Analysis of the Viability of Natural Regeneration for Restoration of Tropical Rainforests:

Seed dispersal and its effects on the practicality of natural regeneration and potential for ecological research at the Mamoní Valley Preserve, Panamá

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Abstract

Natural regeneration of forests is an attractive method for reforestation because of the limited investment required. Like other forms of restoration, it can provide improved ecosystem services, biodiversity, and direct economic benefits to local residents. Noted tropical ecologist Dan Janzen is well-known for, among other things, orchestrating very successful natural regeneration in Costa Rica’s tropical dry forests, but he and others have challenged its potential in tropical rainforests and their pastures. Here relevant barriers to natural regeneration in the Mamoní River Valley of Panamá are assessed through a review of the restoration literature and recommendations are made for how non-profit Earth Train might incorporate natural regeneration into its restoration scheme and research efforts. With careful planning and consideration of the potential need for supplemental planting and removal of anthropogenic disturbances, natural regeneration can work in tropical rainforests, particularly as part of a restoration plan employing multiple methods.

Summary: Can natural regeneration work in tropical rainforests?

Regeneration of forest without direct human assistance is known in the scientific literature as natural regeneration or succession. Its potential for reforesting large areas with minimal financial investment and labor holds great promise for degraded tropical forests, but often, ecological and physiographic factors make natural regeneration difficult to employ.

Tropical ecologist Dan Janzen is well-known for, among other things, extensive successful restoration in the tropical dry forests of Costa Rica. Much of the success the and his colleagues have had at the Area de Conservacion Guanacaste has been to allow natural regeneration by suppression of anthropogenically exacerbated fires (Janzen, 2002). Janzen (2002), though, presents several challenges—all centered around seed dispersal and seedling survival—to the viability of natural regeneration in nearby tropical rainforests (Table 1).

Table 2—Janzen’s Challenges to Natural Regeneration in Tropical Rainforests. All challenges supposed result in slow natural regeneration of forests that do not support the same diversity as local primary forests.

<table>
<thead>
<tr>
<th>Challenge</th>
<th>Brief Explanation of Janzen’s Reasoning</th>
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Lack of wind-dispersed trees at rainforest edges  |  No explanation given; resulting forests will not support diversity of local primary forests
---|---
Lack of animal dispersal to rainforest pastures  |  Rainforest vertebrate dispersers are unlikely to enter pastures where there is little cover or food; resulting forests will not support diversity of local primary forests
Rainforest seedlings will not survive well in pasture  |  Rainforest trees are less well adapted to dry conditions in pasture than are dry forest trees
Rainforest trees have trouble finding mycorrhizal symbionts in pasture  |  Admittedly speculative

In this paper, two of Janzen’s challenges are explored through a review of past tropical rainforest restoration projects. The analysis is carried out with an eye towards making recommendations for natural regeneration reforestation and research in the Mamoní Valley Preserve, on lands owned by the youth leadership and environmental non-profit Earth Train in central Panamá. This is not intended as a complete review of natural regeneration in tropical rainforests; rather it is a targeted exploration of several factors that need consideration if natural regeneration is to be both practically and scientifically productive at and around Centro Madroño, Earth train’s campus. From this review, it is certainly not clear that Janzen’s dismissal of natural regeneration’s feasibility in Guanacaste’s moist forests should be extended to all rainforests, or even to other Latin American ones. Rather, the immense complexity of and variation among tropical rainforests means that natural regeneration has so far been studied effectively only at small scales. Additionally, it is difficult to generalize widely from any studies of natural regeneration. Practitioners at Centro Madroño should go forward with restoration efforts that include natural regeneration while taking the factors discussed below into consideration.
Mamoní River Valley geography, land use and stakeholders

One half of tropical forests are found in the Americas. S. Joseph Wright (2005) of the Smithsonian Tropical Research Institute in Panamá reviewed the state of tropical rainforests and the effects of anthropogenic change on these ecosystems states that a potential 1.05 billion hectares of rainforest could exist in this supra-region, but much has been and continues to be cleared. Over four million hectares (10 million acres) were deforested annually between 1990 and 1997 (Wright, 2005).

The Mamoní River Valley of central Panamá is no exception to these trends. Located at the narrowest point of the isthmus, the valley includes well over a million hectares of intact tropical rainforest, according to a briefing by Earth Train co-director Nathan Gray. The valley falls within one of the most biodiverse regions of the world (Condit et al., 2001) (Figure 1). Since the 1970s, large sections of the region have been cleared for agricultural and ranching use leaving the watershed and its biodiversity under great threat (Gray, *Earth Train Briefing*). A number of groups are working in the region on the complex social and ecological issues underlying the area’s deforestation (Table 2).
Figure 1—Biodiversity in the Mamoní River Valley. From top left to bottom right: A butterfly, a basilisk, the endangered frog *Atelopus limosus*, and a passionflower.

Table 2—Groups Active in the Mamoní River Valley

<table>
<thead>
<tr>
<th>Group</th>
<th>Forest Restoration</th>
<th>Community, Cultural, &amp; Economic Development</th>
<th>Scientific Research</th>
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<tbody>
<tr>
<td>Earth Train</td>
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<td>Peace Corps</td>
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<td>Conservation through Research, Education and Action (CREA)</td>
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Much of the valley today is owned by absentee ranchers, both Panamanian and foreign (Gray, *Earth Train Briefing*¹). Local farmers are contracted to grow culantro, a variety of cilantro, and to ranch cattle on cleared forest lands. Logging companies have

¹ The remainder of the information in this paragraph is from this source, unless otherwise noted.
also entered the area in recent decades and Panamá city is expanding eastward towards the Valley.

**Why are tropical forests and their restoration important?**

Tropical rainforests suffer from a vast array of threats including habitat fragmentation, clear-cutting, agricultural clearing, poaching, over-harvesting, and climate change. Worldwide, over 800 million hectares (2 billion acres) of tropical rainforests have been destroyed or degraded (Lamb, Erskine & Parrotta, 2005), amounting to loss of over half of the once-intact tropical rainforests (Wright, 2005). Ecologically, tropical rainforests are an immensely important biome for their unparalleled diversity. It is estimated that over half of the world’s terrestrial species occur in these forests, although only 6% of the Earth is covered by this ecosystem type (Primack and Corlett, 2005).

The restoration of degraded or destroyed tropical rainforests holds potential ecological, economic and cultural benefits (Lamb et al., 2005) for the five billion people living in tropical nations and dependent on the ecological services (clean air, clean water, wood, non-timber forest products, untapped cultivable species and pharmaceuticals) provided by local ecosystems (Wright, 2005; Perlman and Milder, 2004). A 1997 study in the journal *Nature* estimated that the value of all ecosystem services was anywhere from equivalent to to three times as much as the global gross national product (Costanza et al., 1997).

In Panamá, reforestation in the Canal Zone may decrease the costs associated with recent flooding and erosion, enabling a delay in the need for construction of a new canal (The Economics of Ecosystems and Biodiversity, *An interim report*). The aesthetic value of biodiversity and intact ecosystems can be both enjoyed on its own and tapped for
ecotourism development, noted by both conservation biologists and social scientists (Naidoo & Adamowicz, 2005; Mapes, 2009).

**What are Janzen’s Challenges to Rainforest Natural Regeneration and Are They Valid?**

Janzen presents four primary challenges, two of which are discussed here, and says that together, they conspire to slow natural regeneration in tropical rainforests to a rate far below that in tropical dry forests (Janzen, 2002). Canopy closure in Guanacaste dry forests commonly occurred in as few as five years, but Janzen suggests it takes up to 50 in tropical rainforests. His first challenge is the supposed lack of wind-dispersed trees in tropical rainforests bordering pastures. In a review of regeneration on abandoned neotropical agricultural land, Karen D. Holl (2007), Professor of Environmental Studies at the University of California at Santa Cruz, substantiates Janzen’s suggestion that wind-dispersed trees are less common in moister tropical forests. There is, though, no indication of why this tree guild is particularly absent from the edges of Guanacaste moist forest remnants, and so one cannot immediately judge whether or not this pattern is locally, regionally, or globally important for seed dispersal into pastures.

A study by Castillo and Perez Rios (20082) of the Instituto Politécnico Nacional in Oaxaca offers hope, though, for wind-dispersal and successful natural regeneration at Centro Madroño. In a matrix of differentially aged montane cloud forests in southern Mexico, it was found that young stands tended to harbor wind-dispersed pioneer species in greater numbers than they did animal-dispersed late-successional species. Although, the study included few statistical tests, it did show that in the youngest forests (≈ 7 years) over 70 percent of seeds were abiotically dispersed (mostly wind-dispersed). Many of

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2 The remainder of the information in this paragraph is from this source, unless otherwise noted.
these early successional species likely performed key roles as pioneers, giving a distinct structure to the young forest before later-successional, often animal-dispersed, species invaded and changed the forest compositions (Chazdon et al., 2007).

Seed rain in lowland tropical rainforest pastures around the well-known La Selva Biological Station in Costa Rica showed patterns similar to those found by Castillo and Perez Rios. There, more wind-dispersed seeds were found in natural regeneration plots than in areas planted with either native or exotic trees, either in mixtures or monocultures (Zamora and Montagnini, 2007). Natural regeneration plots did have significantly fewer seeds than did areas where trees had been planted.

Finnegan and Delgado (2000) found that a majority of trees in a 30-year-old secondary tropical rainforest in Costa Rica were wind-dispersed, although a majority of species were vertebrate-dispersed. The site was in the foothills of the Cordillera Central on an abandoned farm which had been cleared and burned previously. Wind-dispersed species were arguably more successful than animal-dispersed species; that they accounted for a greater proportion of the individuals than did animal-dispersed species suggests wind dispersal was not a factor limiting tree establishment. In Mexican riparian rainforest fragments and the surrounding pastures, Cristina Martinez-Garza and Renee González-Montagut (1999) of the Instituto de Ecología and the Mexican Nature Conservation Fund, respectively, also found that the number of wind-dispersed seeds greatly outnumbered animal-dispersed seeds. Their study was conducted around Las Tuxtlas Biological Station which receives close to five meters of rain per year, high even for rainforests.

The success of wind-carried seeds in pastures makes sense. Quite reasonably, it has been suggested in the scientific literature (Castillo and Perez Rios, 2008) that because
wind-carried seeds are dependent on wind, open areas such as pastures and younger forests may allow seeds to be transported greater distances than they would be in a mature forest’s interior. Together, the works of Finnegan and Delgado, Castillo and Perez and Zamora and Montagnini do not mean sure success in natural regeneration at Centro Madroño, but are a good sign that wind-dispersed trees can thrive under the conditions of natural regeneration from the first few years of succession at least through several decades.

Given Janzen’s concern that a lack of wind-dispersed trees around forest edges will limit tropical rainforest succession, it is interesting to note that the vast majority of neotropical tree species, not just those at Guanacaste’s forest edges, are animal-dispersed (Ganade, 2007). Often, better than nine in ten species are animal-dispersed (Howe and Smallwood, 1982). Secondary forests, then, may well invade abandoned pastures even where wind dispersal is, as Janzen has suggested, quite low. It will be critical to determine the dispersal modes of the tree communities surrounding deforested land at Centro Madroño to inform on the importance of wind dispersal.

Janzen’s next challenge to natural regeneration deals with animal dispersal. He observes that tropical rainforests vertebrates are less likely to be found in the adjacent pastures than dry forest vertebrates are in their adjacent pastures (Janzen, 2002). His suggestion is that with few vertebrates in the tropical rainforest pastures, animal dispersal of seeds will be too low for viable natural regeneration. This is somewhat ironic, given that his first challenge, discussed above, was to wind dispersal. Apparently, the trees in Janzen’s tropical rainforests did not get out much. Again, little in the way of reasoning is
presented for why Janzen finds this to be the case at Guanacaste, but other researchers have discussed patterns of animal activity and dispersal of seeds in pastures at length.

The majority of tropical rainforest species are animal-dispersed (Howe and Smallwood, 1982), so it follows that there should be many opportunities for animal dispersal. Although Dosch, Peterson, and Haines (2007) report that many authors agree with Janzen that animal dispersers are quite limited in tropical rainforest pastures, some studies have found significant animal dispersal activity in degraded habitats. In a field survey in southern Costa Rica, it was found that 50 percent of the region’s bird species were using human-dominated landscapes (coffee and tree plantations, pastures, and villages) (Pejchar et al., 2008). Interestingly, seed rain was correlated strongly with bird abundance, but not with bird species richness (Pejchar et al., 2008).

Hooper, Legendre and Condit (2005) did find large-seeded, animal-dispersed trees were rare when natural regeneration occurred in Panamá, a finding in concert with Janzen’s concern. Tropical dry forest regeneration, though, can also be limited by animal dispersal. Panamanian forester José Deago has noted the importance to reforestation of early successional trees like *Cercropia spp.*, but expressed concern that their dispersal may be limited at the margins of the Achetines Forest on the Azuero Peninsula because of low bird activity (Deago, J., personal communication, February, 2009). Thus, it is not clear that the problem is limited to tropical rainforests.

Another study of Costa Rican secondary forests with closed canopies established by natural regeneration showed the understory plant communities to be more diverse than those of planted native, monoculture, or even primary forest communities (Leopold and
Salazar, 2008\textsuperscript{3}). Over 60\% of understory vegetation in these hyper-diverse naturally regenerated areas was animal-dispersed, not far behind the 80\% in primary forest. Very similar numbers of understory species in the primary and secondary forests were wind-dispersed. It is worthy of note, though, that more vines and herbs were present in naturally regenerated areas than in primary forest.

What tradeoffs exist among natural regeneration versus various sorts of facilitated restoration?

In light of the immense threats to tropical rainforests and the benefits they provide, many attempts have recently been made to restore lost forest. A range of facilitated restoration techniques are employed with a range of goals. Chazdon (2008) and Lamb (2005) described continuums of restoration methodologies with varying investments and returns. In general, monocultures of exotic or native species can be planted for wood production and provision of basic ecological services such as watershed protection and erosion prevention (Lamb et al., 2005). These tree farms, though, do not allow the full range of services (such as shade-grown crops and ecotourism money) that a diverse secondary or primary forest can (Lamb et al., 2005; Chazdon, 2008).

Despite plantations’ shortcomings, fast-growing exotic plantation species can be used as part of an effective restoration strategy. Janzen (2002) actually describes the process whereby aggressive tree species such as Caribbean pine (\textit{Pinus carribea}) can be planted and allowed to overtop and shade-out hardy pasture grasses. Following dieback of the grasses, native vegetation can either be planted or allowed to invade naturally, and the exotic or “nurse trees” can be harvested. This sort of process falls intermediately in

\textsuperscript{3} The remainder of the information in this paragraph is from this source, unless otherwise noted.
Lamb’s hierarchy of restoration; it requires a moderate investment in planting, but can yield substantial biodiversity and ecosystem service returns, often faster than unassisted natural regeneration can (Janzen, 2002; Lamb, 2005). There is also a significant short-term economic benefit for selling the harvested nurse trees.

Perhaps the most traditional restoration method is the direct planting of either seeds or nursery-raised seedlings. Leopold (2005) describes such a project in a tropical rainforest of Costa Rica. He documents canopy closure by planted native trees (Leopold, 2005) and accelerated understory succession (Leopold, 2008) within only one decade. In Panamá, the Native Species Reforestation Project (PRORENA) tested nearly two dozen native tree species in restoration research and projects (Winshie et al., 2007). *Acacia mangium, Diphysa robinoides, Gliricidia sepium, Guazuma ulmifolia* and *Ochroma pyramidale* performed best at each of the three sites tested (two tropical rainforests and one tropical dry forest), attaining closed canopies and dense crowns after only two years. Certainly these are impressive results, but both pre- and post-planting investment was very high in this project. All vegetation was cleared and sites were treated with glyphosate, a biodegradable herbicide, prior to seedling transplantation. Dead seedlings were replaced after several weeks and more competing vegetation was cleared.

A particular challenge for those carrying out restoration in Panamá is the aggressive spread of the hardy grass *Saccharum spontaneum*, known locally as paja blanca, meaning “white grass.” Originally brought in to stabilize the banks of the canal, the grass has come to dominate many areas now cleared of native vegetation (Winshie et al., 2007). Another major research effort by PRORENA has been to test methods of paja blanca eradication which can work in concert with forest restoration. In tests of six native

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4 The remainder of the information in this paragraph is from this source, unless otherwise noted.
species and the popularly planted teak (*Tectona grandis*), it was found that more physical clearing of paja blanca and use of herbicide both yielded better growth of young trees (Winshie et al., 2007).

Shono and Durst of the United Nations Food and Agriculture Organization along with researcher Cadawengand, reviewed what they called assisted natural regeneration as a strategy for dealing with paja blanca. As in the case of PRORENA’s plots, physical means were most effective in removing the grass (Shono, Durst and Cadawengand, 2007). They suggest “pressing” the grass to the ground by stepping on it with a wooden board (Figure 2). Following this process they recommend identifying and protecting naturally propagated seedlings and then planting supplemental trees. This method is best used in areas with some remaining natural vegetation. The investment of person-hours is low for assisted natural regeneration when compared to fully facilitated reforestation.

![Figure 2](image)

*Figure 2*—Reproduced from Shono, Durst and Cadawengand, 2007. Pressing down paja blanca using a wooden board.

For those seeking to restore and protect biodiversity at an absolute minimum (potentially zero) investment, natural regeneration remains the most promising reforestation method, and one which is beginning to show great promise. Within the last 30 years, the amount of secondary forest regrowth on abandoned lands in the tropics has

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increased greatly, to the point where for every six-to-seven hectares cleared, one is reestablished as secondary forest (Wright, 2005). In Panamá, areas approximately equal in size to 10 percent of that deforested between 1992 and 2002 were regenerated as forest between 1992 and 1994 (Sloan, 2008). Wherever natural regeneration is performed, it is key that major human disturbances be removed. In the Mamoní River Valley, the most important disturbance is fire set by campesinos to clear forest and create pasture (Gray, *Earth Train Briefing*). For extensive restoration efforts to be truly successful fire must be reduced drastically, as must any unlawful logging.

How does natural regeneration and ecological research fit into the tropical rainforest restoration at Centro Madroño?

The land owned by Earth Train at and around Centro Madroño in the Mamoní River Valley is in various states of degradation. Much is fully cleared pasture with virtually no trees or native species remaining (Figure 3). Significant patches are secondary or primary forest, and some smaller areas are dominated by thick, low vines and shrubs or paja blanca (Personal observation, 2009). This heterogeneity necessitates a variety of restoration methods if forest regeneration is to be optimally successful. As of February 2009, Earth Train was planning to employ both direct planting of seedlings and natural regeneration (Mariscal, E. and Adelson, G., February, 2009; personal communication).
Certain types of vegetation lend themselves to certain restoration techniques. Natural regeneration should be most effective at forest edges. Hooper et al. (2005), working near the Panamá Canal in pastures dominated by paja blanca, showed that seedling density and diversity were significantly higher at 10 m from forest edges than at 35 m. Likewise, Cubíña and Aide (2001) showed a dramatic dropoff in the abundance and diversity of species at less than 10 m from the edge of secondary rainforests in Puerto Rico. A modeling study by two Canadian researchers found that in temperate forests spruce (*Picea*), maple (*Acer*), tamarack (*Larix*), ash (*Fraxinus*), hemlock (*Tsuga*) and pine (*Pinus*) seed density all decrease with distance from the forest edge. This lends further support the plausibility that, in general, forest edges are best suited for natural regeneration (Greene and Johnson, 1996) (Figure 4). Small deforested areas bordered by forest on at least two sides may be ideal spots for natural regeneration, then, in the Mamoní Valley (see Figure 5). By situating Earth Train’s natural regeneration in these areas, the problems of long-distance dispersal of seeds, discussed above, can be limited.
Figure 4—Reproduced from Greene and Johnson (1996). Compare with the observed data from Cubiña and Aide (2001) in Figure 4.

Figure 5—Reproduced from Cubiña and Aide (2001). Open and dark circles represent the number of germinating seedlings at two sites in pastures bordering Puerto Rican rainforests. Note the higher number of seedlings at site two, where predominating winds blew into the pasture.
Figure 5—A schematic representation of the opportunity for utilizing and testing various restoration methodologies around Centro Madroño. The dark green at the bottom and right represents remaining forest, most likely secondary or disturbed. The green dots represent remnant trees in pasture which can serve as seed sources and attractants for seed dispersers. The yellow blotch represents an area covered in paja blanca and the remaining white area represents cleared pasture. NR = sites suitable for natural regeneration, DSP = direct seeding and planting and NT = area for nurse tree experimentation.

In addition to areas adjacent to forest edges, those planning Earth Train’s restoration should consider closely areas where remnant trees are most prevalent. In his short critique of natural regeneration, Janzen (2002) didn’t consider remnant trees, but they are a critical part of the matrix in establishment of restoration. Manning, Fischer, and Lindenmayer (2006) review the benefits of isolated trees for natural regeneration and conservation, in general. Remnant trees can serve as direct seed sources and as attractants for seed-dispersing herbivores, particularly if the tree is one which provides fleshy fruits (e.g. *Ficus sp.*, *Carica sp.*, or *Mangifera sp*.). Lone trees in open pasture also create localized microclimates where tropical rainforest saplings may be more able to colonize, add nutrients to soil in the immediate area and provide some measure of connectivity for both tree and animal populations.

Ultimately, the lesson from all the restoration research and efforts detailed above is that results are always case-specific. Each restoration site is too distinct from each other in it’s hydrology, climate, soils, and ecology to draw any specific rules with truly broad applications. Additionally, nearly all the supposedly long-term research that has been published on tropical rainforest succession is the result of so-called chronosequence studies wherein a group of differently aged sites with purportedly similar conditions are compared to make predictions about the progression and dynamics of restored vegetation

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6 The remainder of the information in this paragraph is from this source, unless otherwise noted.
communities. A review by Chazdon et al. (2007), though, found greater species composition differences across sites used for chronosequence studies than within single sites of the same ages, so these studies may be poor proxies for truly long term monitoring of individual sites. Research in restoration ecology is in its infancy; forests require centuries to regain what is lost in intense degradation and it is too soon to say what works where, when, or why.

In addition to practical restoration, many sorts of valuable restoration research can be carried out in the Mamoní River Valley concurrent with Earth Train’s restoration projects. Earth Train has the opportunity to begin, or encourage others to begin, long term studies of restoration at and around Centro Madroño. For example, some very simply designed observational studies could generate huge data sets on species colonize natural regeneration sites. Just collecting the species, height, diameter-at-breast-height and dispersal method of all trees growing in regeneration plots is valuable. No continuous natural regeneration data from longer than 40 years is available in the literature, so even the simple information proposed above, even collected from perhaps just ten one-acre plots, could be a remarkable data set.

Shorter-term research in the Mamoní Valley could also provide significant insight into previously unanswered questions about design of restoration projects. Any comparisons that could be made among the progression of natural regeneration in different landscapes would be productive. A list of possible comparisons can be found in Table 3.

| Equal-area plots in a strip along a river versus in a square of pasture, both bordering forest edges or not |

\*Table 3—Possible Landscape-Scale Natural Regeneration Progression Comparisons*
Other research might include attempts to entice dispersers into pastures. In Costa Rica artificial roosting structures have been used to successfully recruit frugivorous and nectarivorous bats and to significantly increase seed rain beneath the installed roosts (Kelm, Wiesner and Von Helvesen, 2007). Earth Train might include some artificial perches in pastures and monitor the types and abundances of species which regenerate beneath the structures compared to elsewhere. It would also be valuable to note which bird species use the perches.

Conclusions

Earth Train practitioners should attempt natural regeneration, assisted natural regeneration and direct seeding in appropriate areas of the Mamoní Valley Preserve. Great opportunities exist for improving the native habitats, ecosystem services and economic state of the valley, all through forest restoration.
References


