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RESEARCH ARTICLE

Testing the Performance of Fourteen Native Tropical Tree Species in Two Abandoned Pastures of the Lacandon Rainforest Region of Chiapas, Mexico

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Abstract

The rainforest of Mexico has been degraded and severely fragmented, and urgently require restoration. However, the practice of restoration has been limited by the lack of species-specific data on survival and growth responses to local environmental variation. This study explores the differential performance of 14 wet tropical early-, mid- or late-successional tree species that were grown in two abandoned pastures with contrasting land-use histories. After 18 months, seedling survival and growth of at least 7 of the 14 tree species studied were significantly higher in the site with a much longer history of land use (site 2). Saplings of the three early-successional species showed exceptional growth rates. However, differences in performance were noted in relation to the differential soil properties between the experimental sites. Mid-successional species generally showed slow growth rates but high seedling survival, whereas late-successional species exhibited poor seedling survival at both the study sites. Stepwise linear regressions revealed that the species integrated response index combining survivorship and growth measurements, was influenced mostly by differences in soil pH between the two abandoned pastures. Our results suggest that local environmental variation among abandoned pastures of contrasting land-use histories influences sapling survival and growth. Furthermore, the similarity of responses among species with the same successional status allowed us to make some preliminary site and species-specific silvicultural recommendations. Future field experiments should extend the number of species and the range of environmental conditions to identify site "generalists" or more narrowly adapted species, that we would call "sensitive."

Key words: ***Cynodon plectostachyus*, ecological restoration, land-use history, seedling performance, soil properties, tree plantations.**

Introduction

The Lacandon region of Chiapas (1.25 million ha in size), southern Mexico, contains the major remnant of tropical rainforest in the Mexican territory. It also stretches into Guatemala and Belize, thus constituting the most extensive tract of this biome in Mesoamerica, and one of the largest in the Neotropics (Pennington & Sarukhán 2005). About 60% of this region is still covered with evergreen and semievergreen forests, including the seven protected areas present in the region, which covers approximately 400,000 ha (Mendoza & Dirzo 1999). The remaining 40% has been altered, primarily to logging, cattle ranching, and agriculture during the past 40 years. Between 1970 and 1990, the total area of mature forest decreased nearly one-third (−31%), whereas agricultural land and pasture increased (+21 and +92%, respectively) (De Jong et al. 2000). Pastures for cattle ranching in the Lacandon region are principally dominated by the invasive stargrass *Cynodon plectostachyus* (K. Schum.) Pilg., a C4 grass native to Africa, which reaches an average height of 1.0–1.5 m and quickly forms dense, impenetrable stands (Esquivel et al. 2008). Overgrazing, excessive herbicide application, and/or deliberate and excessive use of fire to control weeds often lead to cattle raising becoming economically unviable. This in turn results in degraded, and often abandoned, pastures that promote fire, and in which native trees have difficulty in recolonizing (Martínez-Ramos & García-Orth 2007).

Many examples in the tropics show the need for active restorative interventions to initiate or accelerate succession toward a forested condition, particularly when the rate of recovery of abandoned areas appears to be slow or in a

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state of arrested succession (Zahawi & Augspurger 1999; Douterlungne et al. 2010; Holl & Aide in press). Ecological restoration also offers an opportunity to recover forest services and benefits, especially in rural communities where socioeconomic goals are the main determinants of management choices (Diemont & Martin 2009; Aronson et al. 2010). The reintroduction of native tree species of different successional status that could potentially be used for handicraft activities and the extraction of forest products, would contribute to the local economy, as well as to biodiversity enhancement by attracting seed dispersers and facilitating natural tree regeneration (Erskine et al. 2006; Rey Benayas et al. 2009).

The current small-scale reforestation projects supported by government agencies and nongovernmental organizations (NGOs) near the Montes Azules Biosphere Reserve in Chiapas are becoming increasingly common in recent years. However, as in many other tropical regions, incipient financial markets and a lack of basic silvicultural data of useful/commercial native rainforest trees impede the widespread adoption of tree plantations for ecological restoration, carbon sequestration, and timber production (Piotto 2008; Milder et al. 2010). Matching species with planting sites appropriately is of vital importance to guarantee successful seedling performance in tree plantations (Butterfield 1995; Shankar Raman et al. 2009). However, productivity among tree plantations and secondary forests, could be affected by local and regional differences in microclimate, soil characteristics, and land-use history (Park et al. 2010; Holl & Aide in press). Nonetheless, the influence of such environmental variation on sapling development of early-, mid- and late-successional native rainforest trees remains poorly studied (Gourlet-Fleury et al. 2005; Russo et al. 2005).

For this study, we examined whether seedling survival and growth of 14 wet tropical native tree species, of three different successional groups, are affected by site conditions of two *Cyn. plectostachyus*-dominated abandoned pastures with contrasting land-use histories. Elsewhere in the tropics, low remnant plant species richness and degraded soil properties after agricultural land use have been related to recent abandonment and intense land-use histories (Cleveland et al. 2003). Furthermore, studies of the responses of tropical tree species to soil nutrient gradients, have revealed that early successional species generally display high growth rates and also a high phenotypic plasticity when exposed to contrasting conditions (Huante et al. 1995; Russo et al. 2005). Therefore, we hypothesized that the conditions for seedling growth would be worse in the site with more intense, recent land-use history, and also that differences in soil properties between sites would influence species responses differentially depending on their successional status.

Methods

Study Sites

The research was conducted within the Lacandon Community, Lacandon region of Chiapas, southern Mexico, north east buffer zone of the Montes Azules Biosphere Reserve (lat 16°50′N, long 91°15′W). The two study sites are located at 35 km from one another and were cleared in the mid 1960s for cattle ranching. After the initial 5–7 years of maize cultivation, pasture stargrass (*Cynodon plectostachyus*) was sown to support extensive cattle ranching. Over the next several decades, fire was used periodically, in both the sites, to eliminate encroaching shrubs and trees and prevent secondary succession, just as is done in cattle pastures throughout the Neotropics (Esquivel et al. 2008). Site 1 was abandoned in 1992, which means that grazing animals were removed 14 years before our experiment was established; site 2 was used as a cattle ranch until 2002, when a large herd of goats was allowed to come in and graze at will, until the site was completely overgrazed and abandoned in 2005, due to nearly null productivity.

The study sites are adjacent to an evergreen tropical rainforest highly fragmented by agricultural fields and abandoned pastures (De Jong et al. 2000). Climate is warm-humid with average annual precipitation greater than 2,000 mm and an average annual temperature of 24.7°C. The dry season (<500 mm) lasts from March to June, and the rainy season (1,500–1,800 mm) from July to October (Pennington & Sarukhán 2005). Predominant soil types are humic acrisols associated with rendzina. These soils are located above calcareous material; they are clay-like and poorly developed (Anonymous 1981).

Species Studied

Fourteen native tree species with traditional or commercial uses in the Lacandon region were included in this study; seed availability, local knowledge of species management, and wide geographical distribution were important criteria used in selecting species for the experiment. Furthermore, we chose species that would potentially constitute three different functional groups in terms of their most frequent appearance in a secondary succession sequence documented previously in the study area (Levy-Tacher & Aguirre-Rivera 2005; Pennington & Sarukhán 2005). The species *Acaciella angustissima* (Mill.) Britton & Rose, *Ochroma pyramidale* (Cav. ex Lam.) Urb., and *Muntingia calabura* L. are, in general, found as pioneer colonizers in open forest, and were considered as "early successional" species (Table 1). The second group, considered as "mid-successional," included the species *Schizolobium parahyba* (Vell.) S.F. Blake, *Cedrela odorata* L., *Spondias mombin* L., *Ceiba pentandra* (L.) Gaertn., *Swietenia macrophylla* King, *Parmentiera aculeata* (Kunth) Seem., *Sapindus saponaria* L., and *Castilla elastica* Sessé ex Cerv. which are also capable of colonizing open areas but are generally long-lived and grow taller than early successional species (Table 1). Finally, the third group was considered as "late-successional," which include the species *Brosimum alicastrum* Sw., *Dialium guianense* (Aubl.) Sand., and *Ampelocera hottlei* (Standl.) Standl. This third group contains species typically present in old growth forests, dispersed almost exclusively by vertebrates, and also all produce market value timber (Table 1) which makes them of interest to local people.

Table 1. Ecological and utilitarian characteristics of the 14 Lacandon rainforest tree species studied.

Species	*Family*	*Adult height (m)*[a]	*Seed dispersal vector*[b]	*Successional status*[c]	*Regional use*[a]
Acaciella angustissima	Fabaceae	10–12	Wind	ES	Fuelwood
Muntingia calabura	Tiliaceae	10–12	Vertebrates	ES	Fruit, fuelwood
Ochroma pyramidale	Bombacaceae	20–25	Wind	ES	Handicraft, timber
Castilla elastica	Moraceae	20–25	Vertebrates	MS	Resin, timber
Cedrela odorata	Meliaceae	30–35	Wind	MS	Timber
Ceiba pentandra	Bombacaceae	35–40	Wind	MS	Fruit (fiber)
Parmentiera aculeata	Bignoniaceae	12–15	Vertebrates	MS	Fruit
Sapindus saponaria	Sapindaceae	12–15	Vertebrates	MS	Soap (fruit), timber
Schizolobium parahyba	Fabaceae	30–35	Wind	MS	Handicraft, timber
Spondias mombin	Anacardiaceae	18–20	Vertebrates	MS	Fruit, timber
Swietenia macrophylla	Meliaceae	50–70	Wind	MS	Timber
Ampelocera hottlei	Ulmaceae	25–30	Vertebrates	LS	Fuelwood, timber
Brosimum alicastrum	Moraceae	35–40	Vertebrates	LS	Fruit, timber
Dialium guianense	Fabaceae	35–45	Vertebrates	LS	Fruit, timber

[a] Pennington and Sarukhán (2005).
[b] http://striweb.si.edu/esp/tesp/plant_species_c.htm
[c] Adapted from Levy-Tacher and Aguirre-Rivera (2005); ES, early-successional; LS, late-successional; MS, mid-successional.

Experimental Design

The experiment was established during the rainy season in September 2006 on the two abandoned pastures described above. Approximately 10–15 days before seedling transplant, all vegetation was cleared with machete and burned to homogenize initial conditions. Experimental areas were fenced, avoiding potential damage by herbivores. A total of 560 seedlings of 14 species (40 individuals per species) per site were transplanted in the cleared area in 40 mixed plots, each measuring 14 × 4 m (Fig. 1). In each plot, 14 seedlings (one stem for each of the 14 species) were planted randomly at a 2 × 2–m spacing and arranged in two rows with seven individuals by row (Fig. 1). This spacing was intended to give preliminary results only during 18 months (the first year is crucial for seedling establishment, De Steven 1991), thus avoiding growth interference between saplings by canopy closure (Elliott et al. 2003). Furthermore, we fit the experimental design and species selection to available land for test sites and to the preferences of tree species by the local people. We observed in the field a potential gradient of soil humidity in site 1 and of different slope in site 2. Therefore, the experiment was designed as a randomized complete block with 10 replications (each block contains four 14 × 4–m plots, Fig. 1) in order to detect possible effects of within-site environmental variation during statistical analysis. A 1-m radius around each seedling was cleared with a machete, approximately every 2 months during the rainy season and every 3 months in the dry season, thereby reducing competition principally with stargrass, which was the strongest competitor in both the sites.

Field Measurements

Approximately 15–20 days before seedling transplant, soil samples were taken in the midpoint of each of the 14 × 4–m plots. Soil cores of 31 cm^3 each were collected at a depth of 0–20 cm. Samples were mixed within each block to obtain one composite sample ($n = 10$ per site). Soil texture (Bouyoucos), organic matter (Walkley & Black), pH (1:2 H_2O), bulk density (pipette), total N (semi-microkjeldhal), available P (Olsen), and cation exchange capacity (ammonium acetate 1N pH 7) were determined for each soil sample (van Reeuwijk 1995). At the same time, 1-m^2 subplots were randomly selected within each block in order to evaluate the plant coverage of dominant species (visually estimated), species richness (total number of species in subplots), and plant diversity (Simpson diversity index) (Magurran 2004). The number of individuals, seedling height (cm), and basal diameter (cm) were assessed 7–10 days and 18 months after seedling transplant. Diameter was measured with calipers at the stem base and height was measured with a ruler.

Data Analysis

Percentage survival was calculated for each species in each block as the percentage of initially planted seedlings still alive 18 months after planting. Minimum acceptable standards for species performance were adapted from Elliott et al. (2003). Survivorship was classified as "excellent" when survival was 76–100%, "good" when 51–75%, "moderate" when 26–50%, and "poor" when less than or equal to 25%. Growth was considered as "exceptional" when saplings were 2.5 m or taller in height and at least 4 cm in basal diameter, "acceptable" when growth was between 1.00–2.49 m in height and 1.50–3.99 cm in basal diameter, and "poor" when seedlings were less than 1 m in height and 1.5 cm in basal diameter 18 months after planting.

To minimize variation in the initial height between individuals and species, we calculated relative growth rates (RGRs) for all surviving seedlings (South 1995). RGR_{height} (cm/mo) was calculated as follows: $RGR_{height} = [ln\ (\text{final height}) - ln\ (\text{initial height})]/18$ months. For $RGR_{diameter}$ (cm/mo) basal diameter was substituted in the formula used to calculate RGR_{height}. An integrated response index (IRI) was calculated for the surviving seedlings at 18 months as a means

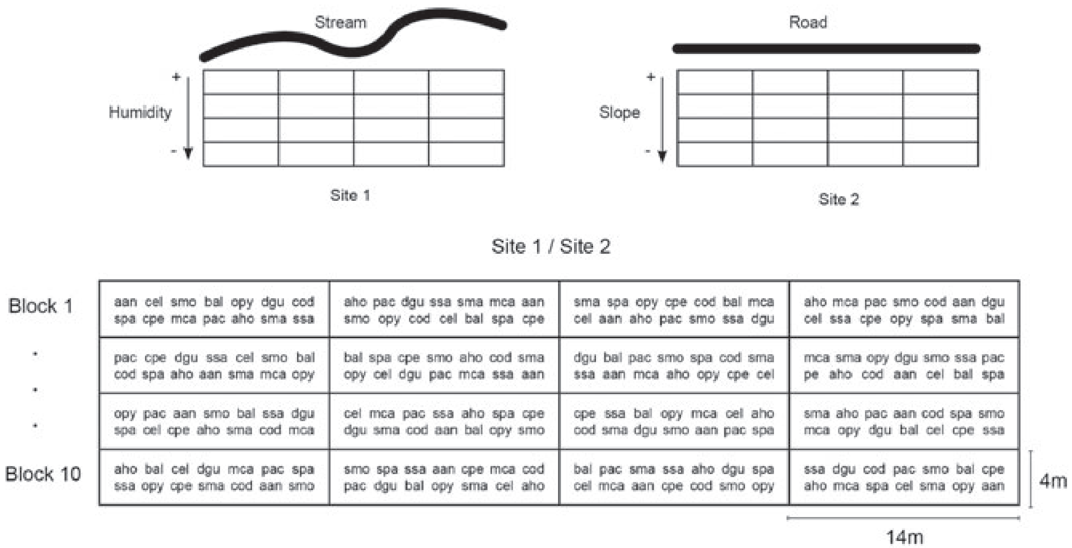

Figure 1. Schematic layout of experimental plantings (aan, *Acaciella angustissima*; aho, *Ampelocera hottlei*; bal, *Brosimum alicastrum*; cel, *Castilla elastica*; cod, *Cedrela odorata*; cpe, *Ceiba pentandra*; dgu, *Dialium guianense*; mca, *Muntingia calabura*; opy, *Ochroma pyramidale*; pac, *Parmentiera aculeata*; sma, *Swietenia macrophylla*; smo, *Spondias mombin*; ssa, *Sapindus saponaria*; spa, *Schizolobium parahyba*).

for comparing total species performance, because it integrates survivorship and growth measurements. IRI was calculated as follows: IRI = survival percentage $\times$ RGR_{height} $\times$ $RGR_{diameter}$ (De Steven 1991).

Analysis of variance (ANOVA) was used to detect differences in RGR_{height} and $RGR_{diameter}$ and IRI by the effect of site and by species within sites (site $\times$ species) in a completely randomized block design. A post hoc analysis (Tukey test) was used to evaluate the interspecies differences in survival percentage, height, and basal diameter within sites. Unpaired t-tests were made to compare: (1) intraspecific differences between sites and (2) differences in soil properties between sites. Previously, the Shapiro–Wilk test was used to assess the normality of the residuals of the response variables. Only survival proportions were arcsin transformed; height (m), basal diameter (cm), RGR_{height} and $RGR_{diameter}$, and IRI showed a normal distribution already and were not transformed.

Multiple regression analysis was used to evaluate the relationship of species IRI with the measured soil parameters. Stepwise method was used to select and keep statistically significant soil variables in the equation. The significance of the relationship was assessed using ANOVA ($p < 0.05$). On the basis of the previous residual analysis (standardized residuals plots and Cook's distance), extreme values (12 of 210) were eliminated to improve multiple regression models (Fry 1993). We performed all statistical analyses and plots using SPSS version 15.0 (Prentice Hall Inc., Upper Saddle River, New Jersey, U.S.A.).

Results

Site Characteristics

The measured variables reveal that, in general, soil conditions were better in site 2 than in site 1. Soil in site 1 showed a heavy clay-like texture (sand = 24%, silt = 31%, and clay = 45%), in contrast with the medium texture registered in site 2 (sand = 48%, silt = 16%, and clay = 36%). Soil in site 1 showed a greater bulk density, less organic matter, greater acidity, less cation exchange capacity, and less total nitrogen than soil in site 2 (Table 2). Also, remarkable changes in humidity at the soil surface were observed in site 1, such as flooding during the rainy season and cracking during the dry period. Pasture in site 1 reached 1.0–1.5 m in height and was mainly composed by herbaceous vegetation before the experiment was established. In site 1, the dominant plant species was stargrass (*Cynodon plectostachyus*) (86% coverage). In site 2, the dominant plant species were stargrass (50% coverage) and scattered individuals of the native shrub *Vernonanthura patens* (Asteraceae) (29% coverage).

Table 2. Soil properties (mean $\pm$ SE) and plant diversity in two abandoned pastures of the Lacandon region (t-test).

	Site 1 (n = 10)	*Site 2 (n = 10)*
Soil properties		
Bulk density (g/cm^3)	1.02 ± 0.02	0.95 ± 0.02*
SOM (%)	11.16 ± 0.63	14.40 ± 0.50**
pH (H_2O)	6.61 ± 0.11	7.49 ± 0.05**
Cation exchange capacity (cmol/kg)	39.26 ± 1.44	52.07 ± 2.03**
Extractable P (mg/kg)	9.57 ± 0.98	9.90 ± 0.35 ns
N (%)	0.57 ± 0.04	0.74 ± 0.03**
Plant diversity		
Species richness (S)	27	29
Simpson diversity index (1 − D)	0.27	0.46

Statistical significant level: ns, not significant; * $p < 0.05$; ** $p < 0.01$. SOM, soil organic matter.

Table 3. Results of ANOVA among seedling performance variables measured after 18 months of transplantation.

		$RGR_{diameter}$		RGR_{height}		IRI	
Source	df	F	p	F	p	F	p
Site	1	0.024	0.877	1.675	0.196	94.683	<0.0001
Species	13	56.251	<0.0001	42.308	<0.0001	74.142	<0.0001
Block	9	1.870	0.055	1.128	0.126	1.084	0.373
Site × species	12	8.196	<0.001	9.325	<0.001	25.199	<0.0001
Site × block	9	1.898	0.051	0.939	0.491	0.646	0.758
Block × species	97	1.171	0.151	0.953	0.604	0.693	0.988
Site × block × species	79	0.814	0.867	0.931	0.641	0.626	0.993
Error	393	—	—	—	—	—	—

Seedling Survival and Growth

The potential effect of environmental heterogeneity within sites was discarded because we did not identify differences on species performance between blocks (Table 3). Survival and IRI were significantly affected by sites and by species within sites (site × species), whereas $RGR_{diameter}$ and RGR_{height} were affected only by species within sites (Table 3). Seven of the fourteen species showed better performance in site 2 than in site 1 at least in one of the variables measured; only one species showed greater IRI in site 1 than in site 2 ($p < 0.05$), whereas three species showed similar performance ($p > 0.05$) in both the sites (Table 4). Stepwise regressions revealed that soil pH and extractable phosphorous (as influenced by pH) were the main soil parameters explaining the IRI of the three early-successional species (Table 5).

Mean survival percentage in site 2 after 18 months (68%) was significantly higher ($F_{1,252} = 108.386$; $p < 0.0001$) than in site 1 (42%). The three early successional species *Muntingia calabura* ($t = -4.210$; degree of freedom [df] = 18; $p = 0.001$), *Ochroma pyramidale* ($t = -3.206$; $df = 18$; $p = 0.007$), and *Acaciella angustissima* ($t = -3.382$; $df = 18$; $p = 0.003$) reached greater survivorship in site 2 than in site 1. The mid-successional species *Cedrela odorata* ($t = -9.000$; $df = 18$; $p < 0.001$), *Spondias mombin* ($t = -2.867$; $df = 18$; $p = 0.012$), *Parmentiera aculeata* ($t = -2.652$; $df = 18$; $p = 0.017$), *Castilla elastica* ($t = -3.943$; $df = 18$; $p = 0.001$),

Table 5. Stepwise linear regression models performed between the species IRI and the soil parameters measured in two abandoned pastures (ANOVA, $p < 0.05$).

Regression models	n	r^2 (%)	p
Muntingia calabura			
IRI = 0.822 + 0.857 (pH)	16	67.9	<0.0001
IRI = 0.872 + 1.079 (pH) − 0.482 (P)	16	87.9	<0.0001
Ochroma pyramidale			
IRI = 1.166 + 0.858 (pH)	15	66.0	<0.0001
IRI = 1.167 + 1.182 (pH) − 0.581 (P)	15	89.3	<0.0001
Acaciella angustissima			
IRI = 1.291 + 0.676 (pH)	17	60.9	<0.0001
IRI = 1.244 + 0.944 (pH) − 0.411 (P)	17	75.9	<0.0001
All early-successional species			
IRI = 1.092 + 0.793 (pH)	48	62.5	<0.0001
IRI = 1.089 + 1.080 (pH) − 0.513 (P)	48	82.9	<0.0001

Table 4. Site effects on performance variables of 14 rainforest tree species according to their successional status 18 months after planting (t-test, $p < 0.05$).

Species	Successional status[a]		$RGR_{diameter}$		RGR_{height}		IRI	
		df	t	p	t	p	t	p
Acaciella angustissima	ES	63	−1.149	0.255	−0.553	0.584	−7.394	<0.001
Muntingia calabura	ES	57	−3.182	0.002	−4.033	<0.001	−12.018	<0.001
Ochroma pyramidale	ES	47	−5.396	<0.001	−4.912	<0.001	−13.384	<0.001
Castilla elastica	MS	29	−1.237	0.250	−1.555	0.143	−6.757	<0.001
Cedrela odorata	MS	42	−2.400	0.006	−5.902	<0.001	−4.922	<0.001
Ceiba pentandra	MS	56	−1.505	0.138	−3.367	0.001	−3.422	0.001
Parmentiera aculeata	MS	60	2.052	0.042	4.652	<0.001	0.765	0.447
Sapindus saponaria	MS	62	5.352	<0.001	4.680	<0.001	5.848	<0.001
Schizolobium parahyba	MS	59	−0.163	0.871	−2.555	0.014	−4.869	<0.001
Spondias mombin	MS	47	4.422	<0.001	−0.087	0.931	−1.634	0.111
Swietenia macrophylla	MS	56	0.541	0.591	0.690	0.493	−0.500	0.619
Ampelocera hottlei[b]	LS	2	—	—	—	—	—	—
Brosimum alicastrum	LS	10	1.286	0.227	1.428	0.250	−1.521	0.159
Dialium guianense[b]	LS	0	—	—	—	—	—	—

[a] ES, early successional; LS, late-successional; MS, mid-successional.
[b] Species with less than 10 individuals at the end of the experiment were excluded from analysis.

and *Sapindus saponaria* ($t = -2.191$; $df = 18$; $p = 0.042$) showed also greater survivorship in site 2 than in site 1. *Brosimum alicastrum* ($t = -3.207$; $df = 18$; $p = 0.006$) was the single late-successional species that showed better survivorship in Site 2 than in Site 1. The mid-successional species *Swietenia macrophylla*, *Ceiba pentandra*, and *Schizolobium parahyba*, as well as the late-successional species *Ampelocera hottlei* and *Dialium guianense* did not show significant differences ($p > 0.05$) in survivorship between sites.

In site 1, good seedling survival (51–75%) was recorded for two of the three early-successional species (*Mun. calabura* and *Aca. angustissima*) as well as for five of the eight mid-successional species studied (*Swi. macrophylla*, *Cei. pentandra*, *Par. aculeata*, *Sch. parahyba*, and *Sap. saponaria*). Moderate seedling survival (26–50%) was registered for the early successional *Och. pyramidale* and for the mid-successional *Spo. mombin*, whereas poor seedling survival (<25%) was recorded for two mid-successional species (*Ced. odorata*, and *Cas. elastica*) (Fig. 2). In site 2, excellent seedling survival (76–100%) was exhibited by the three early-successional species (*Aca. angustissima*, *Mun. calabura*, and *Och. pyramidale*) and by all the mid-successional species (*Swi. macrophylla*, *Ced. odorata*, *Cei. pentandra*, *Spo. mombin*, *Par. aculeata*, *Sch. parahyba*, and *Sap. saponaria*). The three late-successional species (*Bro. alicastrum*, *Amp. hottlei*, and *Dia. guianense*) showed all poor seedling survival in both the sites (Fig. 2).

Saplings of the three early successional species *Mun. calabura*, *Aca. angustissima*, and *Och. pyramidale* showed exceptional growth rates in both sites, reaching mean values at least of 2.5 m in height and 4 cm in basal diameter 18 months after planting. However, the performance of these species was severely affected by environmental variation between sites (Fig. 3; Table 4). Six of a total of eight mid-successional species tested (*Cei. pentandra*, *Spo. mombin*, *Sch. parahyba*, *Swi. macrophylla*, *Ced. odorata*, and *Par. aculeata*) showed acceptable growth rates in both sites attaining mean values between 1.00–2.49 m in height and 1.50–3.99 cm in basal diameter. Poor seedling growth rates (<1 m in height and <1.5 cm in basal diameter) were recorded for two mid-successional species (*Sap. saponaria* and *Cas. elastica*) and for the three late-successional species (*Bro. alicastrum*, *Amp. hottlei*, and *Dia. guianense*) (Figs. 2 & 3).

Discussion

This study provides evidence that the local environmental variation influence sapling survival and growth. More time (years) since land abandonment not necessarily lead into better site conditions for sapling performance. Regardless of 14 years of fallow, site 1 appeared to be in a state of arrested succession due to the high coverage of the grass species *Cynodon plectostachyus*. In turn, the presence of the shrub species *Vernonanthura patens* in site 2 before the experiment was established, suggested that it could recover through natural regeneration. Analyses of soil properties in site 1 also showed a compacted structure and a lower soil capacity to retain and to supply nutrients to plants than in site 2. In contrast, site 2, which has a much longer and more recent history of land use than site 1, showed better soil conditions for tree sapling performance. However, even in site 1, the soil parameters measured could be considered satisfactory when compared to the range over which many of the species described here grow naturally (Cleveland et al. 2003; Diemont & Martin 2009). Our results provide evidence that despite the relatively good soil fertility in the experimental areas, soil variation across sites strongly affected sapling performance of certain species. In particular, the IRI of the three early successional species was greatly enhanced in site 2 and were apparently influenced mainly by changes in soil pH between sites. This result is similar to pot and field experiments, conducted by Huante et al. (1995) and Lawrence (2001), who revealed that early successional tree species grow slowly and allocate more biomass to roots under low resource availability, and grow faster, when resources are not limited, and allocate more biomass to shoots. Evidence on seedling morphology reflect that these species present fine, extensive roots, which have been associated with a more effective exploration and exploitation of zones with high nutrient availability (Paz 2003). Nonetheless, although adaptations for fast growth can provide a competitive advantage, as a result of rapid exploitation of resources when they are relatively abundant, an inability to acclimate to reduced resource availability could lead to increased mortality risk (Russo et al. 2005).

Our results suggest that the three early successional species tested, as well as the mid-successional species *Cedrela odorata* and *Castilla elastica* (and, to a slightly lesser extent, *Schizolobium parahyba*, *Ceiba pentandra*, and *Sapindus saponaria*) could be catalogued as species sensitive (Butterfield 1995) to environmental variation. In contrast, the mid-successional species *Spondias mombin*, *Swietenia macrophylla*, and *Parmentiera aculeata* could be considered as site generalists because of showing similar performance in both the study sites. Furthermore, site sensitive and generalist species could be used for site restoration or for timber production. Thus, each species end use and growth rates requires different planting arrangements depending on site characteristics, local species preferences, and restoration objectives (Haggar et al. 1998; Piotto 2008). Future studies may be focused on the toleration limits to environmental variation within species of different successional status. Research in this topic may contribute to develop theoretical approaches on species functional roles in forest ecosystems (niche vs. neutral theories, Hubbell 2005) that could be applied in silvicultural and ecological restoration (Baraloto et al. 2010; Park et al. 2010).

In our study, tree species with similar ecological characteristics responded in a similar way, and this suggests that these results can be helpful when selecting candidate species for tree plantations. The three early successional species (*Muntingia calabura*, *Ochroma pyramidale*, and *Acaciella angustissima*) exhibited exceptional growth rates, which are necessary to elevate the tree crown above the weeds (Butterfield 1995) and to

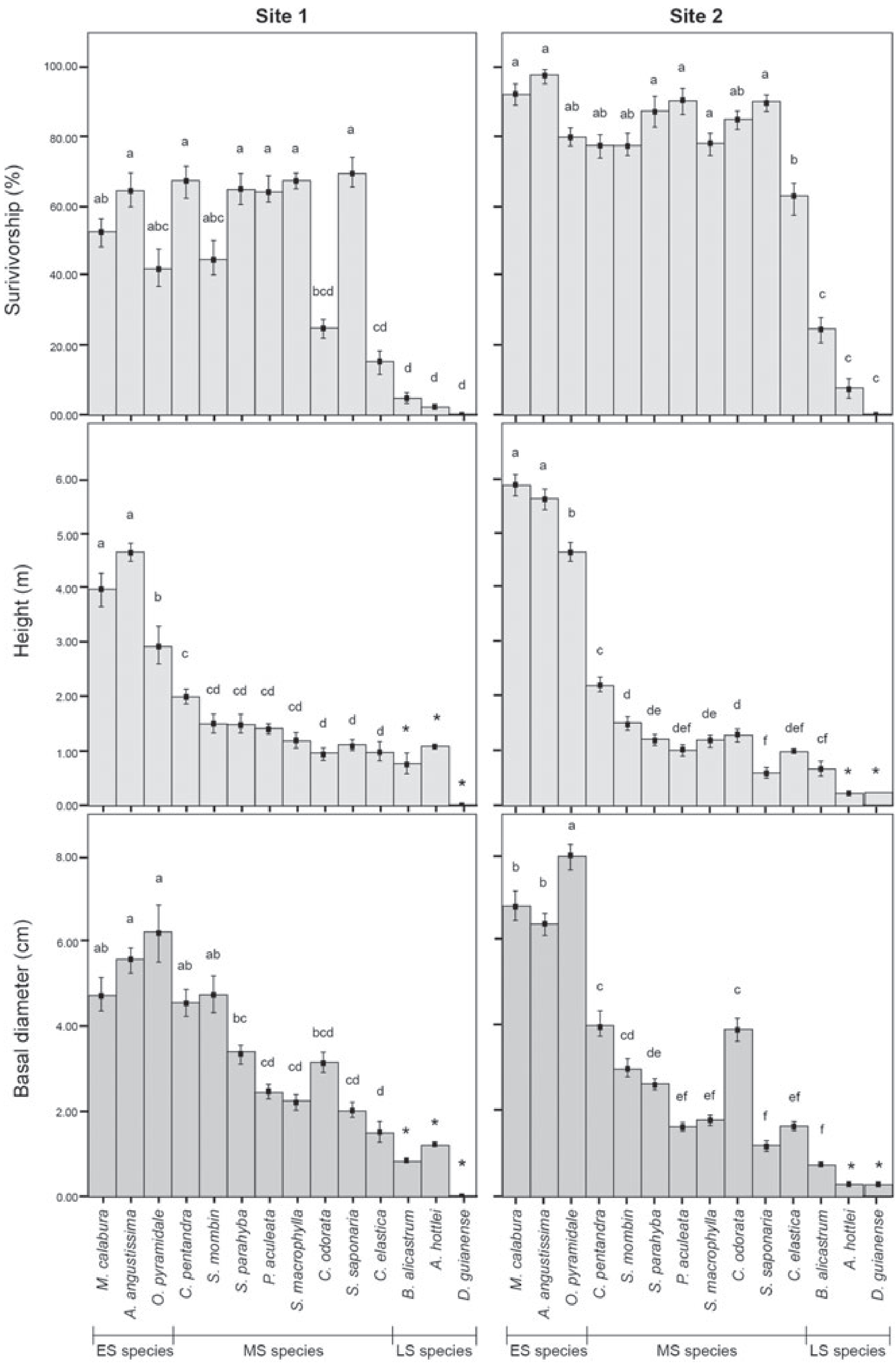

Figure 2. Seedling survival (%), height (m), and basal diameter (cm) of 14 tree species 18 months after transplantation into two abandoned pastures. Different letters expose interspecies differences at a significant level (ANOVA, Tukey's HSD, $p < 0.05$). *Species with less than five observations were excluded from analysis. HSD, honestly significant difference.

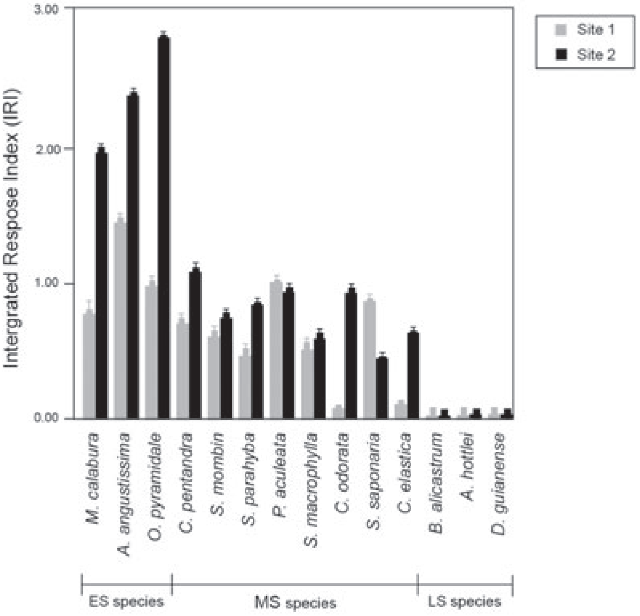

Figure 3. IRI (survival percentage × RGR_{height} × $RGR_{diameter}$) of 14 tree species varying on their successional status 18 months after transplantation into two abandoned pastures. ES, early-successional; LS, late-successional; MS, mid-successional.

improve environmental site conditions rapidly (De Souza & Batista 2004). Almost all the mid-successional species (*Cei. pentandra*, *Spo. mombin*, *Sch. parahyba*, *Par. aculeata*, *Swi. macrophylla*, and *Sap. saponaria*) showed slow growth but acceptable seedling survival rates in both the sites. These performances would be desirable to diversify the canopy structure and create a greater diversity of understorey niches for wildlife and seedling recruitment (Ruíz-Jaén & Aide 2005; Wydhayagarn et al. 2009). The poor seedling survival in site 1 of the mid-successional species *Ced. odorata* and *Cas. elastica*, would be the most important reason to reject these species in order to avoid expensive replanting (Elliott et al. 2003). The three late-successional species (*Brosimum alicastrum*, *Ampelocera hottlei*, and *Dalium guianense*) displayed poor seedling survival at both the study sites,however, should not be discarded or neglected definitely. In view of their slow growth and shade tolerance (Paz 2003), these species can be used in enrichment plantings as a means to establish additional species in a secondary forest or tree plantation (Butterfield 1995; Baraloto et al. 2010).

Many of the mid-successional species tested in our study showed a great potential to be planted together with fast-growing early successional species in abandoned pastures. Spatial and temporal differences in resource requirements of different functional groups is predicted to reduce biological and economic risk, allow greater productivity, and support ecosystem functioning through stable multispecies coexistence (Erskine et al. 2006; Cardinale et al. 2007; Rodrigues et al. in press). Simultaneously, this strategy could benefit rural communities by providing many useful and commercial forest products, as well as—in the near future—with payments for long-term carbon storage through voluntary or mandatory carbon markets (Rey Benayas et al. 2009; Milder et al. 2010). The extension of the experiments to a wider range of conditions within abandoned agricultural land might be helpful to assess the viability of tree plantations as well as to generalize species (or functional group) responses to different environmental gradients.

Implications for Practice

- Environmental variation influences sapling performance and thereby the progress of forest restoration. Early successional species appear to be very sensitive to soil differences among tropical abandoned pastures.
- Despite site performance differences, all early successional, and almost all mid-successional, tree species tested can be successfully established in abandoned pastures of the type we reported on here. Shade-tolerant late-successional species confirmed low survival rates in highly disturbed areas.
- Species performance data across a variety of abandoned agricultural land would be helpful for designing effective restoration strategies through matching adequately functional group species abundances with planting site characteristics.

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