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Subtropical dry forest regeneration in grass-invaded areas of Puerto Rico: Understanding why *Leucaena leucocephala* dominates and native species fail

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ABSTRACT

Throughout the tropics, non-native grasses invade, dominate, and persist in areas where subtropical and tropical dry forests have been highly degraded. In Central America and the Caribbean Islands, forests that regenerate in grass-invaded areas are generally composed of one to a few tree species, usually of the Fabaceae family and often non-native. We investigated the ecological factors that drive these successional patterns in southwestern Puerto Rico, where African grasses dominate extensive areas that are maintained by fires. The non-native legume tree *Leucaena leucocephala* commonly establishes in these areas and forms persistent, mono-dominant stands. We planted 455 saplings of 13 native tree species and *Leucaena* in native forest understory and in grass-invaded areas that were either subjected to or protected from prescribed fires 4 months later. We measured growth and survival to test the following hypotheses: (1) saplings of native species are suppressed in grass-invaded areas compared to the forest understory, (2) *Leucaena* saplings outperform native species in grass-invaded areas, but not in the forest understory, and (3) *Leucaena* saplings are less susceptible to wildfires than native species. After 20 months, 50%, 40%, and 3% of native saplings survived in the forest, unburned-grass, and burned-grass treatments, respectively. Over the same period, 90%, 80%, and 25% of *Leucaena* survived in the same treatments. The fires immediately killed 65% of native saplings and 50% of *Leucaena* saplings. The majority of unburned native saplings died during a seasonal drought, when high irradiance and reduced soil organic matter content likely led to higher mortality in grass-invaded areas than in forest understory. Native species' growth was low in all treatments, yet diameter growth was slightly higher in the unburned grass than the forest understory. *Leucaena* saplings grew faster than the native saplings in all three treatments, especially in the unburned grass. Slow growth and high mortality of native saplings in grass-invaded areas contribute to the dominance of *Leucaena* in forests that regenerate on these sites and suggest that *Leucaena* may play a beneficial role in dry forest restoration in the Caribbean.

1. Introduction

Dry forests accounted for >42% of the forested land area in the tropics before their extent was substantially reduced by conversion to agricultural and urban areas (Murphy and Lugo, 1986a). In many regions, subtropical and tropical dry forests (STDF and TDF; *sensu* Holdridge, 1967) now cover less than 10% of their potential range (Murphy and Lugo, 1986a; Bullock et al., 1995). The remaining fragments of STDF and TDF are threatened by further conversion and degradation, eliciting international concern for their conservation (Lerdau et al., 1991; Miles et al., 2006). In particular, encroachment by introduced grasses and fire threaten remaining small and large fragments of STDF and TDF across much of their range (Janzen, 1988; Brooks et al., 2004; Miles et al., 2006). Non-native grasses, often introduced as forage crops, promote high-frequency fire regimes that inhibit forest regeneration in degraded STDF and TDF (D'Antonio and Vitousek, 1992). Controlling wildfires is therefore a prerequisite for protecting and restoring STDF and TDF, but not a guarantee that forests will regenerate in grass-invaded areas (Litton et al., 2006).

In the absence of wildfires, or other recurrent disturbances, secondary forest regeneration occurs at rates that vary with an array of site factors, such as the intensity of past land use, the proximity of seed sources, and moisture availability (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). The species composition of secondary forests is also influenced by site factors, but usually follows general patterns of succession. Secondary regeneration has been studied extensively in moist and wet tropical forests, where a three-phase sequence of tree recruitment is commonly described (i.e., short-lived pioneer species followed by long-lived pioneer

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species and finally by primary forest species; Brown and Lugo, 1990; Finegan, 1996; Guariguata and Ostertag, 2001).

Successional processes in secondary STDF and TDF are less well understood, but an emerging pattern indicates that a two-phase process of tree recruitment predominates. Commonly, only one to a few pioneer tree species recruit into grass-invaded areas, forming a closed canopy under which primary forest species gradually establish and replace the pioneer species in the canopy (Álvarez-Yépiz et al., 2008; Lebrija-Trejos et al., 2008). In contrast, lightly degraded STDF and TDF, such as charcoal harvesting areas where rootstocks remain intact, tend to regenerate relatively quickly through stump coppicing and do not pass through phases of grass or pioneer tree dominance (Ewel, 1977; Murphy and Lugo, 1990; McLaren and McDonald, 2003a; Lévesque et al., 2011).

In STDF of Central America and the Caribbean Islands, the first phase of tree recruitment into grass-invaded areas tends to be dominated by legume species (i.e., Fabaceae), the particular taxa varying by region (Ray and Brown, 1995a; Roth, 1999; Molina Colón and Lugo, 2006; Romero-Duque et al., 2007; Álvarez-Yépiz et al., 2008; Lebrija-Trejos et al., 2008). In contrast, in more equatorial TDF of Costa Rica and Panama native, non-legume species are common in the first phase of forest regeneration (Kalacska et al., 2004; Griscom et al., 2009; Powers et al., 2009). Secondary forests are often persistent features in disturbed STDF. Legume tree dominance with minor ingrowth of primary forest species may last for several decades or more (Roth, 1999; Molina Colón and Lugo, 2006). Few studies have addressed the factors that determine the patterns of secondary succession in STDF, yet the consistency of legume tree dominance suggests that these trees have an advantage in these areas, perhaps because they can fix nitrogen.

Consistent with these patterns is Puerto Rico, where about 4% of the original STDF area remains forested (Murphy and Lugo, 1995). Areas that burn are invaded by African grasses that are commonly used as forage and are invasive throughout the tropics (Parsons, 1992; Más and García-Molinari, 2006). Highly degraded STDF often form stands that are dominated by the non-native legume tree *Leucaena leucocephala* (hereafter *Leucaena*) (Weaver and Chinea, 2003; Weaver and Schwagerl, 2008). Over time, native trees tend to increase in importance in *Leucaena* stands, however a transition back to primary forest composition has not been documented, even in 60-year-old stands (Francis and Parrotta, 2006; Molina Colón and Lugo, 2006; Pérez Martínez, 2007).

A variety of factors may limit native tree recruitment in highly degraded areas, including a lack of seed arrival, intolerance to microhabitat shifts (e.g., soil degradation, increased solar radiation), or direct competition for resources with grasses. In Puerto Rican STDF, seed arrival to open, grass-invaded areas was not significantly different between native tree species and *Leucaena*, while total seed rain to these areas was minimal (Wolfe, 2008). Grass removal and shading consistently increase seedling survival and growth in STDF and TDF (Ray and Brown, 1995b; Cabin et al., 2002; Griscom et al., 2005). However, direct tests of how performance in grass-invaded areas vs. the forest understory influences secondary succession in STDF and TDF are lacking. We tested the hypothesis that environmental factors suppress the establishment and growth of native trees, but not *Leucaena* in grass-invaded areas and where fires are recurrent. We assessed the performance of planted saplings in grass-invaded areas with and without prescribed fires and in adjacent intact forest stands. Specifically, we tested the following hypotheses: (1) saplings of native species have lower growth and survival rates in grass-invaded areas compared to the forest understory, (2) *Leucaena* outperforms native species in grass-invaded areas, but not in the forest understory, and (3) *Leucaena* saplings are less susceptible to wildfires than native species. An additional objective of this study was to identify native species that could be effective for reforesting grass-invaded areas.

2. Materials and methods

2.1. Study site

This study was conducted in the Guánica Commonwealth Forest and Biosphere Reserve (17°58′N, 66°55′W), a 4500-ha protected area located in the STDF zone of southwest Puerto Rico (Ewel and Whitmore, 1973). Annual rainfall is highly variable and averages 860 mm yr^{-1} with two wet seasons: a major one from August through November and a minor one from April through May (Murphy and Lugo, 1986b). Temperatures fluctuate little throughout the year and average 25.1 °C. Soils are generally shallow, alkaline, and derived from calcareous substrates (USDA, 2008). Guánica Forest has been cited as one of the best-preserved Caribbean dry forests (Ewel and Whitmore, 1973), although areas of it were used for agriculture before the 1930s and for charcoal wood cutting until the 1970s (Murphy and Lugo, 1990). Multi-stemmed trees dominate the canopy, which reaches 5–12 m height (Murphy and Lugo, 1986b).

The coastal area of Guánica Forest was used for this study because this is where the majority of grass invasion and fire occur within the protected area (Murphy et al., 1995). The road that transects this area, PR 333, has facilitated visitor traffic and associated wildfires for nearly 100 years (Miguel Canals, Guánica Forest Manager, personal communication). Since 1986, prescribed fires have been used in grass-invaded areas along the road to limit the encroachment of uncontrolled fires into adjacent forest. Three of these sites, which had burned repeatedly in prescribed or arson fires for at least 10 years, were used for this study. The sites were located <4 km apart, 5–20 m asl, and 5–500 m inland from the coast (Appendix A). The grass-invaded areas ranged 500–5000 m^2. They were dominated by *Pennisetum ciliare* (L.) Link and to a lesser extent *Bothriochloa pertusa* (L.) A. Camus and *Urochloa maxima* (Jacq.) R.D. Webster. The adjacent forest stands used in this study were contiguous with the intact, forested area of Guánica Forest. Their structure and composition were typical of unburned stands (c.f., Lugo et al., 1978). Trees of *Bucida buceras* L. and *Bursera simaruba* (L.) Sarg. formed the canopy.

2.2. Tree species selection and rearing

Saplings of 13 tree species native to the dry forest zone of Puerto Rico and the non-native *Leucaena* were used in this study (Table 1). Native species were selected based on their presence in mature stands of Guánica Forest and on their availability at local nurseries. Availability was considered so that results could be immediately applied to reforestation programs. The native species included the two dominant canopy species (*B. buceras* and *B. simaruba*) and other species common in mature stands in Guánica Forest (c.f., Lugo et al., 1978; Murphy and Lugo, 1986b). One of the species, *Coccoloba uvifera*, is restricted to coastal areas and another, *Pisonia subcordata*, is restricted to moist sites, while the others are distributed throughout the forest. Eight of the native species had been used in planting programs by the US Fish and Wildlife Service (Weaver and Schwagerl, 2008). All eight were rated "good" or "fair" for growth. Seven were rated "good" or "fair" for survival, while *C. uvifera* was rated "poor."

The saplings were 2–3 years old when they were acquired in May–September 2007. They were repotted to 4-L polyvinyl bags with a mixture of soil collected from an intact area of Guánica Forest, commercial potting soil, and composted chicken manure. Within species, plants were randomly assigned to experimental treatments, acclimated in full sun (grass treatments) or the shade of large trees (forest treatment) for 4 weeks prior to planting, and hardened by incrementally decreasing the watering interval

Table 1
Characteristics of the 14 tree species planted in this study. Canopy positions listed as Canopy and Subcanopy refer to mature forest. Dispersal modes were determined based on fruit/seed morphology. Leaf phenology was based on field notes. See Little and Wadsworth (1964) for species authorities.

Family	Species	Canopy position	Dispersal mode	Leaf phenology
Boraginaceae	*Bourreria succulenta*	Subcanopy	Animal	Evergreen
Combretaceae	*Bucida buceras*	Canopy	Unknown	Semi-deciduous
Burseraceae	*Bursera simaruba*	Canopy	Animal	Deciduous
Verbenaceae	*Citharexylum fruticosum*	Subcanopy	Animal	Deciduous
Polygonaceae	*Coccoloba diversifolia*	Canopy	Animal	Evergreen
Polygonaceae	*Coccoloba uvifera*	Coastal sites	Animal	Evergreen
Celastraceae	*Crossopetalum rhacoma*	Subcanopy	Animal	Evergreen
Erythroxylaceae	*Erythroxylum areolatum*	Subcanopy	Animal	Deciduous
Rubiaceae	*Guettarda elliptica*	Subcanopy	Animal	Deciduous
Mimosoideae[a]	*Leucaena leucocephala*	Disturbed sites	Ballistic	Semi-deciduous
Faboideae[a]	*Pictetia aculeata*	Subcanopy	Ballistic	Deciduous
Nyctaginaceae	*Pisonia albida*	Canopy	Clinging	Deciduous
Nyctaginaceae	*Pisonia subcordata*	Moist sites	Clinging	Deciduous
Bignonaceae	*Tabebuia heterophylla*	Subcanopy	Wind	Deciduous

[a] Subfamily of Fabaceae.

to once per week. In late October 2007 (peak rainy season), the saplings were planted into hand-dug holes in the field with their potting substrate and 50 g of granular super-phosphate fertilizer (0–50–0) to encourage rooting. At planting and nine times afterwards, each sapling was watered with eight liters of water to encourage establishment. Watering was applied when 7 consecutive days passed without at least 10 mm of rain and was discontinued after the rainy season in April 2008 to assess plant performance in the seasonal drought conditions that are common in the region (Lugo et al., 1978).

2.3. Planting design and prescribed fire application

At each of the three sites, saplings were planted in three vegetation types: grass (“unburned grass”), grass subsequently subjected to a controlled burn (“burned grass”), and forest understory. Eight planting plots were located in the grass and three plots in the adjacent forest >5 m from the forest edge. The plots were placed 2–20 m apart because rock outcrops prevented uniform spacing. Each plot contained one individual of each species spaced approximately 1 × 1 m. Species that lacked sufficient replicates were excluded from randomly selected plots (Appendix B). In five cases, two plants of the same species were planted in the same plot, so the number of plants per species ranged from 25 to 35 and the total was 455 plants. Five plants that died within a month of planting were not included in the analyses because their deaths were presumably related to transplanting stress.

Four grass plots at each site were randomly selected to be burned during the routine prescribed fires in February 2008, 4 months after planting. Unburned-grass plots were protected during the controlled burns by trimming the grass to ground level and raking away the litter. Trimming reduced aboveground grass biomass and fuel loads, but did not remove grass from the plots, as it vigorously grew back in the next rainy season. The prescribed burns were impacted by three unplanned events. First, one of the burned-grass plots at Site 1 was located too close to the forest edge for it to be burned without danger of the fire escaping into the forest. So it was left unburned, the grass was trimmed, and saplings were placed in the unburned-grass treatment. Second, an arson fire burned at Site 2 two days before the prescribed burns. The fire burned only outside of the firebreaks, leaving protected saplings unaffected, but it precluded measurements of fire characteristics (described below). Third, during the prescribed burn at Site 3, the fire entered three of the fire-protected grass plots and a section of the fourth plot. The saplings in these plots were subsequently placed in the burned-grass treatment for analyses of survival and growth. Thus, after the burns, there were a total of 9 unburned-grass plots and 15 burned-grass plots. Because the unintentionally burned plots had cut grass, they were separated from the intentionally burned plots for analyses of fire characteristics.

2.4. Measurements of environmental parameters

Soil samples were collected for nutrient content analysis in April 2008, 2 months after the prescribed fires. Three randomly located samples were collected in each treatment at each planting site ($n = 27$). Each was a composite of three cores taken one meter apart with a 5.7-cm diameter corer to a depth of 5 cm after clearing away the leaf litter and duff. Samples were air dried, passed through a 2-mm sieve, and analyzed by the USDA Forest Service Institute of Tropical Forestry Laboratory in Rio Piedras, Puerto Rico. Total elements (P, K, Ca, Mg, Al, Mn, and Fe) were assessed using a digestion method (concentrated HNO_3 and 30% H_2O_2; Huang and Schulte, 1985) followed by plasma emission spectrometry. Total N, C, and S were measured with dry combustion at 1450 °C in a LECO CNS analyzer (LECO Corp., St. Joseph, MI). Organic matter was measured as loss on ignition in a muffle furnace at 490 °C. Soil pH was determined in 1:1 soil/H_2O solution.

Leaf area index (LAI, defined as the ratio of one-sided leaf surface area to ground surface area) was measured as a proxy of the shading that the saplings received. Measurements were made with an LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE) at one meter height in nine randomly selected points within each plot and two reference points in a clearing (>30 m from the nearest tree). The grass did not reach 1-m height, so our measurements did not assess the shading that it provided to the lower branches of planted saplings. Measurements were taken once in the dry season (April 2008) and once in the rainy season (November 2008).

Weather measurements from the Western Regional Climate Center (WRCC, www.wrcc.dri.edu) were used for comparison of air temperature, relative humidity, and wind speed during the prescribed fires and daily precipitation throughout the study. The WRCC weather station was located in Guánica Forest, within 2 km of the planting sites.

2.5. Measurements of fire characteristics

Pre-burn fuel loads and fire consumption were measured with paired sampling plots (c.f., Thaxton and Platt, 2006). Six 0.5 × 0.5 m plots were randomly placed at each site and all plant material was collected in half the plot the day before burning and in the other half 2 days after burning. The collections were oven dried at

65 °C, separated between fine and coarse (>5 mm diameter) material, and weighed. Fuel consumption was calculated as the difference between pre- and post-burn mass. Only fine material was analyzed because coarse material was sparse (1.8 ± 0.07% of total fuel load; mean ± SE) and spatially heterogeneous.

Peak fire temperature was measured with temperature-sensitive paints and chalks (Omega Engineering, Stamford, CT). Paints rated to melt at 79, 93, 107, 121, 135, 149, 163, 177, 204, 260, 316, 427, and 538 °C were applied to 10 × 2-cm strips of heavy-duty aluminum foil. Chalks rated to melt at 52 and 66 °C were applied to 5 × 1-cm strips of fine-grain sandpaper. The two strips were enclosed in another layer of foil to create temperature sensors. Sensors were staked to the ground at the base of each sapling immediately before the fires. On taller saplings, sensors were wrapped loosely around the stem at 50 and 100 cm heights. Peak temperature was recorded as the highest temperature paint or chalk that melted. This is an imperfect measure of fire intensity because it does not incorporate flame residence time, yet it is a useful proxy with which to relate biotic responses (Bond and van Wilgen, 1996; Kennard et al., 2005).

2.6. Measurements of sapling performance

Sapling survival was monitored monthly for 20 months. Plants with thoroughly brittle and leafless stems were presumed dead. They were retroactively classified as alive if resprouts were subsequently detected. Sapling size was measured at the time of planting and 3, 8, 12, and 20 months afterwards. Plant height was measured as the distance above the ground of the highest live stem, straightening stems if they were bent. Stems were marked with a permanent marker at 5 cm height, where basal diameter was measured twice perpendicularly with calipers to the nearest 0.1 mm and averaged. Growth rates were calculated for trees that survived at least 1 year after planting as the slope of the linear regression of size over time in units of millimeter per month, using basal diameter and height in separate analyses. Linear regression accurately modeled growth rates (Appendix C). Because many burned saplings resprouted from the base of the stem, their growth was assessed as live stem height and as total auxiliary shoot length (sum of lengths of all shoots branching from the main stem) at 20 months after planting.

2.7. Data analysis

Environmental and fire characteristic data were analyzed using SAS 9.1.3 (SAS Institute Inc.). Peak fire temperature was compared among sites and heights using ANOVA (proc MIXED). Site, height and their interaction were treated as fixed effects. Plots and individual trees were treated as random nested effects, with height split within tree. Temperature sensors that did not register the minimum 52 °C ($n = 0$ at ground level, $n = 5$ at 50-cm height, $n = 4$ at 100-cm height) were assigned the value 38 °C, the midpoint between 52 °C and the mean air temperature during the fires (25 °C).

LAI was compared among sites, treatment, and seasons with ANOVA (proc MIXED). Site, treatment and season were treated as fixed effects. Plots were treated as randomly nested effects with season split within plot. Values were $\log(x + 1)$-transformed before analysis to improve normality and homoscedasticity. Soil nutrient values were compared among planting treatments in separate ANOVAs with planting treatment and site as fixed effects.

Plant performance data were analyzed using R 2.13.1 (R Development Core Team, 2011). Survival rates over the 20 months were assessed using a Cox proportional hazard ratio analysis (package Survival). Survival in the planting treatments and between native species and *Leucaena* were compared by computing hazard ratios (HR) after clustering for the native species and sites. HR > 1 indicates an increased risk of mortality.

The factors that influenced sapling survival during the prescribed fires were assessed using logistic regression modeling for individuals scored as survivors or non-survivors (package LME4). An initial "full" model was created and then fit by sequentially removing random-effect terms then fixed effects terms using likelihood ratio testing (Zuur et al., 2009). In the full model, species were treated as random effects as were plots nested within sites. Fixed effects were provenance (introduced (i.e., *Leucaena*) vs. native), planting site, peak fire temperature at ground level, basal diameter, and height. The minimum adequate model included planting site and peak fire temperature as fixed effects and species as a random effect.

Growth rates in basal diameter and height were compared between native species and *Leucaena* and between the forest and unburned-grass treatments with mixed-model ANOVA (package LME4). Provenance, treatment, and the treatment × provenance interaction were treated as fixed effects and species were treated as random effects. Site and plot nested within site were not included in the model because likelihood ratio testing showed that these factors did not improve the model fit. Because so few saplings in the burned-grass treatment survived to 20 months, growth rates between pooled individuals of native species ($n = 5$) were compared to *Leucaena* ($n = 3$) using Welch's modified t-tests for unequal variance.

3. Results

3.1. Environmental parameters

Soil in the burned- and unburned-grass plots had significantly reduced C, N, S and organic matter compared to the forest plots (Table 2). Soil mineral content was similar among treatments; although, Al, Fe, and Mg contents trended higher in the burned- and unburned-grass treatments than the forest. Soil in the burned- and unburned-grass plots had significantly higher pH than the forest plots.

Mean LAI in the forest plots was 1.25 (1.02–1.50; 95% confidence interval) and 2.79 (2.41–3.22) in the dry and wet seasons, respectively. In the grass plots, mean LAI was 0.05 (−0.01–0.12) and 0.11 (0.04–0.19) in the dry and wet seasons, respectively. LAI varied significantly with treatment, season, and the treatment × season interaction ($p < 0.0001$ for each effect), but not among the planting sites ($p = 0.18$). LAI was near zero in the grass treatments because shade above the grass canopy came only at angles near the horizon from trees near the plots.

3.2. Fire characteristics

Pre-burn fuel loads and fuel consumption did not vary between Site 1 and the uncut areas of Site 3 (Table 3). Peak fire temperature was significantly different among sites (Site 1, Site 3 cut-grass, Site 3 uncut-grass) and heights ($F_{[2,8]} = 11.08$, $p = 0.0049$ and $F_{[2,131]} = 221.71$, $p < 0.0001$, respectively), but not their interaction ($F_{[4,131]} = 2.32$, $p = 0.061$). Peak temperature was highest at ground level at all three sites (Table 3). The removal of grass and topsoil while planting likely reduced the fire temperature adjacent to the saplings. Twelve temperature sensors were staked to the ground in the fuel-load plots. Three of these reached 427 °C, six reached 538 °C, and three had melted aluminum, which occurs at 660 °C. These results indicate that grassy areas undisturbed by planting had a mean peak temperature at ground level of ~540 °C. None of the sensors placed on planted saplings had melted aluminum.

Table 2
Soil nutrient content in the three planting treatments. Values are mean (SE). *F* and *p* values are for the treatment effect in ANOVA analyses. When the effect was significant ($p < 0.05$), Tukey pairwise comparisons were made among treatments. Treatments that share a letter were not significantly different.

Soil character	Forest	Unburned grass	Burned grass	*F*	*p*
pH	7.90 (0.07)[a]	8.16 (0.05)[b]	8.22 (0.05)[b]	107.78	0.0003
Al (mg/g)	23.86 (2.28)	31.79 (1.75)	31.79 (4.1)	6.83	0.0513
Ca (mg/g)	85.26 (14.14)	81.67 (16.02)	70.99 (14.61)	0.17	0.8459
Fe (mg/g)	23.55 (3.86)[a]	37.98 (4.63)[b]	40.45 (1.53)[b]	7.09	0.0484
K (mg/g)	2.90 (0.61)	4.13 (0.89)	4.22 (1.31)	2.22	0.2244
Mg (mg/g)	5.97 (0.21)	8.24 (1.56)	14.10 (3.35)	6.56	0.0546
Mn (mg/g)	0.78 (0.14)	0.96 (0.16)	0.85 (0.09)	0.47	0.6537
Na (mg/g)	0.29 (0.06)	0.22 (0.09)	0.23 (0.09)	0.56	0.6084
P (mg/g)	3.34 (1.3)	2.28 (0.4)	2.13 (0.7)	0.59	0.5954
C (%)	24.11 (1.86)[a]	10.50 (1.39)[b]	7.83 (1.47)[b]	34.19	0.0031
N (%)	2.00 (0.07)[a]	0.81 (0.10)[b]	0.54 (0.13)[b]	80.2	0.0006
S (%)	0.30 (0.01)[a]	0.14 (0.01)[b]	0.11 (0.02)[b]	71.88	0.0007
Organic matter (%)	46.00 (2.30)[a]	24.03 (1.38)[b]	19.98 (3.28)[b]	24.55	0.0057

Table 3
Fire characteristics. Standard errors are in parentheses. Values that share letters within columns do not vary significantly as determined by Tukey pairwise comparisons ($p < 0.05$). Biomass and peak temperature measurements were precluded at Site 2 by an arson fire. The Site 3 cut-grass fire was unplanned. It occurred when the prescribed fire burned areas where the grass was cut to ground level and raked away (see methods).

Burn site	Fire date and time of day	Air temp. (°C)	Relative humidity (%)	Avg. wind speed ($m\ s^{-1}$)	Burn area (m^2)	Pre-fire biomass ($g \cdot m^{-2}$)	Biomass consumed (%)	Mean peak temperature (°C)		
								Ground level	50-cm height	100-cm height
Site 1	Feb. 22, 700 h	22.2	71	0.0	200	616 (72)[a]	90 (4)[a]	376 (22)[a,b]	192 (17)[a]	145 (16)[a]
Site 2	Feb. 20, 1500 h	25.0	72	3.6	5000	–	–	–	–	–
Site 3 uncut-grass	Feb. 22, 1200 h	28.9	46	4.0	500	476 (95)[a]	90 (2)[a]	409 (19)[a]	155 (15)[a]	132 (15)[a]
Site 3 cut-grass	Feb. 22, 1200 h	28.9	46	4.0	300	–	–	289 (22)[b]	80 (16)[b]	69 (21)[a]

3.3. Sapling survival

Overall, 134 of 450 (30%) saplings survived 20 months after planting. Survival of native species was highest in the forest understory, where 57 of 113 (50%) saplings survived, followed by the unburned grass, where 53 of 134 (40%) survived, and the burned grass, where only 5 of 172 (3%) survived (Table 1, Fig. 1). For *Leucaena* survival was 8 of 9 (90%), 8 of 10 (80%), and 3 of 12 (25%), in the forest, unburned-grass, and burned-grass treatments, respectively. High risk of sapling mortality in the burned grass was clear, but Cox proportional hazard analysis also showed that native species had increased risk of mortality in the unburned grass compared to the forest (natives, forest:grass HR = 1.43, $n = 250$ $p = 0.036$). However, this effect was due almost entirely to the increased mortality that occurred during June–August, 2008, when only 32.8 mm of rain fell over 60 days. During this drought, mortality of native saplings was high in all three treatments, yet significantly more died in the unburned grass than in the forest (51 of 122 vs. 21 of 100, chi-square test: $\chi^2 = 13.1$, $p < 0.001$). Native saplings that survived past August 2008 had marginally increased mortality risk in the forest compared to the unburned grass (natives, forest:grass HR = 0.43, $n = 140$, $p = 0.082$). In all treatments, *Leucaena* had lower mortality than native species, however the HR was only statistically significant in the forest (forest, *Leucaena*:natives HR = 6.08, $n = 122$, $p = 0.032$; unburned grass, *Leucaena*:natives HR = 3.65, $n = 144$, $p = 0.07$; burned grass, *Leucaena*:natives HR = 2.07, $n = 188$, $p = 0.28$).

The prescribed fires scorched the entire crown of every sapling in the burned-grass treatment. The leaves were charred in the fire or turned brown within a few days of burning, presumably due to overheating. Those plants that survived burning resprouted from the roots, root collar, or stems up to 175 cm height. Of the 184 saplings that burned, 67 (36%) resprouted, most within 5 months of the fire. All species resprouted, ranging 17–67% of individuals. Model fitting with logistic regression revealed that attributes of plant size (basal diameter and height) and provenance (native vs. *Leucaena*) did not affect burn survival. Peak fire temperature at ground level and planting site significantly affected sapling survival during the burns (temperature coefficient ± SE = 0.010 ± 0.003, $z = 4.09$, $p < 0.0001$; site coefficient ± SE = 1.94 ± 0.61, $z = 3.18$, $p < 0.01$; Fig. 2).

3.4. Sapling growth

Most native saplings grew very little in basal diameter over the 20 months. The average diameter growth rate for natives in the forest understory was just 0.004 ± 0.042 mm $month^{-1}$ (mean ± SE), while in the unburned grass the natives grew 0.081 ± 0.059 mm $month^{-1}$. *Leucaena* in the forest grew in diameter 0.144 ± 0.039 mm $month^{-1}$, which was dwarfed by its growth in the unburned grass, 0.853 ± 0.055 mm $month^{-1}$ (Fig. 3). The ANOVA showed that the effects of planting treatment (grass vs. forest), provenance (*Leucaena* vs. native), and their interaction were significant ($F_{[1,124]} = 87.9$, $p < 0.0001$; $F_{[1,12]} = 227.2$, $p < 0.0001$; $F_{[1,124]} = 114.1$, $p < 0.0001$; respectively). Tukey pairwise testing ($\alpha = 0.05$) showed that diameter growth was higher in the grass than in the forest for both native species and *Leucaena*. *Leucaena* diameter growth was also higher than that of native species in both the forest and the grass. The difference between the growth rates of *Leucaena* and native saplings was 5.5 times greater in the grass than the forest (Fig. 3).

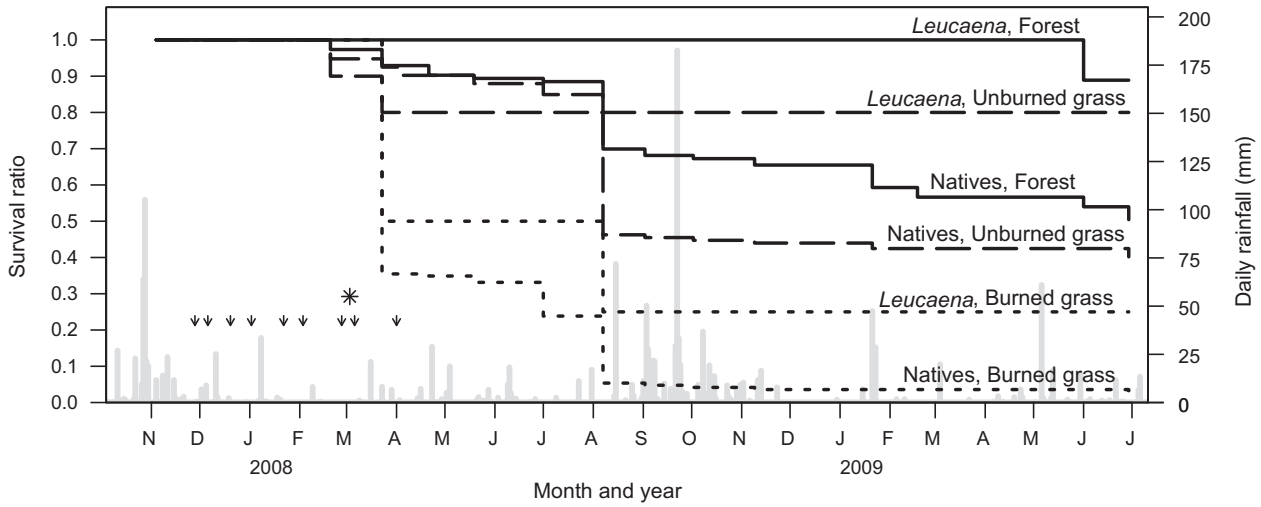

Fig. 1. Daily rainfall (gray bars) and survival ratios of saplings throughout the 20-month project period. Species (natives species pooled and *Leucaena*) and planting treatments are labeled above each line. The asterisk indicates the day of the prescribed fires. Arrows indicate days of supplemental watering.

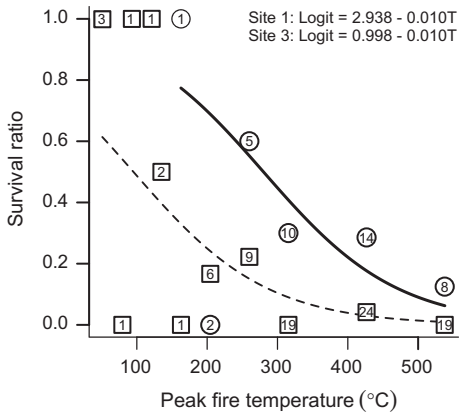

Fig. 2. The ratio of saplings that survived burning in prescribed fires as a function of peak temperature at ground level. Circles represent Site 1. Squares represent Site 3. Fire temperature measurements were precluded at Site 2 by an arson fire. The number of saplings measured at each temperature and site is indicated within each point. The solid and dashed lines represent the probability of survival for Site 1 and Site 3, respectively, as calculated by logistic regression. The logit link function for each site is shown, where *T* equals peak fire temperature at ground level.

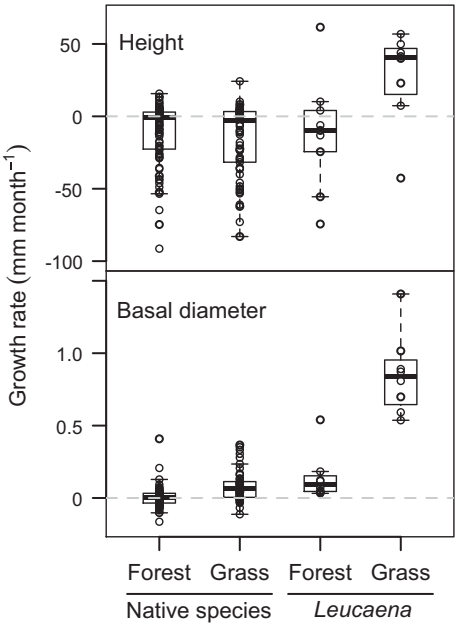

Fig. 3. Growth rates in height (upper panel) and basal diameter (lower panel) for the saplings that survived at least 1 year after planting in the forest understory and unburned grass. Negative height growth rates represent stem dieback. Boxes enclose the 25th and 75th quartiles and are bisected by the medians. Bars extend to the 5th and 95th quartiles. Each sapling is represented as a circle. Dashed lines at zero are shown for reference.

Stem dieback from desiccation was common in all species and treatments, resulting in highly variable growth rates for plant height (Fig. 3). Native sapling dieback rates were -12.8 ± 13.6 mm month^{-1} in the forest and -17.1 ± 12.0 mm month^{-1} in the unburned grass. *Leucaena* also lost height in the forest at a rate of -12.0 ± 13.0 mm month^{-1}, but grew in the unburned grass at 27.5 ± 11.3 mm month^{-1}. The ANOVA model showed that planting treatment and provenance were not significant ($F_{[1,133]} = 0.6$, $p = 0.8$; $F_{[1,12]} = 3.0$, $p = 0.1$; respectively), while their interaction was significant ($F_{[1,133]} = 13.3$, $p = 0.0004$). Tukey pairwise testing ($\alpha = 0.05$) showed that height growth for *Leucaena* was higher in the unburned grass than in the forest. *Leucaena* height growth in the unburned grass was also higher than that of native species in the unburned grass. Native species' height growth did not vary between the forest and unburned grass.

For the saplings that survived to 20 months in the burned-grass plots (Table 1), *Leucaena* was taller (89 ± 23 vs. 31 ± 12 cm; $t = 3.57$, df = 2.67, $p = 0.045$) and had greater total shoot length (284 ± 62 vs. 68 ± 14 cm; $t = 5.41$, df = 4.15, $p = 0.043$) than the native species. They did not differ in the number of shoots per plant (9 ± 2 vs. 6 ± 2 shoots per plant; $t = 1.42$, df = 6.00, $p = 0.20$).

4. Discussion

4.1. Sapling performance in grass-invaded areas and forest understory

All species were highly susceptible to the fires that are common in grass-invaded areas. Saplings were more likely to survive burning when the peak fire temperature at their base was lower, but at any temperature, survival was higher at Site 1 than Site 3 (Fig. 2). Because Site 1 was burned in the early morning, it is possible that dew present on the saplings buffered stem temperatures. Of the saplings that survived the fires, few lived to the next wet season (Fig. 1). The late summer drought reduced survival of burned saplings more quickly and to a greater degree than saplings in the

unburned-grass and forest treatments (Fig. 1), perhaps because the burned saplings allocated their carbohydrate reserves to resprouting and then lacked resources to survive through the drought (Hoffmann et al., 2003; McDowell et al., 2008).

Native saplings in the unburned grass also experienced higher mortality than those in the forest understory during the summer drought (Fig. 1). The lack of overstory shade is probably a principal determinant in this mortality. Ray and Brown (1995b) found that seedlings of ten native tree species planted in an abandoned pasture in a U.S. Virgin Islands STDF had 9-month survival rates of 0–65% (mean = 29%) while seedlings planted under mesh cloth had survival rates of 45–90% (mean = 71%). Similarly, McLaren and McDonald (2003b) found that seedlings of four native tree species sown as seeds in a Jamaican STDF had increased mortality in low-shade treatments, especially during a seasonal drought. In a Costa Rican TDF, Gerhardt (1996) found that canopy thinning decreased the survival rate of three tree species planted as seedlings in the understory, while survival of a fourth species increased. Shade would improve seedling survival during droughts by lowering temperature and evaporative demand (Holmgren et al., 1997). With forest plots having moderate shade during the dry season (LAI = 1.25), our results suggest that the ameliorating effect of shade extends beyond the seedling stage and into the sapling stage as well.

Reduced soil quality in the grass-invaded areas may have contributed to the increased sapling mortality in these areas. Although the 8% total C found in the burned-grass plots (Table 2) would be relatively high in other sites, in Guánica Forest this is inorganic C from calcium carbonate (USDA, 2008). The past fires in the burned- and unburned-grass treatments likely reduced soil C, N, S, and organic matter content, although grass invasion could have influenced these properties independently of fire (Litton et al., 2008). Temperatures as low as 100–300 °C volatilize organic compounds and N (Neary et al., 1999), so even for short durations, the temperatures of the prescribed fires (Table 3) were capable of substantially reducing organic matter content and N at the soil surface. Although S does not volatize at temperatures below 800 °C (Neary et al., 1999), it could have been mineralized and leached out or volatilized by hotter fires in the past. Organic matter improves soil water and nutrient holding capacities and is often reduced after intense fires, which may represent a stable shift in soil condition when forests are converted to grass cover (Johnson and Wedin, 1997; Fearnside and Barbosa, 1998; Kennard and Gholz, 2001).

The seasonality of precipitation experienced by the saplings was typical for Guánica Forest. From June to August 2008, it rained only 32.8 mm (Fig. 1). Four other 60-day or longer periods with less than 33 mm of rain were recorded at the WRCC weather station between June 2005 and May 2009. The high seedling and sapling mortality associated with these droughts (Fig. 1) combined with slow growth and stem dieback (Fig. 3) is a major limitation to native forest regeneration in grass-invaded areas.

Leucaena had a much higher growth rate than native species in the grass-invaded areas (Fig. 3). Moreover, *Leucaena* saplings began producing seeds 8 months after they were planted and by 20 months, six of the eight saplings that survived in the unburned-grass treatment had produced seeds (not shown). High growth and survival rates are common traits among invasive tree species, as are high germination rates, plant biomass, and stem density (Lamarque et al., 2011). The traits that led *Leucaena* to outperform the native species in the grass treatments are likely to be adaptations associated with its functional niche in its native range. In the Yucatán peninsula, Mexico, *Leucaena* is a nitrogen-fixing pioneer that occupies areas after high-intensity wildfires sparked by lightning completely combust the thin organic soils overlaying karstic substrate (Allen et al., 2003; Vargas et al., 2008). Of the two legume tree species native to Puerto Rican STDF, only *Pithecellobium unguis-cati* is known to form nitrogen-fixing nodules, while this trait has not been reported in *Pictetia aculeata* (Sprent, 2001). Since its introduction to Puerto Rico sometime before 1825 (Parrotta, 1992), *Leucaena* appears have played the role of a pioneer tree in highly degraded STDF (Molina Colón and Lugo, 2006; Weaver and Schwagerl, 2008). Because fires were infrequent or absent in Puerto Rican STDF prior to human disturbance (Murphy et al., 1995), this successional pathway was not prevalent for native species. Natural disturbances common in Puerto Rico, such as hurricanes, do not create large clearings in STDF and regeneration is dominated by resprouting (Murphy et al., 1995; Van Bloem et al., 2005). Adaptation to closed-canopy regeneration may explain why native species perform relatively poorly in highly degraded, grass-invaded areas.

4.2. Restoring native dry forest plant communities

Restoring native plant communities is particularly challenging where invasive plants have altered fire regimes and ecosystem properties (Brooks et al., 2004). Reestablishing pre-invasion fire regimes is a practical precursor to restoring pre-grass-invasion plant communities. Reducing fire frequencies in STDF and TDF is greatly facilitated by the formation of closed forest canopies that suppress grass by shading (Janzen, 1988; Aronson et al., 2005). Even when fires occur where grass has been partially suppressed, the reduced fire intensity should allow greater sapling survival (Fig. 2). The native tree species that we planted had very low growth rates, indicating a low potential for forming a closed canopy, exposing them to the deadly threat of grass fires for many years. However, *Leucaena* grew at an exceptional rate in the unburned-grass treatment and recovered relatively well in the burned-grass treatment, showing the potential to form a closed canopy. In a study located ~50 km east of Guánica Forest, where soils were deeper and annual rainfall was slightly higher (mean = 1060 mm yr^{-1}), Francis and Parrotta (2006) showed that stands of planted *Leucaena* suppressed grasses after 5–7 years.

When *Leucaena* stands develop in grass-invaded areas, one novel ecosystem (*sensu* Hobbs et al., 2009) is replaced by another that restores ecosystem function and structure. *Leucaena* has also been shown to act as a nurse tree, promoting the natural regeneration of native forest species and the success of underplanted native trees (Parrotta, 1995; Santiago-García et al., 2008). *Leucaena* is used extensively outside of Puerto Rico in agroforestry, but its application for ecological restoration is rare (Bryan, 1999; Francis and Parrotta, 2006). In degraded areas where *Leucaena* grows without management inputs, passively allowing it to grow provides a low-cost means to reduce fire susceptibility, ameliorate the microclimate, and improve soil conditions. In severely degraded areas where forest regeneration does not occur without management inputs, planting *Leucaena* "may be the most realistic and only satisfactory course of action" (Griscom and Ashton, 2011).

Leucaena is considered a highly invasive species (Rejmanek and Richardson, 1996). In Puerto Rico, *Leucaena* is ubiquitous along untended roadsides and common in highly degraded areas (Little and Wadsworth, 1964). Yet, it does not appear to displace native STDF or regenerate under itself without repeated disturbance (Molina Colón and Lugo, 2006; Pérez Martínez, 2007), perhaps because its growth is suppressed under forest canopies (Fig. 3) and seedlings do not survive well in shade (S.J. Van Bloem, unpublished data). However, in the forest understory we found that *Leucaena* outperformed native species in survival and basal diameter growth, suggesting the ability to establish there once it reaches sapling size. Because considerable time lags may exist between species introduction and invasion (D'Antonio and Meyerson, 2002), caution is warranted when using *Leucaena* as management tool.

Where the risk of wildfires can be effectively reduced by other management techniques, the advantage of fast-growing

introduced species is reduced. Planting native species is a more viable restoration option in these cases. The native species that performed best in grass-invaded areas was *B. simaruba*, which had high survival and consistent growth in both basal diameter and height (although its growth was still much slower than *Leucaena*'s; Appendix D). These attributes also suggest *Erythroxylum areolatum* as a useful species for direct-to-native restoration. Soil-nutrient addition, artificial shading, and reducing grass cover around the base of transplanted or naturally regenerating native species may also improve their growth and survival.

5. Conclusion

Regeneration of native STDF tree species in grass-invaded areas is limited by stochastic and episodic events such as wildfire and drought. The long-term failure of native tree species to establish in grass-invaded areas is probably exacerbated by degraded soil and a lack of drought-ameliorating overstory shade. Recurrent fires pose a strong barrier to saplings; because native species grow slowly in both the forest understory and grass-invaded areas, they are vulnerable to this deadly threat for many years until they reach larger, more resistant sizes. However, native saplings transplanted into grass-invaded areas not subjected to fire grew faster than those planted in forest understory, suggesting an ability for survivors to establish in reforestation projects that effectively control fire. Our results show that the tendency for *Leucaena* to dominate secondary STDF in Puerto Rico is attributable to its much higher growth rate in these areas, lower mortality during drought, and better recovery following burning. These features suggest *Leucaena* as a promising tool for restoring STDF, particularly in areas where it has already become widespread, such as Puerto Rico and many other Caribbean Islands.

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Appendices A–D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.12.015.

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