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Vegetation Response to Grazing and Planting of *Leucaena leucocephala* in a *Urochloa maximum*-dominated Grassland in Puerto Rico

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ABSTRACT.—A considerable portion of the former dry and dry-transition-to-moist forests of Puerto Rico dominated by *Bucida buceras* L. was transformed by land clearing and periodic fires to tall grasslands dominated by *Urochloa maximum* Jacq. and savannas with scattered small trees and shrubs. These communities, maintained by fires, are relatively stable and difficult to reforest. A study was carried out to test whether natural recolonization of forest species might be accelerated by excluding grazing livestock or by planting trees to facilitate natural succession. Experimental treatments included grazing exclusion and planting of *Leucaena leucocephala* (Lam.) de Wit (giant variety) at 2 x 2 m and 4 x 4 m, as well as an unprotected control. Tree growth, herbaceous aboveground biomass, and floristic diversity were monitored in experimental plots for 6 years. Floristic diversity (principally weedy species) increased during the first 3 years in grazed plots but decreased thereafter; biodiversity in grazing-protected plots decreased steadily over time. Herbaceous biomass remained fairly constant in grazed plots, increased gradually in protected plots, and decreased precipitously in planted plots after tree basal area surpassed 8 m^2/ha. The results of this study suggest that while the suppression of dominant grasses, either by controlled grazing or shading by planted trees can facilitate regeneration of native dry forest plant species, this process is both slow and uncertain on highly degraded sites, and likely to require decades before natural succession processes result in vegetation structure and species composition resembling that of native dry forest stands.

KEYWORDS.—forest restoration, dry forests, floristic biodiversity, grazing, natural regeneration, reforestation

INTRODUCTION

Forest loss, and degradation of lands which formerly supported forest, are occurring at unprecedented rates in most tropical and subtropical regions, eroding biological diversity and prospects for sustainable economic development of agricultural and forest resources (FAO, 2003; Lamb et al. 2005). Traditionally the most common response to land degradation has been abandonment, or reliance on natural succession to restore lost soil fertility, species richness, and biomass productivity. Natural succession may be slowed or precluded by persistent physical, chemical and biological barriers, or stresses, which typically include some combination of the following: above- and belowground competition with grasses or ferns, periodic fire, seasonal drought, low seed or rootstock availability, seed and seedling predation, lack of suitable microhabitats for seed germination and seedling establishment, soil nutrient limitations, and absence of obligate fungal or bacterial root symbionts (Parrotta et al. 1997).

Recent studies in many tropical and subtropical countries have shown that planted forests can facilitate forest succession on sites where persistent barriers to succession would otherwise prelude recolonization by native forest species, and thereby serve an important role in forest landscape restoration (ITTO 2002; Carnus et al. 2006). These include a number of studies in Puerto Rico (*cf.* Lugo 1992; Parrotta 1992, 1993, 1999). Once established, planted trees can facilitate succession by first suppressing grasses or other light-demanding species that normally prevent tree seed germination or

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seedling survival, improving light, temperature and moisture conditions for seedling growth, increasing vegetation structural complexity, and accelerating development of litter and humus layers during the early years of plantation growth. These changes lead to increased seed inputs from neighboring native forests by seed dispersing wildlife attracted to the plantations. However, this facilitative effect of planted trees on succession tends to be less pronounced on drier than wetter sites (Parrotta et al. 1997).

Similarly, there is some evidence that moderate, controlled, grazing in degraded pastures formerly occupied by tropical forests can facilitate regeneration of native forest species by suppressing dominant grasses and, under certain conditions, increasing the input and probability of germination and establishment of woody forest species (Janzen 1988; Posada et al. 2000; Zimmerman et al. 2000; ITTO 2002).

In Puerto Rico, the southern coastal plains were historically characterized by dry and dry-transition-to-moist forests dominated by *Bucida buceras* L. Over the past century, or perhaps several centuries, these previously forested landscapes were transformed by land clearing for agriculture, urbanization, and periodic fires (both intentional and accidental) to tall grasslands, dominated by *Urochloa maximum* Jacq., and savannas with scattered small trees and shrubs. These plant communities, maintained by fires, are relatively stable (resistant to natural succession) and difficult to reforest. The present study was carried out to determine the effects livestock grazing, or its exclusion, on natural recolonization of native forest species, and to test the hypothesis that artificial regeneration of forest trees (replanting with *Leucaena leucocephala* (Lam.) de Wit) can be used to facilitate natural succession in the dry forest region of Puerto Rico.

MATERIALS AND METHODS

Study site

Camp Santiago, Puerto Rican National Guard base and training facility, near Salinas, Puerto Rico, is located on the south coastal plain at about 10 m elevation. It is characterized by deep clayey soils in the order Ultisols and a mean annual precipitation of 1060 mm. The site is mostly level or gently sloping, with gradients between 1 and 8 percent. Due to periodic fires and possibly wood cutting, the area lost its forest cover at least before 1936 (this based on examination of the first aerial photos from that year) and probably much earlier. At the start of the study, it was covered with a tall-grass sward dominated by *Urochloa maximum*, with occasional low trees and shrubs.

Sampling design

At the start of the rainy season in late 1994, 16 experimental plots were established in 4 blocks using a randomized complete block design. All plots measured 32 x 32 m each (1024 m^2). Each block included one plot of the following treatments: unprotected control (subject to grazing), protected control, planted with *Leucaena leucocephala* (giant variety) at 2 by 2 m spacing, and planted with *L. leucocephala* (giant variety) at 4 by 4 m spacing. Other treatments involving direct seeding with 16 woody species were originally included in the experimental design but were abandoned due to germination failure caused by poor soil moisture conditions after seeding. A barbed-wire fence enclosed the grazing-protected treatments; grazed plots were located outside the fenced area. The grazed plots and some of the control plots were mistakenly mowed for hay in the year of establishment, but not thereafter. The grazed plots were moderately to heavily grazed by cattle and horses except during the last year (2000), when the cattle were unexpectedly withdrawn and only horses grazed the area with lower impact. The study came to an abrupt end when a large fire swept through the entire area in early 2001.

Seedlings of *L. leucocephala* were initially planted as dibbled plugs in September 1994; gaps caused by post-planting mortality were replanted approximately one month later with seedlings grown in 1 liter plastic bags. A complete species list of vascular plants in each plot was made at establishment and every year thereafter in late October or early November. The identity of several unknown species was established by consulting local taxonomists and comparing pressed samples with reference samples in the University of Puerto Rico Herbarium. Spelling and authority of scientific names were verified by consulting with the Natural Resources Conservation Service (2003) plants database. To evaluate the possible influence of experimental treatments on plant species composition in the study plots, we used a multi-way ANOVA using block, treatment, and year as independent variables, and arcsine-transformed species presence data from each plot as the dependent variable.

Height and diameter at breast height (d.b.h., 1.37 m above ground level) of all trees were measured at the end of each growing season (January). Stems per hectare (of trees at least 1.37 m in height) were enumerated, and basal area was calculated as the sum of cross sectional areas of stems at d.b.h. of all trees per plot, expressed on a per hectare basis. In December of each year of the study, four temporary 1 m^2 circular plots marked by a heavy wire hoop were randomly placed in each plot and oven-dry herbaceous biomass was sampled. Herbaceous biomass was cut 1 cm above the ground, placed in paper bags, pre-dried in a solar dryer for 1 month, and oven dried at 105°C in a forced-air dryer for 24 hours before weighing.

RESULTS

The plant species recorded during the annual inventory of experimental plots are shown in Table 1. Although 97 species were observed over the course of the study, many were annuals that are only seen when disturbance and rainfall is favorable. At least two tree species regenerated from seed after a flood in 1997 but did not survive into the second year. For the combined data for all experimental plots, species numbers are somewhat higher after the first two years. However, when the treatments are separated (Fig. 1), this increase appears to be confined to the grazing-protected treatment. Analysis of plot-wise species composition data showed significant differences among blocks (ANOVA, $P < 0.001$) for all years, and among treatments (ANOVA, $P < 0.01$) at 3 and 4 years after establishment of the experiment (1997 and 1998).

Five species, *Bothriochloa pertusa*, *Desmanthus virgatus*, *Leucaena leucocephala*, *Teramnus labialis*, and *Urochloa maxima*, were present in most or all plots and made up the bulk of the biomass and plant numbers. *Urochloa maxima*, a tall grass, was the dominant vegetation and tended to suppress all other species except where it was eventually shaded by the planted *L. leucocephala*. *Leucaena leucocephala*, in its native, shrubby form, grows naturally in the area and occurred in most of the plots at the beginning of the study and in all of them by its end. A large percentage of the species occurring at this site are weedy and many of them exotic; relatively few are from the dry forest that originally covered the area. Figure 1 shows the average number of plant species per plot segregated by treatment over the course of the study. Apart from year-to-year fluctuations presumably related at least in part to inter-annual variations in rainfall, which ranged from 661 to 1358 mm yr^{-1} over the course of the study (NOAA 2005), there is an obvious downward trend in species richness after 1998 for all the protected treatments; for the unprotected (grazed) treatment, species richness showed an increase during the early years of the study followed by a decline during the last two years.

The number of stems (of both natural and planted trees) per hectare, mean tree heights, and basal areas by treatment are given in Table 2. The planted *L. leucocephala* increased rapidly in height (up to 2 m/yr) and basal area. Tree heights and basal areas increased somewhat over time in the protected controls, attributable mainly to the naturally occurring shrubby *L. leucocephala* and *Prosopis juliflora* in those plots. *Acacia farnesiana* contributed appreciably to stem numbers but these were short and added little to basal area. Numbers of stems per hectare increased dramatically over time, especially in the control plots.

In the year of establishment, biomass val-

TABLE 1. Plant species and the number of plots where these were observed each November during the study.

Species	Life Form*	Year						
		1994	1995	1996	1997	1998	1999	2000
		No. of plots (of 16) where found						
Acacia farnesiana (L.) Willd.	S	6	9	10	10	10	10	10
Achyranthes aspera L.	H	1	0	2	2	2	4	2
Aeschynomene americana L.	H	2	3	1	1	1	1	1
Alysicarpus vaginalis (L.) DC.	H	0	1	2	2	1	0	1
Amaranthus crassipes Schlecht.	H	0	0	0	3	0	0	0
Amaranthus dubius Mart. ex Thellung	H	0	0	0	1	1	0	0
Bastardia bivalvis (Cav.) Kunth	S	13	12	11	10	8	8	6
Bastardia viscosa (L.) Kunth	H	0	0	0	0	3	2	4
Bidens alba (L.) DC.	H	0	0	0	0	0	1	0
Boerhavia coccinea P. Mill.	H	0	3	1	1	0	0	0
Bothriochloa pertusa (L.) A. Camus	G	16	16	16	16	15	15	13
Bourreria succulenta Jacq.	H	1	1	1	1	1	1	1
Bucida buceras L.	T	1	1	1	1	0	0	0
Calotropis procera (Ait.) Ait.f.	S	15	14	12	15	13	13	14
Capraria biflora L.	S	6	6	9	11	9	6	5
Chamaesyce hirta (L.) Millsp.	H	1	1	0	1	1	1	0
Chamaesyce hyssopifolia (L.) Small	H	2	2	2	1	0	0	0
Chloris barbata Sw.	G	0	0	0	0	0	1	0
Cissus verticillata (L.) D.H. Necols. & Jarvis	H	1	0	1	0	0	1	0
Cleome viscosa L.	H	1	1	1	3	1	0	1
Clitoria ternatea L.	H	3	4	3	4	7	4	4
Commelina diffusa Burm.f.	H	0	0	0	0	1	1	2
Commelina erecta L. var. *erecta*	H	0	0	0	0	0	1	0
Corchorus aestuans L.	H	12	14	3	0	1	0	2
Corchorus hirsutus L.	H	0	0	2	5	6	5	2
Corchorus hirtus L.	H	1	3	2	0	0	0	1
Cucumis anguria L.	H	2	5	0	4	3	3	2
Cyperus ochraceus Vahl	G	1	0	1	1	0	1	1
Cyperus rotundus L.	G	5	2	4	4	1	2	1
Desmanthus virgatus (L.) Willd.	H	16	16	16	16	15	15	12
Desmodium glabrum (P. Mill.) DC.	H	12	12	7	0	6	3	2
Desmodium tortuosum (Sw.) DC.	H	0	2	1	2	8	7	5
Digitaria sanguinalis (L.) Scop.	G	0	0	0	1	0	0	0
Echinochloa colona (L.) Link	G	0	0	0	0	0	1	1
Euphorbia heterophylla L.	H	1	1	1	0	0	0	0
Flueggea acidoton (L.) G.L. Webster	S	3	6	4	6	6	6	4
Galactia striata (Jacq.) Urban	H	0	0	0	0	3	5	2
Heliotropium angiospermum Murr.	S	0	1	1	3	0	1	2
Heteropterys purpurea (L.) Kunth	S	0	2	2	2	1	1	1
Indigofera suffruticosa P. Mill.	S	0	0	0	1	2	1	0
Ipomoea indica (Burm.f.) Merr.	H	16	16	8	15	13	14	10
Ipomoea triloba L.	H	0	4	2	2	4	3	1
Jasminum fluminense Vell.	S	0	0	1	0	0	1	0
Jatropha gossypiifolia L.	S	0	1	1	2	1	1	0
Lagascea mollis Cav.	H	1	1	1	1	1	1	1
Leucaena leucocephala (Lam.) de Wit	S/T**	12	16	16	16	16	16	16
Ludwigia octovalvis (Jacq.) Raven	S	0	0	0	0	1	1	0
Macroptilium lathyroides (L.) Urban	H	4	6	2	4	4	3	3
Malachra alceifolia Jacq.	H	6	2	1	1	1	1	1
Malachra capitata (L.) L.	H	2	0	0	0	0	0	0
Malvastrum americanum (L.) Torr.	H	1	0	1	1	10	8	5

TABLE 1. Continued.

Species	Life Form*	Year						
		1994	1995	1996	1997	1998	1999	2000
		No. of plots (of 16) where found						
Malvastrum coromandelianum (L.) Garcke	H	2	0	1	0	0	6	2
Matelea variifolia (Schlechter) Woods.	H	0	0	0	1	0	0	0
Melochia pyramidata L.	S	4	8	8	7	3	1	1
Merremia aegyptia (L.) Urban	H	9	9	2	5	3	4	3
Merremia quinquefolia (L.) Hallier f.	H	0	3	3	1	5	3	2
Parkinsonia aculeata L.	S	1	1	2	1	1	1	1
Parthenium hysterophorus L.	H	2	1	2	0	1	1	1
Passiflora foetida L.	H	0	0	0	0	1	0	0
Passiflora suberosa L.	H	1	1	0	3	1	1	0
Pennisetum ciliare (L.) Link var. *ciliare*	G	1	0	3	4	1	2	2
Phyllanthus amarus Schumacher	H	0	1	0	2	1	1	1
Phyllanthus niruri L.	H	2	0	0	0	0	1	1
Physalis angulata L.	H	0	0	0	0	1	1	0
Pithecellobium dulce (Roxb.) Benth.	T	1	1	2	4	6	5	7
Pithecellobium unguis-cati (L.) Benth.	S	6	6	8	8	7	6	6
Portulaca oleracea L.	H	0	0	1	1	0	0	0
Prestonia agglutinata (Jacq.) Woods.	H	0	0	2	1	1	2	1
Priva lappulacea (L.) Pers.	S	4	3	1	1	1	1	1
Prosopis juliflora (Sw.) DC.	T	9	9	9	13	12	12	15
Pseudabutilon umbellatum (L.) Fryxell	H	0	0	0	0	1	0	0
Pterocarpus macrocarpus Kurz	T	0	0	0	1	0	0	0
Rauvolfia viridis Willd. ex Roem. & J.A. Schultes	S	1	1	2	4	2	2	2
Rhynchosia minima (L.) DC.	H	4	11	10	3	13	6	9
Rhynchosia reticulata (Sw.) DC.	H	0	0	0	0	0	2	1
Ruellia tuberosa L.	H	6	4	9	11	3	4	3
Samanea saman (Jacq.) Merr.	T	1	1	1	2	1	1	1
Senna obtusifolia (L.) Irwin & Barneby	H	5	6	0	0	0	1	1
Sesbania sericea (Willd.) DC.	S	1	1	1	0	0	0	0
Sida abutifolia P. Mill.	H	6	6	14	10	7	3	3
Sida rhombifolia L.	S	11	11	12	3	5	1	4
Sida salvifolia K. Presl	H	0	0	0	0	4	5	2
Sidastrum multiflorum (Jacq.) Fryxell	H	0	13	11	8	5	3	4
Spermacoce confusa Rendle	H	5	4	2	0	1	2	1
Stigmaphyllon emarginatum (Cav.) A. Juss.	S	3	2	4	7	3	6	7
Stylosanthes hamata (L.) Taubert	H	1	0	0	1	0	0	0
Swietenia macrophyllum × *mahagoni*	T	0	0	0	1	0	0	0
Synedrella nodiflora (L.) Gaertn.	H	0	1	1	1	0	0	0
Tephrosia cinerea (L.) Pers.	H	4	5	9	7	6	6	5
Teramnus labialis (L.f.) Spreng.	H	16	16	16	16	16	15	16
Tillandsia recurvata (L.) L.	H	1	1	1	1	2	2	2
Tridax procumbens L.	H	0	3	0	1	1	0	1
Urochloa maxima (Jacq.) R. Webster	G	16	16	16	16	16	16	16
Urochloa platyphylla (Munro ex Wright) R. Webster	G	0	0	0	0	1	0	0
Vernonia sericea L.C. Rich.	S	1	0	0	0	0	0	0
Wissadula amplissima (L.) R.E. Fries	H	4	0	11	1	1	3	1
Wissadula periplocifolia (L.) K. Presl ex Thwaites	S	0	0	2	1	1	0	1
Xanthium strumarium L. var. *glabratum* (DC.) Cronq.	H	0	0	0	2	1	1	1
Number of species present		58	59	65	70	69	72	67

*T = tree, S = shrub, H = herb, S = grass and grass-like

**Giant variety (tree) planted; shrubby variety growing naturally

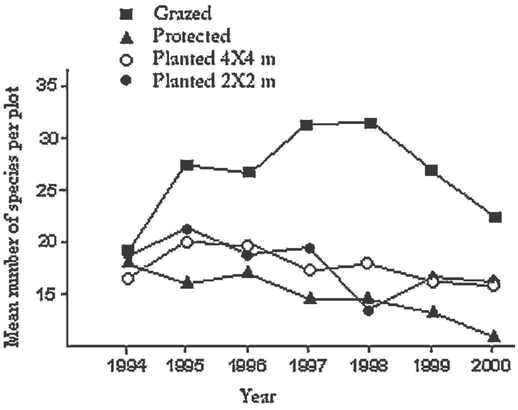

FIG. 1. Mean number of plant species observed in experimental plots. Plotted values are means of four replicate plots per treatment.

ues were low due to the lower than average rainfall that year and the reduced vigor of the perennial grass plants following years of mowing and possibly grazing (Table 3). In most of the following years, the herbaceous biomass was considerably less in the grazed than in the protected (ungrazed) plots except in the last year when the cattle had been withdrawn. Herbaceous biomass in the plots with 2 x 2 m spaced *L. leucocephala* declined from the 4th year onwards. The wider spaced (4 x 4 m) *L. leucocephala* plots showed some apparent reductions in herbaceous biomass during the last 2 years. The relation between dry herbaceous biomass and basal area of trees in the 12 protected plots (both planted and unplanted controls) in the last year of the study (2000) are presented in Fig. 2. This relation shows a negative, approximately linear, trend (adjusted $R^2 = 0.617$; $P = 0.0015$).

We estimate that about 40 percent of the species observed in the study were probably part of the original dry forest, although there is considerable uncertainty since dry forest in this particular area no longer exists for comparison purposes. About 7 species of the dry forest (herbs and subshrubs) seem to have established themselves during the course of the study. This was offset, however, by the apparent loss of about 3 species, one of which was the dominant dry forest tree species (*Bucida buceras*), represented by a single individual in the study area, which was lost due to blow-down. One can never be certain, in the case of annual herbs, whether a species has been gained or lost in a period as short as this study.

DISCUSSION

We cannot fully explain the apparent increase in plant species richness seen in the grazed plots during the first 2 years. However, the initial increase in species richness in these plots, followed by a decline after

TABLE 2. Mean heights, stand density, and basal areas of naturally occurring plus planted trees.

Mean tree height (m)	1995	1996	1997	1998	1999	2000
Grazed	1.98	2.42	2.19	2.32	2.57	2.56
Protected Control	1.56	2.03	2.32	2.64	3.11	3.29
Planted 4 × 4 m	1.59	1.95	2.77	4.16	5.10	5.48
Planted 2 × 2 m	1.43	2.04	2.89	4.44	6.21	6.40
Stems/ha						
Grazed	576	1238	1162	1714	2520	3635
Protected Control	193	618	1079	1521	1733	2224
Planted 4 × 4 m	493	652	1465	1375	1753	1704
Planted 2 × 2 m	2285	2581	4546	4358	4292	4127
Basal Area (m^2/ha)						
Grazed	—	0.32	0.32	0.41	0.65	0.94
Protected Control	—	0.29	0.45	0.51	0.86	1.08
Planted 4 × 4 m	—	0.10	0.44	1.62	2.98	3.67
Planted 2 × 2 m	—	0.76	1.55	4.76	6.97	8.31

— = data not collected

TABLE 3. Mean herbaceous biomass (kg/ha dry weight) harvested on four plots per treatment over the 7-year study period.

	1994	1995	1996	1997	1998	1999	2000
Treatments				kg/ha			
Grazed	3,750	5,820	8,430	3,330	11,230	7,530	13,120
Protected	3,600	9,240	11,270	9,580	14,270	11,540	13,590
Planted 4 × 4 m	3,760	9,350	11,080	10,550	11,690	9,350	11,820
Planted 2 × 2 m	3,960	8,670	11,680	8,070	7,640	3,510	4,620

year 4, suggests that the cessation of regular mowing (applied to the entire study area prior to establishment of the experiment) permitted the regeneration of a wider range of herbaceous species, but the reestablishment of dominance by grasses after 4 years resulted in a suppression of many of the less tolerant herbaceous species, particularly the annuals. This hypothesis is consistent with our data on herbaceous biomass (predominantly grasses), which was generally much higher in the ungrazed and planted treatments than in the grazed treatment through the first 4 years of our study (Table 3). One clear finding from these results is that moderate grazing is less detrimental to plant biodiversity than unchecked *Urochloa maxima* competition, lending support to the view that competition from grasses is the principal barrier to regeneration of native dry forest species and to biodiversity more generally at this site and in similarly degraded dry tropical forest landscapes.

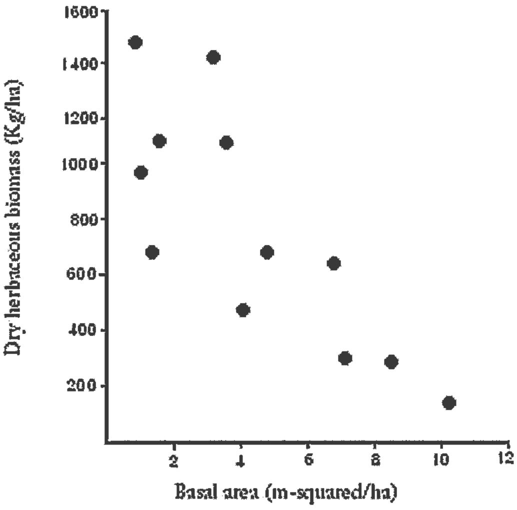

FIG. 2. Relationship between tree basal area and herbaceous biomass in experimental plots protected from livestock grazing. Data are for the 6th and final year of the study (2000), and include results from the protected control, 4 x 4-m planted, and 2 x 2-m planted treatments.

Leucaena leucocephala, established without supplemental water and weeded only during the first year, grew exceptionally well, competing successfully with *U. maxima*. The species is recommended as a biological means of suppressing growth of this exotic grass. Based on our results, close spacing (no greater than 2 by 2 m) and periods of 5 to 7 years will be necessary to bring the grass under control.

Although herbaceous biomass under *L. leucocephala* stands was never fully suppressed, it appears from the relationship seen in Fig. 2 that the growth of dominant grasses is significantly suppressed when basal area reaches or exceeds 8 m^2/ha. Low tree basal areas (below about 4 m^2/ha) appear to have relatively little effect on grass growth. One mechanism that may offset suppression by low basal area stands is that nitrogen fixed by the *L. leucocephala* trees enables greater growth of understory species: *Urochloa maxima* plants growing near the trees were greener than those situated at a distance from them.

While the *L. leucocephala* stands create at least some of the conditions necessary for reestablishment of native dry forest species, this study provides little data to help answer the question of how long the recolonization by native forest species will take. The nearest remnants of dry forest are located on hills about 0.8 km distant from the study site. Although some light wind-dispersed seeds of forest species may be carried this far during storms, the more effective means of seed transport would be by birds. Only three species of birds, *Ze-*

naida aurita, *Crotophaga ani*, and *Tyrannus dominicensis*, were observed on the plots during the study. The first two, which are granivores and seed predators, were observed to nest within the plot. The last is insectivorous and was observed foraging. Perhaps fruit-bearing species, selected to attract seed-dispersing frugivores, might be planted in future reforestation projects in this region. Obviously, effective fire suppression must be part of any reforestation project. Finally, the role and impact of grazing on reforestation should be revisited. The arresting effect of *U. maxima* (and possibly other exotic grasses) is overwhelming in this disturbed environment, both for the suppression of other vegetation and because it is an effective carrier of fire. Grazing consumes most of the fuel and alleviates the suppression. Although some desirable species are eaten by the grazers, others are allowed to grow and eventually create a forest canopy (authors' personal observation).

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