Does a native grass (Imperata brasiliensis Trin.) limit tropical forest restoration like an alien grass (Melinis minutiflora P. Beauv.)?

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Research Article

Does a native grass (*Imperata brasiliensis* Trin.) limit tropical forest restoration like an alien grass (*Melinis minutiflora* P. Beauv.)?

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Abstract

Abandoned pastures are increasingly targeted for forest restoration in the neotropics. However, the dominance of such areas by fodder grasses imposes a challenge for efficient and low cost control. Therefore, we questioned whether alien and native grasses equally affect: (1) natural regeneration; (2) natural regeneration under artificial perches; and (3) planted seedling development. Our study was carried out in an abandoned pasture in southeastern Brazil, in the Atlantic Forest biome. For (1) we installed plots in grass patches of *Melinis minutiflora* (molasse grass, an alien grass) and *Imperata brasiliensis* (satintail, a native grass that occurs in degraded areas); for (2) we installed plots under perches in alien and native grass patches; and for (3) we compared overall planted seedling mortality and development of four tree species in alien and native grass patches. Density and diversity of woody species in natural regeneration and under perches were similar for invasive and native grass patches. However, species composition differed between alien and native grass patches (Ellenberg similarity of 28% for perches and 35% for natural regeneration in different grass patches). Seedling mortality was similar for both alien and native grasses. Except for two tree species, development was similar for both native and alien grass patches. Our results indicate that the biological barriers imposed by a given grass species for forest succession and restoration must not be estimated based only on the species' origin.

Keywords: restoration ecology, alien species, biological barriers.

Resumo

A restauração florestal nos neotrópicos é geralmente realizada em pastagens degradadas. No entanto a dominância de tais áreas por gramíneas agressivas demandam o desenvolvimento de metodologias para seu controle. Ao mesmo tempo, pouco se sabe sobre a interação das espécies de gramíneas com os métodos de restauração e na sucessão em áreas degradadas. Desta forma, questionamos se gramíneas invasoras e nativas afetam igualmente a regeneração natural (1); regeneração sob poleiros artificiais (2); e desenvolvimento de mudas plantadas (3). Para (1) instalamos parcelas em áreas dominadas por *Melinis minutiflora* (capim-gordura, uma gramínea invasora) e *Imperata brasiliensis* (sapê, uma gramínea nativa que ocorre em áreas degradas); para (2) instalamos parcelas sob poleiros artificiais em áreas com gramíneas invasoras ou nativas; e para (3) comparamos a mortalidade das mudas plantadas e o desenvolvimento de quatro espécies de mudas arbóreas nativas plantadas em áreas dominadas por gramíneas nativas ou invasoras. A densidade e diversidade de espécies lenhosas regenerando naturalmente e recrutadas sob os poleiros artificiais foram semelhantes em gramíneas exóticas e invasoras. No entanto, a composição florística dos regenerantes arbóreos diferiu entre as gramíneas invasoras e nativas (Similaridade de Ellenberg entre as diferentes gramíneas de 28% para poleiros e 35% para a regeneração natural). A mortalidade das mudas plantadas foi semelhante nas duas gramíneas. Exceto para duas espécies de arbóreas, o desenvolvimento das mudas foi semelhante nas duas gramíneas. Concluímos que as barreiras biológicas impostas por uma gramínea nativa podem ser tão restritivas para a restauração de áreas degradadas como uma espécie invasora.

Palavras-chave: ecologia da restauração, espécies invasoras, barreiras biológicas

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Introduction

Worldwide, approximately 13 million ha of natural forests were destroyed between 2000 and 2010 [1]. Most of this deforestation occurred in tropical forest regions [2]. The intense loss of vegetation cover has impaired both biodiversity and ecosystem services such as water flow regulation, nutrient cycling, and climate regulation [3]. Additionally, degraded areas created by deforestation are more vulnerable to colonization by alien species [4].

Alien species are any taxa in a given area brought in either intentionally or unintentionally by humans from another region where they are native, or that arrived in a new area from a region where they are alien [5]. Alien species may overcome barriers for their establishment and spawn reproductive offspring, usually expanding their distribution range. When these conditions are met the alien species is considered an invasive species in its new habitat [6].

Invasive species alter biological communities [7-9], abiotic factors [10, 11] and disturbance regimes [12] of their new habitat, but their effect may be null depending on the ecosystem attribute observed [8, 13, 14]. On the other hand, forest degradation may favor the proliferation of ruderal native species [15], which in turn hinder biodiversity and change abiotic factors [16] and disturbance regimes [17]. Therefore, one should not predict the ecological effects of a species based solely on its origin without further investigation [13].

Extensive pasturelands of alien fodder grasses are a common land use in deforested tropical areas [18]. For instance, this land use covers approximately 75% (211 million ha) of the total deforested land in Brazil [19]. Such areas are common targets for forest restoration projects, since they present lower opportunity costs than agriculture [20, 21]. However, the biological filter imposed by fodder grasses challenges ecological restoration in these areas by severely limiting native woody species establishment [20, 22], and development [23]. Open pastures therefore often show arrested or even reversed succession [24]. Finally, given the resilience of invasive grass populations, their control represents a significant share of the costs of tropical forest restoration and conservation [9, 25].

Most of the grasses used for cattle fodder in the neotropics are African grasses of high resiliency and biomass. One common invasive grass species in areas under restoration in southeastern Brazil is *Melinis minutiflora* P. Beauv. (molasse grass), which produces up to 4,900 kg.ha^{-1} of dry biomass and has intense seed production, which can lie dormant in the soil for long periods; it is also tolerant of drought, inter- and intra-specific competition, and low soil fertility, making this a very adaptable species with high invasive potential [26, 27]. On the other hand, native grasses may also spontaneously occupy areas under restoration, agricultural lands, and abandoned or poorly-managed pastures. *Imperata brasiliensis* Trin. (satintail) is well known to occupy large gaps created by fire in tropical montane moist forest [28] or after cropping in Amazonian wet forests [29]. Wagner et al. [30] pointed out the negative competitive effects of *I. brasiliensis* in commercial forestry. It also occurs in the states of Louisiana and Alabama in USA, where it is considered an invasive species [31, 32].

Several ecological restoration techniques can overcome biological barriers to secondary succession in pasturelands: artificial perches may attract seed-dispersing fauna and help to overcome the dispersion barrier in pastures [33]; planting native seedlings tackles the grass competition establishment barrier by inserting nursery-grown plants in the community [34]; finally, assisting natural regeneration – by fertilizing woody individuals and removing grasses - favors growth and survival of native tree individuals that naturally surpass grass competition and become established in pasturelands [35], thus reducing the effects of the development barrier.

Grasses impose barriers to forest restoration and succession in tropical pastures [24]. However, we lack knowledge about the specific barriers imposed by invasive and native grasses in these areas [23, 36].The objective of this study is to compare the effect of invasive and native grasses on natural regeneration, recruitment under perches, and planted native seedling mortality and development in a neotropical pastureland.

Methods

Study Area

This work was carried out on 132 hectares of abandoned pasture bordering the "Cachoeira" reservoir, located in southeastern Brazil between the approximate coordinates of 23°00'50"S and 46º16'47"W, in the county of Piracaia, São Paulo State (Fig. 1). The experimental site lies within the Atlantic Forest biome, one of the most diverse and threatened biomes in the world [37]. The Brazilian Atlantic Forest retains only about 12% of its original extent [38], but the region supports 62% of the Brazilian population and produces 80% of its gross national product.

The climate of the region is classified as Cwa according to Köppen, characterized by rainy, warm summers, and cold, dry winters, with an annual mean temperature of 20ºC (average minimum temperature of 13.8ºC and maximum of 26.2ºC) and annual rainfall of 1,513 mm. According to the meteorological data from the Brazilian Company for Agriculture Research [39], there is no hydric deficit at any time of the year in our study area. The soil is classified as Dystrophic Ultisol, with high clay content. Past grazing increased leaching and soil density of our study area. There are six tropical seasonal semideciduous montane forest remnants, with different degrees of degradation, surrounding the study area. The pasture where our study was carried out is characterized by scattered patches of grasses, mainly the indigenous grass *Imperata brasiliensis* Trin. (hereafter native) and the invasive African grass *Melinis minutiflora* Beauv. (hereafter invasive).

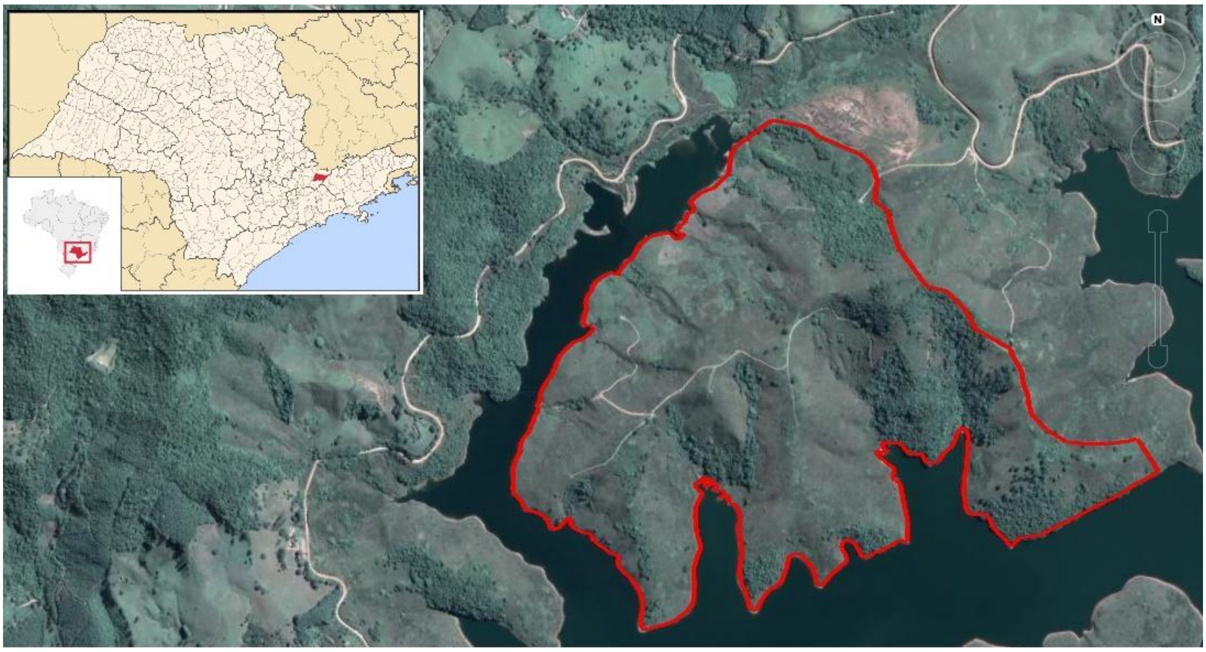

Fig. 1: Location of the study area (upper left corner) and aerial photograph of the 350 ha pasture where this work was carried out. Source: Google Earth 7.1.

Almeida et al. [40] reported that 81 (63%) of the 129 bird species in our study area move through open, anthropized, and forest border areas.; additionally, 19% of individual birds sampled and 22% of the bird species in our study area were potential seed dispersers, while 68% of the trees with diameter at breast height greater than 15 cm in forest remnants were animal-dispersed.

In March 2009, two years before our work, the study area was isolated from degradation factors such as grazing and fire. In 2010, from March to August, restoration techniques were carried out in the area (see next topic). Data gathering occurred in 2011, one year after implementation of restoration techniques.

Restoration Techniques Description

Artificial perches: 2 × 2 m squares were hoed to remove grasses, and bamboo poles measuring three to five meters in height were fixed into the ground. No herbicide was used to control grasses. The upper part of the poles had three one-meter bamboo sticks set perpendicularly to function as a perching site for birds. This restoration technique is intended to attract seed dispersers to the pasture, thereby tackling the dispersion barrier. Grasses recolonized the exposed soil under the perches two months after hoeing. There was no natural regeneration under perches when they were installed. There are six forest remnants of different sizes (ranging from 4 to 33 hectares) and varying degrees of degradation scattered over the study area, with distances varying from 30 to 500 meters from the nearest perch.

Group planting (Anderson nuclei): 2-m diameter circles were hoed to remove grasses and five tree seedlings were planted in a cross design spaced 0.5 m away from each other, with one slow-growing species surrounded by four fast-growing species that would ideally provide shade against grasses, as detailed by Corbin and Holl [41]. No herbicide was used to control grasses. Planting groups were spaced 15 m from each other. During planting, seedlings were fertilized with 20 g of ammonium sulfate + 60 g of a phosphorus and calcium-based fertilizer + 30 g of potassium chloride. After planting, two cover fertilizations were carried out in one year by pouring 30 g of ammonium sulfate + 30 g of potassium chloride next to each seedling. Leaf cutter ants were suppressed every three months by spreading sulfonamide-based baits around the ants' nests. Seedlings were planted from both tubes and plastic sacks, and all species ranged around 30-80 cm height at the time of planting; seedling size varied according to seedling species, but seedlings of the same species had similar size. Seedlings were grown in local nurseries for approximately 8 months before planting. This technique negates the dispersal barrier, but seedlings still have to overcome the establishment barrier imposed by grasses. Grasses recolonized the exposed soil approximately two months after planting. The list of species sampled in the Anderson nuclei and their ecological function in the nuclei (i.e. fast-growing and slow-growing species) can be found in the Appendix 1.

Assisted natural regeneration: in order to facilitate the development of woody individuals that spontaneously overcame the dispersion and establishment barriers, the regenerating trees and shrubs received two cover fertilizations identical to the one applied to the planted seedlings, and all grasses within one meter of the plant were manually removed using a hoe.

Experimental design

Data collection was carried out one year after restoration interventions. All plots mentioned hereafter are 1.5 m x 1.5 m squares. When quantifying natural regeneration we considered only woody individuals taller than 0.3 m. Plots were installed on restoration techniques (to analyze grasses effect on artificial perches and Anderson nuclei) or next to restoration techniques (to analyze grass effect on natural regeneration). Both grass species studied occurred in small patches scattered in the study area. Thus, the number of plots was not the same in both grasses for the parameters studied. However, statistical analysis was not compromised by different numbers of repetitions in each grass patch.

The area was mostly occupied by a dense cover of the studied grass species (i.e. *I. brasiliensis* and *M. minutiflora*). Other species, such as *Urochloa decumbens* (Stapf.) Webster and *Andropogon bicornis* L., occurred in small patches (around 1-5 m^2) but plots were never placed over these grasses, and their cover in our plots never surpassed 10 %. The short-lived shrub *Baccharis dracunculifolia* showed very high (2,453 individuals per hectare) and variable densities in the study area; this species disrupted data analysis by adding too much variability to statistical analysis and hiding the effect of grasses on natural regeneration. Also, this species provides little shade that could suppress grasses and favor restoration of the area, and has shown allelopathy in laboratory studies[42].We therefore had to exclude plots containing this species from the data processing. The experimental design for each parameter evaluated in the area is as follows:

Natural regeneration under perches in different grass patches: we installed plots under 27 perches on invasive grass patches and nine perches on native grass patches. Regenerating species were identified and counted. We classified regenerating species according to their dispersal syndrome (zoochoric and non-zoochoric) in order to evaluate whether artificial perches were assisting the regeneration of animal dispersed species.

Seedling establishment on grass patches: in order to compare the effect of native and invasive grasses on seedling establishment, we quantified the mortality in 48 and 50 planting groups in invasive and native grass patches respectively. We measured height and crown diameter (calculated as the length between the northern and southern extremities of the seedling's crown) of four fast-growing species: *Inga vera* Willd – Fabaceae (with 25 and 31 individuals measured on invasive and native grass patches, respectively); *Ceiba speciosa* (St.-Hill.) Ravenna – Malvaceae (25 and 15 individuals); *Schinus terebinthifolia* Raddi –Anarcadiaceae (22 and 28 individuals); and *Anadenanthera colubrina* Vell – Fabaceae (35 and 23). The complete list of the individuals found in the group plantings is in the Appendix 1.

Natural regeneration on grass patches: we placed 112 and 38 plots on invasive and native grass patches, respectively. Plots were placed every 15 meters in randomly selected sectors of the study area. Individuals from natural regeneration were identified and counted.

Statistical Analysis

Since the number of plots differed for each grass, we carried out rarefaction (10,000 simulations) procedures before calculating species richness. Shannon diversity[43] was calculated to quantify species abundance and richness; Pielou evenness [44] and Ellenberg [45] similarity indices were calculated to compare woody plant populations between both grasses studied. These indices were employed to compare natural regeneration under perches and natural regeneration in assisted natural regeneration areas on both grass patches.

We compared the number of regenerating woody individuals under perches for both grasses using the chi-square test ($\alpha = 0.05$). Since the number of repetitions (plots) on each grass differed, we assumed that the number of individuals would be proportional to the number of plots in each grass patch.

When evaluating seedlings planted in Anderson nuclei in both grass species, we used arc-sin transformation on data referring to percent mortality before performing the chi-square test ($\alpha = 0.05$) to compare seedling mortality among planting groups in both grass patches. Height and crown diameter of seedlings planted in native and invasive grass patches were compared via multi-comparison ANOVA ($\alpha = 0.05$).

We compared natural regeneration density for both grass patches using the chi-square test ($\alpha = 0.05$). Since the number of repetitions (plots) for each grass differed, we assumed that the number of regenerating woody individuals would be proportional to the number of plots in each grass patch.

When data for any of the above parameters were non-parametric, we ranked them before carrying on statistical tests.

Results

Natural regeneration under perches

Average grass cover in plots under perches was of 71 ± 17 % and 60 ± 18 % for plots in *M. minutiflora* (invasive) and *I. brasiliensis* (native) grasses, respectively. The remainder cover was mostly grass litter. Density of regenerating individuals under perches was similar ($\chi^2_{1,21}$ = 2.91, p = 0.088) for both invasive (0.56 ± 0.16 individuals/m²) and native (0.78 ± 0.28 individuals/m²) grasses (Fig. 2). The density of animal-dispersed individuals under perches was 0.18 ± 0.09 individuals/m² and 0.22 ± 0.15 individuals/m² for invasive and native grass respectively. Statistical analysis of animal-dispersed individuals could not be carried out for comparison among these treatments due to the very low number of plots with animal-dispersed individuals. Density of wind-dispersed individuals under perches was also similar for both alien and native grasses ($\chi^2_{1,21}$ = 0.44, p = 0.505). Density of wind-dispersed woody individuals under perches was 0715 ± 0.77 and 0.44 ± 0.52 individuals/m² for invasive and native grass, respectively. All species recruiting under perches were native pioneers. The complete list of the species found under artificial perches for each grass is in Appendix 2.

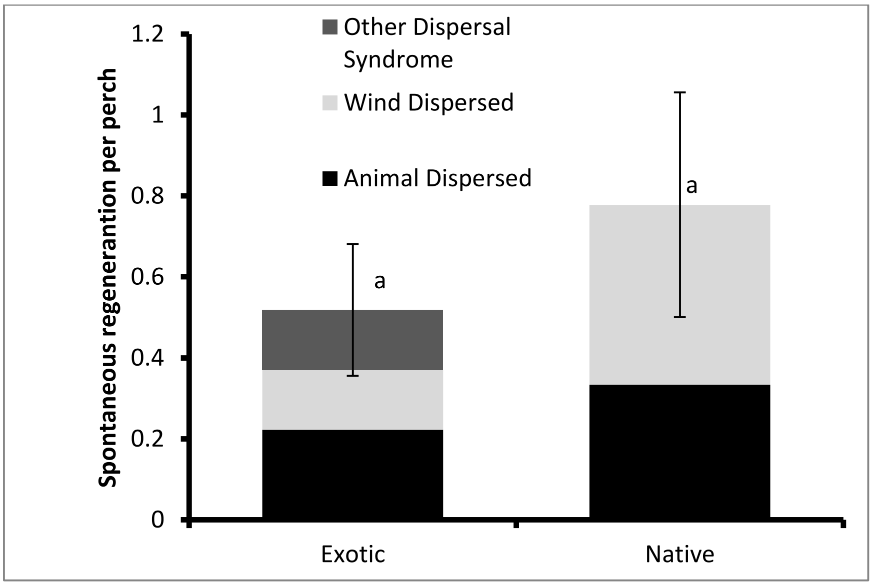

Fig. 2: Woody species natural regeneration density and dispersal syndromes under perches within invasive and native grass patches, in southeastern Brazil. Bars followed by the same letter do not differ (Chi-square test, p = 0.088). Error bars represent mean standard error. There were also no differences for animal or wind dispersed spontaneous regeneration in each grass.

Seedling establishment on grass patches

Grass cover in plots on Anderson nuclei was 68 ± 20 % and 59 ± 20 % for plots in *M. minutiflora* (invasive) and *I. brasiliensis* (native) grasses, respectively. The remaining cover was mostly grass litter. Regarding competition with young woody individuals, native grass was similar to invasive grass. Planted seedling mortality was 22.2 ± 2.2%, with similar results ($\chi^2_{1,98}$ = 0.17, p = 0.68) for invasive (25.4 ± 3.5%) and native (19.2 ± 2.7%) grasses.

Seedlings of *S. terebinthifolia* were taller ($F_{1,48}$ = 4.21, p = 0.0458) in invasive grass patches (90.4 ± 34.9 cm and 75.8 ± 33.9 cm within invasive and native grasses, respectively) and seedlings of *A. colubrina* had marginally greater ($F_{1,55}$ = 3.79, p = 0.056) crown diameter in native grass patches (33.5 ± 13.0 cm and 40.4 ± 13.8 cm within invasive and native grasses, respectively). No differences were found between grass patches for seedlings of *I. vera* ($F_{1,53}$ = 2.48, *p* = 0.121 for height and $F_{1,53}$ = 0.73, *p* = 0.395 for crown); *C. speciosa* ($F_{1,37}$ = 0.03, *p* = 0.869 for height and $F_{1,37}$ = 0.56, *p = 0*.458 for crown); *S. terebinthifolia* crown diameter (F1,53 = 0.73, *p* = 0.396) or *A. colubrina* height ($F_{1,55}$ = 0.03, *p =* 0.871).

Natural regeneration on grass patches

Grass cover in these plots was 84 ± 15 % and 72 ± 20 % for plots in *M. minutiflora (invasive)* and *I. brasiliensis* (native) grasses, respectively. The remaining cover was mostly grass litter. The mean density of regenerating individuals was similar ($\chi^2_{1,51}$ = 3.45, *p* = 0.0632) for both invasive (1310 ± 243 individuals/m²) and native (988 ± 550 individuals/m²) grass patches (Fig. 3). All regenerating species were native pioneers.

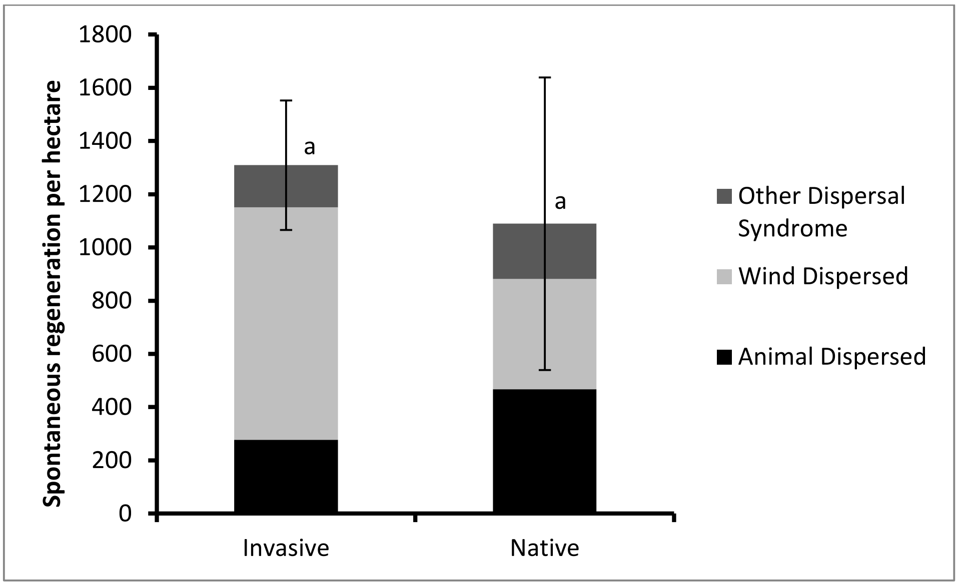

Fig. 3: natural regeneration density and dispersion syndromes on grass patches. Bars followed by the same letter do not differ (Chi-square test, *p =* 0.0632).

Species richness and Shannon diversity index were similar for both native and invasive grasses (Table 1). However, Ellenberg similarity was only 24%, indicating that species composition between invasive and native grass differed (Table 1). The most common species for invasive grass patches were *Chromolaena laevigata*, *Vernonanthura phosphorica* and *V. platensis,* while the most common species for native grass patches were *V. platensis* and *Gaya pilosa*. The complete list of species regenerating on each grass patch is in Appendix 3.

Table 1 Indices for the community of woody plants > 0.3 m height regenerating in grass patches under artificial perches and where natural regeneration was assisted, for both native (*Imperata brasiliensis*) and invasive (*Melinis* minutiflora)grasses. n: number of plots in each grass. Diversity: Shannon diversity index. Evenness: Pielou evenness index. Similarity: Ellenberg similarity index.

	n	Plots with at least one individual***	Richness*	Shannon's Diversity Index*	Pielou's Evenness*	Ellenberg's Similarity*
Artificial Perches						
Native	9	1 (11.1%)	2**	0.69	1	28%
Invasive	27	13 (48.2%)	5**	1.58	0.98	
Assisted Natural Regeneration						
Native	38	11 (28.9%)	9**	2.89	0.43	35%
Invasive	112	25 (22.3%)	20**	2.15	0.87	

*Considering only plots with at least one individual.
** Note the different number of plots (n).
*** 1.5-m side square plots.

Discussion

Effect of grasses on recruitment under artificial perches

Seed arrival under perches is not sensitive to distance from forest remnants. [46, 47]. Based on background scientific literature and the presence of animal-dispersed trees and seed dispersers in nearby forest remnants, we considered seed rain to be similar among artificial perches.
The invasive grass in this study imposes barriers to seedling recruitment under perches [48], and *I. brasiliensis,* a native grass, imposes equally intense barriers. Although the specific processes behind these barriers were not examined in the current study, both grass species had similar density, ecological groups, and dispersal syndromes for the natural regeneration established under perches.
In general, the mean density of regenerating individuals under each perch was low (0.61 individuals/perch). Given that no individual higher than 1.3 m was found, and most were smaller than 0.8 m, we argue that, in our study, density dependent interactions play a very small role in determining established seedling density. Such low density is critical especially for animal-dispersed individuals, since this is the ecological group that perches should facilitate. Various studies point out that perches increase seed rain, but the dense grass layer and grass competition prevent recruitment of seeds from the seed rain [46, 48-50]. In areas devoid of intense grass coverage, perches do increase seedling recruitment [51].

We argue that the fixation of bamboo perches *per se* is not a successful technique to increase natural regeneration of bird-dispersed woody plants in pastures densely dominated by *M. minutiflora* and *I. brasiliensis.* Artificial perches could be substituted, for example, with natural perches such as the planting of birddispersed treesof a fast growing species, known as “filling” group [34, 52]. Tree-like perches foment more seed rain than pole-like perches [46,] and would offset the relatively high number of shrubs regenerating under perches (Appendix 2). Unlike bamboo perches, those trees function not only as resting perches but also attract dispersive birds by providing food (fruits and seeds) and nesting sites [22, 53-55], as well as shading invasive grasses [56].

Seedling establishment on grass patches

Overall seedling mortality and growth were similar between both grass species patches. This contrasts with the results found by Ortega-Pieck et al. [23], who observed greater mortality of seedlings planted within invasive grass than in native grass. However, the grass species studied by Ortega-Pieck were different from this study. We emphasize the importance of further research addressing the species-specific biological barriers imposed by certain species – especially grasses - for forest regeneration, regardless of species origin.

Competition with invasive grasses may encourage seedling growth in some species [57, 58], as observed in our study for *S. terebinthifolia* and *A. colubrina*. This phenomenon is also observed in neotropical arborized savannas and on seedlings planted under the shade of other plants [7, 23, 57]. However, in abandoned pasture restoration, the presence of invasive grasses is detrimental to indigenous seedling establishment compared to seedlings planted in areas devoid of grasses [59, 60], and we argue that the small growth increase for some tree species would not offset overall seedling suppression by grasses.

Natural regeneration on grass patches

Although our experimental design did not include a treatment devoid of any grass cover, the literature provides strong evidence that dense grass cover - such as observed in our study area - hinders natural regeneration in tropical forests [11, 24, 49, 61-63], leading to arrested or even reverse succession [24, 36].

Species composition was very different between both invasive and native grass species, despite diversity and richness being similar. We could not determine any functional characteristics of the natural regeneration that would explain their occurrence in one grass species and not the other. Additionally, our study did not analyze whether the distribution of grass species is related to another factor, such as soil, that also affects natural regeneration species composition. But it is clear that invasive and native grasses affect composition of the natural regeneration differently in tropical abandoned pastures, probably altering successional trajectories.

Implications for conservation

In tropical pastures, the native grass *I. brasiliensis* imposes biological barriers to density and diversity of natural regeneration similar to *M. minutiflora*, an invasive grass. However, barriers imposed by these grasses are species-specific and affect woody species establishment and growth differently. By not assisting natural regeneration on native grass patches – simply because the grass is native – we would neglect certain woody species that are more likely to occur on native grass patches and alter floristic composition of the restored community. Thus, restoration projects in abandoned pasturelands can benefit a wider array of woody species if both native and invasive grasses are managed to facilitate woody individual regeneration. Also, unless both native and invasive grasses are managed, we do not recommend artificial perches to increase seedling recruitment in grass-dominated abandoned pastures.

References

[1] Fao. 2010. *Global forest resources assessment 2010: main report.* Rome, Italy. http://www.fao.org/docrep/013/i1757e/i1757e.pdf

[2] Zarin, D. 2012. Carbon from tropical deforestation. *Science.* 336: 1518-1519

[3] Chazdon, R. L. 2008. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. *Science.* 320: 1458-1460

[4] Silverio, D. V., Brando, P. M., Balch, J. K., Putz, F. E., Nepstad, D. C., Oliveira-Santos, C. and Bustamante, M. M. 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philos Trans R Soc Lond B Biol Sci.* 368:

[5] Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson , M. and Kirschner, J. 2004. Alien plants in checklists and floras: towards etter communication between taxonomists and ecologists. *Taxon.* 53: 131-143

[6] Pyšek, P. and Richardson, D. M. 2006. The biogeography of naturalization in alien plants. *Journal of Biogeography.* 33: 2040-2050

[7] Hoffmann, W. A. and Haridasan, M. 2008. The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology.* 33: 29-36

[8] Martins, C. R., Hay, J. D. V., Walter, B. M. T., Proença, C. E. B. and Vivaldi, L. J. 2011. Impacto da invasão e do manejo do capim gordura (*Melinis minutiflora*) sobre a riqueza e biomassa da lora nativ do Cerrado sentido restrito. *Revista Brasileira de Botânica.* 34: 73-90

[9] Pyšek, P. and Richardson, D. M. 2010. Invasive Species, Environmental Change and Management, and Health. *Annual Review of Environment and Resources.* 35: 25-55

[10] Ehrenfeld, J. G., Kourtev, P. and Huang, W. 2001. Change in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological applications.* 11: 1287-1300

[11] Thaxton, J. M., Cordell, S., Cabin, R. J. and Sandquist, D. R. 2012. Non-Native Grass Removal and Shade Increase Soil Moisture and Seedling Performance during Hawaiian Dry Forest Restoration. *Restoration Ecology.* 20: 475-482

[12] Setterfield, S. A., Rossiter-Rachor, N. A., Douglas, M. M., Wainger, L., Petty, A. M., Barrow, P., Shepherd, I. J. and Ferdinands, K. B. 2013. Adding fuel to the fire: the impacts of non-native grass invasion on fire management at a regional scale. *PLoS One.* 8:

[13] Davis, M. A., Chew, M. K., Hobbs, R. J., Lugo, A. E., Ewel, J. J., Vermeij, G. J., Brown, J. H., Carroll, S. P., Thompson, K., Pickett, S. T. A., Stromberg, J. C., Tredici, P. D., Suding, K. N., Ehrenfeld, J. G., Grime, J. P., Mascaro, J. and Briggs, J. C. 2011. Don't judge species on their origins. *Nature.* 474: 153-154

[14] Parr, C. L. 2010. Habitat complexity and invasive species: the impacts of gamba grass (*Andropogon gayanus*) on invertebrates in an Australian tropical savanna. *Biotropica.* 42: 688-696

[15] Tabarelli, M., Peres, C. A. and Melo, F. P. L. 2012. The 'few winners and many losers' paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation.* 155: 136-140

[16] Schnitzer, S. A. and Carson, W. P. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters.* 13: 849-857

[17] Allen, B. P., Pauley, E. F. and Sharitz, R. R. 1997. Hurricane impacts on liana populations in an old-growth southeastern bottomland forest. *Torrey Botanical Society.* 124: 34-42

[18] Houghton, R. A. 2012. Carbon emissions and the drivers of deforestation and forest degradation in the tropics. *Current Opinion in Environmental Sustainability.* 4: 597-603

[19] Sparovek, G., Berndes, G., F, K. I. L. and Barretto, G. O. P. 2010. Brazilian agriculture and environmental legislation: status and future challenges. *Environmental Science & Technology.* 44: 6046-6053

[20] Florentine, S. K. and Westbrooke, M. E. 2004. Restoration on abandoned tropical pasturelands—do we know enough? *Journal for Nature Conservation.* 12: 85-94

[21] Brancalion, P. H. S., Viani, R. a. G., Strassburg, B. B. N. and Rodrigues, R. R. 2012. Finding the money for tropical forest restoration. *Unasylva.* 63: 25-34

[22] Holl, K. D., Loik, M. E., Lin, E., H. V. and Samuels, I. A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology.* 8: 339-349

[23] Ortega-Pieck, A., López-Barrera, F., Ramírez-Marcial, N. and García-Franco, J. G. 2011. Early seedling establishment of two tropical montane cloud forest tree species: the role of native and exotic grasses. *Forest Ecology and Management.* 261: 1336-1343

[24] Zahawi, R. A. and Augspurger, C. K. 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica.* 31: 540-552

[25] Nave, A. G., Brancalion, P. H. S., Coutinho, E. and Cesar, R. G. 2009. *Descrição das ações operacionais de restauração.* BioAtlântica Institute. São Paulo

[26] Castro, C. R. T., Garcia, R., Carvalho, M. M. and Couto, L. 1999. Produção forrageira de gramíneas cultivadas sob luminosidade reduzida. *Rev. Bras. Zootec.* 28: 919-927

[27] Martins, C. R., Hay, J. D. V. and Carmona, R. 2009. Invasion potential of two cultivar of *Melinis minutiflora* in the Brazilian cerrado - seed characteristics and seedling establishment. *Revista Árvore.* 33: 713-722

[28] Carvalho, M., M., Xavier, D., F., Freitas, V., P. and Verneque, R., S. 2000. Correção da acidez do solo e controle do capim-sapê. *Rev. Bras. Zootec.* 29: 33-39

[29] Fujisaka, S., Escobar, G. and Veneklaas, E. 1998. Plant community diversity relative to human land uses in an Amazon forest colony. *Biodiversity and Conservation.* 7: 41-57

[30] Wagner, R. G. 2005. The role of vegetation management for enhancing productivity of the world's forests. *Forestry.* 79: 57-79

[31] Lelong, M. G. 1977. Annotated list of vascular plantis in Mobile, Alabama. *Sida.* 7: 118-146

[32] Allen, C. M. 1974. Nineteen species of grasses (Poacea) new to Louisiana. *Proc. Louisiana Acad.* 37: 18-20

[33] Reis, A., Bechara, F. C. and Tres, D. R. 2010. Nucleation in tropical ecological restoration. *Scientia Agricola.* 67: 244-250

[34] Rodrigues, R. R., Gandolfi, S., Nave, A. G., Aronson, J., Barreto, T. E., Vidal, C. Y. and Brancalion, P. H. S. 2011. Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management.* 261: 1605-1613

[35] Shono, K., Cadaweng, E. A. and .B., D. P. 2007. Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology.* 15: 620-626

[36] Esquivel, M. J., Harvey, C. A., Finegan, B., Casanoves, F. and Skarpe, C. 2008. Effects of pasture management on the natural regeneration of neotropical trees. *Journal of Applied Ecology.* 45: 371-380

[37] Laurance, W. F. 2009. Conserving the hottest of the hotspots. *Biological Conservation.* 142: 1137

[38] Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J. and Hirota, M. M. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? . *Biological Conservation.* 142: 1141-1153

[39] Embrapa. 1970. *Climatic Data from brazil: Piracaia - SP*. http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=&COD=422

[40] Almeida, A., Padovezi, A. and Lima, R. a. F. 2011. *Projeto cachoeira: monitoring birds and vegetation.* The nature conservancy Brasil. Brasília - DF, Brazil.

[41] Corbin, J. D. and Holl, K. D. 2012. Applied nucleation as a forest restoration strategy. *Forest Ecology and Management.* 265: 37-46

[42] Gusman, G., S., Bittencourt, A., H. C. and Vestena, S. 2008. Allelopathy of *Baccharis dracunculifolia* DC. on the germination and development of cultivated species. *Acta Sci. Biol. Sci.* 30: 119-125

[43] Shannon, C. E. 1948. A mathematical theory of communication. *The bell system technical Journal.* 27: 379-423 and 623-656

[44] Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. *Theoretical Biology.* 13: 131-144

[45] Mueller-Dombois, D. and Ellenberg, H. 1974. *Aims and Methods of Vegetation Ecology.* John Wiley and Sons. New York, USA

[46] Holl, K. D. 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pastures? *Restoration Ecology.* 6: 253-261

[47] Mcclananhan, T. R. and Wolfe, R. W. 1987. Dispersal of ornithochorous seeds from forest edges in central Florida. *Vegetatio.* 71: 107-112

[48] Reid, J. L. and Holl, K. D. 2013. Arrival ≠ Survival. *Restoration Ecology.* 21: 153-155

[49] Aide, T. M., Zimmerman, J. K., Herrera, L., Rosario, M. and Serran, M. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management.* 77: 77-86

[50] Graham, L. L. B. and Page, S. E. 2011. Artificial bird perches for the regeneration of degraded tropical peat swamp forest: a restoration tool with limited potential. *Restoration Ecology.* no-no

[51] Zanini, L. and Ganade, G. 2005. Restoration of *Araucaria* forest: the role of perches, pioneer vegetation, and soil fertility. *Restoration Ecology.* 13: 507-514

[52] Nave, A. G. and Rodrigues, R. R. 2007. Combination of species into filling and diversity groups as forest restoration methodology. In: *High Diversity Forest Restoration in Degraded Areas.* Rodrigues, R. R., Martins, S. V. and Gandolfi, S. (Eds.), pp. 130-126. Nova Science Publishers, NEw york

[53] Herrera, J. M. and García, D. 2009. The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad. *Biological Conservation.* 142: 149-158

[54] Laborde, J., Guevara, S. and Sánchez-Rios, G. 2008. Tree and shrub dispersal in pastures: the importance of rainfores trees outside forest fragments. *Écoscience.* 15: 6-16

[55] Zahawi, R. A. and Augspurger, C. K. 2006. Tropical forest restoration: tree islands as recruitment foci in degraded lands of honduras. *Ecological Applications.* 16: 464-478

[56] Loik, M. E. and Holl, K. D. 1999. Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. *Restoration Ecology.* 7: 382-391

[57] Loik, M. E. and Holl, K. D. 2001. Photosynthetic responses of tree seedlings in grass and under shrubs in early-successional tropical old fields, Costa Rica. *Oecologia.* 127: 40-50

[58] Ammondt, S. A. and Litton, C. M. 2012. Competition between Native Hawaiian Plants and the Invasive Grass Megathyrsus maximus: Implications of Functional Diversity for Ecological Restoration. *Restoration Ecology.* 20: 638-646

[59] Griscom, H. P., Ashton, P. M. S. and Berlyn, G. P. 2005. Seedling survival and growth of native tree species in pastures: Implications for dry tropical forest rehabilitation in central Panama. *Forest Ecology and Management.* 218: 306-318

[60] Hooper, E., Legendre, P. and Condit, R. 2005. Barriers to forest regeneration of deforested and abandoned land in Panama. *Journal of Applied Ecology.* 42: 1165-1174

[61] Royo, A. A. and Carson, W. P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research.* 36: 1345-1362
[62] Sampaio, A. B., Holl, K. D. and Scariot, A. 2007. Does restoration enhance regeneration of seasonal deciduous forests in pastures in central Brazil? *Restoration Ecology.* 15: 462-471
[63] Campoe, O. C., Stape, J. L. and Mendes, J. C. T. 2010. Can intensive management accelerate the restoration of Brazil's Atlantic forests? *Forest Ecology and Management.* 259: 1808-1814

APENDIX 1

List of planted seedlings found in the group plantings (individuals alive during data collection, one year after planting). R = fast growing species with wide canopy, planted in the edges of the Anderson nuclei to quickly cover the area and favor slow growing species; D = slow growing species planted in the center of the Anderson nuclei in order to add species and functional richness to the area under restoration.

Family and species	Individuals	Group
Anarcadiaceae	**24**	
Schinus terebinthifolia Raddi	24	R
Araucariaceae	**3**	
Araucaria angustifolia (Bertol.) Kuntze	3	D
Arecaceae	**1**	
Syagrus romanzoffiana (Cham.) Glassman	1	D
Bignoniaceae	**1**	
Handroanthus heptaphyllus Mattos.	1	D
Boraginaceae	**5**	
Cordia superba Cham.	5	R
Euphorbiaceae	**8**	
Alchornea glandulosa Poepp. & Endl.	2	R
Croton floribundus Spreng.	1	R
Croton urucurana Baill.	5	R
Fabaceae-Caesalpinoideae	**8**	
Copaifera langsdorffii (Desf.)	1	D
Hymenaea courbaril Hayne	7	D
Fabaceae-Faboideae	**8**	
Centrolobium tomentosum Guill. ex Benth.	1	R
Lonchocarpus muehlbergianus Hassl.	3	D
Myrocarpus frondosus Allemão	3	D
Pterocarpus sp.	1	D
Fabaceae-Mimosoideae	**87**	
Acacia polyphylla DC.	1	R
Albizia polycephala (Benth.) Killip ex Record	10	R
Anadenanthera colubrina (Vell.) Brenan	42	R
Enterolobium contortisiliquum (Vell.) Morong.	2	R
Inga vera Willd.	28	R
Piptadenia gonoacantha (Mart.) Macbr.	1	R
Pithecolobium incuriale (Vellozo) Bentham	3	R
Lauraceae	**8**	
Nectandra lanceolata Nees et Mart	8	D

Lecythidaceae	**3**	
Cariniana estrellensis (Raddi) Kuntze	3	D
Malvaceae	**25**	
Ceiba speciosa (St.-Hil.) Ravenna	23	D
Pseudobombax grandiflorum (Cav.) A. Robyns.	2	D
Meliaceae	**3**	
Cedrela fissilis Vell.	3	D
Moraceae	**4**	
Ficus guaranitica Schodat	2	D
Maclura tinctoria (L.) D. Don. Steud.	2	D
Myrtaceae	**11**	
Eugenia involucrata DC	3	D
Eugenia uniflora L.	4	D
Psidium cattleianum Sabine	1	D
Psidium guajava L.	2	R
Psidium rufum Mart. ex DC	1	R
Primulaceae	**2**	
Myrsine coriaceae (Sw.) R. Br. Ex Roem. & Schult.	2	D
Rubiaceae	**1**	
Rubiaceae - Non-identified	1	D
Rutaceae	**1**	
Esenbeckia grandiflora Mart.	1	D
Sapindaceae	**1**	
Cupania vernalis Camb.	1	R
Tiliaceae	**7**	
Luehea grandiflora Mart. & Zucc.	7	R
Verbenaceae	**4**	
Aegiphila sellowiana Cham.	1	R
Citharexylum myrianthum Cham.	3	D
Unidentified	**3**	
Unidentified 1	1	D
Unidentified 2	1	D
Unidentified 3	1	D
Total Individuals found	**218**	
Dead Individuals	**82**	
Total Individuals originally planted	**300**	

APPENDIX 2

Species regenerating under artificial perches on *M. minutiflora* and *I. brasiliensis* grass patches. Zoo = animal dispersed, An = wind dispersed, Au = other dispersal syndrome, P = pioneer, NP = non pioneer. The "Group" column refers to the species sucessional group.

Species	***M. minutiflora* (invasive)**	***I. brasiliensis* (native)**	**Life form**	**Dispersion**	**Group**
Chromolaena laevigata (Lam.) R.M.King & H.Rob.	X		shrub	An	P
Gaya pilosa K. Schum.	X		shrub	Au	P
Leucochloron incuriale (Vell.) Barneby & J.W. Grimes	X		tree	Au	P
Machaerium hirtum (Vell.) Stellfeld	X		tree	An	P
Meliaceae - unidentified	X		tree	-	-
Ocotea sp.	X		tree	Z	-
Solanum stipulaceum Roem & Schult.	X		tree	Z	P
Solanum variabile Mart.	X	X	tree	Z	P
Vernonanthura phosphorica (Vell.) H.Rob.	X	X	tree	An	P
Vernonia platensis Spreng.	x		shrub	An	P

APPENDIX 3

Natural regeneration on *M. minutiflora* and *I. brasiliensis* patches on plots with assisted natural regeneration. Zoo = animal dispersed, An = wind dispersed, Au = other dispersal syndrome, P = pioneer, NP = non pioneer. The "Group" column refers to the species sucessional group.

Species	*M. minutiflora*	*I. brasiliensis*	Life form	Dispersion	Group
Acacia polyphylla DC.	X		tree	An	P
Aegiphila sellowiana Cham.	X		tree	*Z*	P
Alchornea triplinervia (Sprengel) Müller Argoviensis	X		tree	Z	P
Baccharis sp.	X		shrub	An	P
Chromolaena laevigata (Lam.) R.M.King & H.Rob.	X		shrub	An	P
Chromolaena maximilianii (Schrad. ex DC.) R. M. King & H. Rob.	X		shrub	An	P
Ficus insipida Willd.		X	tree	Z	P
Gaya pilosa K. Schum.	X	X	shrub	Au	P
Gochnatia polymorpha (Less.) Cabrera	X		tree	An	P
Luehea divaricata Mart.	X		tree	An	P
Machaerium hirtum (Vell.) Stellfeld	X	X	tree	An	P
Machaerium villosum Vog.	X		tree	An	St
Peltophorum dubium(Spreng.) Taub.	X		tree	An	Si
Piper sp.	X	X	shrub	Z	-
Pithecollobium incuriale (Vellozo) Bentham	X		tree	Au	P
Psidium guajava L.	X		tree	Z	P
Pterocarpus sp.	X		-	An	-
Myrsine umbellata Mart.		X	tree	Z	P
Solanum pseudoquina A. St.-Hill.	X	X	tree	Z	P
Solanum stipulaceum Roem & Schult.		X	tree	Z	P
Solanum variabile Mart.	X		tree	Z	P
Trema micrantha (L.) Blume		X	tree	Z	P
Vernonanthura phosphorica (Vell.) H.Rob.	X	X	shrub	An	P
Vernonia platensis (Spreng.) Less.	X	X	shrub	An	P
Vernonia scorpioides (Lam.) Pers.	X		shrub	An	P