A Strategy for Restoration of Montane Forest in Anthropogenic Fern Thickets in the Dominican Republic

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Abstract

Deforested tropical areas are often colonized by competitive ferns that inhibit forest succession. In thickets of such a fern (*Dicranopteris pectinata*), we investigated methods for initiating restoration of tropical montane forest in the Ébano Verde Scientific Reserve (Dominican Republic). In clearings in the thickets, growth and survivorship of 18 common early- and late-successional woody species were tested, with and without fertilizer (poultry litter). Three years after sowing, life history did not affect survivorship, but early-successional species grew faster than late-successional species (height increase 153 ± 103 cm vs. 81 ± 67 cm [mean ± 1 SD]). *Inga fagifolia*, a late-successional species, and *Alchornea latifolia*, an early-successional species, had 160 ± 62 cm mean height increase, and low mortality rates (<4%). In contrast, four late-successional species (*Cyrilla racemiflora, Myrcia deflexa, Prestoea acuminata* var. *montana*, and *Mora abbottii*), and one early-successional species, *Ocotea leucoxylon,* had approximately 39% mortality and height increase of 43 ± 48 cm. *Brunellia comocladifolia* had high mortality (55%), but averaged 340 ± 201 cm height increase, and was the only species whose growth was improved by fertilization. Fertilization improved survivorship of only one species, *Piper aduncum*. After three years, soils in the clearings had low pH and available P and did not differ significantly from soils in thickets. However, based on the growth rates and survivorship of sown woody plants, these soils did not appear to be a barrier for restoration. Although a complementary study demonstrated substantial natural regeneration, active planting should be used to increase plant density and diversity, especially where natural regeneration is poor.

Key words: arrested succession, *Dicranopteris pectinata*, Dominican Republic, Ébano Verde Scientific Reserve, inhibition, invasive species, native tree species, restoration, tropical montane forest, woody seedling survival and growth.

Introduction

Although tropical forests were once thought of as fragile ecosystems (Richards 1964; Gómez-Pompa et al. 1972), more recent studies have found that secondary forest can recover after light- to medium-intensity anthropogenic disturbances (e.g., small forest clearings, cattle pastures used for no more than 12 years) (Buschbacher et al. 1988; Uhl et al. 1988; Brown & Lugo 1990; Aide et al. 1995; Zimmerman et al. 1995; Aide et al. 2000). However, when anthropogenic disturbances are more severe, succession of tropical forests is often arrested, and plant communities of different species composition establish. In these plant communities the establishment of forest plants is prevented by seed predation, dispersal limitation, infertile soils, and repeated disturbance (e.g., burning, cutting, grazing, soil erosion) (Aide & Cavelier 1994; Nepstad et al. 1996; Holl 1998; Holl et al. 2000; Slocum & Horvitz 2000; Wijdeven & Kuzee 2000; Zimmerman et al. 2000). In addition, colonizing species are often exceptionally competitive in postdisturbance conditions and thereby inhibit (sensu Connell & Slayter 1977) the establishment of forest species. In the tropics these colonizing species are often grasses (Cavelier et al. 1998; Cabin et al. 2002) or ferns (García et al. 1994; Cohen et al. 1995; Walker & Boneta 1995; May 2000; Slocum et al. 2000).

The ferns *Dicranopteris pectinata* (Willd.) Underw. (Gleicheniaceae) of the New World tropics and *D. linearis* (Burm. f.) Underw. of the Old World tropics often inhibit forest succession after anthropogenic disturbance (Cohen et al. 1995; Walker & Boneta 1995). These ferns form thickets over large areas after abandonment of agriculture (García et al. 1994; Cohen et al. 1995; Slocum et al. 2000) (Fig. 1). The capacity of these ferns to competitively dominate these sites seems to stem from their ability to

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Figure 1. *Dicranopteris pectinata* can form thickets over extensive areas. Photo from the southwestern part of the EVSR, Dominican Republic.

colonize primary and secondary successional sites (landslides, mountain ridges, and lava flows) where soil fertility can be exceptionally low (Walker 1994; Russell et al. 1998). *Dicranopteris linearis*, for example, has an extremely high phosphorus-use efficiency, creates a canopy greater than 2 m tall with high leaf area indexes (>16), and creates abundant litter with low decomposability, and thus may contribute to oligotrophic conditions (Russell et al. 1998). Less is known about the physiology of *D. pectinata*, but it also creates thickets and layers of nutrient-poor litter (Walker 1994). These characteristics apparently allow *D. linearis* and *D. pectinata* to survive on inhospitable sites and exclude the colonization of native woody species.

Attempts to release forest succession in *Dicranopteris* thickets have met with mixed success. Several studies found that *D. pectinata* rhizomes did not survive burning but recovered rapidly by lateral growth from adjacent unburned thickets (Walker & Boneta 1995; May 2000). Similarly, physically removing thickets can release forest succession but only if regrowth of the fern is kept in check (Cohen et al. 1995; Slocum et al. 2004). The exception to this was a study by Russell et al. (1998); three years after removal of *D. linearis* thickets, fern cover was 2% compared with 80% in the uncut treatment. The increase in dominance by trees and other herbs was primarily the result of growth of individuals present before ferns were cleared and not by colonization of new individuals.

In all these attempts to release forest succession, forest regrowth was species poor and patchy. It therefore makes sense to couple these efforts with active planting. Planting should be limited to areas with low natural regeneration or low diversity. In this study we planted seedlings of native woody species to create a forest canopy in thickets of *D. pectinata*. The study was carried out in a nature preserve that used to be montane forest (the Ébano Verde Scientific Reserve [EVSR], Dominican Republic) and was conducted concurrently with a study on natural regeneration (Slocum et al. 2004). Our approach included (1) clearing ferns with machetes to release woody plants from competition; (2) applying a locally abundant and cheap fertilizer (poultry litter) to overcome potential nutrient limitation; (3) planting a variety of native woody plants (18 species of early- and late-successional shrubs and trees) to maximize chances of finding species capable of overcoming potentially harsh conditions; and (4) determining if cutting the fern improved soils and tree nutrition relative to that in the thickets. We postulated that the local conditions were so degraded (i.e., low soil fertility) that *D. pectinata* was the best species for these conditions, and after its removal, only a few woody species would be able to tolerate the poor soil conditions. Alternatively, soils under *D. pectinata* thickets may have been sufficiently fertile to allow high survivorship and growth of a variety of species. Our approach is an initial effort to restore these thickets to a species composition representative of the region's previously extant montane forest.

Methods

Study Site

The study took place in the EVSR (23 km^2), located in the Cordillera Central (Central Range) of the Dominican Republic (lat 19°06′N, long 70°33′W). In the reserve, elevation ranges from 800 to 1,565 m above sea level, and rainfall ranges from 1,500 to 3,000 mm/year, with no distinct dry season (García et al. 1994). The reserve is administered by the Fundación para el Mejoramiento Humano (PROGRESSIO). The original vegetation was subtropical montane forest dominated by the tree Ébano verde (*Magnolia pallescens* Urb. and Ekman, Magnoliaceae; García et al. 1994). At present, the reserve contains species-poor secondary forest concentrated along streams (Slocum et al. 2000) and small isolated patches of mature forest that contain the majority of the reserve's woody species (274 species; García et al. 1994). Besides these forests, the reserve contains expansive thickets of *Dicranopteris pectinata* (Fig. 1), which colonized in the 1970s after logging, agriculture, burning, and subsequent soil erosion (García et al. 1994). Although precise estimates of cover for the thickets over the entire reserve are not known, 90% of the southwestern part of the reserve is covered by the fern (Slocum et al. 2000). In these areas, the thickets consist of a layer of living fronds (mean ± 1 SD: 125 ± 56 cm deep, $n = 17$), a layer of dead fronds and stems (97 ± 38 cm deep), and a root mat (34 ± 18 cm deep) (Fig. 2). The few trees and shrubs in the fern thickets are small, occur at low densities, and consist of only approximately 25 species (García et al. 1994; Slocum et al. 2000). It appears that these trees in the thickets probably arrived and grew to a sufficient height before the fern canopy was fully established because regeneration under the thickets is extremely limited (Slocum et al. 2004). Similar thickets of

Figure 2. A *Dicranopteris pectinata* thicket in the EVSR, Dominican Republic. The pole is 2 m long and is resting at the base of the thicket.

D. pectinata, and its congener, *D. linearis*, are found throughout the tropics and have similar effects on woody vegetation (Walker 1994; Cohen et al. 1995; Walker & Boneta 1995; Mejía & Jiménez 1998; Russell et al. 1998).

Plant Species Selection

Selection of woody plant species was based on several criteria. First, we looked for species that already grew commonly in the thickets and therefore showed potential to grow and survive there after fern removal. We found seven such species, six early-successional and one late-successional (Slocum et al. 2004; Table 1). Second, in order to maximize our chances of finding some species that would have good rates of growth and survivorship, we collected roughly equal numbers of early- and late-successional species, and trees and shrubs (Table 1). Life history assignments were based on the habitats the species colonized (Weaver 1986; García et al. 1994; Slocum et al. 2000). Third, we only collected species that were common in the southwestern part of the reserve, so that their seeds and seedlings could be easily collected both for this study and for future efforts and that their collection would not cause further degradation in the reserve.

Plant Survivorship and Height Increase

Seedlings were collected from November 1998 to January 1999 and grown until early June 1999. They were grown in nursery bags ($4.5 \times 10 \times 12$ cm) in a shade house (50% incident sunlight). They were regularly watered and fertilized with poultry litter (poultry manure mixed with bedding material). This litter had 18 ± 0.9 g/kg N, 14 ± 0.5 g/kg P, and 21 ± 0.3 g/kg K (mean $\pm$ 1 SD, n = 3). Before out-planting, all plants were placed outside of the shade house for two weeks to adjust them to full sunlight. At the

Table 1. Species sown in the clearings, including life history characteristics, growth form, and dispersal syndrome.

Species, Authors, and Family	*Life History*[a]	*Growth Form*	*Dispersal*
Myrcia deflexa (Poir.) DC., Myrtaceae	L	shrub	animal
Myrcia splendens (Sw.) DC., Myrtaceae	L	shrub	animal
Inga fagifolia G. Don, Fabaceae	L	tree	animal
Prestoea acuminata (Willd.) H.E. Moore var. *montana* (Graham) A. Henderson & Galeano, Arecaceae	L	tree	animal
Mora abbottii Rose & Leonard, Fabaceae	L	tree	animal
Cyrilla racemiflora L., Cyrillaceae[b,c]	L	tree	animal
Coccoloba wrightii Lindau, Polygonaceae	L	tree	animal
Tabebuia berteroi (DC.) Britton, Bignoniaceae	L	tree	animal
Piper aduncum L., Piperaceae	E	shrub	animal
Tabebuia bullata A.H. Gentry, Bignoniaceae[c]	E	shrub	wind
Baccharis myrsinites Pers., Asteraceae[c]	E	shrub	wind
Psychotria berteriana DC., Rubiaceae	E	shrub	animal
Clidemia umbellata (Mill.) L.O. Williams, Melastomataceae	E	shrub	animal
Turpinia occidentalis (Sw.) G. Mon, Staphyleaceae	E	tree	animal
Ocotea leucoxylon (Sw.) Laness., Lauraceae[c]	E	tree	animal
Alchornea latifolia Sw., Euphorbiaceae[c]	E	tree	animal
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult., Myrsinaceae[c,d]	E	tree	animal
Brunellia comocladifolia Bonpl., Brunelliaceae[c,e]	E	tree	wind

Nomenclature is based on the Missouri Botanical Garden's VSAT nomenclatural database (http://mobot.mobot.org/W3T/Search/vast.html).
[a] L = late successional; E = early-successional.
[b] *Cyrilla racemiflora* colonizes bare substrates such as landslides, but persists as a canopy emergent in mature forest (Weaver 1986).
[c] Species that commonly grow in thickets in the reserve (Slocum et al. 2004).
[d] *Myrsine coriacea* attains high growth rates in gaps but can persist as seedlings in the forest understory (Sugden et al. 1985).
[e] Obligate gap-demander (Sugden et al. 1985).

time of planting (mid-June 1999), seedlings selected for out-planting were robust (mean ± 1 SD, 20 ± 11 cm tall, $n = 2{,}280$).

For out-planting, three blocks were randomly located along an old logging road in the southwest part of the reserve. These blocks (each approximately 45 × 30 m) were located more than 100 m away from the road and approximately 250 m from each other. These blocks all had different aspects and slopes and were representative of fern thickets in this part of the reserve, but they may not be representative of thickets on steeper slopes or at higher elevations.

In the blocks, thickets were removed using machetes between January and March 1999. Ferns were cut to the root layer, and the debris was piled up into rows, 1–2 m apart, leaving cleared rows in between. As much as possible, these rows were placed along contour lines to minimize erosion. Erosion was also reduced by not removing the root mat, but we cut the root mat to reduce the chance of it resprouting.

Along the cleared rows, seedlings were planted 1 m apart. This high density was used because we anticipated high mortality and that a large number of seedlings would be needed to shade out recolonizing fern. In each block, approximately 50 seedlings of each species were planted, and half were fertilized with approximately 100 mL of poultry litter placed at the bottom of the planting hole. No additional fertilizer was applied after planting. The position of each seedling along the cleared rows was random, regardless of its species or fertilizer treatment. Plant height was measured at the time of planting, and plant height and mortality were determined 12, 24, and 36 months after planting.

In our study the impact of the fern thickets on the seedlings was not tested. It was clear that the ferns presented a strong competitive barrier at our study site (Figs. 1 & 2), as well as at other sites where the characteristics of the thickets and their effects on colonizing plants were tested (Cohen et al. 1995; Walker & Boneta 1995; Russell & Vitousek 1997; Russell et al. 1998). Therefore, we decided that planting seedlings in the ferns would not be a viable restoration method.

Soil Characteristics and Leaf Nutrients

To understand how clearing the fern affected soils, cores of soil (12 cm deep × 5 cm diameter) were collected in the cleared blocks and compared to those collected in nearby thickets. For each block, six randomly selected points along its edges were selected. At each point, a core was taken 3 m into the cleared block and 3 m into the thicket. A total of 36 cores were collected (3 blocks × 2 fern treatments × 6 replicates). Soil samples were weighed, air-dried at 65°C, and weighed again to determine bulk density. Soil pH was determined on a 1:1 soil: water slurry using a Fisher Scientific Accumet 1000 Series handheld pH/mV/ion meter (Fisher Scientific International, Inc., Hampton, NH, U.S.A). From the dried soils, extractions were conducted to determine elemental concentrations, including exchangeable K, Ca, and Mg using a Mehlich 3 extraction (Mehlich 1984), available PO_4-P using a Mehlich 1 extraction (Nelson et al. 1953), and available NH_4-N and NO_3-N using 2 M KCl (Keeney & Nelson 1982). Exchangeable Al and Ca were extracted using $SrCl_2$, and a Ca/Al ratio was calculated as an Al toxicity test (Joslin & Wolfe 1989). Acidity was determined using the SMP (Shoemaker, McLean & Pratt 1961) buffer method (Eckert & Sims 1995). Cation exchange capacity was determined by adding Ca, K, Mg, and acidity (Brown & Warncke 1988). Elemental concentrations in extractions of exchangeables were analyzed on a Spectro Ciros^{CCD} inductively coupled argon plasma emission spectrometer (ICP, Spectro A.I., Inc., Fitchburg, MA, U.S.A.). Available PO_4-P, NH_4-N, and NO_3-N were analyzed by flow-injection analysis on a Lachat QuikChem 8000 (Lachat Instruments, Loveland, CO, U.S.A). Total N and C were determined using combustion methods on a Perkin-Elmer 2400 CHN Elemental Analyzer (Perkin Elmer, Inc., Wellesley, MA, U.S.A.) (Bremner 1996; Nelson & Sommers 1996).

The effect of fern removal on foliar nutrient concentrations was determined by collecting leaves from adult trees of *Myrsine coriacea* and *Brunellia comocladifolia*. We assumed that these trees were approximately 25 years old because they appeared to have established when agricultural activities ceased and before the fern thickets became fully established (Slocum et al. 2004). Three years after clearing (June 2002), two recently matured leaves were collected from three trees of each species in each block. In the adjacent thickets, leaves were also collected from three trees of each species, for a total of 36 samples (3 blocks × 2 fern treatments × 2 tree species × 3 replicates). The two leaves from each tree were combined, separated from their petioles, dried at 60°C, and ground. Total C and N were determined by combustion on a Perkin-Elmer 2400 CHN Elemental Analyzer. Elemental concentrations of Al, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn were determined on the ICP after a digestion with nitric acid and H_2O_2 (Huang & Schulte 1985).

Data Analysis

For the sown seedlings, mortality by the third year was analyzed using a binary logistic regression with the fixed effects species, fertilizer, and block. In this model, block was included as a fixed effect because mixed models for logistic regression are currently in development (Allison 1999:206; P. D. Allison 2005, Department of Sociology, University of Pennsylvania, personal communication). Height increase by the third year was analyzed with a randomized block factorial, including the main effects species and fertilizer, block as a random effect, and the appropriate interactions.

Variables describing soils were analyzed with a multivariate analysis of variance (MANOVA), with presence/absence of the fern as the main effect and block and the block by fern interaction as random effects. Given significant results, the MANOVA was followed by one-way analysis of variance of individual variables. Significance levels for these tests were Bonferroni corrected. Data for the plant leaves were analyzed in the same way as the soils, with each tree species being analyzed separately.

For all statistical tests, natural log or square root transformations were used when necessary to improve normality. Based on examinations of the residuals, the assumptions of normality and homogeneity of variance were not violated in any of the analyses. Tukey–Kramer Honestly significant different (HSD) tests were used to make pairwise comparisons. The SAS GLM procedure was used to conduct MANOVAs, the MIXED procedure was used for factorial analyses, and the GENMOD procedure was used for mortality analyses (Littell et al. 1996; Allison 1999; SAS Institute 1999). For the MIXED procedure, degrees of freedom were estimated using the ddfm=satterth option.

Results

Soil Characteristics, Poultry Litter, and Leaf Nutrients

The soils in the cleared blocks did not significantly differ from those in the thickets overall (Wilk's lambda = 0.51; $F_{[15,16]} = 1.0$, $p = 0.46$). Soils in the clearings and thickets both had a pH of 4.6, a cation exchange capacity of 15 cmol/kg, 2.6 g/kg nitrogen, and a C:N ratio of 16 (Table 2). Similarly, foliar nutrient concentrations did not differ between fern thickets and cleared plots for either of the two tested tree species, *Myrsine coriacea* (Wilk's lambda = 0.4, $F_{[4,13]} = 0.4$, $p = 0.88$) or *Brunellia comocladifolia* (Wilk's lambda = 0.09, $F_{[4,13]} = 3.8$, $p = 0.12$) (Table 3).

Table 2. Mean ± 1 SD of soil characteristics in fern thickets and cleared plots in the EVSR, Dominican Republic.

Soil Characteristic	*Clearing**	*Thicket**
Bulk density (g/cm^3)	0.62 ± 0.11	0.64 ± 0.10
pH	4.6 ± 0.3	4.6 ± 0.3
Total C (g/kg)	46 ±13	41 ± 20
Total N (g/kg)	2.7 ± 0.7	2.5 ± 1.1
C/N ratio	17 ± 2.7	16 ± 2.7
NH_4-N (mg/kg)	15 ± 4	14 ± 7
NO_3-N (mg/kg)	2.5 ± 3.3	3.4 ± 4.5
PO_4-P (mg/kg)	1.6 ± 1.1	1.1 ± 0.6
K (cmol/kg)	0.16 ± 0.10	0.12 ± 0.05
Ca (cmol/kg)	1.1 ± 0.7	0.6 ± 0.4
Mg (cmol/kg)	0.7 ± 0.3	0.4 ± 0.2
Acidity (cmol/kg)	15 ± 5	16 ± 4
Cation exchange capcity (cmol/kg)	15 ± 2	15 ± 2
Ca (mg/kg)	91 ± 35	74 ± 40
Al (mg/kg)	13 ± 8	17 ± 10
Ca/Al (molar)	13.9 ± 22.2	5.6 ± 6.5

Soil characteristics in thickets did not differ significantly from those in clearings.
* $n = 18$.

Plant Mortality and Height Increment

After three years, overall mortality of the woody plants was 21%. Mortality was not significantly affected by block ($\chi^2_{[2]} = 0.01$, $p = 0.99$), fertilizer ($\chi^2_{[1]} = 0$, $p < 0.97$), or any of their interactions (spp. × block: $\chi^2_{[34]} = 40$, $p = 0.22$; fertilizer × block: $\chi^2_{[2]} = 0.21$, $p = 0.90$; spp. × fertilizer × block: $\chi^2_{[34]} = 34$, $p = 0.47$). There was, however, a significant species by fertilizer interaction ($\chi^2_{[17]} = 28$, $p = 0.05$). Only one species, *Piper aduncum*, had significantly greater mortality (73%) when not fertilized (test within *P. aduncum* only; $\chi^2_{[1]} = 15$, $p < 0.0001$). The strongest effect was a significant effect of species ($\chi^2_{[17]} = 328$, $p < 0.0001$). Almost no seedlings of *Inga fagifolia* died, whereas more than 50% of the seedlings of *Cyrilla racemiflora* and *B. comocladifolia* died (Fig. 3). Some species appeared to have higher mortality in the first year, including *B. comocladifolia, Myrcia deflexa, Prestoea acuminata* var. *montana, Turpinia occidentalis*, and *Psychotria berteriana*. Others species had constant mortality over all three years, including *C. racemiflora, Ocotea leucoxylon, Clidemia umbellata*, and *P. aduncum*. There was no clear effect of life history on woody seedling mortality (Fig. 3).

Plant height increase after three years was significantly affected by species ($F_{[17,68]} = 75$, $p < 0.0001$) and an interaction of species with fertilizer ($F_{[17,68]} = 2.9$, $p = 0.001$). Although fertilizer lead to an overall 10-cm height increase (all species combined), this was statistically significant for only one species, *B. comocladifolia,* which had the highest mean height increase of the tested species (Fig. 4) and which grew 73 cm/year faster when fertilized (Tukey–Kramer HSD, $p < 0.05$).

After three years, average plant height increase was 126 ± 103 cm, with 28% of the plants growing more than 2 m in height. Early-successional species grew about twice as rapidly as late-successional species (153 ± 103 vs. 81 ± 67 cm), whereas trees grew 25% faster than shrubs (141 ± 105 vs. 111 ± 90 cm). The six species with the most rapid height increase included five early-successional species (*B. comocladifolia, P. berteriana, Alchornea latifolia, C. umbellata*, and *M. coriacea*), and one late-successional species (*I. fagifolia*) (Fig. 4). On average these species grew more than 1.5 m in three years, with 5% of their individuals growing more than 4 m. The six slowest growing species included four late-successional species (*C. racemiflora, P. acuminata* var. *montana, M. deflexa,* and *Mora abbottii*) and two early-successional species (*Tabebuia bullata* and *O. leucoxylon*) (Fig. 4). On average these species grew between 28 and 67 cm in height over three years, with only 0.4% of their individuals growing more than 2 m in three years.

Discussion

Soil Condition

The soils at our study site were rich in carbon (Silver et al. 1994; Tian 1998; Tornquist et al. 1999) but had low to moderate total N (González & Fisher 1994; Silver et al.

Table 3. Elemental concentrations (%) in leaves of two tree species found in fern thickets of *Dicranopteris pectinata* and in areas cleared of the fern in the EVSR, Dominican Republic.

	Brunellia comocladifolia		*Myrsine coriacea*	
Element	*Thicket**	*Clearing**	*Thicket**	*Clearing**
C	46.3 ± 0.6	45.9 ± 0.6	52.3 ± 0.8	52.1 ± 0.7
N	1.4 ± 0.1	1.5 ± 0.2	1.7 ± 0.1	1.6 ± 0.2
P	0.07 ± 0.02	0.09 ± 0.01	0.09 ± 0.01	0.09 ± 0.02
K	0.8 ± 0.1	0.9 ± 0.1	0.9 ± 0.2	0.9 ± 0.3
Ca	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1
Mg	0.11 ± 0.02	0.11 ± 0.02	0.07 ± 0.01	0.07 ± 0.02
S	0.12 ± 0.03	0.12 ± 0.03	0.19 ± 0.07	0.18 ± 0.06
Al	0.02 ± 0.05	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
Cu	0.0005 ± 0.0002	0.0006 ± 0.0002	0.0005 ± 0.0001	0.0006 ± 0.0002
Fe	0.005 ± 0.002	0.005 ± 0.001	0.006 ± 0.00	0.007 ± 0.001
Mn	0.08 ± 0.05	0.12 ± 0.04	0.01 ± 0.00	0.01 ± 0.00
Na	0.09 ± 0.03	0.07 ± 0.02	0.26 ± 0.07	0.26 ± 0.07
Zn	0.005 ± 0.001	0.005 ± 0.001	0.006 ± 0.002	0.006 ± 0.002

For each tree species, elemental concentrations in tree leaves from thickets did not significantly differ from that in leaves from clearings.
*$n = 18$.

1994; Motavalli et al. 1995; Tornquist et al. 1999), resulting in a high C:N ratio (Erickson et al. 2001). Available NH_4-N and NO_3-N also appeared to be at low to moderate levels (Davidson et al. 1998; Erickson et al. 2001). Compared with other tropical soils, levels of exchangeable cations were high (Silver et al. 1994; Motavalli et al. 1995; Menzies & Gillman 1997; Davidson et al. 1998). In particular, exchangeable Ca was high and may have offset high levels of exchangeable Al and its toxicity in the soil (Joslin & Wolfe 1989). Last, our soils had pH levels typical of a highly weathered tropical soil (Motavalli et al. 1995) and had low levels of available phosphate similar to that reported in other studies (Davidson et al. 1998; Dias et al. 2000; Doberman et al. 2002).

Cutting the fern and leaving the debris on site led to nonsignificant changes in soil chemistry. Similarly, nutrient concentrations in the leaves of the two tree species we tested in the clearings (*Brunellia comocladifolia* and *Myrsine coriacea*) were not improved relative to those found in the thickets. The foliar N and P concentrations of our two tested species were similar to those found in leaves of the tree *Metrosideros polymorpha* growing on volcanic soils (Vitousek & Farrington 1997) and were considerably lower than those found for 11 tropical tree species growing on highly degraded soils in Ecuador (Davidson et al. 1998). None of these tree species had N and P foliar concentrations lower than that found in leaves of *Dicranopteris linearis* growing on oligotrophic sites in Hawaii (Russell et al. 1998).

Our fertilizer treatment (poultry litter) increased height increment of only one species, *B. comocladifolia*, and the survivorship of another, *Piper aduncum*. This result may be explained by our use of only a small amount of the poultry litter (a single application of approximately 100 mL), which was decided upon when preliminary experiments (M. G. Slocum, Louisiana State University; T. M. Aide, University of Puerto Rico; J. K. Zimmerman, University of Puerto Rico; and L. Navarro, Universidad de Vigo, Spain, unpublished data) showed that some species exhibited high mortality when fertilization with poultry litter was repeated. A limited response to fertilization may also be explained by the fact that our poultry litter had concentrations of N (1.8%) and P (1.4%) lower than the average found in poultry litter in the U.S.A. (4.9% N and 2.1% P) (Sharpley et al. 1998). Percent K of our litter (2.1%) was the same as the U.S. mean. Alternatively, Davidson et al. (1998) suggest that nutrients released by fertilizer might have been sorbed by the soil and have become unavailable for uptake by plants. Two other studies conducted on acidic, highly weathered tropical soils found a similar lack of response of woody plants to fertilizer (Harcombe 1977; Davidson et al. 1998).

We do not have data on the effects of agriculture on the soils in our study area (25 years ago), but it is likely that agriculture severely degraded the soils because of the intensity and frequency of the disturbance and because of the steep slopes and high rainfall in the region. Once agriculture ceased, the colonization and presence of *D. pectinata* likely improved soil conditions. Several studies have documented the ability of *Dicranopteris* to colonize and tolerate low nutrient substrates such as fresh lava flows (Russell & Vitousek 1997; Russell et al. 1998) and the upper zones of landslides (Walker 1994). In these studies, *Dicranopteris* gradually improves and creates soils by trapping atmospheric inputs and creating organic matter (Maheswaran & Gunatilleke 1988; Russell & Vitousek 1997; Russell et al. 1998). In our site, once the fern was removed, the growth and survival of native shrub and tree species suggest that the soils had sufficient fertility and were not a major barrier for forest recovery.

Woody Plant Survival and Height Increment

Our 18 sown species performed well in the clearings, having 21% mortality overall and a mean height

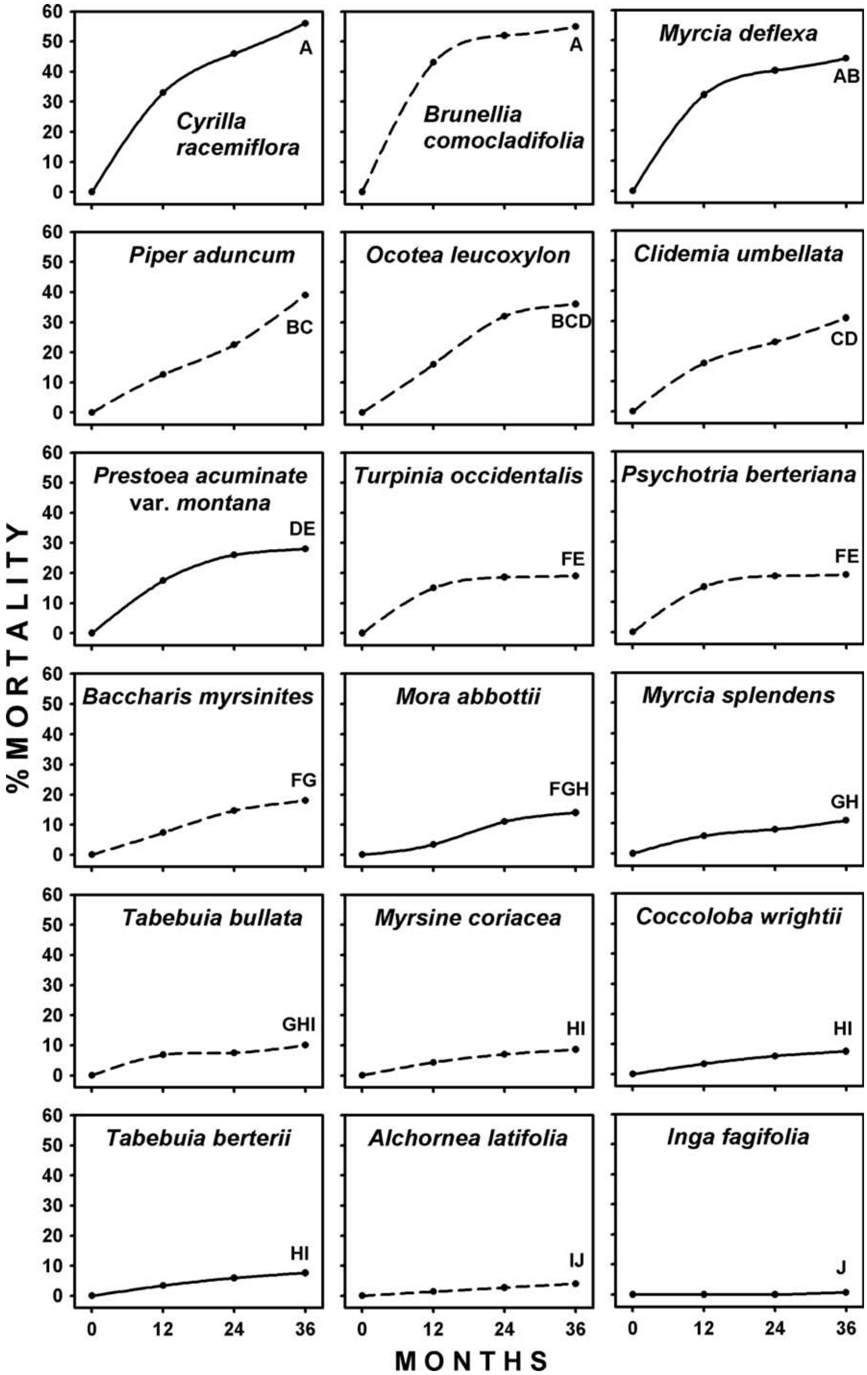

Figure 3. Percent mortality of seedlings of 18 native woody species planted in clearings in fern thickets at the EVSR, Dominican Republic. Species with solid lines are late-successional species, and those with dashed lines are early-successional species (Table 1). In the third year, points that do not share the same letter are significantly different (Tukey–Kramer HSD, $p < 0.05$). Figure depicts data summed across fertilizer treatment and blocks.

increment of 0.3 to 3.4 m after three years. Similar results have been found for native species in a number of tropical studies. For example, Davidson et al. (1998) planted native early- and late-successional species in a premontane forest site that was highly degraded by agriculture. These species had a height increment similar to ours (0.2 to 3.7 m in 2.5 years) but had higher mortality rates (half of their species had >50% mortality). In lowland wet forest sites with slightly higher soil fertility, species averaged at least 3 m in height increase in three years, with some species averaging 12 m (González & Fisher 1994; Butterfield 1996; Kanmegne et al. 2000). Mortality was low (28% in the study by Butterfield [1996] and 8.6% in the study by González & Fisher [1994]).

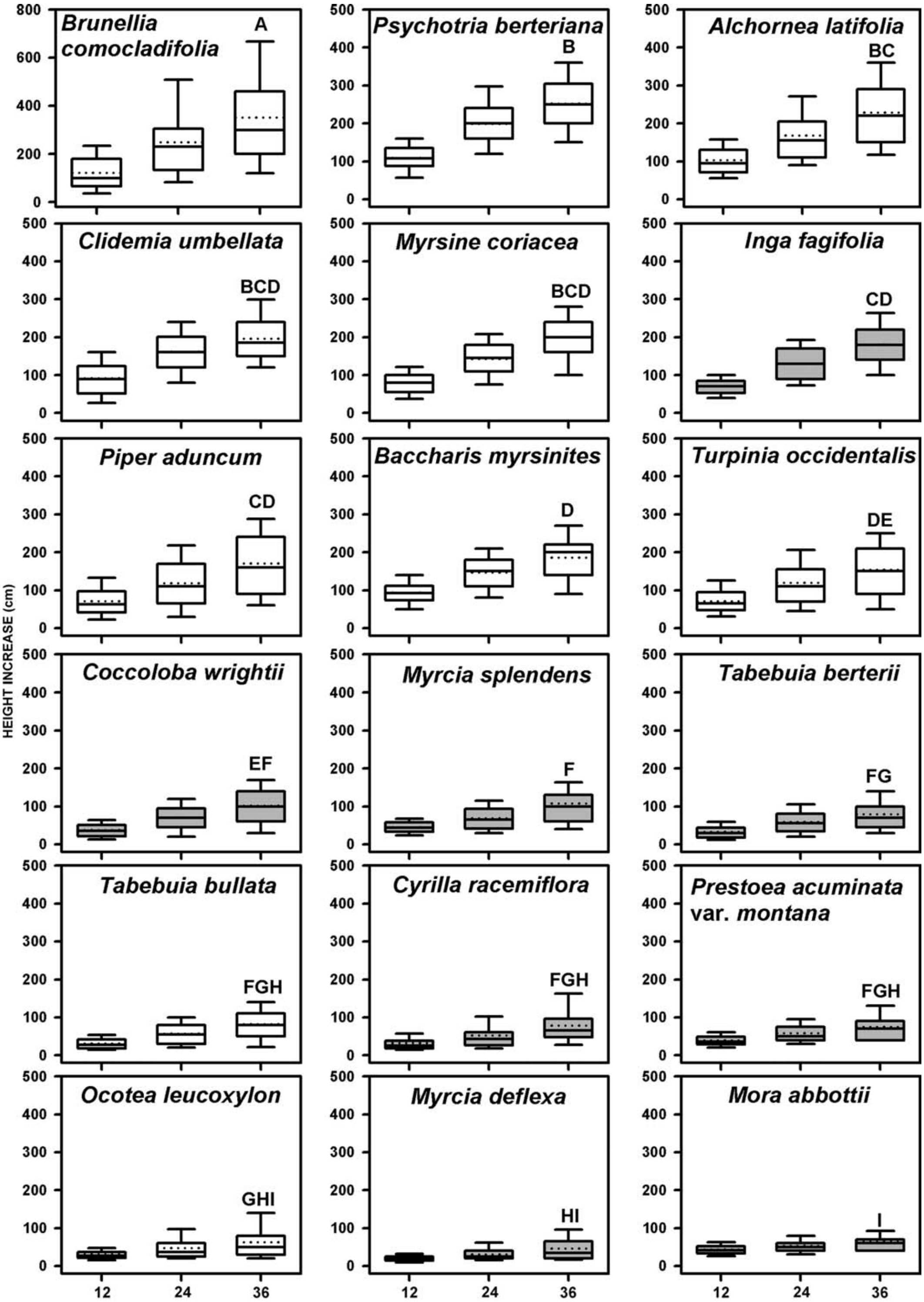

Figure 4. Cumulative height increment of seedlings of 18 native woody species planted in clearings in fern thickets at the EVSR, Dominican Republic. Box and whisker plots show 10, 25, 50, 75, and 90th percentiles. Means are indicated by dotted lines (sometimes hidden by the 50th percentile). Shaded box plots are late-successional species, and open box plots are early-successional species (Table 1). Species are ordered by mean height increase in the third year and are on the same scale of height increase (except for *Brunellia comocladifolia*). In the third year, bars that do not share the same letter are significantly different (Tukey–Kramer HSD, $p < 0.05$). Figure depicts data summed across fertilizer treatment and blocks.

By using a large number of native species that varied in life history characteristics, we were able to identify promising species for future reforestation efforts. We expected that *M. coriacea* and *B. comocladifolia* would possibly have the highest growth rates and survivorship because they are the dominant tree species in the thickets (Slocum et al. 2004). However, once the fern was eliminated, these species did not perform better than species that were rare or that did not occur in the thickets. The species with the best combination of growth and survivorship included one that was moderately common in the thickets (*Alchornea latifolia*) and one that did not occur in the thickets (*Inga fagifolia*). The latter is a late-successional nitrogen fixer, achieved a mean height increment of 159 cm and had almost no mortality over three years. In the same time period, *A. latifolia*, an early-successional species, grew an average of 207 cm in height and had only 4% mortality.

This project of sown seedlings was conducted concurrently with a study of natural regeneration in the clearings (Slocum et al. 2004). Natural regeneration was substantial after clearing the thickets (2.3 ± 1.5 stems/m^2 [stems >20 cm tall only]), with many individuals growing more than 2 m in height from seed in 3 years. In addition, three years after clearing, regrowth of *D. pectinata* reached only 16% cover. Most of this regrowth could be easily controlled because it stemmed from thickets along clearing edges.

From these results it is evident, that after clearing the thickets, natural regeneration alone could be a cost-efficient way to restore forest in the EVSR. However, we found that natural regeneration was patchy and species poor; in our clearings, only 23 species established and only 12 had good growth rates (Slocum et al. 2004). To some extent this lack of species could be overcome with time because secondary forest establishes and promotes the arrival of more species by attracting seed-dispersing animals (Holl et al. 2000). This process, however, may be slow and may allow the reestablishment of ferns or other competitors, so planting woody plants should be used to increase species diversity and to fill in areas where natural regeneration is limited.

Based on our initial assessment of our study species, we recommend that open areas be planted with *I. fagifolia* and *A. latifolia* to shade out competitors and perhaps to improve soils. Given their high survivorship, these species could be planted using a wider separation (every 3–4 m) than used in this study (1-m spacing). Once they have created a closed canopy, planting of late-successional canopy and understory species (Ashton et al. 2001), such as *Cyrilla racemiflora, Prestoea acuminata* var. *montana, Myrcia deflexa,* and *Mora abbottii*, could help increase site diversity. To increase the pool of species that could be planted in clearings, additional studies would be needed to learn how to collect and establish propagules of species from patches of primary forest in the EVSR. Overall, our restoration effort would be similar to that of Ashton et al. (1997), who found that the best results were accomplished by first creating a nurse canopy that eliminated herbaceous competitors and improved soils. After sowing seedlings, they then experimented to see what conditions improved growth for particular species (e.g., they thinned the nurse canopy to increase light availability).

Conclusions

Although *Dicranopteris pectinata* has inhibited natural succession at the EVSR for more than 20 years, this study has demonstrated that by simply clearing large plots and planting a mixture of native woody species, one can initiate forest restoration in the southwestern part of the EVSR. The soils of the site were apparently sufficiently fertile to support the growth of sown woody plants and of natural regeneration. Although natural regeneration in our clearings was substantial, sowing woody plants would complement this regeneration by increasing species diversity and by filling in areas that had no woody plants. These treatments are relatively inexpensive and could easily be tested in other montane ecosystems where *D. pectinata* covers thousands of hectares.

Implications of Practice

- After anthropogenic disturbance, *D. pectinata* and other species of fern can form thickets that prevent natural regeneration.
- Manual clearing of this fern was necessary to promote natural regeneration and provide habitat for restoration.
- In clearings, natural regeneration was patchy and species poor. Sowing seedlings of woody plants was necessary to increase plant density and diversity.
- Although plant species varied considerably in growth and survivorship, there was no sign that plants were substantially limited by soil conditions.
- These methods could be used in other parts of the EVSR and in other tropical regions where ferns inhibit natural regeneration.

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