29 Limitations of Animal Seed Dispersal for Enhancing Forest Succession on Degraded Lands

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Introduction

Each year, approximately 127,300 km^2 of tropical forests are cleared, 55,000 km^2 are logged and as much as 30,000 km^2 are burned (Food and Agriculture Organization, 1999). Thus, the amount of tropical forest either deforested, logged or burned annually is approximately 212,000 km^2. Against these statistics is the hope that, with enough biological knowledge and political and economic change, forests can be restored on degraded lands. These restored forests can provide such ecosystem services as soil and water conservation, CO_2 sequestration and extractive use (Brown and Lugo, 1990, 1994). Because degradation is often severe, intervention is probably needed to restore forests in a time frame useful to current conservation goals (Parrotta, 1993).

There are two major challenges to 'regreening' the tropics. First, little is known about the process of forest succession on degraded lands. Most of what is known is limited to descriptions of vegetative change after land abandonment; studies of the underlying processes are few (Chazdon, 1994). Secondly, widespread forest restoration on degraded lands may be cost-prohibitive. Though there may be future subsidies for restoration via international agreements, such as the Kyoto Protocol to the United Nations Framework Convention on Climate Change, restoration strategies using natural processes (e.g. animal-mediated seed dispersal) will be the most widely applicable and affordable.

For the purposes of this review, we define degraded land as formerly forested area where human activities have reduced tree cover more than 90%. Forest recovery on these lands requires abiotic resources (e.g. soil nutrients), the absence of recurrent disturbances (e.g. fire) and adequate floristic resources (e.g. soil seed bank, seedlings, adult trees) (Uhl *et al.*, 1981; Brown and Lugo, 1994). Generally, as the severity of land degradation increases, the available floristic resources decrease (Uhl *et al.*, 1982, 1988; Nepstad *et al.*, 1991; Brown and Lugo, 1994) and post-disturbance seed dispersal becomes increasingly important for forest regrowth (Da Silva *et al.*, 1996; Nepstad *et al.*, 1996). In many degraded systems, lack of seed dispersal to degraded areas is considered one of the leading obstacles to forest regrowth (Nepstad *et al.*, 1991; Holl, 1999). Given that most tree species in the moist tropics produce animal-dispersed seeds (Howe and Smallwood, 1982; Chapman and Chapman, 1999), frugivores may be especially important in restoration efforts.

We review mechanisms that limit animal-mediated seed dispersal during forest succession on degraded tropical lands. We illustrate these limitations with examples from the system we know best, Kibale National Park in Uganda, and relate our findings to work done throughout the moist tropics. We then evaluate several proposed strategies to overcome seed-dispersal and recruitment limitations on degraded lands, and conclude with questions we think are important to address in the near future. While our focus is on the moist tropics, the principles we discuss are relevant to forest succession in other tropical and temperate regions.

Limitations to the Role of Seed Dispersal in Forest Succession

Challenges to tree recruitment on degraded lands

To understand the role that animal seed dispersal plays in forest succession on degraded lands, it is important to consider the harsh conditions facing trees establishing from seeds in this environment. Degraded tropical areas are typically hot and dry, and soil quality is often poor (Adedeji, 1984; Aide and Cavelier, 1994; Brown and Lugo, 1994). These conditions can make it difficult for tree seeds to germinate and seedlings to establish, even for many early-successional tree species ('pioneers'). However, fast-growing grasses and vines often establish in such environments and can dominate or 'arrest' succession (Borhidi, 1988; Uhl *et al.*, 1988). These species often limit tree seedling establishment and growth through competition (Nepstad *et al.*, 1991) and by creating a flammable habitat in which periodic fires kill the few tree seedlings and saplings that have established (Uhl and Buschbacher, 1985; Uhl and Kauffman, 1990; Kuusipalo *et al.*, 1995).

The numbers of seeds dispersed into degraded areas

One of the major constraints on regeneration of forest on degraded lands is that few animal-dispersed seeds are brought into disturbed areas by frugivores even when forest is nearby (Aide and Cavelier, 1994; Holl, 1998, 1999). This constraint is illustrated by three studies at Kibale. In the first, we examined seed rain by bats and birds below isolated trees within 150 m of forest edge (Duncan and Chapman, 1999). Of 1593 tree seeds collected, only 0.93% were of forest species and, of 11 tree species collected, only three were forest species. In a second, ongoing, study, we are examining seeds dispersed by birds in a successional forest at Kibale. Our preliminary results show that, of the 11,685 seeds we collected from mist-netted birds, only 11.2% were from plant species not fruiting on the site. Of these, 10.4% were of a single early-successional, light-demanding tree (*Maesa lanceolata*), whose seeds were probably unable to establish in the understorey. In a third study, Zanne and Chapman (2001) found that recruitment densities of animal-dispersed species declined with increasing distance from the forest edge in softwood plantations within Kibale. In addition, a plantation 15 km away from the forest had much lower recruitment densities of animal-dispersed stems than plantations within the park (see also Parrotta *et al.*, 1997; Wunderle, 1997).

There are several possible reasons why few forest seeds are dispersed into degraded areas. Typically, there is little incentive for forest-dwelling frugivores to visit degraded areas because fruit abundance there is usually low (Da Silva *et al.*, 1996). Forest frugivores may also be more at risk of predation in open degraded areas than in forest (Janzen *et al.*, 1976; Wegner and Merriam, 1979; Janzen, 1990). Similarly, disturbance-dwelling frugivorous species may avoid the unfamiliar habitat of the forest. These factors probably explain why many researchers have found a steep decline in seed dispersal with increasing distance from the forest edge (Charles-Dominique, 1986; Gorchov *et al.*, 1993; Aide and Cavelier, 1994; Holl, 1998, 1999).

The low numbers of seeds dispersed into degraded areas may be insufficient to initiate widespread forest succession. Our exploration of seed fate at Kibale suggests that hundreds of seeds may be needed for one seedling to establish. In another ongoing study, we are examining the fates of tree seeds dispersed into a 5-year-old successional forest on a logged cypress (*Cupressus lusitanica*) plantation. We monitored eight seed species (25 stations per species, five to 12 seeds per station) for 10 months. Because seed predation was very high, we caged some seed stations to exclude vertebrate granivores and allow seedling germination. We removed cages several weeks after germination to allow vertebrate herbivory. At open stations, only 4.8% of seeds germinated and 98.7% of seeds and germinated seedlings disappeared or were eaten (Table 29.1). In contrast, survival of seedlings germinating below cages was high (44%) at 10 months after dispersal, suggesting that in some systems seed predation may be a greater barrier to establishment than seedling mortality. Duncan and Duncan (2000) found that, of 1600 seeds (of eight species) set out in seed stations in grass-dominated abandoned agricultural areas at Kibale, only 20% of seeds survived 6 months. While 95% of seedlings (of six species) planted in the grassland survived 6–8 months, their growth was extremely slow, averaging only 1.8 cm $year^{-1}$. Chapman and Chapman (1999) sowed seeds of four early-successional species (one to four seeds per square metre) into grass-dominated abandoned cropland. After 4 years, densities of these species ranged from 0 to 0.027 seedlings m^{-2}, and were no greater than densities of these species in control plots. These low densities may have been due to the aggressiveness of the dominant grass species (*Pennisetum purpureum*) or to rodent seed predation. These experiments suggest that seeds dispersed into successional habitats face very low probabilities of recruitment.

Together, these results suggest that across different stages of succession few seeds are dispersed into degraded areas, and those seeds that do arrive face high seed predation, moderate seedling mortality and slow seedling growth. Others have also found that seed

Table 29.1. Results of seed predation and seedling survival experiments (mean ± SD). Open stations allowed access to seeds by seed predators. Caged stations protected seeds from predators to allow germinations; cages were removed soon after germination. Seed survival averages include seeds and seedlings that survived to 10 months. For the smaller-seeded *T. orientalis* and *C. africana*, seed number was not monitored. No *M. myristica* or *T. orientalis* seeds germinated from caged stations.

		Open stations			
Species	Initial seed no. per station	Mean no. seeds surviving at 10 months	Mean no. total germinations per station	No. seedlings surviving to 10 months	Caged stations: time to 50% mortality (months)
Bridelia micrantha (*Euphorbiaceae*)	5	0.16 ± 0.37	0.96 ± 1.10	0.16 ± 0.37	2.9
Celtis africana (*Ulmaceae*)	5	–	0.54 ± 1.30	0.14 ± 0.47	6.7
Diospyros abyssinica (*Ebenaceae*)	5	0.08 ± 0.4	0.04 ± 0.20	0	4.5
Mimusops bagshawei (*Sapotaceae*)	10	0	0	0	> 13.0
Monodora myristica (*Annonaceae*)	10	0.26 ± 1.25	0	0	–
Prunus africana (*Rosaceae*)	5	0	0.33 ± 1.13	0	4.0
Trema orientalis (*Ulmaceae*)	12	–	0	0	–
Uvariopsis congensis (*Annonaceae*)	10	0.22 ± 1.04	0.09 ± 0.42	0.09 ± 0.42	> 11.0

predation is high in degraded tropical lands and that most seeds are depredated within the first few weeks after dispersal (Nepstad *et al.*, 1991, 1996; Whelan *et al.*, 1991; Osunkoya, 1994). Seedling survival and growth rates are often low in other degraded systems, and it has been suggested that water stress and low levels of soil nutrients are to blame (Nepstad *et al.*, 1991, 1996; Gerhardt, 1993; Aide and Cavelier, 1994).

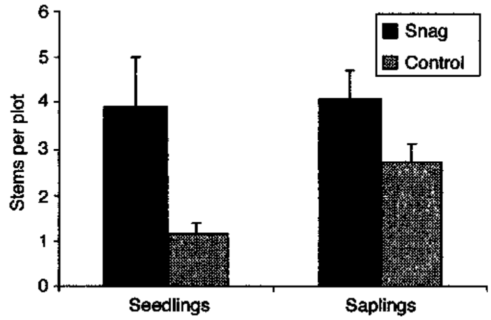

Fig. 29.1. Mean (+ SE) seedling and sapling numbers below snags (n = 20) and in adjacent open areas (control) in an early successional habitat at Kibale. All shrubs and trees of animal-dispersed species were counted in 2 m^2 plots. Snag plots had more seedlings and saplings than control plots (P = 0.014 and 0.016, respectively).

Location of seeds dispersed into degraded areas

A second constraint on animal seed dispersal into degraded areas is that there tends to be little dispersal into open areas where tree recruitment is most needed. Most animal-mediated seed dispersal tends to be concentrated below emergent structures (e.g. remnant or pioneer trees). Duncan and Chapman (1999) found that seed rain below isolated trees in an agricultural area was 90-fold greater than in adjacent grassland. Such patterns seem to affect seedling recruitment. In an ongoing study, we are examining seedling recruitment of animal-dispersed species below isolated snags and into adjacent areas (5 m away) in a 2-year-old succession. Densities of animal-dispersed seedling (height $\leq$ 0.25 m) and sapling (height $\geq$ 1.0 m) species were greater below snags than in adjacent plots (paired T-test, P = 0.018) (Fig. 29.1).

Greater seed rain below trees in degraded areas has been found in several tropical systems, and is most probably a result of seed dispersal by bats and birds (Guevara *et al.*, 1986; Uhl, 1987; Willson and Crome, 1989; Guevara and Laborde, 1993; Vieira *et al.*, 1994; Da Silva *et al.*, 1996; Nepstad *et al.*, 1996; Harvey, 2000). Others have also shown that seedling recruitment is greater in the shade below trees, probably due to lower temperatures, higher humidity and reduced competition with grasses (Guevara *et al.*, 1986; Vieira *et al.*, 1994; Toh *et al.*, 1999).

While seed rain to trees in degraded areas is frequently lauded as important for initiating forest succession on degraded lands and use of artificial perches has been proposed as a management tool, there may be limitations to the effectiveness of increasing seed rain. Trees in heavily degraded areas are often at low densities; thus their site-wide effect on tree seedling establishment will be small. In addition, areas with low tree densities are more vulnerable to fires, which kill young trees (Kuusipalo *et al.*, 1995; Toh *et al.*, 1999). Finally, where recruitment is successful below trees, the spread of vegetation into adjacent open areas may be slow, and decades or centuries may be needed for canopy closure (Toh *et al.*, 1999).

Seeds are sometimes dispersed to locations much less favourable to seedling establishment than below trees. This became evident in our survey of recruitment from seed dispersal by baboons (*Papio anubis*) into young successions on logged conifer plantations at Kibale. Baboons occasionally visit disturbed areas, where they feed, socialize and rest. During their visits they can disperse seeds of large-seeded mature forest species that are rarely or never dispersed by smaller-bodied, more abundant frugivores (e.g. birds). Thus, we expected baboon dispersal to contribute an important component to the species composition of recruited seedlings. We conducted surveys in these young successional areas to quantify the numbers and locations of baboon defecations and the seeds they contained. Defecation sites were subsequently monitored to quantify seedling establishment. We found that 62% of 52 defecations were in locations where conditions for seedling establishment and survival seemed unfavourable (Fig. 29.2). To date (~24 survey months), surveys have failed to find any tree seedlings recruiting from either favourable or unfavourable locations. Thus, most of the seeds dispersed by baboons into these degraded areas are placed into unfavourable microhabitats, where subsequent recruitment is unlikely.

The composition of seeds dispersed into degraded areas

Ideally, the composition of seeds dispersed into degraded areas would have high proportions of tree seeds, including early-, mid- and late-successional species. The early-successional species would quickly establish and, as they matured, provide an understorey environment conducive for survival and growth of mid- and late-successional species. However, the species composition of seeds dispersed into degraded areas often contains few tree seeds, and these are predominantly early-successional species. In our study of seed dispersal to trees in degraded agricultural lands adjacent to forest (Duncan and Chapman, 1999), only 14% of seeds were tree species; the majority were hemi-epiphytic figs, unable to germinate from the ground (Fig. 29.3). Furthermore, 99.9% of seeds recovered were early-successional species already present and fruiting on the site. A high proportion of early-successional species may be expected, since these species often produce larger numbers of seeds compared with mid- and late-successional species. However, the recruitment of these latter species is very important for advancing forest succession past the pioneer stage. From our ongoing study of seeds dispersed by birds in a 5-year-old successional forest, 21% of recovered seeds were tree seeds, and 47% of these were one early-successional species that could no longer germinate in the shaded understorey of the site. Most seeds were early-successional shrub species fruiting in the site (Fig. 29.3). Finally, in our study of baboon seed dispersal into logged plantations, 16% of seeds were tree species (Fig. 29.3). Ninety-seven per cent of these were mature forest species, but none have established in 24 months. Most seeds were mature forest herbs (99%), which also have low establishment rates.

In some regions, a majority of seeds dispersed into degraded areas can be tree species, but most of these are early-successional species, such as *Cecropia* spp. (Nepstad *et al.*, 1991; Guevara and Laborde, 1993; Da Silva *et al.*, 1996). For example, Holl and Lulow (1997) reported that tree seeds comprised 46% of seeds collected below artificial perches in abandoned pasture in Costa Rica, but only 29% of species and roughly 29% of seeds were species only found in forest.

Where there is poor establishment or limited dispersal of tree seeds, shrub seed dispersal to degraded areas may be important in initiating forest succession (Nepstad *et al.*, 1991). Vieira *et al.* (1994) found that shrubs

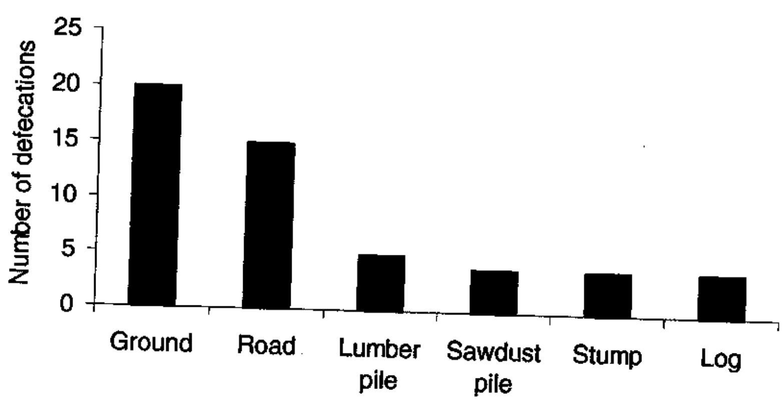

Fig. 29.2. Locations where baboon defecations were found in young successional habitat at Kibale. Only the ground location seems potentially favourable for seedling establishment and survival.

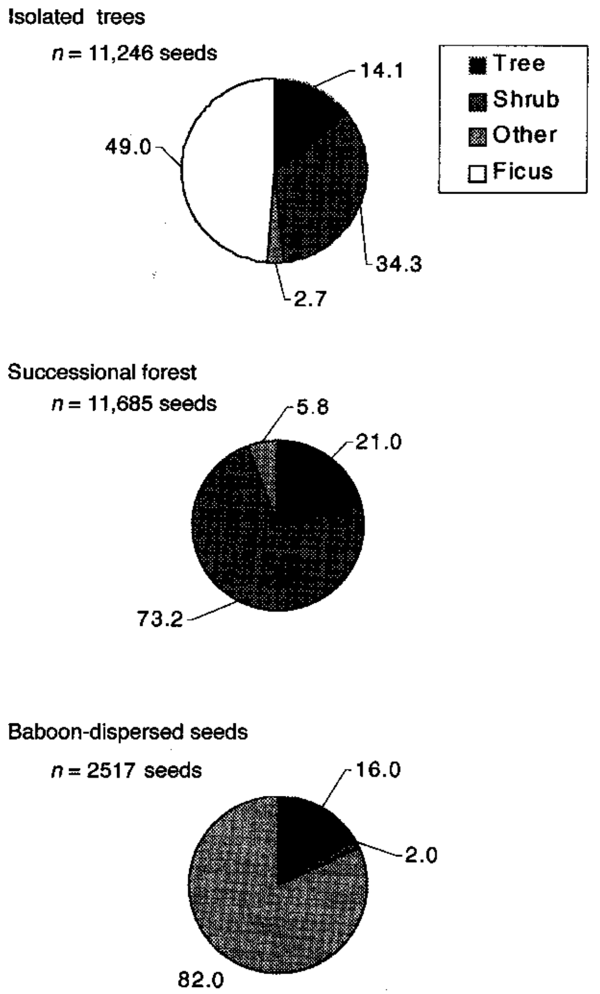

Fig. 29.3. Categories of seeds dispersed to isolated trees in agriculture near forest, by birds into a 5-year-old successional forest and by baboons (*Papio anubis*) into recently logged (< 2 years) conifer plantations.

recruiting on degraded pasture in Brazil attracted seed-dispersing birds and provided a microclimate conducive to the establishment of the tree seeds they dispersed. Zahawi and Augspurger (1999) found greater tree establishment in abandoned pastures with guava shrubs than in pastures without shrub cover. Establishment of shrubs as cover prior to the establishment of tree seedlings may be a successful successional pathway towards secondary forest in many degraded areas where tree recruitment is initially poor.

The timing of seed dispersal into degraded areas

Dispersal of seeds to degraded areas may or may not result in stem recruitment. Early-successional species must recruit soon after disturbance, when sunlight is abundant and before aggressive grasses or vines take over (Uhl and Clark, 1983). Mid- and late-successional species may only recruit after development of a shady, humid understorey. Their establishment may be necessary to prevent reinvasion of aggressive vines, shrubs and grasses after the short-lived pioneers begin to senesce.

We examined timing of seed deposition by birds into a chronosequence of successions (1, 2 and 4–6 years old) on logged *Pinus* spp. and *C. lusitanica* plantations. We quantified the seed banks present before logging, estimated seed deposition rates and surveyed seedling densities (height ≤ 0.25 m) of animal-dispersed species after logging. We found two seedling recruitment pulses, one at 1 year and one at 4–6 years after logging (Fig. 29.4). The first pulse seemed to be mostly due to recruitment from the soil seed bank, not seeds dispersed after logging. However, the second pulse seemed mainly dependent on post-disturbance seed dispersal. During the second year, seed dispersal into the succession was high, but seedling recruitment was very low. These results suggest there may be windows of time when seedling recruitment in successions may be more or less likely.

More evidence for the importance of timing for seed dispersal comes from our study of dispersal and recruitment into a 5-year-old succession on a logged cypress plantation. The early-successional tree *Trema orientalis* comprised 47% of 2455 tree seeds we recovered from captured birds. However, no *T. orientalis* seeds from caged stations protected from rodents (25 stations, 250 seeds) have germinated in this site after 21 months. We presume this early-successional species is unable to germinate in the shaded understorey of this successional forest. In addition, the poor establishment of mid- and late-successional tree seeds dispersed by baboons into recently logged plantations may be due to the harsh abiotic conditions facing seeds and seedlings in these cleared areas. These results suggest that the probability for recruitment of species varies through time and may often be a result of establishment limitations, not necessarily seed-dispersal limitations (for a temperate system, see Kollmann, 1995).

Strategies to Overcome Seed Dispersal and Recruitment Limitations

The four limitations described above provide a framework for understanding why seed dispersal often fails to promote forest succession of degraded lands. Consequently, land managers have considered ways of overcoming barriers to forest regrowth. For any given location, designing the best strategy will depend on the local ecological, economic and political conditions, and how they interact with management goals.

Sites with sufficient resources for forest cover to quickly establish may not need much intervention during the first few years. In more heavily degraded sites, the first priority may be slowing soil erosion and/or reducing the probability of fire. It can take many decades for topsoil to develop, and most tree species are probably incapable of establishing without it. Fire-breaks may be needed to prevent fires from quickly destroying years of restoration and perpetuating the dominance of grasses. In

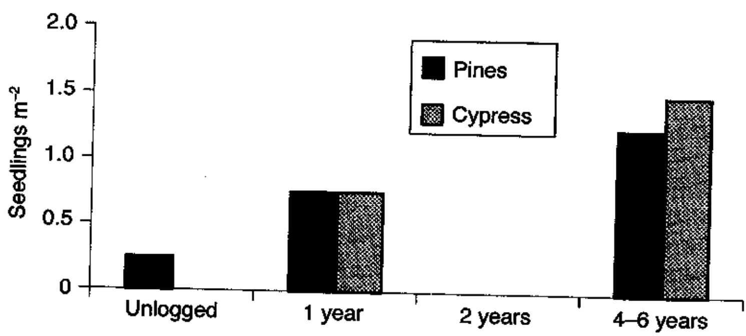

Fig. 29.4. Changes in median seedling density of animal-dispersed trees and shrubs during the first years of forest succession following harvest of exotic pine (*Pinus caribeae* and *Pinus patula*) and cypress (*Cupressus lusitanica*) plantations at Kibale.

1994, fire destroyed native trees planted by the Forest Absorbing Carbon Dioxide Emission (FACE) foundation in 500 ha of degraded grassland at Kibale.

When the area is secured from the threat of fire or other recurrent disturbances, the next steps towards reafforestation will depend on financial resources and the time frame within which forest cover is needed. Now, we consider the advantages and disadvantages of several management strategies.

Constructing perches or planting trees to increase seed rain

Animal-dispersed seed rain in degraded areas tends to be concentrated below the few trees present, and the microclimate below them can be better for seedling establishment than in adjacent open areas. Thus, some researchers have suggested that planted trees or artificial perches will initiate forest succession in degraded areas (McClanahan and Wolfe, 1987, 1993; Aide and Cavelier, 1994; Holl, 1998; Toh *et al.*, 1999). Trees planted in clumps may be more attractive to seed-dispersers than single trees (Toh *et al.*, 1999). Furthermore, planted trees or perches could be placed in the landscape to increase seed-disperser movement between isolated forest patches.

While vegetation can establish below and spread away from trees or perches in degraded tropical systems, it may take many years before canopy closure over a large area is attained (Toh *et al.*, 1999). Artificial perches would be needed in high densities to enhance recruitment over a large area. This will probably be expensive and may dilute seed rain among perches. Also, artificial perches may do little for recruitment if their shade is inadequate to reduce the density of herbaceous vegetation and the threat of fire around them. Holl (1998) investigated recruitment below artificial perches of two types in abandoned pasture and found no difference in recruitment below these perches relative to recruitment in nearby open areas. If trees are planted to become perches, several years may be needed before they attract seed rain and are no longer vulnerable to fires (Chapman and Chapman, 1999). Despite these drawbacks, the use of artificial or natural perches may be effective in small degraded areas or when financial resources are limited and complete canopy cover is not needed for many years.

Seed sowing

Sowing seeds is another means of increasing seed density in degraded areas (Sun *et al.*, 1995; Pinard *et al.*, 1996; Hau, 1997; Chapman and Chapman, 1999). Seeds of many species can be easily collected, prepared and dispersed over a large area. Managers can select which species to sow and where to sow them.

Chapman and Chapman (1999) had limited success with distributing seeds of early- and mid-successional species into recently abandoned cropland in Kibale. Others have also found limited or no success with seed sowing, or found that it was less effective than planting seedlings (Ray and Brown, 1995; Pinard *et al.*, 1996; Parrotta and Knowles, 1999). The timing of seed sowing may be important to consider, especially for early-successional species that may have a short window of time during which they can establish. Site preparation, especially removal of grasses or vines, may be important for successful seed sowing in many systems (Sun *et al.*, 1995; Sun and Dickinson, 1996; Sarmiento, 1997). Because rodent seed predation in degraded areas can be very high (Osunkoya, 1994; Nepstad *et al.*, 1996), distributing well-protected or large seeds less vulnerable to small rodents may be successful (Uhl, 1987; Hau, 1997). In summary, seed sowing may work in some systems with some species, but trials will be needed to identify the species and site-preparation strategies that will be successful.

Tree plantings

Planting native trees in degraded areas is a more direct way of facilitating succession (Tucker and Murphy, 1997). Managers can choose the species to plant and where to plant them. But the greatest advantage of this strategy is that it avoids the stages of seed dormancy, germination and establishment, when mortality is typically highest.

Unfortunately, trial plantings will be needed, because little is known about propagation of native species in most regions. Restoration ecologists could learn from agroforestry trials that identify native species with commercial value for propagation in agricultural areas (Davidson *et al.*, 1998; Stanley and Montagnini, 1999; Eibl *et al.*, 2000). Once species are identified, the construction and maintenance of propagation facilities may be costly. In many systems, continued interventions may be needed to ensure the survival of planted seedlings. For example, every 6 months the FACE project at Kibale must cut grasses around planted seedlings and saplings to reduce competition and fire-risk. Fire-breaks must also be maintained. The combined costs of native-species reafforestation via planting efforts may be great. Parrotta and Knowles (1999) report that reafforestation by planting on degraded mines in Brazil costs US$250,000 km^{-2}.

In light of obstacles to reafforestation with native species, many have suggested using plantations of exotic fast-growing fuel wood or timber species to catalyse succession on degraded lands (Parrotta *et al.*, 1997). Many such species (e.g. *Acacia* spp., *Pinus* spp., *Eucalyptus* spp.) grow well on degraded lands, compete successfully with aggressive herbaceous growth and reduce the threat of fire within a few years of planting (Lugo, 1997). Furthermore, the protocols for successful planting of such species are well developed. But the main reason why plantations have attracted so much attention from restoration ecologists is that they can attract frugivores that disperse seeds into an understorey whose microclimate is suitable for the establishment of these species (Wunderle, 1997). Mature plantations within Kibale and throughout the world often harbour a dense and species-rich population of native stems, especially if remnant forest is nearby as a seed source (Chapman and Chapman, 1996; Fimbel and Fimbel, 1996). Finally, the harvest and sale of these timber species could help pay for the restoration effort (Chapman and Chapman, 1996).

Unfortunately, there are numerous drawbacks to using exotic timber plantations to facilitate forest succession. Some timber species may invade adjacent undisturbed habitats (Binggeli, 1989), although many frequently planted timber species do not seem to be invasive (e.g. pine, eucalyptus). The species recruiting from animal seed dispersal into plantations tend to be small-seeded early-successional species (Wunderle, 1997). If mid- and late-successional species fail to recruit in sufficient densities, then, when the timber species are gone (via harvesting or natural death), remaining stands of early-successional species may eventually be replaced by arrested successions (Wunderle, 1997). Thus, plantations may only be successful when they are in close proximity to primary forest (Parrotta *et al.*, 1997). Another limitation arises because timber species are often planted in high densities. As they are harvested or die and fall, native species in the understorey may be crushed.

The goals of managing plantations for profit versus enhancing native tree establishment can conflict. Native stems in plantation understories could slow the growth of timber species and reduce their market value (Lamb, 1998). Thus, some managers may keep plantations clear of native stems. Even if native stems are allowed to grow, they may be severely damaged during harvest, as in Kibale, where most native stems are cut to roll logs off-site. Less destructive harvesting techniques (e.g. directional felling) typically increase harvesting costs. After harvest, managers may want to replant these areas with timber species, thus preventing forest succession to more mature phases. Finally, if reafforestation with timber plantations becomes widespread and demand for plantation timber does not grow accordingly, the surplus of timber on the global market could further reduce the financial benefits of this strategy (Leslie, 1999).

Despite these potential pitfalls, reafforestation via timber production remains one of the most widely discussed methods of restoring biological productivity on degraded lands and may be one of the most practical strategies yet proposed. Lamb (1998) and Wunderle (1997) discuss strategies for designing plantations in ways that would help overcome some of the biological obstacles. Ashton *et al.* (1997, 1998) have studied ways of integrating commercial harvest of plantation species and plantings of native stems for forest restoration. However, there are still many unaddressed questions about the practicality of plantations in restoring forests, among which seed-dispersal-orientated questions figure prominently.

Directions for Future Research

Many questions need to be addressed regarding the role of seed dispersal in forest restoration on degraded tropical lands. First, many of the points raised in this chapter have only been investigated by a few studies that inadequately represent the diversity of habitats and geographical areas where reafforestation is needed. More work is needed to test the generality of the existing patterns. Here we outline additional research directions that may be important for realizing the potential of animal-mediated seed dispersal in ecological restoration.

To attract seed-dispersing animals from the forest into degraded areas, some have suggested planting fast-growing, fleshy-fruit-producing species (Green, 1993; Whittaker and Jones, 1994; Sarmiento, 1997; Tucker and Murphy, 1997; Duncan and Chapman, 1999; but see Toh *et al.*, 1999; Zahawi and Augspurger, 1999). These species could be established as plantations, in small clusters or as corridors to draw animals from the forest (Toh *et al.*, 1999). For example, abandoned *Musa* plantations on degraded land in Kibale have facilitated the establishment (almost to canopy closure) of native tree saplings dispersed from the forest in only 6 years. More research is needed to investigate these and other possible ways to increase use of degraded lands by forest frugivores.

However, the risks of drawing animals away from the forest need investigation. Such a strategy could disrupt processes within the forest if frugivores spend much time in degraded areas. For example, seeds of invasive exotic species may be brought back into the forest from degraded areas (Binggeli, 1989). Forest animals in degraded areas may be exposed to increased predation and hunting (Janzen *et al.*, 1976; Wegner and Merriam, 1979; Janzen, 1990). Animals may raid nearby agricultural areas, thus souring farmers' attitudes towards preserves and restoration (Naughton-Treves, 1998; Naughton-Treves *et al.*, 1998). Finally, frequent use of degraded pastures by forest species may increase potential for disease transmission between native and domestic animal species.

To avoid these risks, managers could rely on seed dispersal by frugivores that live in degraded habitats (Da Silva *et al.*, 1996; Holl, 1998). Managers could plant selected native trees in and near degraded areas to provide these frugivores with seeds to disperse and perches to use. Ecologists and agroforesters could collaborate to find native tree species useful to people and good for establishing in degraded areas.

These suggestions and much of the work done in restoration ecology in the tropics have focused on getting a first cohort of trees established on degraded lands. However, we also need to better understand the role of animal-mediated seed dispersal and plant recruitment in older successional forests (Finegan, 1996; Guariguata *et al.*, 1997; Holl and Kappelle, 1999). Where early-successional tree species are able to establish, will their dominance be followed by that of mid- and late-successional species dispersed to the site? If succession is failing, then to successfully intervene we shall need to know if the problem is a lack of dispersers, poor dispersal quality or poor establishment of dispersed seeds. Finding cost-effective ways of helping succession overcome these obstacles would be of great use to managers. We also need to know whether/how manipulations of secondary forests can increase forest regrowth. For example, Chapman *et al.* (2001) removed grasses and shrubs in 5-year-old successional forest on a former conifer plantation and found that reduced competition did not benefit the remaining trees (but see Guariguata, 1999).

Another area needing attention is the impact of woody-stemmed, invasive exotic species in secondary forest succession (Brown *et al.*, 1998; Russell *et al.*, 1998; Stadler *et al.*, 2000). Because many invasive exotics are early-successional species, they may become an important component of secondary forests. Examples from Africa include *Cecropia obtusifolia* (Richards, 1996), *Maesopsis eminii* (Binggeli, 1989) and *Cedrela odorata* (Zanne and Chapman, 2001). It is unknown how much of a threat these species are to secondary forest development or whether they can be used as part of a successful restoration strategy (Kuusipalo *et al.*, 1995; Otsamo, 2000).

Finally, where secondary forests will be managed to benefit populations of rare plants and animals, we need to know how to enhance these habitats to benefit such species. This will require knowledge about the habitat requirements of these species and an understanding of how management of successional forest may affect them.

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