SHORT COMMUNICATION

Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic

Matthew G. Slocum^{*1}, T. Mitchell Aide^{*}, Jess K. Zimmerman[†] and Luis Navarro[‡]

* Department of Biology, University of Puerto Rico, P.O. Box 22360, San Juan, Puerto Rico 00931–3360, USA

† Institute for Tropical Ecosystem Studies, University of Puerto Rico, San Juan, Puerto Rico 00936, USA

‡ Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Vigo, 36200-Vigo, Spain

(Accepted 16th August 2003)

Key Words: arrested succession, competition, *Dicranopteris pectinata*, dispersal limitation, disturbance, Dominican Republic, Reserva Científica Ébano Verde

Tropical forests can recover after anthropogenic disturbances of light to moderate intensity (Aide *et al.*) 1995, 1996, 2000; Uhl 1987, Uhl et al. 1988); however, severe disturbances (e.g. compaction or loss of soil) often result in conditions that prevent forest recovery. These degraded sites are often dominated by grasses (Aide & Cavelier 1994, Cabin et al. 2002, Cavelier et al. 1998, Uhl et al. 1988) and ferns (Cohen et al. 1995, García et al. 1994, Slocum et al. 2000, Walker & Boneta 1995) that can impose barriers for tree regeneration and arrest the succession process. Important barriers for tree regeneration include: (1) competition with grasses and ferns for soil moisture, nutrients and light (Aide & Cavelier 1994, Guimarães-Vieira et al. 1994, Holl et al. 2000, Nepstad et al. 1996, Russell et al. 1998, Walker 1994, Zimmerman et al. 2000), and (2) dispersal limitation given that grasses and fernlands offer few resources that attract seed dispersers (Guevara & Laborde 1993, Holl et al. 2000, McDonnell & Stiles 1983, Slocum & Horvitz 2000, Zimmerman et al. 2000).

Forest restoration in these grasslands and fernlands can be accelerated by increasing seed arrival by attracting seed dispersers with trees or artificial perches (McDonnell & Stiles 1983), and by clearing herbaceous vegetation and reducing competition (Robinson & Handel 2000). To determine an efficient strategy for restoring subtropical montane forest, we evaluate the success of natural regeneration 3 y after removing the dominant fern, *Dicranopteris pectinata* (Willd.) Underw. (Gleicheniaceae). For a control, we compared this recruitment with that in fernlands > 25 y old. Within the cleared areas we also compared recruitment under trees and in areas with no tree cover to evaluate the importance of remnant trees in attracting seed dispersers.

The study was conducted in the Ébano Verde Scientific Reserve (23 km²), located in the Cordillera Central of the Dominican Republic (19°06'N, 70°33'W). Elevation ranges from 800 to 1565 m asl and rainfall ranges from 1.5 to 3 m y^{-1} , with no distinct dry season (García *et al.* 1994). The original vegetation in this region was subtropical montane forest dominated by the tree Ébano Verde (Magnolia pallescens Urb. & Ekm., Magnoliaceae, García et al. 1994). During the early 1970s most of this region was subjected to logging and swidden agriculture. Following the abandonment of these activities, most areas have been colonized by D. pectinata (Garcia et al. 1994, Slocum et al. 2000), a species that commonly colonizes landslides (Walker 1994). The fern forms thickets consisting of a layer of living fronds (125 \pm 56 cm deep), a second layer of dead fronds and stems $(97 \pm 38 \text{ cm deep})$, and a root mat $(34 \pm 18 \text{ cm})$ deep; mean ± 1 SD; n = 17). Within these thickets, trees and shrubs occur at low densities (Slocum et al. 2000), and casual observation by botanists (García et al. 1994) and locals also suggest that forest succession has been arrested in the reserve since agricultural abandonment. Similar thickets of D. pectinata, and its congener, D. linearis (N. L. Burm.) Underw. (Gleicheniaceae), are found throughout the tropics, and have similar inhibitory effects on woody vegetation (Cohen et al. 1995, Mejía & Jiménez 1998, Russell et al. 1998, Walker 1994, Walker & Boneta 1995).

¹Corresponding author. Present address: Wetland Biogeochemistry Institute, Louisiana State University, Baton Rouge, LA 70803, USA. E-mail: mateo457@yahoo.com.

In the thickets we randomly located three sites (each $\sim 45 \times 30$ m). Between January 1998 and March 1999, ferns were cut to the root layer with machetes and debris was piled into rows, 1–2 m apart. To avoid erosion, the root mat was not removed, but it was cut to reduce resprouting. In each cleared site, we randomly picked ~ 14 isolated trees to sample woody recruits, as well as ~ 7 'open' areas (i.e. no tree canopy within 2 m). Three y after the sites had been cleared, we counted, identified and measured the heights of woody recruits > 20 cm tall in circular plots (2 m radius, 12.6 m²) around each tree trunk and in the open plots. In addition, fern cover was estimated in each plot to the nearest 10%. Species nomenclature was based on a local survey (García *et al.* 1994).

To test how trees and open areas differed in density of stems and species, we used a randomized block design using the MIXED procedure of SAS version 8 (SAS Institute Inc. 1999). This design included the tree/open treatment as a fixed effect, cleared site as a random effect, and the interaction between the tree/open treatment and site as a random effect. A naturallogarithm transformation was used to normalize the distribution of woody plant density.

To document woody plants growing in the thickets, we established plots $(10 \times 20 \text{ m})$ between December 1998 to January 1999 every 100 m along the logging road (22 plots). Each plot was set 5 m into the thickets from the road. In the plots, we identified and counted all woody plants projecting above the fern canopy (i.e. plants > 125 cm). The density and species composition of the thickets was compared to plants > 125 cm tall in the three cleared sites. Recruitment and growth in the thickets occurred during the last 25 y following agricultural abandonment, while recruitment and growth in the cleared sites occurred during the last 3 y.

Three y after clearing, 23 species of woody plants had established in the sampling plots (Table 1). The most common species was the animal-dispersed shrub Psychotria berteriana. Other common animal-dispersed species included Clidemia umbellata, Trema micrantha, Myrsine coriacea and Miconia mirabilis. The two most common wind-dispersed species were Baccharis myrsinites and Brunellia comocladifolia. The mean density of woody plants > 20 cm tall was 2.3 ± 1.5 stems m⁻² (Table 1). The species that colonized these sites were mainly smallseeded, early successional species that represented less than 10% of the 274 known woody species in the reserve (García et al. 1994). One potential reason for the low diversity was a lack of nearby seed sources: patches of mature forest are more than 1000 m from our cleared sites. Other seed sources, including secondary forest along streams (> 100 m distant) and trees within the thickets, were closer, but these sources include a limited pool of species (García et al. 1994, Slocum

et al. 2000). Alternatively, the low diversity may be due to harsh conditions in the cleared sites (e.g. infertile soils). However, seedlings of 18 species of native trees and shrubs sown in the cleared sites had 79% survival after 3 y, and growth rates averaging 42 cm y^{-1} (M. Slocum *et al.*, unpubl. data).

In the cleared sites, density of woody plants under trees did not significantly differ from those in open areas $(2.5 \pm$ 1.5 stems m⁻² under trees (n = 43) v. 2.0 \pm 1.4 stems m^{-2} in the open (n = 23); $F_{1,64} = 2.0$; P = 0.16; Table 1). Similarly, plots under trees had similar densities of species $(5.8 \pm 1.9 \text{ species plot}^{-1}, n = 43)$ as plots in the open $(5.2 \pm 2.0 \text{ species plot}^{-1}, n = 23; F_{1.64} = 1.8, P = 0.18).$ The lack of a 'tree-perch effect' may be related to the methods of site preparation. Seeds may have accumulated in the litter underneath the trees, deposited there by gravity and seed-dispersers. These seeds would have been unintentionally spread around the site when the site was cleared. A second explanation is that trees in our site were closely spaced together (usually within 5 m), whereas in other studies trees were more spread out (Guevara et al. 1992, Slocum & Horvitz 2000).

There were large differences in density and species diversity of plants > 125 cm tall between the fern thickets and cleared plots (Table 1). Density of woody plants >125 cm was eight times greater in the 3-y-old cleared plots $(0.75 \pm 0.73 \text{ stems m}^{-2})$ than in the fern thickets $(0.09 \pm 0.01 \text{ stems } \text{m}^{-2})$, where regeneration has occurred for the last 25 y. These results suggest that the fern has severely inhibited recruitment of woody plants. Species richness was greater in the thickets (28 species) than in the cleared plots (12 species), but there was a large difference in the area sampled (4400 m^2) and 829 m^2 , respectively) (Table 1). The most common species in the fern thickets were *M. coriacea*, *B. myrsinites*. B. comocladifolia and the introduced species Pinus caribaea. In the clearings, the most common species > 125 cm tall were Psychotria berteriana, B. myrsinites, T. micrantha, C. umbellata and M. mirabilis (Table 1).

In the cleared plots, the recovery of the fern did not have a major impact on forest recovery. Three y after clearing, fern cover was $16 \pm 25\%$ (n = 63). Ferns did not resprout from the root mat, as has been described for D. linearis (Cohen et al. 1995), but mainly colonized by spreading from the edge of the cleared sites $(> 1 \text{ m y}^{-1})$. This pattern of regrowth from existing clumps, and not from root sprouts, was also documented by Walker & Boneta (1995) in D. pectinata thickets that had been burned. In our cleared sites, there was a negative relationship between fern cover and woody plant regrowth (In-transformed fern cover vs. stem density: $r_s = -0.20$; P = 0.02; lntransformed fern cover vs. species density: $r_s = -0.17$; P = 0.05; n = 66), demonstrating the inhibitory effects of the fern on forest recovery and the need for large plots to reduce the edge to area ratio.

Table 1. Densities (stems 100 m^{-2}) of woody plants found at the Ébano Verde Scientific Reserve, Dominican Republic. Included are densities of woody plants > 20 cm tall in artificial clearings in the fern thickets, including densities found under trees and in the open (i.e. not under trees). Also included are densities of woody plants > 125 cm tall in the clearings and in the thickets. Densities are sorted by the total of all columns. For the last two columns, densities of species per plot are not shown because the sampling plots are of different sizes. Species nomenclature was based on a local survey (García *et al.* 1994).

| Species (family) | Traits [‡] | Plants > 20 cm tall in clearings | | Plants > 125 cm tall | |
|--|---------------------|----------------------------------|---------------|-------------------------|---------------|
| | | Open | Trees | Clearings | Thickets |
| Psychotria berteriana (Rubiaceae) | S A | 120 | 127 | 43 | 0.2 |
| Baccharis myrsinites (Asteraceae) | S W | 18 | 30 | 11 | 1 |
| Clidemia umbellata (Melastomataceae) | S A | 14 | 20 | 4 | 0.4 |
| Miconia mirabilis (Melastomataceae) | S A | 9 | 20 | 4 | 0.05 |
| Myrsine coriacea (Myrsinaceae) | ΤА | 11 | 17 | 2 | 3 |
| Brunellia comocladifolia (Brunelliaceae) | ΤW | 13 | 9 | 4 | 1 |
| Trema micrantha (Ulmaceae) | ΤА | 4 | 8 | 6 | _ |
| Alchornea latifolia (Euphorbiaceae) | ΤА | 3 | 3 | 0.7 | 0.3 |
| Solanum rugosum (Solanaceae) | S A | 3 | 3 | _ | _ |
| Piper aduncum (Piperaceae) | S A | 1 | 2 | 0.4 | _ |
| Ocotea leucoxylon (Lauraceae) | ΤА | 0.3 | 1 | 0.2 | 0.7 |
| Cecropia peltata (Cecropiaceae) | ТА | 0.7 | 0.9 | 0.1 | 0.02 |
| Cyrilla racemiflora (Cyrillaceae) | ТА | 0.7 | 0.7 | _ | 0.1 |
| Pinus caribaea (Pinaceae) | ТР | _ | _ | _ | 1.4 |
| <i>Cyathea</i> sp. 1 (Cyatheaceae) | FW | _ | _ | _ | 0.9 |
| Tabebuia bullata (Bignoniaceae) | S W | 0.3 | 0.2 | 0.1 | 0.1 |
| Gomidesia lindeniana (Myrtaceae) | ТА | _ | 0.5 | _ | 0.2 |
| Turpinia occidentalis (Staphyleaceae) | ТА | _ | 0.5 | _ | 0.05 |
| llex tuerckheimii (Aquifoliaceae) | ТА | _ | 0.2 | _ | 0.02 |
| Citrus sp. 1 (Rutaceae) | ТА | 0.3 | _ | _ | _ |
| Poitaea campanilla (Fabaceae) | SU | 0.3 | _ | _ | _ |
| Prestoea acuminata var. montana (Arecaceae) | ТА | _ | 0.2 | _ | 0.07 |
| Psychotria plumieri (Rubiaceae) | S A | _ | 0.1 | _ | 0.04 |
| Miconia sp. 1 (Melastomataceae) | S A | _ | 0.1 | _ | _ |
| Myrcia splendens (Myrtaceae) | S A | _ | 0.1 | _ | _ |
| Coccoloba wrightii (Polygonaceae) | ТА | _ | _ | _ | 0.1 |
| Styrax ochraceus (Styracaceae) | SU | _ | _ | _ | 0.07 |
| Persea krugii (Lauraceae) | ТА | _ | _ | _ | 0.05 |
| Clusia clusioides (Clusiaceae) | ΕA | _ | _ | _ | 0.02 |
| Ficus sp. 1 (Moraceae) | ТА | _ | _ | _ | 0.02 |
| <i>Guatteria blainii</i> (Annonaceae) | ТА | _ | _ | _ | 0.02 |
| Haenianthus salicifolius var. obovatus (Oleaceae) | ΤU | _ | _ | _ | 0.02 |
| Dreopanax capitatus (Araliaceae) | ТА | _ | _ | _ | 0.02 |
| Syzygium jambos (Myrtaceae) | ТА | _ | _ | _ | 0.02 |
| Forralbasia cuneifolia (Celastraceae) | ΤU | - | _ | _ | 0.02 |
| Density of stems per 100 m ² (mean \pm sd): | | 200 ± 141 | 245 ± 153 | 75 ± 7 | 8.7 ± 1.0 |
| Density of species per plot (mean \pm sd): | | 5.2 ± 2.0 | 5.8 ± 1.9 | _ | _ |
| Number of species: | | 16 | 21 | 12 | 28 |
| Number of plots: | | 23 | 43 | 66 | 22 |
| Total sampling area (m^2) : | | 289 | 540 | 829 | 4400 |

^{\ddagger} Life-history traits, including life form (S = shrub, T = tree, F = tree fern, E = epiphytic tree), and dispersal syndrome (U = unknown, A = animal dispersed, W = wind dispersed, P = directly planted). All species are natives except for *Syzgium jambos*.

In conclusion, clearing of fern thickets in the Ébano Verde Scientific Reserve caused rapid recruitment of woody species followed by limited regeneration of the fern thickets. Colonization of the cleared areas was dominated by a limited group of early successional species, suggesting that a second phase of enrichment planting with mature forest species will help to accelerate the recovery process (Ashton *et al.* 2001, Davidson *et al.* 1998, Slocum *et al.*, submitted).

ACKNOWLEDGEMENTS

We thank the staff of the Fundación para el Mejoramiento Humano (Progressio), the administrators of the Ébano Verde Scientific Reserve. In particular, we thank Ramón Elias Castillo for helping initiate the project, and José Bueno Marmolejo for help in the field. Funding for this project was provided by NASA-IRA (NAGW-4059) and by the Xunta de Galicia and Ministry for Education and Science of the Spanish Government to Luis Navarro.

LITERATURE CITED

- AIDE, T. M. & CAVELIER, J. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2:219–229.
- AIDE, T. M., ZIMMERMAN, J. K., HERRERA, L., ROSARIO, M. & SERRANO, M. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management* 77:77–86.
- AIDE, T. M., ZIMMERMAN, J. K., ROSARIO, M. & MARCANO, H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 18:537–548.
- AIDE, T. M., ZIMMERMAN, J. K., PASCARELLA, J., MARCANO-VEGA, J. & RIVERA, L. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* 8:328–338.
- ASHTON, M. S., GUNATILLEKE, C. V. S., SINGHAKUMARA, B. M. P. & GUNATILLEKE, I. A. U. N. 2001. Restoration pathways of rain forest in southwest Sri Lanka: a review of concepts and models. *Forest Ecology and Management* 154:409–430.
- CABIN, R. J., WELLER, S. G., LORENCE, D. H., CORDELL, S., HADWAY, L. J., MONTGOMERY, R., GOO, D. & URAKAMI, A. 2002. Effects of light, alien grass, and native species additions on Hawaiian dry forest restoration. *Ecological Applications* 12:1595–1610.
- CAVELIER, J., AIDE, T. M., SANTOS, C., EUSSE, A. M. & DUPUY, J. M. 1998. The savannization of moist forests in the Sierra Nevada de Santa Marta, Colombia. *Journal of Biogeography* 25:901–912.
- COHEN, A. L., SINGHAKUMARA, B. M. P. & ASHTON, P. M. S. 1995. Releasing rain forest succession: a case study in the *Dicranopteris linearis* fernlands of Sri Lanka. *Restoration Ecology* 3:261–270.
- DAVIDSON, R., GAGNON, D., MAUFFETTE, Y. & HERNANDEZ, H. 1998. Early survival, growth and foliar nutrients in native Ecuadorian trees planted on degraded volcanic soil. *Forest Ecology and Management* 105:1–19.
- GARCÍA, R., MEJÍA, M. & ZANONI, T. 1994. Composición floristica y principales asociaciones vegetales en la Reserva Científica Ébano Verde, Cordillera Central, República Dominicana. *Moscosoa* 8:86– 130.
- GUEVARA, S. & LABORDE, J. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* 107/108:319–338.
- GUEVARA, S., MEAVE, J., MORENO-CASASOLA, P. & LABORDE, J. 1992. Floristic composition and structure of vegetation under

isolated trees in Neotropical pastures. *Journal of Vegetation Science* 3:655–664.

- GUIMARÃES-VIEIRA, I. C., UHL, C. & NEPSTAD, D. 1994. The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* 115: 91–99.
- HOLL, K. D., LOIK, M. E., LIN, E. H. V. & SAMUELS, I. A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* 8:339–349.
- MCDONNELL, M. J. & STILES, E. W. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–116.
- MEJÍA, M. & JIMÉNEZ, F. 1998. Flora y vegetacion de Loma la Humeadora, Cordillera Central, República Dominicana. *Moscosoa* 10:10–46.
- NEPSTAD, D. C., UHL, C., PEREIRA, C. A. & CARDOSO DA SILVA, J. M. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76:25–39.
- ROBINSON, G. R. & HANDEL, S. N. 2000. Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecological Applications* 10:174–188.
- RUSSELL, A. E., RAICH, J. W. & VITOUSEK, P. M. 1998. The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawaii. *Journal of Ecology* 86:765–779.
- SAS INSTITUTE INC. 1999. *SAS/STAT user's guide*, version 8, volume 2. Cary, North Carolina. 1307 pp.
- SLOCUM, M. G. & HORVITZ, C. C. 2000. Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology* 149:51–62.
- SLOCUM, M. G., AIDE, T. M., ZIMMERMAN, J. K. & NAVARRO, L. 2000. La vegetación leñosa en helechales y bosques de ribera en la Reserva Científica Ébano Verde, República Dominicana. *Moscosoa* 11: 38–56.
- UHL, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. *Journal of Ecology* 75:377–407.
- UHL, C., BUSCHBACHER, R. & SERRÃO, E. A. S. 1988. Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession. *Journal* of Ecology 76:663–681.
- WALKER, L. R. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science* 5:525– 532.
- WALKER, L. R. & BONETA, W. 1995. Plant and soil responses to fire on a fern-covered landslide in Puerto Rico. *Journal of Tropical Ecology* 11:473–479.
- ZIMMERMAN, J. K., PASCARELLA, J. B. & AIDE, T. M. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8:350–360.