
Does Restoration Enhance Regeneration of Seasonal Deciduous Forests in Pastures in Central Brazil?

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Abstract

The goal of restoration is to accelerate ecosystem recovery, but in ecosystems that naturally regenerate rapidly restoration techniques need to be selected carefully to facilitate rather than impede natural recovery. We compared the effects of five restoration techniques, such as plowing the soil, removing grasses, adding forest litter, seeding, and planting nursery-growing seedlings, on the regeneration of seasonal deciduous forest trees in four abandoned pastures in central Brazil. We monitored all woody stems immediately prior to treatments and again 14 months after the treatments. We recorded an average of 16,663 tree stems per hectare and a total of 83 species before implementing treatments. Planting strongly increased species richness; adding litter and seeding had weaker positive effects on richness; and plowing and grass removal had no effect.

Plowing substantially reduced the density of naturally established stems. Despite the high survival of planted seedlings, stem density in planting treatments did not change because the tractor and digging holes to plant seedlings caused mortality of naturally regenerating seedlings. Tree stems grew more in the grass release plots than in the control plots. Our results suggest that early succession of seasonal deciduous forest in pastures in the region studied does not need to be stimulated once the perturbation is stopped and that intensive restoration efforts may actually slow recovery. We recommend only enrichment planting of seedlings that are not able to resprout.

Key words: Cerrado biome, colonization, Coppice shooting, dry forest, forest succession, pasture, regrowth, resilience, resprout.

Introduction

Restoration ecologists have long recognized that restoring an ecosystem requires a subtle understanding of the natural recovery process. This understanding is particularly important in diverse systems, such as tropical forests, where it is impossible to reintroduce all species, and, therefore, the aim should be to facilitate succession (Holl 2002a). Such an approach will result in the most cost-efficient methods to restore the large areas of land degraded globally. Nonetheless, restoration practitioners often intervene with “tried and true” methods, such as planting trees to increase canopy architecture because they are widely used and show short-term results. There are numerous examples worldwide, however, of how such efforts may actually inhibit ecosystem recovery (Chambers et al. 1994; Murcia 1997; Holl 2002b; Holl & Cairns 2002; Souza & Batista 2004).

If trees regenerate naturally in anthropogenically impacted systems, this should be managed as an efficient and cheap way to restore the forests, rather than clearing abandoned agricultural lands before planting tree seedlings which may actually slow recovery. In tropical pastures, in Brazil and elsewhere, planting nursery-grown tree seedlings is the most widely utilized technique to restore forests (Holl 2002a; Souza & Batista 2004; Ruiz-Jaen & Aide 2005) but few studies have tested planting seedlings without completely mowing and/or plowing the area before planting (Tucker & Murphy 1997; Leopold et al. 2001). Clearing the area facilitates planting and reduces seedling competition with grasses, which often limits plant growth in abandoned tropical pastures (Nepstad et al. 1996; Holl 1998; Holmgren et al. 2000; Hooper et al. 2002; Otsamo 2002; Jones et al. 2004). But, clearing may destroy naturally regenerating plants.

Most concern about tropical deforestation and concomitant restoration efforts has been focused on tropical wet and moist forests, although forest loss is even more severe in tropical dry forest regions (Janzen 1988; Lerdau et al. 1991; Whitmore 1997). Strategies for tropical wet and moist forest restoration may not be appropriate for dry forests, given many ecological differences (Vieira & Scariot 2006). For example, in tropical dry forests, unlike moister forests, seasonal availability of water can limit seed germination and plant establishment (Gerhardt 1996; Cabin et al. 2002; Vieira & Scariot 2006), thereby limiting

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recovery. On the other hand, regeneration by coppicing, common for dry forest trees, may sustain the system resilience and jump start succession in abandoned fields (Ewel 1980; De Rouw 1993; Miller & Kauffman 1998). Acquiring information about natural regeneration identifies the major constraints to recovery that should be managed in order to accelerate succession.

The goal of this study was to document natural regeneration in abandoned pastures in dry forest in the Parana River Valley, state of Goias, Central Brazil and to compare the efficiency of different management techniques to facilitate natural regeneration. We chose treatments feasible at large scale that were cheaper than the standard approach of planting native tree seedlings in a cleared area. We also chose techniques to test specific ecological hypotheses about the sprouting ability of trees and grass competition. Specifically, we tested planting mixed species of tree seedlings without soil plowing or grass mowing because it causes less damage to the established natural regeneration and is cheaper. Seeding of diverse tree species in between grass tussocks is a low impact and even less expensive technique. Litter input from forests to pasture comprises a potentially inexpensive way of introducing a high diversity of seeds. Plowing the soil eliminates the grass cover one time and possibly stimulates root sprouts of woody plants (Vieira et al. 2006). Grass removal by manually removing the grass tussocks is not feasible at a larger scale and is an expensive technique. We used it to test the effect of grasses on tree regeneration and, to a certain degree, it simulates grass removal with species-specific herbicide, which could be used at a large scale.

Because dry forests in this region have considerable natural tree regeneration even after lengthy disturbance (Vieira et al. 2006; Sampaio et al. in press), we expected that low-impact management of natural regeneration, such as seeding and litter input, would be the best ways to improve the stem density and species richness of trees in pastures, rather than simply excluding cattle or using restoration techniques that cause damage to the natural regeneration of trees. We also expected enhanced seedling growth in the grass removal treatment compared to the control.

Methods

Study Area

We conducted the study in the Parana River Basin in Central Brazil. This region is in the Cerrado biome that is characterized by a lengthy seasonal dry period, where savanna-like vegetation dominates the landscape. Forests in this region occur in mesic areas near watercourses and/or in areas of rich soils. This study was conducted in sites originally covered by seasonal deciduous forests that occur in patches surrounded by savanna and associated with flat terrain, lower altitudes, karst geology and alfisols soils rich in calcium (Ca) and magnesium (Mg) (Scariot &

Sevilha 2000). It is likely that more than 80% of the original forest has been converted to pastures, and most remaining forest fragments are smaller than 1 ha (Luiz 1998; Andahur 2001). To conserve seasonal deciduous forests in this region it will be necessary to restore forest in order to create larger fragments or increase their connectivity.

The climate of this region is tropical with a well-defined wet and dry season (Aw–Koppen; Fig. 1). Annual precipitation is approximately 1,000–1,300 mm, 95% of which falls between September and March, with a median of 3 months without rain (Brazilian Agency for Water–ANA). Annual mean temperature is 21–24°C, with temperatures ranging from an average of 24–27°C in September and October to 18–21°C in June and July (Brazilian Climatology Institute–INMET; life zone of dry forest *sensu* Holdridge 1967).

Pastures

We conducted this study in four pastures separated from each other by 10–40 km (13°39'S, 46°45'W). All the pastures were formerly seasonal deciduous forests, are located on flat terrain, and were planted with *Andropogon gayanus* Kunth (African pasture grass). The pastures differ in clearing and management history, time since abandonment, and surrounding vegetation (Table 1). Pastures I and IV are adjacent to *Cerrado* forest vegetation and have regenerating trees floristically similar to this physiognomy, whereas the other two pastures are surrounded by seasonal deciduous forests. Therefore, the pastures varied in composition, structure, and density of tree regeneration at the outset of the study (Table 1). The pastures with more intensive and mechanized management had lower

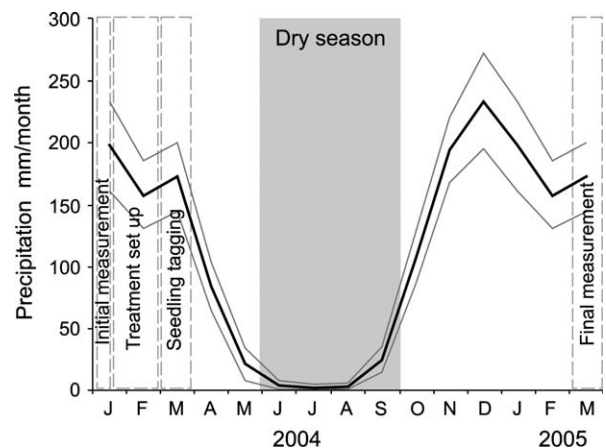


Figure 1. Timing of precipitation and experimental set up. Black solid line is the average of 35 years of daily precipitation data at the nearest measurement station (approximately 15–30 km from the pastures; Brazilian Agency for Water–ANA); gray solid lines are the confidence intervals (95%) of the measurements. The dotted lines indicate the different stages of the experimental set up and sampling of tree regeneration in the pastures.

Table 1. Characteristics of the four pastures studied. Stem density, species richness, and stems height of tree species calculated by plot (10 × 10 m).

Pastures	Years Used as Pasture	Deforestation and Management	Years Abandoned before Experiment	Area Fenced (ha)	Approximate Distance to the Nearest Forest Fragment (m)	Stem Density Mean (min-max)	Species Richness Mean (min-max)	Height (cm) Third quartile
I	Approximately 40	Manual	0	0.6	10	264 (115–512)	26 (17–41)	55
II	Approximately 15	Manual	2	5.0	10	274 (64–644)	22 (12–29)	94
III	<5	Mechanized	0	1.6	200	83 (39–156)	11 (6–18)	87
IV	>20	Mechanized	2	10.0	200	45 (9–128)	12 (6–18)	146

densities of natural tree regeneration and those abandoned for longer periods had taller tree saplings (Table 1). The soils of the pastures range in pH from 5.6 to 7.0, are rich in nutrients such as Ca (5.4–12.4 meq/100 g) and Mg (1.8–4 meq/100 g), and have low levels of aluminium (0–0.1 meq/100 g).

Experimental Design

Immediately prior to the experiment, we fenced the experimental area in all pastures to exclude cattle and ceased all management activities, including mowing, plowing, and grass seeding. We set up the experiment as a randomized complete block design replicated four times in four pastures (4 blocks × 4 pastures, 2.4 ha/pasture). The treatments and control were randomly assigned to one of six adjacent 10 × 10 m plots within each block and set up during the rainy season of 2004 (Fig. 1). At the beginning of the dry season, we cleared a 5-m buffer around the

fences, leaving bare soil to protect from potential adjacent fires.

Planting. Tree seedlings of 18 species were planted on a 2-m grid, with two extra lines of trees planted in between the 2-m lines (Fig. 2). The species were chosen with the aim of maximizing richness, so species available during the study period were selected that had a variety of growth rates. The quantity and position of the seedlings planted was systematically chosen according to the growth rate of the species (Table 2). Fast growing species were planted in higher quantity at the border and in the interior of the plot, intermediate growing species were planted in between the fast growing species in a lower quantity, and the slowest growing species were planted in the two extra lines (Fig. 2). The position of each species within the same growth category was chosen randomly. Forty-two seedlings were planted in each 10 × 10-m plot.

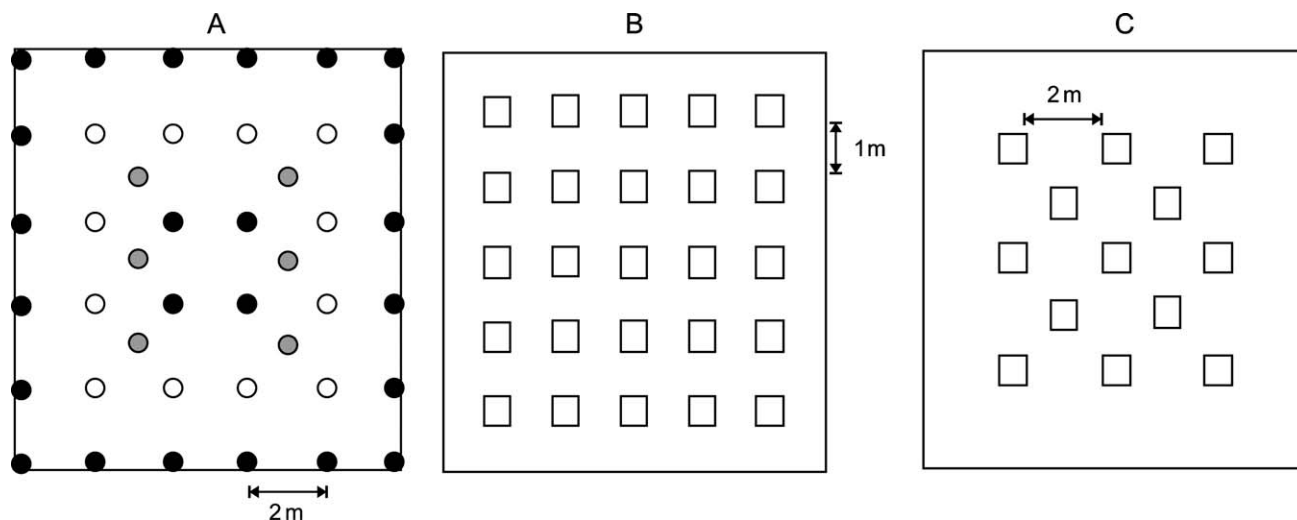


Figure 2. Experimental plot set up in the pastures to test the planting of nursery-grown seedlings, seeding tree species, and litter input on forest regeneration. The larger squares indicate the plots of 10 × 10 m where the treatments were set up (Planting, A). The circles indicate the position of planted seedlings; black circles indicate fast-growing species; open circles indicate medium-growing species; gray circles indicate slow-growing species. The smaller squares indicate the subplots (70 × 70 cm) where the seeds were buried (Seeding, B) or where the litter was added (Litter, C). See Tables 2 and 3 for seedling and seed species lists.

Table 2. Planted species' growth category, age at time of planting, number of seedlings, percent survival, and height increase (mean \pm SE) 14 months after planting.

Species	Growth Category	Age (mo)	Seedlings per plot	Survival (%)	Height Increase (cm)
<i>Schinopsis brasiliensis</i> Engl.	Intermediate	6	2	100	36.1 \pm 4.3
<i>Lonchocarpus muehlbergianus</i> Hassl.	Intermediate	18	2	97	1.1 \pm 5.2
<i>Pseudobombax tomentosum</i> (C. Martius & Zuccarini) Robyns	Intermediate	6	2	97	10.3 \pm 3.0
<i>Jacaranda</i> sp.	Fast	18	2	91	22.3 \pm 3.6
<i>Guazuma ulmifolia</i> Lam.	Fast	18	4	88	37.0 \pm 4.4
<i>Myracrodruon urundeuva</i> Allemão	Intermediate	6	2	87	30.1 \pm 6.0
<i>Anadenanthera colubrina</i> (Vell.) Brenan	Intermediate	6	2	85	44.8 \pm 6.2
<i>Bauhinia acuruana</i> Moric.	Fast	6	4	81	17.8 \pm 3.4
<i>Albizia hassleri</i> (Chodat) Burkart	Fast	6	4	77	29.9 \pm 4.8
<i>Aspidosperma pyrifolium</i> Mart.	Slow	6	1	75	7.2 \pm 3.7
<i>Machaerium scleroxylum</i> Allemão	Slow	6	1	75	12.8 \pm 3.2
<i>Amburana cearensis</i> (Allemão) A.C. Sm.*	Fast	18	4	72	18.5 \pm 2.4
<i>Hymenaea courbaril</i> L.	Slow	6	1	69	18.2 \pm 6.0
<i>Acacia paniculata</i> Willd.	Fast	6	4	68	31.8 \pm 7.5
<i>Machaerium villosum</i> Vogel	Slow	6	1	60	7.8 \pm 3.6
<i>Erythrina</i> sp.	Fast	6	4	54	35.7 \pm 7.6
<i>Callisthene fasciculata</i> Mart.	Slow	18	1	31	12.2 \pm 9.7
<i>Copaifera langsdorfii</i> Desf.	Slow	6	1	19	-2.0 \pm 5.3

* A species of the family Fabaceae that was not found naturally regenerating in the pastures.

The holes used for seedlings, 40 cm diameter \times 70 cm deep, were made by a tractor drill. We planted the seedlings manually. The seedlings were not handled in between the planting and final measurements.

Seeding. In the seeding treatment, we direct seeded 10 tree species in 25, 0.7 \times 0.7 m subplots (0.5 m²) regularly spaced within 10 \times 10-m plots (Table 3; Fig. 2). The regular position of the subplot was shifted slightly (<20 cm) depending on the position of the grass tussocks, in order to place the seeds in between tussocks on bare soil. Species were chosen with the aim of maximizing richness, based on the availability during the study period and viability of seeds just before seeding. The amount of seeds of each species seeded per subplot varied depending on the availability (Table 3). In the dry season, just before the

beginning of the experiment, we collected seeds from at least two trees of each species in an area of approximately 10 km radius surrounding the pastures. We mixed, scattered, and hand buried the seeds in the subplots. The seeds viability was tested with tetrazolium in a sample of 100 seeds per species, about 1 month before setting up the seeding treatment. The minimum viability was 80%.

Litter Input. Litter was moved from a nearby, undisturbed forest to the subplots in the litter treatments plots (Fig. 2). The litter was gathered in September 2003, the time of year when the litter layer is thicker (about 10 cm of dry leaves) and has a larger amount of seeds (357 \pm 67 viable seeds/m², L. Z. Andrade & A. Scariot, unpublished data) because most wind dispersal of seeds occurs during the dry season. We stored the litter from the time of collection

Table 3. Seed species' seeding density, percent establishment, and height increase (mean \pm SE) 14 months after seeding.

Species	Seeds/Plot	Establishment (%)	Height Increase (cm)
<i>Copaifera langsdorfii</i> Desf.	250	41.2	10.1 \pm 0.2
<i>Machaerium scleroxylum</i> Allemão	75	21.3	8.2 \pm 0.9
<i>Enterolobium contortisiliquum</i> (Vell.) Morong ^a	375	9.3	24.8 \pm 2.2
<i>Aspidosperma pyrifolium</i> Mart.	100	6.0	10.5 \pm 1.4
<i>Myracrodruon urundeuva</i> Allemão ^b	1000	2.5	9.4 \pm 1.2
<i>Guazuma ulmifolia</i> Lam. ^{a,b}	1000	0.7	4.7 \pm 1.0
<i>Schinopsis brasiliensis</i> Engl.	375	0.5	8.5 \pm 2.5
<i>Amburana cearensis</i> (Allemão) A.C. Sm.	50	0	—
<i>Anadenanthera colubrina</i> (Vell.) Brenan	300	0	—
<i>Aspidosperma subincanum</i> Mart.	225	0	—
Total	3750	5.2	—

^a Seeds with physical dormancy.

^b Seeds with less than 0.5 mm diameter; other species have seeds with greater than 1 cm diameter.

until the application in plastic mesh-bags in a ventilated room at ambient temperature. The litter was placed on the soil in 13, 0.7×0.7 -m subplots regularly spaced in the plots. The amount of litter applied to the subplots was similar to that found on the forest floor (in average $0.1 \text{ m}^3/\text{m}^2$). We assumed that all seedlings established in the subplots germinated from seeds present in the litter.

Grass Removal. At the beginning of the study, the grasses were pulled out by the roots using hoes throughout the whole 10×10 -m plot, without removing other plants. No additional grass removal was done thereafter.

Plowing. The plowing treatment consisted of tilling the soil with a tractor twice immediately after the initial measurement in order to destroy all the plants and leave bare soil. We tilled the soil to a depth of 10 cm in order to remove the grass roots, but not the tree roots.

Measurements

In early January 2004, immediately prior to the initiation of experimental manipulations, we identified, tagged, and measured the height of all tree stems in the 10×10 -m plots (initial measurement; Fig. 1). We also measured and tagged all out-planted seedlings immediately following planting. In order to maximize the chance of finding seedling traits, all the plots were resampled and the new seedlings were tagged, at the end of the first rainy season (March 2004; Fig. 1). We classified a plant as a seedling by the presence of cotyledons or fruit/seed traits. We classified sprouts by the presence of stumps and basal bifurcations. Plants without cotyledons or sprout characteristics remained unclassified. In March 2005 (final measurement; Fig. 1), we sampled all the plots to record all new recruits, measure survival of stems tagged during initial measurements, and record stem height. We considered new recruits to be all tree stems recorded in March 2005 that were not tagged during initial measurements. Stems that were first tagged in March 2004 and survived until March 2005 were considered in new recruits, but if March 2004 stems did not survive until the final measurement, they were not included in the total number of new recruits.

For those species we were unable to identify in the field, we collected a sample for posterior literature and herbarium analysis. The species nomenclature was updated and standardized according to the Missouri Botanical Garden (<http://mobot.mobot.org/W3T/search/vast.html>). The specimens collected were deposited in the Embrapa Genetic Resources and Biotechnology (Cenargen) Herbarium, Brasília, Brazil (CEN).

Data Analysis

We evaluated the net changes in the tree community regenerating in the whole plots, that is, the difference in the stem density, average height, and species richness in

each plot between the initial measurement (all stems recorded prior to treatments) and the final measurement (all stems, including naturally established, planted, and seeded). We chose this approach, rather than the usual separate analysis of introduced or naturally established individuals because the goal of most restoration efforts is to increase the net species richness and stem density.

In order to compare the efficiency of treatments in increasing stem density and species richness, we analyzed the variable change (final measurement–initial measurement) using analysis of variance (ANOVA) with a split-plot model. The pastures were analyzed as whole plots and the treatments were the subplots of the split-plot model; a block term was also included. The treatment effect was analyzed using treatment \times block interaction as the error term. We ranked the stem density and species richness change values, which showed strongly skewed distributions, prior to analysis. To determine whether the median changes in species richness and stem density were different than zero, we tested the values by resampling 1,000 times the calculated values with a bootstrap technique (Sokal & Rohlf 1995).

Because increase in tree height is a desired result of forest restoration, we used repeated measures ANOVA to compare the initial and final measurements of mean stem height in the control, plowing, and grass release plots. The data for the seeding, litter input, and seedling planting plots were not considered in that analysis because the seeds and seedlings we introduced as part of the treatments could cause an artificial decrease in the mean stem height.

In order to evaluate the effect of grass competition, we compared the stem growth of surviving stems in the grass removal plots to the control plots. The competition cannot be evaluated by the mean height of all stems in the plots because the actual growth is confounded by recruitment and mortality. Therefore, we only considered individuals that existed before the treatment and survived 14 months after.

To compare the costs of the different methods, we estimated the cost of each technique tested, based on the costs to do the experimental 10×10 -m plots and then extrapolated those to 1 ha.

Results

We recorded an average of 16,663 tree stems per hectare and a total of 83 species in our initial survey (Appendix), before implementing treatments in the four pastures. At the final measurement (after 14 months), the mean stem height increased by 26.3 ± 3.8 cm (SE) and an average of 1,518 new tree stems per hectare were recorded, in across all pastures and treatments. Of the new tree stems, 10% of the individuals were seedlings (150 stems, 149 in pasture I) and 54% were resprouts (784 stems); for 36%, we were not able to determine the origin (523 stems without stumps or cotyledons). Only three species clearly

recruited from seeds, *Dypterix alata*, *Platypodium elegans*, and *Myracrodruon urundeuva*; the first two exclusively recruited from seeds. Fifty-two species resprouted. We were unable to classify only six species as resulting from either sprouts or seedlings. No species colonized the pastures during the study that were not recorded in the initial survey.

The treatments had a significant effect on species richness ($F_{[5,15]} = 38.3$, $p < 0.001$, Fig. 3). The change in species richness after 14 months was statistically equal to zero in control, grass removal, and plowing plots (Bootstrap resampling of median, $p = 0.4$, 0.2 , 0.9 , respectively); in the other treatments, the change was significantly greater than zero ($p < 0.001$, litter $p = 0.003$). Planting substantially increased species richness (Fig. 3) due to the high survival (>60%) of almost all planted species except *Copaifera langsdorffii* and *Callisthene fasciculata* (Table 2). Only two species had >20% establishment in the seeding treatment (Table 3); despite the low establishment, this treatment increased species richness slightly (Fig. 3). The litter treatment increased species richness minimally because the establishment was very low; only 34 seedlings total belonging to eight species were established from litter seeds.

Anadenanthera macrocarpa was the planted species with the most growth. *Enterolobium contortisiliquum* grew most rapidly among seeded species. *M. urundeuva* and *Schinopsis brasiliensis* grew more when planted as seedlings than when seeded (Tables 2 & 3).

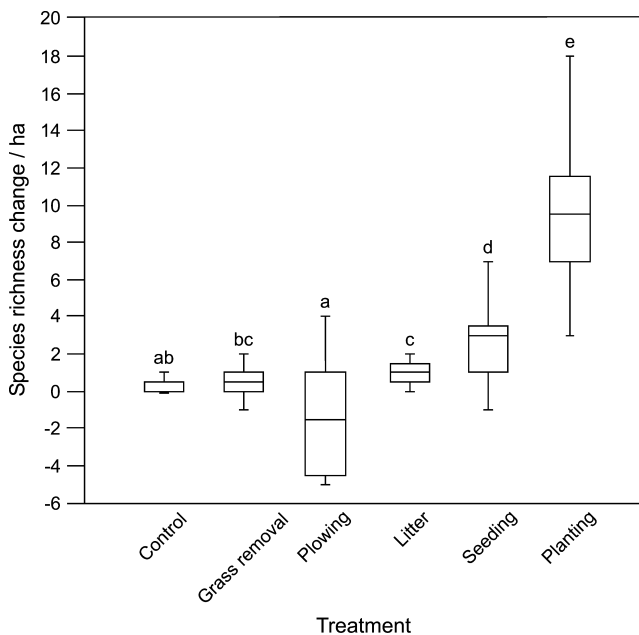


Figure 3. Change in tree species richness between initial and final measurements. Boxes indicate the median and first and third quartiles; bars indicate the minimum and maximum values. Treatments with the same letter are not significantly different using Tukey test ($\alpha = 0.05$).

Plowing dramatically reduced stem density ($F_{[5,15]} = 21.2$, $p < 0.001$, Fig. 4) because the recruitment did not compensate for the 100% mortality of stems caused by plowing the soil. For the other treatments, including the control, stem density increased during the study (Bootstrap resampling of median, $p < 0.001$). Seeding was the only treatment that significantly increased the stem density compared to the control, although the difference was small (Fig. 4). Interestingly, despite the high survival of planted seedlings (Table 2), the planting treatment had no effect on net stem density compared to the control (Fig. 4). The higher mortality of naturally regenerating stems in the planting plots (30% of stems), compared to all treatments (<5%) except plowing, was due to damage from hole digging and the tractor running over stems.

The final average height of tree stems was higher in grass removal than plowed plots, although neither differed significantly from the control (repeated measures of ANOVA, $F_{[1,15]} = 439.4$, $p < 0.001$; measurements \times treatments, $F_{[5,15]} = 14.8$, $p < 0.001$, Fig. 5). The initial and final height of tree stems did not differ in the plowed plots (repeated measures of ANOVA, $F_{[1,15]} = 0.3$, $p = 0.6$, Fig. 5).

The tree stems that were there before the treatment and survived until the final measurement grew more in the grass release than the control plots (mean \pm SE, grass removal = 40.5 ± 3.9 cm, control = 26.1 ± 2.8 cm, $t = 3$, $df = 30$, $p = 0.006$).

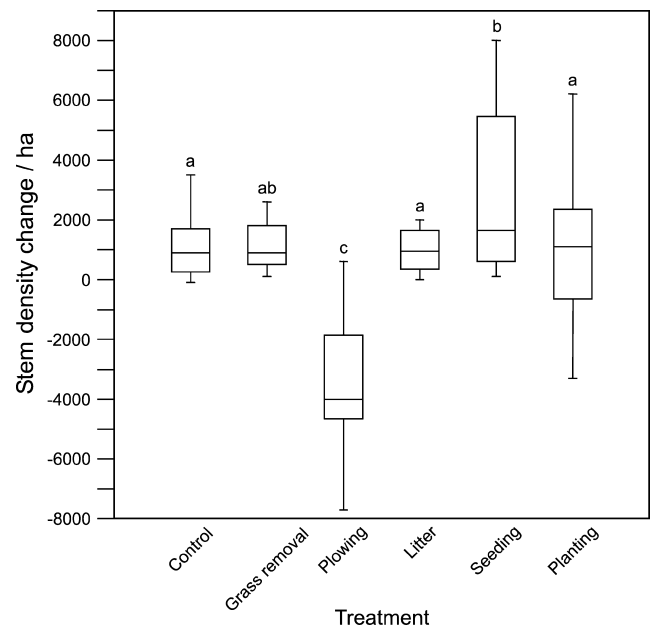


Figure 4. Change in stem density between initial and final measurements. Boxes indicate the median and first and third quartiles; bars indicate the minimum and maximum values. Treatments with the same letter are not significantly different using Tukey test ($\alpha = 0.05$).

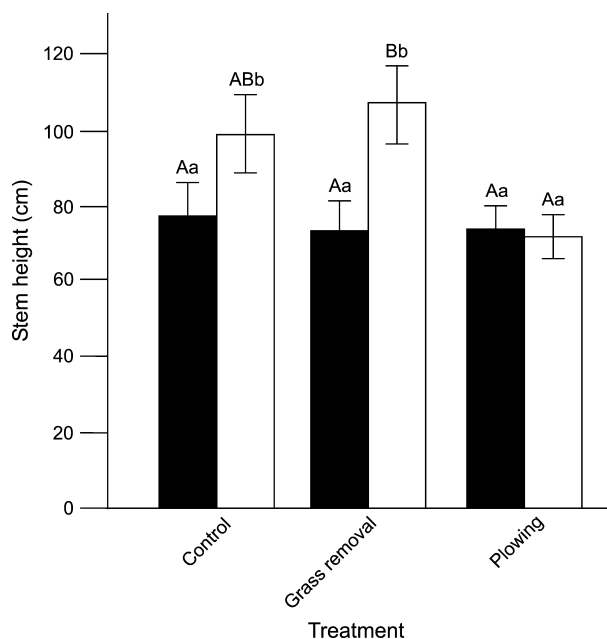


Figure 5. Tree stems height at time of initial and final measurements. Solid bars = initial measurement, open bars = final measurement. Error bars indicate one SE. Upper case letters indicate statistical difference among treatments and lower case letters indicate differences at the two measurement times ($\alpha = 0.05$).

Planting trees without plowing costs approximately US\$2,000 per hectare, including seed collection, growing seedlings in the nursery, and planting costs. The seeding cost was about half of the planting cost, but was still expensive due to the cost of collecting a high quantity of seeds (seeding density of 375,000 seeds/ha) of species where seeds are not available commercially. Litter input (approximately US\$400/ha) and plowing (approximately US\$100/ha) were much less expensive. The most expensive technique was removing manually the grass tussocks (approximately US\$3,000/ha). The costs are not always directly related to the area, thus the values present here should be considered cautiously.

Discussion

Several studies have reported minimal spontaneous regeneration of trees by seeds or sprouts in heavily used tropical pastures (e.g., Uhl et al. 1988; Aide et al. 1995; Nepstad et al. 1996; Miller & Kauffman 1998; Holl 1999; Moran et al. 2000; Peterson & Haines 2000; Rivera et al. 2000; Slocum 2000; Cubina & Aide 2001; Ferguson et al. 2003). In striking contrast, this and other studies (Vieira et al. 2006; Sampaio et al. in press) show that in the Cerrado region of Brazil, even pastures intensively used for several years or decades still have a considerable natural regeneration, which can be managed to accelerate the succession. A few other studies suggest that some dry forest systems may be able to recover rapidly after intense disturbance

(e.g., Miller & Kauffman 1998; Janzen 2002; McLaren & McDonald 2003), in part due to extensive resprouting.

We recorded high species richness and a considerable amount of stem sprouts even in the more disturbed pastures (III and IV). Sprouts grow faster than seedlings (Kennard 2002), especially young shoots (McLaren & McDonald 2003). This indicates that at least some secondary woody vegetation will establish in those pastures without any management. The few pastures in the region that have been abandoned for about 4 years have trees approximately 2 m in height, forming a canopy (A. B. Sampaio, manager, Brazilian Environmental Agency-IBAMA, personal observation, 2004). Old secondary forests in Panama and Brazil were described with similar structure to their primary forest reference system, although several mature forest species, including some dominants, are still missing (Finegan 1996; Tabarelli & Mantovani 1999; Aide et al. 2000).

Planting tree seedlings using tractors did not increase the density of tree regeneration compared to the control after just 14 months because even the high survival of the planted seedlings was barely sufficient to compensate for the mortality caused by the tractor during the hole digging. Likewise, the mortality caused by soil plowing was not compensated by the resprouts, although plowing has been suggested to stimulate root sprouting (Vieira et al. 2006). Therefore, techniques that damage natural regeneration, such as the combination of plowing and mechanically planting trees might delay succession in areas with extensive natural regeneration, particularly if standard planting techniques were used, that include repeated clearing around seedlings. It is likely that manual planting of trees would cause less damage, but this planting method is less cost-effective and was not tested in our study.

No new species were naturally established from seed during the 14 months of monitoring, even in pastures next to forest fragments. The probability of colonization and establishment of native species in open pastures is highly limited (Holl 2002a; Vieira & Scariot 2006), although in pastures with remnant trees the dispersal of seeds is much higher (Guevara et al. 1992; Toh et al. 1999; Zahawi & Augspurger 1999; Slocum 2001). It is important to note that the present study was conducted over a short period to sufficiently characterize patterns of colonization by seed. We found some colonization by seed, but these seedlings included just three species and were highly clustered, possibly originating from remnant trees.

Resprouting was an important source of recruitment, mainly in the plowing treatment. In the other treatments, there were less new sprouts during the study period probably because there was less damage to natural regeneration at the initiation of the study. Our results suggest that without management the early stage of succession will be mostly limited to the species initially present in the pastures and to those with sprouting ability.

Our results concur with recommendations that tropical forest restoration efforts should provide for the full

complement of species by introducing species that are unlikely to colonize abandoned lands (Martínez-Garza & Howe 2003). *Cavanillesia arborea* (Willdenow) K. Schum., *Cedrela fissilis* Vell. and *Amburana cearensis* (Allemão) A.C. Sm. are examples of species that should be planted because they were not found naturally regenerating in the pastures of the present study nor in 25 other pastures sampled in the region (Sampaio et al. in press).

At our site, the nonresprouting species can be efficiently introduced by planting a small number of nursery-grown seedlings without repeated clearing of grasses to minimize damage to natural regeneration. Although seeding increased both species richness and stem density significantly, seedling establishment was low. Dormant seeds, such as *Enterolobium contortisiliquum* (Vell.) Morong and *Guazuma ulmifolia* Lam. may remain viable in the soil and germinate in the future (Nepstad et al. 1996; Zimmerman et al. 2000; Camargo et al. 2002), but other species may have germinated and the seedlings died during the dry season (Cabin et al. 2002). Past studies suggest that broadcast seeding of multiple tree species in areas dominated by exotic grasses is generally not very successful and highly species specific (Engel & Parrotta 2001), especially in dry forests where the emerging seedlings need to endure some months with soil water deficit (Cabin et al. 2002). Likewise, our attempt to introduce multiple species by adding forest litter was unsuccessful. However, a few selected species can be successfully introduced by direct seeding (Parrotta & Knowles 2001; Camargo et al. 2002), such as *Copaifera langsdorffii* in our study. Considering that planting is expensive, seeding could be used as a complementary technique depending on the species characteristics, in order to reduce the costs of the restoration efforts.

Both this and past studies (Holl 1998; Hau & Corlett 2003) show that grass competition may limit tree growth. Despite the short-term release of competition in our study, it was during the rainy season, the only period when the plants grow in dry forest regions (Murphy & Lugo 1986). When water is a limiting resource, competition seems to be more evident (Cabin et al. 2002). Therefore, removing the grasses, even just at the time of planting, may help to enhance stem growth. Ongoing reduction of grass competition might further enhance growth, but it is both resource intensive and may damage naturally regenerating stems.

This study evaluated 14 months of the initial secondary succession of seasonal dry forests converted to pastures. During this short time, it is impossible to characterize pathways of the succession (Brown & Lugo 1994). However, our short study did clearly highlight the importance of the natural regeneration in this system. The resprouting ability of the trees characteristic to these forests is evident and leads to rapid early regeneration when anthropogenic disturbance ceases. This natural regeneration of trees should not be overlooked in designing restoration efforts. Research on the effect of restoration treatments on long-term succession in tropical dry forests in this region is needed.

Implications for Practice

- This and related studies show that certain types of long-disturbed forests can show a high degree of resilience, particularly if many plant species can resprout from roots. In such cases, intervention to enhance the early succession of seasonal deciduous forest is not necessary once the perturbation is stopped.
- Soil and vegetation disturbances, such as plowing or mechanically digging holes to plant seedlings may reduce the density of naturally regenerating trees and thereby, actually slow recovery.
- Tropical dry forest seedlings can be planted with high survival rates even in between grass tussocks (*Andropogon gayanus*).
- Complete removal of grass (*Andropogon gayanus*) cover, even once, improves the growth of established tree stems in abandoned pastures in Central Brazil.
- Nonresprouting trees should be reintroduced to accelerate the establishment of the full complement of deciduous forest species.

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Appendix. Species sampled regenerating naturally in the four pastures studied.

Family	Species
Anacardiaceae	<i>Astronium fraxinifolium</i> Schott ex Spreng. <i>Myracrodruon urundeuva</i> Allemão <i>Schinopsis brasiliensis</i> Engl. <i>Spondias mombin</i> L.
Apocynaceae	<i>Aspidosperma pyrifolium</i> Mart. <i>A. subincanum</i> Mart.
Arecaceae	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.
Bignoniaceae	<i>Jacaranda</i> sp. <i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook. f. ex S. Moore <i>T. impetiginosa</i> (Mart. ex DC.) Standl. <i>T. ochracea</i> (Cham.) Standl. <i>T. roseoalba</i> (Ridl.) Sandwith
Bombacaceae	<i>Pseudobombax tomentosum</i> (C. Martius & Zuccarini) Robyns
Boraginaceae	<i>Cordia</i> sp.
Celastraceae	<i>Maytenus floribunda</i> Reissek
Chrysobalanaceae	<i>Licania araneosa</i> Taub.
Clusiaceae	<i>Kielmeyera</i> sp.
Combretaceae	<i>Combretum duarteianum</i> Cambess. <i>Terminalia argentea</i> Mart.
Dilleniaceae	<i>Curatella americana</i> L.
Ebenaceae	<i>Diospyros</i> sp.
Erythroxylaceae	<i>Erythroxylum</i> sp. 1 <i>Erythroxylum</i> sp. 2 <i>Erythroxylum</i> sp. 3
Euphorbiaceae	<i>Sebastiania brasiliensis</i> Spreng.
Fabaceae	<i>Acacia farnesiana</i> (L.) Willd. <i>A. glomerata</i> Benth. <i>A. paniculata</i> Willd. <i>A. polyphylla</i> DC. <i>Acosmium dasycarpum</i> (Vogel) Yakovlev <i>Albizia hassleri</i> (Chodat) Burkart <i>Anadenanthera colubrina</i> (Vell.) Brenan <i>Bauhinia acuruana</i> Moric. <i>Bauhinia</i> sp. <i>B. unguilata</i> L. <i>Copaifera langsdorffii</i> Desf. <i>Cumaruna alata</i> (Vogel) Kuntze <i>Enterolobium contortisiliquum</i> (Vell.) Morong <i>Erythrina</i> sp. <i>Hymenaea courbaril</i> L. <i>Lonchocarpus muehlbergianus</i> Hassl.

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Appendix. Continued

Family	Species
	<i>M. brasiliense</i> Vogel <i>M. scleroxylon</i> Tul. <i>M. stipitatum</i> (DC.) Vogel <i>M. villosum</i> Vogel <i>Platypodium elegans</i> Vogel <i>Sclerolobium paniculatum</i> Vogel <i>Senna spectabilis</i> (DC.) H.S. Irwin & Barneby
	<i>Swartzia multijuga</i> Vogel <i>Sweetia fruticosa</i> Spreng. <i>Vatairea macrocarpa</i> (Benth.) Ducke
Flacourtiaceae	<i>Xylosma</i> sp.
Lythraceae	<i>Lafoensia pacari</i> A. St.-Hil.
Malpigiaceae	<i>Byrsonima</i> sp.
Moraceae	<i>Brosimum gaudichaudii</i> Trécul
Myrtaceae	<i>Eugenia dysenterica</i> DC. Unidentified 1 Unidentified 2 Unidentified 3
Olacaceae	<i>Ximena americana</i> L.
Opiliaceae	<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook. f.
Polygonaceae	<i>Triplaris gardneriana</i> Wedd.
Rhamnaceae	<i>Rhamnidium elaeocarpum</i> Reissek
Rubiaceae	<i>Alibertia edulis</i> (Rich.) A. Rich. ex DC. <i>Amaioua guianensis</i> Aubl. <i>Guettarda viburnoides</i> Cham. & Schltdl. <i>Randia armata</i> (Sw.) DC. <i>Tocoyena formosa</i> (Cham. & Schltdl.) K. Schum.
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.
Sapindaceae	<i>Dilodendron bipinnatum</i> Radlk. <i>Magonia pubescens</i> A. St.-Hil. <i>Pouteria gardneri</i> (Mart. & Miq.) Baehni
Sapotaceae	<i>Simarouba amara</i> Aubl.
Simaroubaceae	<i>Guazuma ulmifolia</i> Lam.
Sterculiaceae	<i>Sterculia striata</i> A. St.-Hil. & Naudin
Tiliaceae	<i>Luehea divaricata</i> Mart.
Ulmaceae	<i>Celtis iguanaea</i> (Jacq.) Sarg.
Verbenaceae	<i>Vitex polygama</i> Cham.
Vochysiaceae	<i>Callisthene fasciculata</i> Mart. <i>Qualea grandiflora</i> Mart. <i>Q. multiflora</i> Mart.
Unidentified	Unidentified 4 Unidentified 5