46 grazed pastures in Muy Muy, Nicaragua

Characteristics of samples and community	Seedlings	Saplings	Adults
Plots (<i>n</i>)	835	441	46
Area (ha)	0.6	17.6	46.0
Abundance (total no. of individuals)	6378	5698	1769
Observed species (no.)	60	70	72
Expected species by Chao 1 (no.)	82	88	83
Species with one or two individuals (%)	35	30	35
Species with more than 50% of individuals (%)	23	6	7
Species registered in one or two paddocks (%)	47	40	40
Species registered in more than 50% of paddocks (%)	22	20	15
Tree density (no. ha ⁻¹)	10 630	354	40
Shannon's diversity index (mean ± SE)	1.56 ± 0.07 ^a	1.66 ± 0.08 ^a	1.76 ± 0.07 ^a
Pielou's evenness index (mean ± SE)	0.71 ± 0.02 ^b	0.73 ± 0.02 ^b	0.83 ± 0.02 ^a

Different letters in the same row indicate significant differences (Tukey test, $P < 0.05$).

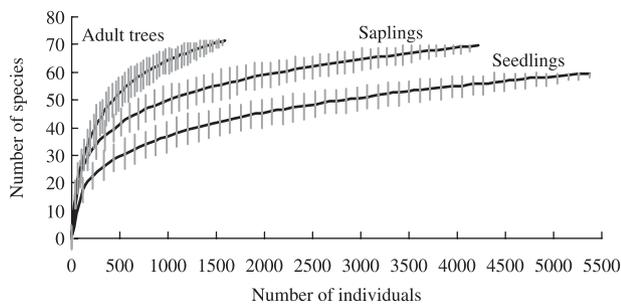


Fig. 1. Species accumulation curves for three size classes (with standard errors) as a function of the number of individuals sampled in 46 grazed pastures in Muy Muy, Nicaragua.

pastures and (ii) species with limited natural regeneration (Table 3). The first group comprised 37 of the 85 tree species registered (44%) and consisted of those species with individuals in all three size classes (seedlings, saplings and adults).

Six of the species in this group had the highest IVI in all three size classes, indicating that these species dominated the tree cover in pastures. Another 10 species were common, with high IVI in one or two size classes. The remaining 21 species with adequate natural regeneration were species that had low abundances or frequencies in all three size classes.

The second group of species, i.e. those with limited natural regeneration, comprised 48 of the 85 species registered (56%) and consisted of species that had individuals present only in one or two of the three size classes (Table 3). Of these species, 16 were present only as adults in the pastures. These species (mainly relicts of the original forest) appeared to face the strongest limitation to natural regeneration in active pastures. Another 14 species were not represented by seedlings despite the presence of saplings and adult trees. These 14 species, compared with the 16 described above, might regenerate infrequently at specific windows of opportunity limited to specific microsites that were not present in the

Table 2. Tree species with the highest importance value indices (IVI, IVI_s) in 46 grazed pastures in Muy Muy, Nicaragua. Species are presented in decreasing order of adult IVI

Species	Habitat	Dispersal vectors	Uses	IVI _s		IVI
				Seedlings	Saplings	Adults
<i>Guazuma ulmifolia</i>	RF, AL	WA, C	Fo, Wo	99	109	82
<i>Cassia grandis</i>	AL	C	S	46	83	80
<i>Tabebuia rosea</i>	RF, SF, AL	Wi	Wo	99	78	80
<i>Albizia saman</i>	SF, AL	C	Wo, Fo, S	33	58	74
<i>Bursera simaruba</i>	RF, SF, AL	WA	Fw, Fo, LF	41	18	63
<i>Enterolobium cyclocarpum</i>	SF, AL	C	Fo, S	91	108	52
<i>Cordia alliodora</i>	SF, AL	Wi	Wo	84	48	47
<i>Leucaena shannoni</i>	AL	C	Fo	48	57	45
<i>Gliricidia sepium</i>	SF, AL, C	E	Fo, LF	28	31	40
<i>Spondias mombin</i>	AL, C	WA	Fr, LF	31	24	37
<i>Cordia collococca</i>	SF, AL	WA	Wo, Fo	26	41	25
<i>Platymiscium parviflorum</i>	SF	Wi	Wo	37	34	24
<i>Psidium guajava</i>	AL, C	WA, C	Fr, Fo	18	55	22
<i>Genipa americana</i>	SF, AL, C	WA	Fr	53	31	14

Habitat: riparian forest (RF), secondary forest (SF), agricultural lands (AL), cultivars (C). Seed dispersal vectors: wild animals (WA), wind (Wi), cattle (C), explosive (E). Farm uses: forage (Fo), wood (Wo), firewood (FW), shade (S), live fences (LF), fruit trees (Fr).

IVI (adults) = relative abundance + relative frequency + relative dominance.

IVI_s (saplings and seedlings) = relative abundance + relative frequency.

Table 3. Total abundance of seedlings, saplings and adults of the five most abundant tree species by regeneration category in 46 grazed pastures in Muy Muy, Nicaragua

Regeneration category	Species	Abundance			Total
		Seedlings ($n = 835$)	Saplings ($n = 441$)	Adults ($n = 46$)	
I Adequate natural regeneration (individuals present in all three size classes)					
IA High abundance and frequency in all three size classes					
	<i>Cordia alliodora</i>	2717	239	102	3058
	<i>Enterolobium cyclocarpum</i>	525	1200	82	1807
	<i>Tabebuia rosea</i>	750	597	226	1573
	<i>Guazuma ulmifolia</i>	358	898	251	1507
	<i>Cassia grandis</i>	44	293	189	526
IB Low abundance in one or two size classes					
	<i>Platymiscium parviflorum</i>	533	206	40	779
	<i>Albizia saman</i>	43	228	118	389
	<i>Cedrela odourata</i>	264	4	66	334
	<i>Gliricidia sepium</i>	138	138	57	333
	<i>Psidium guajava</i>	25	264	12	301
IC Low abundance in all three size classes					
	<i>Lonchocarpus parviflorus</i>	45	175	7	227
	<i>Tabebuia ochracea</i>	60	156	4	220
	<i>Trichilia americana</i>	98	13	8	119
	<i>Acrocomia mexicana</i>	12	79	1	92
	<i>Sapium macrocarpum</i>	54	5	13	72
II Limited natural regeneration (individuals present in only two size classes)					
IIA Only adults present					
	<i>Ficus isophlevia</i>	0	0	12	12
	<i>Robinsonella lindeniana</i>	0	0	8	8
	<i>Zuelania guidonea</i>	0	0	6	6
	<i>Myrciaria floribunda</i>	0	0	5	5
	<i>Lysiloma auritum</i>	0	0	2	2
IIB Only seedlings and/or saplings present					
	<i>Capparis frondosa</i>	88	24	0	112
	<i>Randia armata</i>	32	52	0	84
	<i>Curatella americana</i>	20	47	0	67
	<i>Casearia corymbosa</i>	3	63	0	66
	<i>Cupania guatemalensis</i>	1	15	0	16
IIC Only adults and saplings present					
	<i>Vitex gaumeri</i>	0	11	2	13
	<i>Croton draco</i> spp. <i>panamensis</i>	0	6	4	10
	<i>Zanthoxylum elephantiasis</i>	0	4	5	9
	<i>Ceiba pentandra</i>	0	1	4	5
	<i>Ceiba aescutifolia</i>	0	1	3	4

pastures studied. If not, their low abundances appear to limit their natural regeneration within grazed pastures. The remaining 18 species did not have adult trees present within the pastures but were represented by seedlings and/or saplings. These species appeared able to regenerate in the pastures but were later eliminated by cattle and pasture management (weeding).

PASTURE MANAGEMENT EFFECTS ON TREE SEEDLINGS

Pastures with different grass species showed significant differences in the tree seedling species richness (species m^{-2}). Seedling species richness was higher in *Brachiaria* pastures than in naturalized or *Cynodon* pastures (ANOVA, $F_{2,40} = 6.23$, $P = 0.004$; Fig. 2a). Tree seedling abundance in different types of pastures was highly variable across sites and the number of seedlings per m^2 did not show differences across the different

types of pastures and their associated management practices (ANOVA, $F_{2,40} = 0.58$, $P = 0.566$; Fig. 2b). There were no interactions between the effects of grass species composition and fire-use history on the mean number of species of tree seedling per m^2 (ANOVA, $F_{2,40} = 0.23$, $P = 0.797$) or on the number of seedlings per m^2 (ANOVA, $F_{2,40} = 0.55$, $P = 0.579$). Fire-use history had no effect on the mean number of species (ANOVA, $F_{2,40} = 0.23$, $P = 0.797$) or on seedling abundance (ANOVA, $F_{1,40} = 0.46$, $P = 0.502$).

Seedling species composition was principally affected by grass composition (B, N, C) and the composition of the adult tree cover within the pastures and in surrounding areas, but not by fire-use history. Despite differences in fire-use histories, the seedling species composition was more similar between pastures with *Cynodon* grasses (CBr and CnBr) and between pastures with naturalized grasses (NBr and NnBr) in the cluster diagrams (Fig. 3a). Only the *Brachiaria* pastures showed differences in seedling species composition as a result

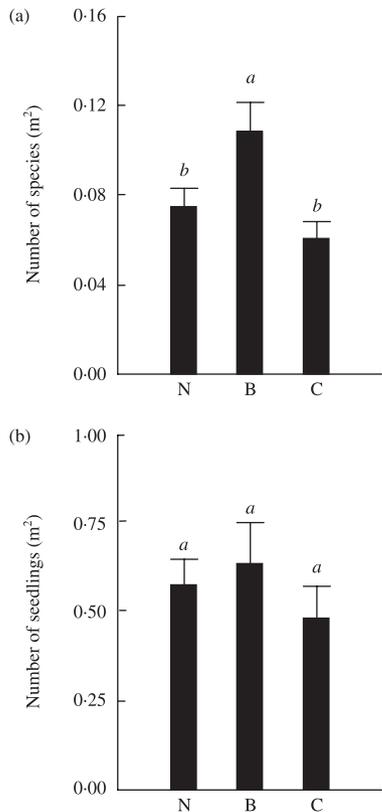


Fig. 2. Tree seedling (a) species and (b) density per m² in 46 grazed pastures with different grass compositions [*Brachiaria* spp. (B), *Cynodon* spp. (C), naturalized pastures *Paspalum* spp. (N)] in Muy Muy, Nicaragua. Different letters indicate significant differences among pasture types (Tukey $P = 0.05$).

of fire-use history (BBr vs. BnBr). Of the 17 species that were found exclusively in a single pasture type, 11 were found in *Brachiaria* pastures that had not been recently burned (BnBr), five in recently burned *Brachiaria* pastures (BBr) and one in *Cynodon* pastures. Differences were also found in the species composition of adult trees in *Brachiaria* pastures with different fire histories (BBr and BnBr) (Fig. 3b). These differences in seedling composition were influenced by the high tree cover in *Brachiaria* pastures and their proximity to secondary forest (Table 4).

A high proportion of the variation in the abundance of tree seedlings was explained by grass composition, fire history, cattle management, tree species richness, tree density and the type of neighbouring land use (CA, Monte Carlo, $P = 0.002$, $r = 0.945$). The particular type of cattle grazed in the pastures (i.e. lactating cows, non-lactating cows, heifers or calves) and the location of the pasture relative to forest cover (i.e. next to riparian forests or secondary forests or not) were correlated with the different types of grass species (Table 4). *Brachiaria* pastures were associated with a greater density and species richness of adult trees, were generally grazed by lactating cows and tended to be located near secondary forests. The naturalized pastures, in contrast, were located near riparian forests and were used principally for non-lactating cows, while the pastures with *Cynodon* spp. were located near

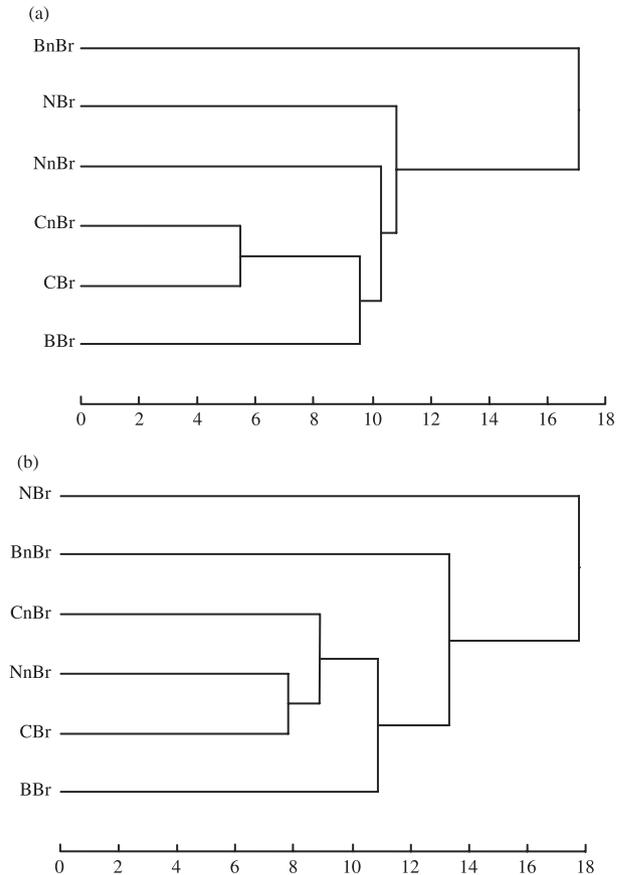


Fig. 3. Cluster diagrams of (a) seedlings and (b) adult tree species composition using Euclidean distances and the Ward grouping method in 46 grazed pastures with different grass species and different fire histories in Muy Muy, Nicaragua. Grass species include *Brachiaria* spp. with or without recent burns (BBr, BnBr), *Cynodon* spp. with or without recent burns (CBr, CnBr) and naturalized grasses *Paspalum* spp. with or without recent burns (NBr, NnBr).

cattle corrals or farmhouses and were used primarily for calves.

The number of seedling species was positively related to the number of adult tree species present in the pastures for each of the three grass species (B, $R^2 = 0.63$, $F = 15.38$, $P = 0.003$; C, $R^2 = 0.62$, $F = 15.56$, $P = 0.002$; N, $R^2 = 0.49$, $F = 14.65$, $P = 0.001$; Fig. 4a). However, the significance of the linear regressions of tree seedling density on adult tree density depended on pasture type, with seedling density being significantly higher in pastures with greater tree densities in pastures of *Brachiaria* spp. ($R^2 = 0.78$, $F = 31.89$, $P = 0.0003$) but not in pastures dominated by *Cynodon* spp. ($R^2 = 0.10$, $F = 1.27$, $P = 0.283$) or in naturalized pastures ($R^2 = 0.10$, $F = 0.01$, $P = 0.092$; Fig. 4b).

Discussion

RICHNESS AND DIVERSITY OF NATURAL REGENERATION OF TREES IN PASTURES

A significant number of tree species are able to regenerate naturally within managed pastures. In 1 ha of grazed pasture,

Table 4. Pasture management variables explaining the abundance variability of tree seedlings and their correlations with grass composition, tree variables, pasture management and type of land use in neighbouring areas in 46 grazed pastures in Muy Muy, Nicaragua. Grass species include *Brachiaria* spp. (B), *Cynodon* spp. (C) and naturalized grasses *Paspalum* spp. (N)

Environmental variables	CCA		CA (R)			χ^2
	F	P	B	C	N	P
Tree cover	2.02	0.01	0.22	-0.26	-0.04	0.63
Tree density	2.03	0.02	0.42	-0.40	-0.16	0.13
Tree richness	3.04	0.01	0.52	-0.46	-0.23	0.44
Manual weeding	1.55	0.07	-0.29	0.49	-0.06	0.05
Herbicide	1.29	0.14	0.66	-0.23	-0.57	0.07
Non-lactating cows	1.70	0.02	-0.28	-0.30	0.45	0.01
Lactating cows	1.24	0.18	0.45	-0.09	-0.33	0.01
Weaned calves	0.91	0.54	-0.22	0.53	-0.17	0.01
Secondary forest	1.13	0.35	0.08	0.03	-0.11	0.08
Riparian forest	0.95	0.48	-0.63	0.24	0.53	0.05
Tacotalas	1.68	0.03	-0.23	-0.16	0.39	0.02
Farmyard	1.77	0.03	-0.41	0.28	0.24	0.08
Farm house	1.61	0.04	-0.45	0.39	0.16	0.08

CCA, canonical correspondence analysis and Monte Carlo test ($P < 0.05$); CA, correspondence analysis ($P < 0.05$; R, matrix index values); χ^2 , chi-square analysis ($P < 0.05$).

we found an average of 10 630 seedlings and 354 saplings belonging to 60 and 30 tree species, respectively. The extensive cattle management traditionally used in Muy Muy (manual weeding, infrequent use of herbicides, large paddocks and infrequent rotation of cattle) probably favours the natural regeneration of trees in the pastures. The fact that such management practices characterize a large proportion of the cattle production regions of Central America (Carr & Langhammer 2005) suggests that it is possible to maintain populations of native tree species in managed pastures and illustrates the potential for managing natural regeneration as a means to conserve tree diversity within tropical agricultural landscapes (Gordon *et al.* 2003).

Our results suggest that there are two different groups of tree species present in pastures: (i) those with an adequate natural regeneration and (ii) those with a limited natural regeneration. These two groups reflect different capacities of tree species to establish seedlings, saplings and adults in active pastures, because of ecological conditions in pasture systems and farmers' management practices.

Forty-six per cent of the 85 tree species found in pastures appeared to have high probabilities of maintaining their populations in active pastures through natural regeneration, as individuals of these species were found in all three size classes. The tree species with the highest importance indices (IVI and IVI_s) within this group were pioneer species that are dispersed by cattle or wind and have high resprouting capacities (Stevens *et al.* 2001). These characteristics favour the regeneration of these species, allowing them successfully to overcome the low availability of seeds, high solar radiation, high evapotranspiration, degraded soils, grazing and trampling by cattle, and the extraction and pollarding of trees by farmers,

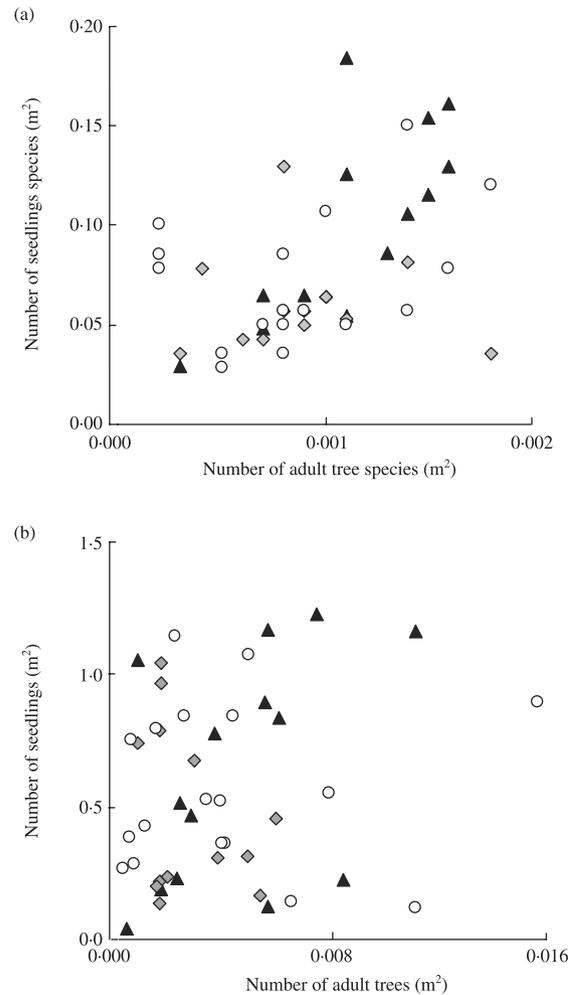


Fig. 4. Relations between (a) adult and seedling species richness and (b) adult tree and seedling abundance in 46 grazed pastures with different grass species, *Brachiaria* spp. (triangles), *Cynodon* spp. (rhombuses) and naturalized grasses *Paspalum* spp. (circles), in Muy Muy, Nicaragua.

which are considered important barriers to tree establishment on pastures elsewhere (Nepstad *et al.* 1996; Holl 1999).

Tree species with the highest IVI showed different strategies to overcome natural regeneration barriers in grazed pastures. Species dispersed by cattle (e.g. *Guazuma ulmifolia*, *Cassia grandis*, *Enterolobium cyclocarpum* and *Leucaena shannonii*) are probably favoured by the presence of cattle and may be widely dispersed in cattle dung in the paddocks (Janzen 1981; Somarriba 1986; Radford *et al.* 2001; Traba, Levassor & Begoña 2003). Wind-dispersed pioneer species, such as *Tabebuia rosea* and *Cordia alliodora*, are readily dispersed from nearby forest borders into the adjacent pastures (Augsburger & Franson 1988). The presence of remnant forest patches and isolated trees in pastures also enhances seed dispersal by wild animals into the pastures (Holl 1999; Harvey 2000). Tree species with high resprouting capacity, such as *Guazuma ulmifolia* and *Gliricidia sepium*, have a reduced mortality of seedlings and saplings caused by cattle browsing and trampling (Hobbs & Mooney 1985; Cordero & Boshier

2003). In addition, many of the common tree species that regenerate in pastures are retained by farmers because of their value as forage (leaves or fruits), timber or shade for cattle (Harvey & Haber 1999; Cordero & Boshier 2003).

Fifty-six per cent of the 85 tree species found in these pastures were represented in only one or two of the three size classes evaluated, suggesting that they have limited natural regeneration and low probabilities of maintaining their populations on active pasturelands. This group of species includes both species that seem to be unable to regenerate within the pastures, and others that may be regenerating but are removed by current management practices. For example, 16 species within this group appear to be unable to recruit new individuals to maintain their populations in pastures. These species are unable to regenerate in these pastures because of low densities of adults in the landscape, inbreeding or unfavourable microsite conditions in pastures (Janzen 1986). However, these trees could still disperse pollen to other trees in the landscape (fragments or continuous forest) and may contribute to gene exchange and species population dynamics at the landscape level (White, Boshier & Powell 2002).

Another 18 tree species appear able to colonize pastures but do not survive to an adult stage. The absence of adult trees of these species, despite the presence of seedlings and saplings, could be the result of natural growth patterns (e.g. small tree species that rarely reach a diameter of 10 cm, such as *Capparis frondosa*) or of limited regeneration conditions (Stevens *et al.* 2001). The absence of individuals in the largest size class could also indicate that these species have just recently colonized the pastures and have not yet reached the adult stage, as has been observed in other colonization studies with pioneer species (Lichstein, Grau & Aragón 2004). Alternately, the high temperature and humidity fluctuations could limit establishment and growth of seedlings and saplings of these tree species in open pastures (Conrado, Chavelas & Camacho 1993; Gerhardt 1999; Hooper, Legendre & Condit 2005). In addition, the absence of adult trees of these species on active pasturelands could be the result of cattle activity (trampling, browsing) and/or pasture management practices (e.g. manual weeding with machetes), which have been identified as strong selective factors driving population dynamics of some tree species in active pastures elsewhere (Camargo *et al.* 1999; Kindt, Simon & Van Damme 2004).

Fourteen tree species were absent in the seedling size class and may be unable to colonize active pastures. There are several potential explanations for the absence of seedlings of these species. First, it is possible that some of these species were actively regenerating within the pastures but were not found as seedlings because (i) the trees were already taller than 30 cm at the time the study was conducted, (ii) these species only regenerate in specific microhabitats or under certain climatic conditions that were not present during the study period, or (iii) these species may regenerate in pulses (that occur supra-annually) and their seedlings were absent during the survey because it was potentially an unfavourable year for seedling establishment (Cornett *et al.* 2000). Secondly, these

species may be unable to establish within the active pastures because of the pressures from cattle grazing and manual weeding, as has been reported for some tree species elsewhere (Camargo *et al.* 1999).

PASTURE MANAGEMENT EFFECTS ON TREE SEEDLINGS

The species richness, density and composition of tree seedlings in the pastures were influenced by the composition of the grass layer, as well as the particular management practices associated with each pasture type. The fact that the greatest species richness of seedlings was found in pastures dominated by *Brachiaria* spp. compared with pastures with naturalized grass or pastures with *Cynodon* spp. is probably not only because of the growth characteristics of this grass species under active management (which may permit a large number of seeds to reach the soil and germinate) but because of the high density and species richness of adult trees in these pastures, as well as the cattle management and the closeness of these pastures to forest patches. The erect bunch-forming growth of *Brachiaria* spp. in this region (up to 1 m tall; Johnson *et al.* 2005) probably increases the availability of microsites appropriate for the germination and establishment of tree seedlings, particularly during the dry season (Gerhardt 1999), in comparison with the creeping, mat-forming architecture of *Cynodon nlemfuensis* (Fairfax & Fensham 2000), which impedes tree seeds from reaching the soil (M.J. Esquivel, personal observation). At the same time, the location of the *Brachiaria* pastures next to secondary forests and the fact that these pastures tend to have a high density and species richness of adult trees (Sánchez *et al.* 2005) increase the probability that these pastures receive a large seed rain (Holl 1999).

Finally, differences in the way in which the different types of pastures are managed may have an impact on seedling mortality. In *Brachiaria* pastures, where cattle are usually managed on a rotational basis (with individual paddocks being grazed for 4 days, followed by 30 days of recovery), seedling mortality by trampling is probably low (Simon *et al.* 1997). In contrast, the naturalized pastures are usually grazed continuously (i.e. without any recovery periods in dry seasons) and seedlings in these pastures are therefore likely to suffer greater mortality.

The history of fire use, on the other hand, showed no clear effect on seedling species richness or density. Studies elsewhere have shown that the use of fire in pastures can positively select for species with seeds that are fire tolerant or experience enhanced germination under fire (Conrado, Chavelas & Camacho 1993), while reducing the emergence of seedlings of other species that are negatively affected by the changes in understorey cover and microclimatic conditions in burnt areas (Setterfield 2002). However, our study found no clear effects of fire on regeneration patterns. There were no effects of burning on natural regeneration within either *Cynodon* or *Paspalum* pastures. The observed differences in seedling composition between *Brachiaria* pastures with different fire-use histories most probably reflects differences

in the proximity of the pastures to forest, rather than a fire-history effect *per se*. The *Brachiaria* pastures that were not recently burned were located closer to secondary forests than *Brachiaria* pastures that had been burnt within the last 5 years, making it difficult to distinguish a fire-history effect from the effects of higher seed rain from the adjacent forest. It is possible, however, that the effects of burning are only obvious in the first months or years following burning, rather than the 5-year time frame used here, so additional research is merited.

CONCLUSIONS

The results of this study provide evidence against the commonly held notion that tropical trees in pastures are 'living dead' and incapable of maintaining their populations in active pastures, and instead point to the potential of natural regeneration in pastures to contribute significantly to the conservation of tree diversity in agricultural landscapes. Our results suggest that a significant number of the tree species censused can overcome the regeneration barriers that exist in pastures. In addition, our results show that the current pasture management conditions, such as grass composition, type of cattle grazing, farmer management of adult tree density and composition in the pastures and the presence of nearby forests, collectively determine the composition, richness and density of tree seedlings in active pastures.

However, unless specific measures are taken, the species richness and diversity of tree cover in these agricultural landscapes will gradually decrease over the long term because of the limited regeneration of certain tree species. Selective retention of saplings or seedlings during pasture management practices and protection against cattle activities could enhance the probability of some of these species reaching adult stages (Camargo *et al.* 1999). Manual dispersal of seeds into pastures, seedling transplantation from other habitats to favourable microsites on pastures, the use of more selective weeding practices (that retain more seedlings), the prevention of overgrazing (controlled rotation) and the physical protection of saplings from cattle could also enhance the natural regeneration of species with early colonization limitations (Simon *et al.* 1997; Martínez-Garza & Howe 2006). In addition, the retention of a high diversity of tree cover (particularly forest cover) within farms could help to ensure the continued dispersal of propagules into pastures (Holl 1999; Esquivel, Calle & Silverstone 2001; Harvey, Tucker & Estrada 2004). Collectively, these changes in pasture management could greatly enhance the natural regeneration of trees within active pastures and thereby contribute to the long-term conservation of tree diversity within the agricultural landscapes that dominate much of the tropics.

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