

---

# Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment

Karen D. Holl<sup>1,2</sup>

Michael E. Loik<sup>1</sup>

Eleanor H. V. Lin<sup>3</sup>

Ivan A. Samuels<sup>1,3</sup>

## Abstract

Tropical forests are being cleared at an alarming rate although our understanding of their ecology is limited. It is therefore essential to design restoration experiments that both further our basic knowledge of tropical ecology and inform management strategies to facilitate recovery of these ecosystems. Here we synthesize the results of research on tropical montane forest recovery in abandoned pasture in Costa Rica to address the following questions: (1) What factors limit tropical forest recovery in abandoned pasture? and (2) How can we use this information to design strategies to facilitate ecosystem recovery? Our results indicate that a number of factors impede tropical forest recovery in abandoned pasture land. The most important barriers are lack of dispersal of forest seeds and seedling competition with pasture grasses. High seed predation, low seed germination, lack of nutrients, high light intensity, and rabbit herbivory also affect recovery. Successful strategies to facilitate recovery in abandoned pastures must simultaneously overcome numerous obstacles. Our research shows that establishment of woody species, either native tree seedlings or early-successional shrubs, can be successful

in facilitating recovery, by enhancing seed dispersal and shading out pasture grasses. On the contrary, bird perching structures alone are not an effective strategy, because they only serve to enhance seed dispersal but do not reduce grass cover. Remnant pasture trees can serve as foci of natural recovery and may enhance growth of planted seedlings. Our results highlight the importance of: (1) understanding the basic biology of an ecosystem to design effective restoration strategies; (2) comparing results across a range of sites to determine which restoration strategies are most generally useful; and (3) considering where best to allocate efforts in large-scale restoration projects.

**Key words:** bird perching structures, grass competition, microclimate, reforestation, seed dispersal, seed germination, seed predation, shrubs, soil nutrients.

## Introduction

More than a decade ago, Bradshaw (1987) wrote that "the successful restoration of a disturbed ecosystem is the acid test of our understanding of that ecosystem." Although this quote has often been restated, little research in restoration ecology has been rigorously designed to test the complex interactions between abiotic and biotic factors that affect the rate and direction of recovery. Nowhere is the need to take this approach greater than in the tropics, where forests are being cleared at an alarming rate although a thorough understanding of their ecology is lacking.

An estimated 8% of tropical forests were destroyed during the 1980s alone (WRI 1997), and clearing has continued over the past decade at only a slightly lower rate (FAO 1997). The primary cause of deforestation in Latin America over the past few decades has been creation of pastures for cattle grazing (Amelung & Diehl 1992; Fearnside 1993); for example, Costa Rica, a country that was once almost entirely forested, is now almost half (46%) covered by pasture (WRI 1998). Clearly, conservation efforts in the tropics must focus on slowing deforestation and providing alternative sources of income to people living in countries with tropical forests. At the same time, there is a need to develop strategies to restore degraded forests or, at minimum, to return the land to more productive uses. Given that knowledge of tropical forests, particularly highly disturbed tropical forests, is sparse, it is necessary to do research that furthers our understanding of how tropical ecosystems work and simultaneously informs selection of restoration strategies.

Over the past five years, we have studied montane forest recovery in abandoned pasture in southern Costa Rica. Given the complexity of tropical ecosystems, it is not possible to reintroduce all of the myriad species. Rather, it is necessary to design strategies to accelerate the natural

---

<sup>1</sup>Department of Environmental Studies, University of California, Santa Cruz, CA 95064, U.S.A.

<sup>2</sup>Address correspondence to K. D. Holl, email kholl@cats.ucsc.edu.

<sup>3</sup>Department of Biology, University of California, Santa Cruz, CA 95064, U.S.A.

recovery process. Therefore, our research has aimed to answer two broad questions: (1) What factors limit tropical forest recovery in abandoned pasture? and (2) How can we use this information to design strategies to facilitate ecosystem recovery? We have asked these questions concurrently. Results from experiments to identify factors impeding recovery have informed our selection of restoration strategies. Likewise, testing these strategies has furthered our understanding of the ecology. In this article, we synthesize the results from both published and unpublished research at our study site; for those data that are presented elsewhere, we refer readers to the appropriate sources for the details of experimental design.

### Study Area

The majority of this research was conducted in abandoned pasture adjacent to the Las Alturas Biological Station in southern Costa Rica (8°57'N, 82°50'W, 1,500 m elevation). Average annual rainfall is approximately 3,000 mm, more than 95% of which normally falls between April and December (Instituto Costarricense de Electricidad, unpublished data). Average annual maximum and minimum temperatures are 24.6 and 13.2° C, respectively (Instituto Costarricense de Electricidad, unpublished data).

The pasture directly abuts primary, seasonal montane wet forest (Holdridge et al. 1971) creating an

abrupt forest/pasture edge. The primary forest is part of the Las Tablas Protected Area (19,602 ha), which is contiguous with La Amistad Biosphere Reserve. The 5 ha pasture where most of the research was conducted (Fig. 1) is part of a mosaic of agricultural land uses covering approximately 2,500 ha. Some data on reforestation with native species were collected in other pastures on this property. The focal study area was cleared 25 years ago using heavy machinery. The land was used for 15 years for the cultivation of coffee and for the subsequent 10 years for cattle grazing. Cattle were removed from the pasture in February 1995. At that time, the pasture vegetation consisted predominantly of non-native grasses such as *Axonopus scoparius* (Flügge) Kuhlm., *Digitaria decumbens* Stent, and *Melinis minutiflora* Beauv. Isolated trees, primarily *Inga edulis* Mart. and *Inga punctata* Willd. (Fabaceae), were scattered throughout the pasture. Shrubs began to colonize the pasture soon after abandonment; common shrub species include *Piper arboreum* Aublet (Piperaceae), *Rubus urticaefolius* Poir. (Rosaceae), *Solanum rudepannum* Dunal (Solanaceae), *Solanum umbellatum* Willd. (Solanaceae), and *Vernonia patens* H. B. K. (Asteraceae).

### Obstacles to Forest Recovery

For forest to recover in abandoned pasture, a number of processes must occur, including dispersal, avoidance of



Figure 1. Focal abandoned pasture where the majority of the research was conducted, one year after abandonment. Note crossbar perching structure on left and remnant trees and recently established shrub patches throughout pasture.

predation, and germination of seeds, as well as survival and growth of seedlings (Fig. 2). Each of these processes is influenced by a number of factors (Fig. 2); for example, seed germination is affected by light, temperature, and moisture, which are in turn influenced by vegetative cover. Research at various neotropical sites demonstrates that many factors may impede tropical forest succession in areas of pasture land, including a lack of soil nutrients, soil compaction, competition with pasture grass, seasonal drought, low rates of seed colonization, and high seed and seedling predation (e.g., Uhl 1987; Buschbacher et al. 1988; Nepstad et al. 1991; Aide & Cavelier 1994; Reiners et al. 1994; Aide et al. 1995; Fernandes & Sanford 1995; Nepstad et al. 1996). The relative importance of these factors often varies greatly over small spatial and temporal scales. Few studies have evaluated a number of factors at a single site, which would allow for the possibility to prioritize those factors most important in limiting recovery. Such information is essential for designing effective restoration strategies; therefore, we aimed to isolate the effect of various biotic and abiotic factors on different processes influencing seedling establishment.

#### Seed Availability—Dispersal and Predation

The first important question in studying recovery of any ecosystem is whether propagules of target species are present in the disturbed area. Recovery of tropical forest in abandoned pasture is generally dependent on dis-

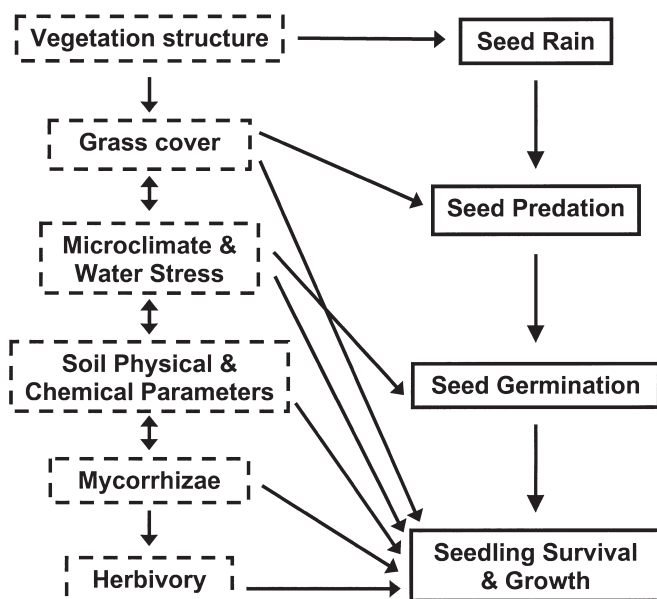


Figure 2. Factors limiting pasture recovery. Processes that influence seedling establishment are in boxes with solid lines. Factors affecting the magnitude of these processes are in boxes with dashed lines.

persal of seeds of forest species, because many tropical forest seeds have an extremely short duration of viability and are, therefore, not present in the seed bank (Uhl 1987; Garwood 1989; Nepstad et al. 1996). We monitored seed rain in seed traps at distances from 250 m into the forest to 250 m into the pasture for a one year period, beginning in May 1995. Seed rain was dramatically lower in open pasture (no nearby trees) with an average of 1,670 seeds  $\text{m}^{-2} \text{yr}^{-1}$  falling in forest traps and 190 seeds  $\text{m}^{-2} \text{yr}^{-1}$  (not including grasses) falling in open pasture traps (Holl 1999). Dispersal of animal-dispersed seeds was particularly low, only 3 seeds  $\text{m}^{-2} \text{yr}^{-1}$ ; seeds of only one genus, *Solanum*, a widespread pasture shrub, fell in pasture traps beyond 5 m of the forest edge (Holl 1999). This result is not surprising, given the minimal movement of birds, one of the primary agents of seed dispersal, between the forest and pasture at this site (Sisk 1991). Several other studies have also indicated that lack of seed dispersal, particularly of animal-dispersed seeds, is a primary factor limiting tropical forest recovery in large disturbed areas (Kolb 1993; Aide & Cavelier 1994; González Montagut 1996; Nepstad et al. 1996; Hardwick et al. 1997; Zimmerman et al. 2000).

If seeds are dispersed into open areas, the question arises as to whether they will survive until germination. Although tropical forest seeds often germinate within a few weeks of dispersal, our results suggest that seed predation can be high even over short time periods. Overall, approximately two-thirds of seeds were removed from seed depots within thirty days (Holl & Lulow 1997). Levels of predation of the ten native forest species studied were highly species specific, ranging from 0 to 87% of seeds remaining in the pasture at the end of the study (Holl & Lulow 1997), which may affect patterns of recovery. Other studies have reported similarly high and species-specific rates of seed predation in tropical pastures (Uhl 1987; Aide & Cavelier 1994; Osunkoya 1994; Nepstad et al. 1996; González Montagut 1996).

#### Seed Germination

For seedlings of forest species to establish, seeds dispersed into the pasture must be able to germinate. Previously, we measured germination rates of twelve woody species in abandoned pasture and have compared their germination rates with those of seeds in either primary forest or under shrubs in pasture (Holl 1999; Holl, unpublished data). We have recorded a wide range of germination rates, from 0 to 78%. In most cases, germination rates were similar in abandoned pasture with dense grasses, as compared to primary forest or under pasture shrubs (Holl 1999; Holl, unpublished data). Other studies have reported a comparable range of germination rates in abandoned pastures, with very high germination of some species and no germina-

tion of other species (Aide & Cavelier 1994; González Montagut 1996; Hardwick et al. 1997). Our results, as well as those of others (Aide & Cavelier 1994; González Montagut 1996; Hardwick et al. 1997; Zimmerman et al. 2000), indicate that germination of some species is lower in areas cleared of pasture grasses where microclimatic conditions are more stressful. For most of the species we studied, lack of germination did not appear to be as important as lack of seed dispersal in limiting recovery. Very low seed germination in a few species may have been due to lack of appropriate triggers for seed germination, such as passing through the guts of birds (Lieberman & Lieberman 1986; Ellison et al. 1993) or the required light quantity or quality (Vazquez-Yanes & Orozco-Segovia 1993; Metcalfe 1996).

### Seedling Survival and Growth

Clearly, seedling establishment in abandoned pastures is limited foremost by lack of dispersal and secondarily by high seed predation and low germination rates in some species. If seedlings do become established, a suite of abiotic and biotic factors may, subsequently, reduce seedling survival and growth (Fig. 2). These factors include competition with pasture grasses, stressful microclimatic conditions, lack of soil nutrients, reduced mycorrhizal inoculum, and herbivory. Our research indicates that competition with pasture grasses is the primary factor impeding seedling survival, although the other factors slow seedling growth to a lesser extent.

At our study site, pasture grasses commonly grow to a height of 1.5 m and create a dense litter layer, approximately 10 cm deep. We have studied the effects of pasture grass on seedling survival in two ways. First, we cleared areas of pasture grass and monitored vegetation composition in cleared and uncleared areas after six months. Species richness and cover of broadleaved species was approximately five times higher in cleared than in non-cleared quadrats (Table 1). Second, we transplanted recently germinated seedlings (1–4 cm tall) of four early colonizing woody species, *Cecropia polyphlebia* Donn. Smith. (Moraceae), *Hasseltia floribunda* Kunth (Flacourtiaceae), *Heliocarpus appendiculatus* Turcz. (Tiliaceae), and *Sorocea trophoides* Burger (Moraceae), in areas of dense pasture grass (99% grass cover) and below pasture shrubs (24% grass cover). After eighteen months, seedling survival of three of the four species was significantly higher under shrubs; *C. polyphlebia* showed very low survival in both habitats (Table 2). Together, these results and those of other studies (González Montagut 1996; Sun & Dickinson 1996; Posada et al. 2000) suggest that pasture grasses play a major role in limiting survival of forest seedlings.

As with many previous studies, we have documented higher soil and air temperatures, light levels, and vapor

**Table 1.** Mean cover and species richness for seedlings of broadleaved species in areas cleared of grasses and areas not cleared of grasses, before clearing and six months following clearing. Values are means  $\pm$  1 SE.  $n = 6$ .

Time of Sampling	Cover (%)		Species Richness	
	Cleared	Not Cleared	Cleared	Not Cleared
Before clearing	7.7 $\pm$ 9.2 <sup>a</sup>	10.2 $\pm$ 12.2 <sup>a</sup>	2.2 $\pm$ 2.0 <sup>a</sup>	2.2 $\pm$ 2.1 <sup>a</sup>
6 months	69.5 $\pm$ 18.1 <sup>a</sup>	12.5 $\pm$ 18.3 <sup>b</sup>	8.2 $\pm$ 1.9 <sup>a</sup>	1.5 $\pm$ 1.9 <sup>b</sup>

Note: Means with the same letter are not significantly different across treatment using a *t*-test.

pressure deficit in areas of pasture cleared of grass compared to areas in the forest (Holl 1999). Pasture grasses, however, reduce soil temperature and light intensity at the soil surface to levels similar to those in the forest (Holl 1999). We have measured soil and plant water potential during the dry season in a number of years; the results suggest that soil moisture at our site rarely drops to a level sufficiently low to be stressful to plants (Holl 1999; Loik & Holl, unpublished data). In contrast, Nepstad and colleagues (1996) report high levels of water stress for seedlings planted in pasture in Amazonia; this difference in results is likely due to the comparatively longer dry season at their research site. It is also important to note that our study site is at a much higher elevation than most previous research on tropical forest recovery; accordingly, maximum temperatures are lower than those reported from lowland tropical pastures (Vieira et al. 1994; González Montagut 1996). Our research has demonstrated that light intensity in the open pasture is in excess of that needed for maximal photosynthesis, which can be stressful for seedlings of certain species once they reach a sufficient height to overtop the grasses (Loik & Holl 1999).

Research at other sites suggests that soil compaction (Reiners et al. 1994; Sun et al. 1995) and lack of nutrients (Aide & Cavelier 1994; Vieira et al. 1994) may reduce

**Table 2.** Mean percent survival after 18 months<sup>1</sup> of early-successional tree seedlings planted in areas of dense pasture grass and below pasture shrubs. Values are means  $\pm$  1 SE.  $n = 8$  plots with 16 seedlings in each plot.

Species	Percent Survival	
	Grass	Shrub
<i>Cecropia polyphlebia</i>	1 $\pm$ 1 <sup>a</sup>	2 $\pm$ 1 <sup>a</sup>
<i>Hasseltia floribunda</i>	1 $\pm$ 1 <sup>a</sup>	36 $\pm$ 1 <sup>b</sup>
<i>Heliocarpus appendiculatus</i>	0 $\pm$ 0 <sup>a</sup>	10 $\pm$ 3 <sup>b</sup>
<i>Sorocea trophoides</i>	2 $\pm$ 2 <sup>a</sup>	31 $\pm$ 8 <sup>b</sup>

<sup>1</sup>Due to phenological differences, *S. trophoides* was planted three months later than the other species, so survival rates for *S. trophoides* are reported after 15 months. Note: Means with the same letter are not significantly different across habitat type using a *t*-test.

seedling growth in abandoned agricultural land. We have documented much higher soil compaction in the pasture compared to forest (Holl 1999), although we have not tested the effects of soil compaction on seedling growth directly. Our research also indicates that phosphorus levels are extremely low in both the forest and pasture at our site (Holl 1999). To test whether these levels limited seedling growth, we fertilized seedlings of three commercially valuable tree seedlings with 50 g of 10:30:10 NPK fertilizer when the seedlings were planted in the field and before the start of the following rainy season. Seedlings were planted in three mixed-species blocks on a 3 × 3 m grid in the pasture; six fertilized and six unfertilized seedlings were planted in each block. Seedling height and cover increased significantly more for fertilized seedlings, indicating that seedling growth was slowed by available nutrients (Fig. 3).

Janos (1996) has suggested that lack of mycorrhizal inocula may slow recovery in degraded areas in the tropics. We measured percent root infection with arbuscular mycorrhizae (AM) of seedlings of four native forest tree species (*Calophyllum brasiliense* Camb. (Clusiaceae), *Ocotea glaucosericea* Rohwer (Lauraceae), *Ocotea whitei* Woodson (Lauraceae), and *Sideroxylon portoricense* Urb. (Sapotaceae)) planted in forest, in open pasture, and in pasture below remnant trees. All four species were infected with AM; percent root infection ranged from 10–90% (Lin 1999). Both of the species for which sample sizes were sufficient to make quantitative comparisons (*C. brasiliense* and *S. portoricense*) had simi-

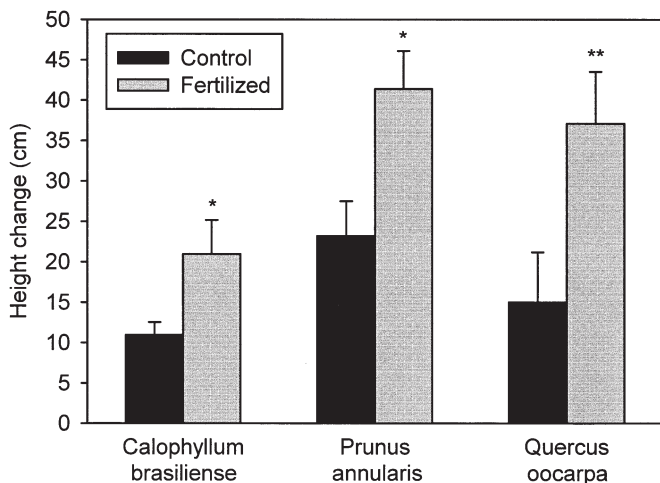


Figure 3. Height increase of fertilized and unfertilized native tree seedlings (*Calophyllum brasiliense*, *Prunus annularis* Koehne (Rosaceae), and *Quercus oocarpa* Liebm. (Fagaceae)) between June 1996 and June 1997. Seedlings were fertilized with 50 g of 10:30:10 NPK fertilizer in June 1996 and February 1997.  $n = 12$ – $18$  for each species fertilization treatment. Error bars represent 1 SE. \* =  $p < 0.05$ , \*\* =  $p < 0.01$  using a  $t$ -test.

lar percent infection in forest and open pasture; percent infection of *C. brasiliense* was higher under remnant trees (Table 3). The higher infection rate below trees may reflect differences in spore numbers or composition (not measured) and/or differences in other factors, such as nutrient availability or microclimatic conditions (discussed later). A number of other studies have reported similar or higher levels of mycorrhizal spores and/or mycorrhizal infection of roots in tropical pastures compared to forests (Fischer et al. 1994; Johnson & Wedin 1997; Allen et al. 1998). Some studies, however, have found different species composition of mycorrhizal spores in highly degraded pastures compared to primary or secondary forest (Allen et al. 1998; L. Carpenter 1999, personal communication).

A final factor that reduces seedling survival and growth at our site is rabbit herbivory. In a trial using native tree species for reforestation, 64% of seedlings (0.1–0.5 m tall) were cut by rabbits within 2 years (Holl & Quiros Nietzen 1999). Although some seedlings survived cutting by rabbits and resprouted, survival and growth were greatly reduced in cut seedlings (Holl & Quiros Nietzen 1999). Whereas herbivory due to leaf cutter ants (*Atta* spp.) has been reported in abandoned tropical pastures (Butterfield 1995; Nepstad et al. 1996; L. Carpenter 1995, personal communication), our research is the first to document the importance of rabbit herbivory. This result has strong implications for the potential of tropical reforestation programs in the region of our study.

### Strategies for Facilitating Recovery

In summary, our research, as well as that of others, suggests that multiple factors retard recovery in abandoned tropical pastures. Some problems seem to be widespread (e.g., lack of seed dispersal and nutrient limitation), and others tend to be more site-specific

**Table 3.** Percent arbuscular mycorrhizal infection of roots of two-year-old seedlings of *Calophyllum brasiliense* and three-year-old seedlings of *Sideroxylon portoricense* planted in open pasture, under trees in pasture, and in primary forest. Roots were stained with Trypan Blue (Lin 1999). Values are means  $\pm$  1 SE for  $n = 6$  seedlings. Arcsine transformed infection rates were analyzed using a one-way ANOVA for each species and Tukey's LSD mean comparison procedures.

Species	Percent Infection	
	<i>C. brasiliense</i>	<i>S. portoricense</i>
Open pasture	42.6 $\pm$ 2.4 <sup>a</sup>	20.3 $\pm$ 9.3 <sup>a</sup>
Under tree	62.4 $\pm$ 4.8 <sup>b</sup>	36.8 $\pm$ 10.0 <sup>a</sup>
Forest	30.4 $\pm$ 6.9 <sup>a</sup>	26.0 $\pm$ 5.1 <sup>a</sup>

Note: Means with the same letter are not significantly different across habitat type using Tukey's LSD.

(e.g., water stress and herbivory). At the site of our research, the primary factors inhibiting recovery are lack of forest seeds and competition with pasture grasses, whereas other factors, such as nutrient availability and herbivory, also influence recovery. These results suggest that the most effective restoration strategies will simultaneously overcome a range of obstacles to regeneration. Our research on strategies to facilitate recovery confirms this point. We have tested a number of strategies for facilitating the early stages of recovery in abandoned pasture, including bird perching structures, establishing native seedlings and shrubs, and retaining pasture trees. This research has helped to further our understanding of both natural successional processes in abandoned pastures, and our ability to recommend management strategies.

### Bird Perching Structures

One potential method for increasing seed dispersal, and thereby facilitating recovery, is the use of artificial bird perching structures. Increased vertical structure may attract birds farther into the pasture and enhance seed dispersal. Artificial perching structures have successfully encouraged seed dispersal into disturbed temperate ecosystems (McDonnell 1986; McClanahan & Wolfe 1987, 1993), but have received little study in tropical rain forest ecosystems. Perches would seem to be particularly useful in tropical forests where the seeds of 50–90% of canopy trees and nearly 100% of shrubs and sub-canopy trees have adaptations for animal dispersal (Howe & Smallwood 1982).

To test this strategy, we monitored bird activity, seed dispersal, and seedling establishment below two types of perches: (1) crossbar perches consisting of 5-m tall posts with 2.2 m crossbars attached perpendicularly at the top and (2) branch perches consisting of 5-m tall branches of *Inga* spp. We found that branch perches served to increase dispersal of some forest species (Holl 1998b). Seedling establishment, however, was not higher below branch perches than in open pasture (Holl 1998b). This result is not surprising, given the fact that perches serve only to increase seed dispersal and do not help to overcome other obstacles to recovery, in particular competition with pasture grasses. These results highlight the importance of using seedling establishment, rather than seed rain alone, as a measure of success. Combining the use of bird perching structures with efforts to reduce pasture grasses through clipping or herbicides may help to facilitate recovery (Ferguson 1995; Miriti 1998) but has not been tested on a large scale. More promising seem to be efforts to establish woody species that simultaneously overcome a number of obstacles to recovery.

### Planting Native Tree Seedlings

Seedlings of native and exotic tree species can help to increase seed dispersal, shade out pasture grasses, ameliorate stressful microclimatic conditions, and improve soil structure and soil nutrient availability, which all lead to higher understory diversity (Montagnini & Sancho 1990; Prinsley 1991; Parrotta 1992; Montagnini et al. 1995; Haggard et al. 1997; Parrotta et al. 1997). Trees can also provide income to land owners from future logging. In recent years, efforts have increasingly focused on planting native tree species to restore degraded areas in the tropics. Our research demonstrates that some native tree species grow quickly in abandoned pastures. We measured seedling height of three species of trees that were planted by the land owner on an approximately 3 × 3 m mixed-species grid at a site located approximately 5 km from the primary study site. Seven years after planting, surviving seedlings were an average of 7–11 m tall (Fig. 4). A number of other studies have also demonstrated that some native species show growth rates in disturbed areas in the tropics similar to those of more commonly used exotic species (Kartawinata 1994; Alfaro Bonilla & Barrantes Arias 1995; Butterfield 1995; Ashton et al. 1997; Stanley & Montagnini 1999) and may serve to facilitate forest regeneration.

Our research also shows that the success of efforts to reforest with native tree species may be highly variable. As discussed previously, in localized areas we found high rabbit herbivory on native seedlings. Fencing the seedlings tripled the cost of planting, which would likely be cost prohibitive for large-scale planting efforts (Holl & Quiros Nietzen 1999). Similarly, we have recorded highly variable growth rates for the same spe-

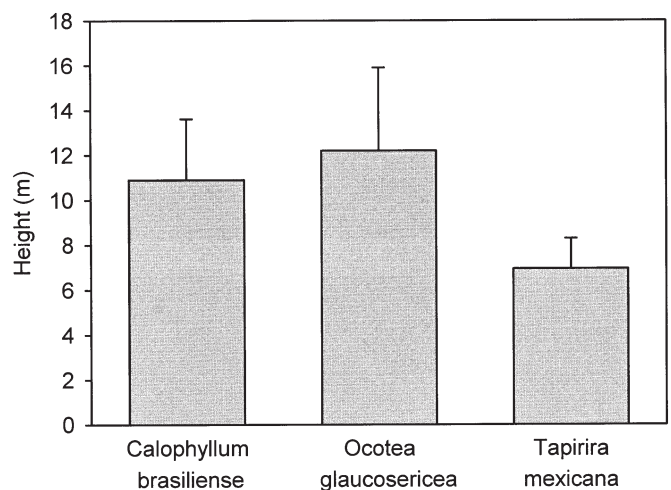


Figure 4. Heights of three native tree seedlings (*Calophyllum brasiliense*, *Ocotea glaucosericea*, and *Tapirira mexicana* Marchand (Anacardiaceae)) seven years after planting in abandoned pastures.  $n = 50$  for each species. Error bars represent 1 SE.

cies at different locations within the 10,000 ha landholding where we work. For example, *Ocotea glaucosericea* planted by the land owner grew nearly two meters per year over a period of 7 years (Fig. 4), whereas the seedlings we planted of the same species grew 0.36 meters per year over a 2-year period (Loik & Holl 1999). Likewise, other projects in Costa Rica focused on testing native tree species for reforestation have recorded highly variable growth rates at different sites (Butterfield & Espinoza 1995; Alfaro Bonilla & Barrantes Arias 1995). Variable growth would be expected with differences in soil type, climate, degree of land degradation, and existing vegetation. These results suggest that planting native tree seedlings may be useful as a strategy for accelerating forest recovery at many disturbed sites in the tropics and highlight the importance of testing any restoration strategy on a small scale at each site to evaluate appropriate species.

### Seeding Shrubs

Increasingly, it is being recognized that naturally colonizing shrubs and trees may play a critical role in ameliorating adverse conditions and facilitating succession in abandoned tropical pastures (Vieira et al. 1994; Aide et al. 1995). Many shrub species attract birds, thereby increasing dispersal of forest seeds (Willson & Crome 1989; Vieira et al. 1994; Saab & Petit 1992; Cardoso da Silva et al. 1996; Nepstad et al. 1996). As with tree seedlings, shrubs may help to overcome other obstacles to recovery such as ameliorating stressful microclimatic conditions, increasing soil nutrients, and shading out pasture grasses (Vieira et al. 1994; Holl 1998a). In contrast, some research in the tropics suggests that shrubs may inhibit recovery (Anaya Lang 1976; Zahawi & Augspurger 1999).

In February 1996 and February 1998, 1 and 3 years after abandonment, respectively, we surveyed shrub cover in 4 ha of the focal study area that had not been disturbed by experiments. Our results indicated that shrub cover increased from 2.4 to 6.1% during this time period, but large areas were still covered by dense grass with no establishment of shrubs or tree seedlings. The shrub patches measured in both years increased an average of  $6.9 \pm 11.0$  m<sup>2</sup> in cover between sampling periods, indicating that, once established, patches spread at a rapid, but highly variable, rate. The vast majority of seedlings of animal-dispersed forest trees established below remnant trees, shrubs, or both (Table 4). Clearly, shrubs may compete with forest seedlings (Holl 1998a), but these results suggest that, overall, shrubs and remnant trees facilitate the establishment of woody seedlings.

Seeding early-successional shrubs may be an inexpensive strategy to facilitate recovery, as many shrubs produce copious seeds year round, and are easily collected. We tested this strategy by seeding each of nine

**Table 4.** Distribution of tree seedlings in 4 ha of abandoned pasture in February 1996 and 1998.

Variable	1996	1998
Number of tree seedlings <sup>1</sup>	100	80
Number of animal-dispersed forest tree seedlings <sup>2</sup>	37	31
Percent of seedlings of animal-dispersed forest species below:		
Shrubs only	32%	23%
Trees only	24%	29%
Shrub and trees	16%	26%
Open pasture	27%	23%

<sup>1</sup>This number includes tree seedlings greater than 0.5 m and less than 5 m. For 1996 all seedlings are reported. For 1998 all seedlings established since 1996 are reported.

<sup>2</sup>This number excludes wind-dispersed species (primarily *Cedrela tonduzii* and *Heliocarpus appendiculatus*) and species for which fruiting individuals were predominantly located in the pasture (primarily *Inga edulis* and *I. punctata*).

common shrub (900 seeds/m<sup>2</sup>) or early successional tree species (100 seeds/m<sup>2</sup>), in 3 × 3 m plots in abandoned pasture in August 1997; the species include *Cecropia polyphlebia* Donn. Smith., *Heliocarpus appendiculatus* Turcz., *Miconia dodecandra* (Desr.) Cogn. (Melastomataceae), *Piper arboreum*, *Salvia tiliaefolia* Vahl (Lamiaceae), *Saurauia montana* Seem. (Actinidiaceae), *Solanum umbellatum*, *Tournefortia glabra* L. (Boraginaceae), and *Vernonia patens*. We seeded five paired areas that either had dense grass cover, or where grasses had been cleared. After one year, no shrub seedlings established in control areas (dense grass with no seeding), and few shrub seedlings established in areas that were seeded but not cleared. Shrub cover was much higher in plots that were cleared and seeded

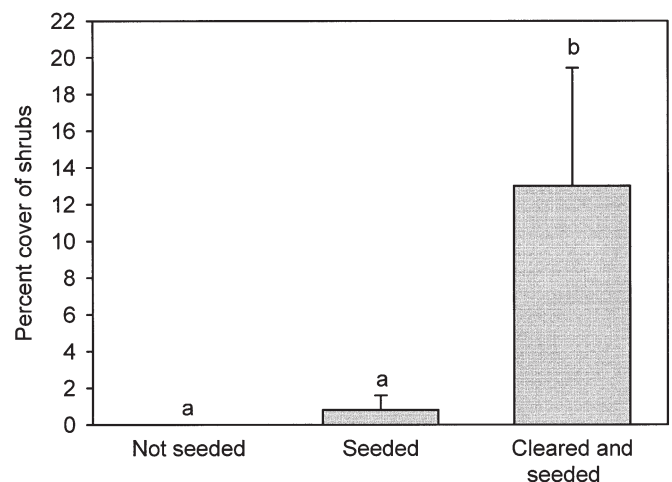


Figure 5. Cover of shrubs one year after seeding in areas that were not seeded with shrubs, were seeded with shrubs, and were seeded with shrubs and cleared of existing vegetation immediately prior to seeding. Error bars represent 1 SE.  $n = 5$  for each treatment. Means with the same letter are not significantly different across habitat type using Tukey's LSD.

(Fig. 5). An average of only 3.8 seedlings/m<sup>2</sup> established in seeded and cleared plots, indicating that a low percentage of seeds became established. This result is not surprising, given the high rates of predation and variable germination recorded in previous experiments. Regardless, these seedlings have the potential to cover a substantial area, given their rapid growth rates. This result, combined with our surveys of natural shrub distribution in the pasture, suggests that a relatively small amount of effort could be invested in seeding shrubs in areas far from existing patches to accelerate the process of nucleation (Yarranton & Morrison 1974). Clearly, additional monitoring is needed to determine whether shrubs facilitate recovery over the long term.

### Remnant Trees

Much previous work has focused on the critical role remnant pasture trees play in natural forest recovery by increasing seed dispersal, ameliorating microclimatic conditions, and increasing soil nutrients (Janzen 1988; Belsky et al. 1989; Guevara & Laborde 1993; Sarmiento 1997; Rhoades et al. 1998; Otero-Arnaiz et al. 1999). Our results confirm the importance of remnant pasture trees in facilitating forest recovery in abandoned pasture. Twenty-seven species of frugivorous birds were recorded perching in pasture trees (Samuels 1998). Accordingly, the number of animal-dispersed seeds falling under remnant pasture trees was similar to that in the forest and two orders of magnitude higher than in open pasture (Table 5). Consequently, the majority of seedlings of animal-dispersed species established under remnant trees (Table 4). Likewise, a large portion of shrub cover (36% in 1996 and 38% in 1998) was located below trees, despite the fact that there were few trees (5.5 trees/ha) in the pasture.

Our results also show that planting seedlings under remnant trees compared to open pasture enhances seedling growth. As discussed previously, we planted seedlings of four native forest tree species (*Calophyllum brasil-*

*ense*, *Ocotea glaucosericea*, *Ocotea whitei*, and *Sideroxylon portoricense*) in open pasture, under remnant trees in the pasture, and in primary forest. After two years, all species but one (*S. portoricense*) showed higher growth rates under remnant pasture trees than in either of the other two habitats (Lin 1999; Loik & Holl 1999). We have studied three potential mechanisms to explain this enhanced growth. First, litterfall under trees was 20 times that in open pasture (6.7 vs. 0.4 mg ha<sup>-1</sup> yr<sup>-1</sup>) and was comparable to that for many tropical forests (Vitousek 1984). Second, mycorrhizal infection was slightly higher for seedlings planted under remnant pasture trees compared to open pasture or forest (Table 3; Lin 1999). Third, the light levels under remnant trees were more favorable for seedling growth compared to the higher light levels in open pasture and very low light levels in the forest (Loik & Holl 1999). Clearly, these factors interact, and separating the relative importance of each would require more experimentation. Regardless, these results suggest that remnant trees may serve to enhance seedling growth through a number of interacting mechanisms. As a result, given limited resources for reforestation efforts, one strategy may be to plant seedlings at the edge of the canopy of remnant trees.

### Conclusions and Recommendations for Future Research

A number of general conclusions stem from our research and other studies on tropical forest recovery and restoration. First, numerous factors limit forest recovery in abandoned pastures. Therefore, successful strategies to facilitate recovery will need to overcome multiple factors simultaneously. The most promising strategies appear to be establishing woody species, either through retaining some remnant pasture trees when possible or through seeding or planting shrubs or native tree seedlings.

Second, the most effective combination of these strategies and species will be site-specific. Restoration would be much easier if general prescriptions could be made. But, given the varying site conditions and high species turnover between sites, general strategies will need to be tailored to specific situations. Our work highlights the importance of doing small-scale experiments to learn more about the ecology of specific sites, before implementing restoration strategies over a larger scale. For example, reforesting a large area with native tree seedlings that were subsequently cut by rabbits would result in a significant financial loss to a landowner. Our review also illustrates the importance of comparing results across a range of sites to identify which factors seem to be important most consistently and which strategies have a high probability of success.

Third, in scaling up from small-scale studies like ours, it is important to consider how to allocate restoration efforts most efficiently over a large scale. Given

**Table 5.** Number of animal- and wind-dispersed seeds falling in open pasture, below remnant pasture trees, and in forest. Seeds were collected between 1 May 1995 and 30 April 1996. Values are means  $\pm$  1 SE for  $n = 6$  sites, which are averages of three seed traps at each site.

Habitat	Seeds m <sup>-2</sup> yr <sup>-1</sup>	
	Animal-Dispersed	Wind-Dispersed
Open pasture	3.1 $\pm$ 1.1 <sup>a</sup>	114.0 $\pm$ 65.9 <sup>a</sup>
Remnant pasture tree	956.7 $\pm$ 461.7 <sup>b</sup>	42.2 $\pm$ 9.3 <sup>a</sup>
Forest	1150.5 $\pm$ 665.2 <sup>b</sup>	292.9 $\pm$ 25.0 <sup>b</sup>

Note: Means with different letters are significantly different across habitat type using Tukey's LSD on log-transformed values.



limited resources, it is unlikely that most land owners will be able to replant or reseed the large areas of degraded pastures in Latin America. Therefore, it may be most efficient to restore small islands of native seedlings or shrubs that will increase in size with little subsequent input (Kolb 1993). More research is needed on a larger scale to evaluate how best to allocate the limited resources available for restoration.

Finally, our research demonstrates how difficult restoring tropical forests will be. It is too early to know whether we can truly restore tropical forests to a semblance of pre-disturbance condition. It is unlikely that the numerous species present before disturbance will all recolonize. Therefore, we should view tropical forest restoration as a necessary activity given existing land uses, and must, simultaneously, focus efforts on conserving existing forest.

### Acknowledgments

This research would not have been possible without the dedicated field assistance of numerous people: A. Bullard, E. Catanese, A. Cathcart, L. Dunleavy, J. Holl, M. Holl, M. Lulow, N. Messmore, E. Quiros-Nietzen, C. Reese, J. Small, 21 Earthwatch volunteers, and 9 interns from the Colegio Agropecuario de Sabanilla. Funding was provided by the American Philosophical Society, the Center for Field Research, the U.S. Department of Energy, the Lindbergh Foundation, the National Science Foundation, and the University of California, Santa Cruz. We are grateful to Roig and Maria Mora for their support in this research, and to Mitch Aide for organizing this special feature and reading an earlier draft of this manuscript.

### LITERATURE CITED

- Aide, T. M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2:219–229.
- Aide, T. M., J. K. Zimmerman, L. Herrera, M. Rosario, and M. Serrano. 1995. Forestry recovery in abandoned tropical pasture in Puerto Rico. *Forest Ecology and Management* 77:77–86.
- Alfaro Bonilla, C. M., and P. Barrantes Arias. 1995. Estudio de adaptabilidad preliminar de 15 especies de altura en la zona sur de Costa Rica. B.S. thesis. Instituto Tecnológico de Costa Rica, Cartago.
- Allen, E. B., E. Rincon, M. F. Allen, A. Perez-Jimenez, and P. Huante. 1998. Disturbance and seasonal dynamics of mycorrhizae in a tropical deciduous forest in Mexico. *Biotropica* 30:261–274.
- Amelung, T., and M. Diehl. 1992. Deforestation of tropical rainforests: economic causes and impact on development. Mohr, Tübingen, Germany.
- Anaya Lang, A. L. 1976. Consideraciones sobre el potencial alelopático de la vegetación secundaria. Pages 428–445 in A. Gomez-Pompa, C. Vazquez-Yanes, S. del Amo Rodriguez, and A. Butanda Cervera, editors. Investigaciones sobre la regeneración de selvas altas en Veracruz, Mexico. Compañía Editorial Continental, Mexico City, Mexico.
- Ashton, P. M. S., S. Gamage, I. A. U. N. Gunatilleke, and C. V. S. Gunatilleke. 1997. Restoration of Sri Lankan rainforest: using Caribbean pine *Pinus caribaea* as a nurse for establishing late-successional tree species. *Journal of Applied Ecology* 34:915–925.
- Belsky, A. J., R. G. Admunson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* 26:1005–1024.
- Bradshaw, A. D. 1987. Restoration: an acid test for ecology. Pages 23–29 in W. R. Jordan, M. Gilpin, and J. D. Aber, editors. *Restoration ecology*. Cambridge University Press, Cambridge, England.
- Buschbacher, R., C. Uhl, and E. A. S. Serrao. 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *Journal of Ecology* 76:682–699.
- Butterfield, R. P. 1995. Promoting diversity: advances in evaluating native species for reforestation. *Forest Ecology and Management* 75:111–121.
- Butterfield, R. P., and M. Espinoza C. 1995. Screening trial of fourteen tropical hardwoods with an emphasis on species native to Costa Rica: fourth year results. *New Forests* 9:135–145.
- Cardoso da Silva, J. M., C. Uhl, and G. Murray. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology* 10:491–503.
- Ellison, A. M., J. S. Denslow, B. A. Loiselle, and D. Brenès M. 1993. Seed and seedling ecology of neotropical Melastomataceae. *Ecology* 74:1733–1749.
- Fearnside, P. M. 1993. Deforestation in Brazilian Amazonia: the effect of population and land tenure. *Ambio* 2:537–545.
- Ferguson, B. G. 1995. Overcoming barriers to forest regeneration in a degraded tropical pasture: an evaluation of restoration techniques. M.S. thesis. University of Michigan, Ann Arbor.
- Fernandes, D. N., and R. L. Sanford, Jr. 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. *Conservation Biology* 9:915–922.
- Fischer, C. R., D. P. Janos, D. A. Perry, R. G. Linderman, and P. Sollins. 1994. Mycorrhiza inoculum potentials in tropical secondary forest succession. *Biotropica* 26:369–377.
- Food and Agriculture Organization of the United Nations (FAO). 1997. *State of the World's Forests*. FAO, Rome.
- Garwood, N. C. 1989. Tropical soil seed banks: a review. Pages 149–208 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of soil seed banks*. Academic Press, Inc., San Diego, California.
- González Montagut, R. 1996. Establishment of three rain forest species along the riparian corridor-pasture gradient in Los Tuxtlas, México. Ph.D. dissertation. Harvard University, Cambridge, Massachusetts.
- Guevara, S., and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* 107/108:319–338.
- Haggard, J., K. Wightman, and R. Fisher. 1997. The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. *Forest Ecology and Management* 99:55–64.
- Hardwick, K., J. Healey, S. Elliott, N. Garwood, and V. Anusarnunthorn. 1997. Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand. *Forest Ecology and Management* 99:203–214.
- Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, Oxford.
- Holl, K. D. 1998a. Effects of above- and belowground competition of shrubs and grass on *Calophyllum brasiliense* (Camb.) seedling growth in abandoned tropical pasture. *Forest Ecology and Management* 109:187–195.

- Holl, K. D. 1998b. The role of bird perching structures in accelerating tropical forest recovery. *Restoration Ecology* 6:253–261.
- Holl, K. D. 1999. Factors limiting tropical moist forest regeneration in agricultural land: soil, microclimate, vegetation and seed rain. *Biotropica* 31:229–242.
- Holl, K. D., and M. E. Lulow. 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. *Biotropica* 29:459–468.
- Holl, K. D., and E. Quiros Nietzen. 1999. The effect of rabbit herbivory on reforestation of an abandoned pasture in southern Costa Rica. *Biological Conservation* 87:391–395.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- Janos, D. P. 1996. Mycorrhizas, succession, and the rehabilitation of deforested lands in the humid tropics. Pages 129–162 in J. C. Frankland, N. Magan, and G. M. Gadd, editors. *Fungi and environmental change*. Cambridge University Press, Cambridge, England.
- Janzen, D. H. 1988. Guanacaste National Park: tropical ecological and biocultural restoration. Pages 143–192 in J. Cairns, Jr., editor. *Rehabilitating damaged ecosystems*. CRC Press. Boca Raton, Florida.
- Johnson, N. C., and D. A. Wedin. 1997. Soil carbon, nutrients, and mycorrhizae during conversion of dry tropical forest to grassland. *Ecological Applications* 7:171–182.
- Kartawinata, K. 1994. The use of secondary forest species in rehabilitation of degraded forest lands. *Journal of Tropical Forest Science* 7:76–86.
- Kolb, S. R. 1993. Islands of secondary vegetation in degraded pasture of Brazil: their role in reestablishing Atlantic coastal forest. Ph.D. dissertation. University of Georgia, Athens.
- Lieberman, M., and D. Lieberman. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Tropical Ecology* 2:113–126.
- Lin, E. H. V. 1999. Mycorrhizal colonization of seedlings planted to restore abandoned pasture in southern Costa Rica. B.S. thesis. University of California, Santa Cruz.
- Loik, M. E. and K. D. Holl. 1999. Photosynthetic responses to light for rain forest seedlings planted to restore abandoned pasture, Costa Rica. *Restoration Ecology* 6:253–261.
- McClanahan, T. R., and R. W. Wolfe. 1987. Dispersal of ornithochorous seeds from forest edges in central Florida. *Vegetatio* 71:107–112.
- McClanahan, T. R., and R. W. Wolfe. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology* 7:279–288.
- McDonnell, M. J. 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bulletin of the Torrey Botanical Club* 113:6–11.
- Metcalfe, D. J. 1996. Germination of small-seeded tropical rain forest plants exposed to different spectral compositions. *Canadian Journal of Botany* 74:516–520.
- Miriti, M. N. 1998. Regeneraco florestal em pastagens abandonadas na Amaznia Central: competico, predaco, e disperso de sementes. Pages 179–191 in C. Gascon and P. Moutinho, editors. *Floresta Amaznia: dimica, regeneraco e manejo*. Instituto Nacional de Pesquisa da Amaznia, Manaus, Brazil.
- Montagnini, F., A. Fanzeres, and S. Guimaraes da Vinha. 1995. The potentials of 20 indigenous tree species for soil rehabilitation in the Atlantic forest region of Bahia, Brazil. *Journal of Applied Ecology* 32:841–856.
- Montagnini, F., and F. Sancho. 1990. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio* 19:386–390.
- Nepstad, D. C., C. Uhl, C. A. Pereira, and J. M. Cardoso da Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76:25–39.
- Nepstad, D. C., C. Uhl, and E. A. S. Serrao. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* 20:248–255.
- Osunkoya, O. O. 1994. Postdispersal survivorship of north Queensland rainforest seeds and fruits: effects of forest, habitat and species. *Australian Journal of Ecology* 19:52–64.
- Otero-Arnaiz, A., S. Castillo, J. Meave, and G. Ibarra-Manriquez. 1999. Isolated pasture trees and the vegetation under their canopies in the Chiapas coastal plain, Mxico. *Biotropica* 31:243–254.
- Parrotta, J. A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. *Agriculture, Ecosystems and Environment* 41:115–133.
- Parrotta, J. A., J. W. Turnbull, and N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99:1–7.
- Posada, J., M. Aide, and J. Cavelier. 2000. Cattle and weedy shrubs as restoration tools for tropical mountain rainforest. *Restoration Ecology* 8:370–379.
- Prinsley, R. T. 1991. The role of trees in sustainable agriculture: an overview. Pages 87–117 in R. T. Prinsley and J. Allnutt, editors. *The role of trees in sustainable agriculture*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Reiners, W. A., A. F. Bouwman, W. F. J. Parsons, and M. Keller. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecological Applications* 4:363–377.
- Rhoades, C. C., G. E. Eckert, and D. C. Coleman. 1998. Effect of pasture trees on soil nitrogen and organic matter: implications for tropical montane forest restoration. *Restoration Ecology* 6:262–270.
- Saab, V. A., and D. R. Petit. 1992. Impact of pasture development on winter bird communities in Belize, Central America. *Condor* 94:66–71.
- Samuels, I. A. 1998. The role of riparian corridors and isolated pasture trees in facilitating bird movement in tropical pasture. B.S. thesis. University of California, Santa Cruz.
- Sarmiento, F. O. 1997. Arrested succession in pastures hinders regeneration of Tropicandean forests and shreds mountain landscapes. *Environmental Conservation* 24:14–23.
- Sisk, T. D. 1991. Distribution of birds and butterflies in heterogeneous landscapes. Ph.D. dissertation. Stanford University, Stanford, California.
- Stanley, W. G., and F. Montagnini. 1999. Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica. *Forest Ecology and Management* 113:91–103.
- Sun, D., and G. R. Dickinson. 1996. The competition effect of *Brachiaria decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in tropical north Australia. *Biotropica* 28:272–276.
- Sun, D., G. R. Dickinson, and A. L. Bragg. 1995. Direct seeding of *Alphitonia petriei* (Rhamnaceae) for gully revegetation in tropical northern Australia. *Forest Ecology and Management* 73:249–257.
- Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture. *Journal of Ecology* 75:377–407.
- Vazquez-Yanes, C., and A. Orozco-Segovia. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics* 24:69–87.
- Vieira, I. C. G., C. Uhl, and D. Nepstad. 1994. The role of the shrub *Cordia multispicata* Cham. as a succession ‘facilitator’ in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* 115:91–99.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–298.

- Willson, M. F., and F. H. J. Crome. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. *Journal of Tropical Ecology* 5:301–308.
- World Resources Institute (WRI). 1997. *World Resources 1997–1998*. Oxford University Press, Oxford.
- World Resources Institute (WRI). 1998. *World Resources 1998–1999*. Oxford University Press, Oxford.
- Yarranton, G. A., and R. G. Morrison. 1974. Spatial dynamics of a primary succession: nucleation. *Journal of Ecology* 62:417–428.
- Zahawi, R. A., and C. K. Augspurger. 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica* 31:540–552.
- Zimmerman, J., J. Pascarella, and M. Aide. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8:328–338.