Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar

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Papers

1. *Ingar Pareliussen, E. Gunilla A. Olsson, Sølvi Wehn*, *Joel Ratsirarson*. Natural establishment of trees in the grasslands between forest fragments in upland Madagascar. (Manuscript)
2. *Ingar Pareliussen, E. Gunilla A. Olsson, W. Scott Armbruster*. Factors limiting the survival of native tree seedlings used in conservation efforts at the edges of forest fragments in upland Madagascar. (Accepted for publication in Restoration Ecology)
3. *Ingar Pareliussen, W. Scott Armbruster, E. Gunilla A. Olsson, Mary Edwards, Joel Ratsirarson*. Factors limiting the growth of native tree seedlings at the edges of forest fragments in upland Madagascar. (Manuscript)
4. *Sølvi Wehn, E. Gunilla A. Olsson, and Ingar Pareliussen*. Natural recovery of trees after fire in the edges of forest fragments in Ambohitantely forest, upland Madagascar. (Submitted)

Contents

General introduction

Introduction

Tropical forests cover just 7 percent of the Earth's surface, and yet they are home to fully 50 to 70 percent of the planet's animal and plant species (Bierregaard et al. 1992). During the 1990's the global forest loss was estimated at 14.6 million hectares (FAO 2001). Deforestation leads to an unprecedented fragmentation of forested areas and subsequent loss of biodiversity, from genes and species to whole families of plants and animals. Madagascar, the focus for this thesis, is renowned for the high level of endemism, found in its forests (Ganzhorn et al. 2001), and as an area where the fauna and flora are under the greatest threat from deforestation (Myers et al. 2000).

Roads to deforestation and fragmentation

Wildfire

Most tropical forest are subject to wildfires from time to time (Uhl 1998). A study of the soils in the Upper Rio Negro region of Amazonas (Sanford et al. 1985), showed abundant charcoal deposits that indicated there had been frequent fires in the last 6000 years there had been frequent fires. The fires corresponded with what is believed to be dry periods in the area. However, most tropical forests are resistant to fire; even after several weeks of drought, litter on the tropical forest floor can be difficult to ignite (Ginsberg 1998).

Agriculture

In many areas of the tropics humans have practiced small scale slash-and-burn agriculture. This practice can be sustainable as long as the forests are large enough to allow recovery time between uses. However, population increases and the concomitant increase in agricultural uses of forests can lead to deforestation and fragmentation in areas where slash-and-burn agriculture had once been sustainably practiced (Harcourt et al. 1992). Modern mechanical agricultural practice have further intensified this destruction. Tractors and other modern farming equipment need large cleared areas to be used efficiently.

The impact of slash-and-burn agriculture (tavy) on the forests of Madagascar has been strongly intensified in the last 100 years with the introduction of cash crops (Jarosz 1996). Tavy is practiced in the rain forests on the east-coast of Madagascar (Kull 2000*a*). Some of the best areas for cultivation, previously used for rice production, were expropriated and used for the cultivation of corn and coffee. To produce rice, the Malagasy turned to the forest and intensified old methods of slash and burn, dry rice agriculture. To reduce tavy, the government outlawed shifting cultivation. The Malagasy people, however, refused to abide by this law. They claimed that it was a pretense on the part of a government trying to force them into wage work, a kind of work that was seen by the Malagasy as a form of enslavement (Jarosz 1996).

Grasslands dominates the highlands of Madagascar. Large areas are burned annually, even though laws ban the practice. When asked why they burn the grassland, farmers say that they burn to get a green fodder for their cattle, and to get rid of pests and disease (Kull 2000*b*). Even if the target was grasslands, the fires may spread and hit a forest fragment. Repeated burning increases the probability of new fires and increases the intensity of subsequent fires in the fragment, killing more trees for each burning (Cochrane et al. 1999).

Logging

Logging in Africa for the global market has increased and shifted focus in the last decade (Sizer & Plouvier 2000). Most the timber previously went to Europe, but emerging economies in Asia, having depleted their own resources, are importing more and more hardwood. The international timber trade from Madagascar, however, seems to be limited and restricted (Teholy 2002).

Most of the energy for cooking in Madagascar comes from charcoal. In the cities and larger towns of Madagascar, an estimated 275 000 kg of charcoal is consumed every day (Rajaonah 2000). Much of the wood used for charcoal production comes from *Eucalyptus spp.* and *Pinus spp.* plantations, but some is taken from native forests.

Ecological effects of deforestation and fragmentation

The direct abiotic impact of fragmentation on remnant habitats is called an edge effect (Freidenburg 1998) and includes an increase in wind and light penetration (Saunders et al. 1991; Murica 1995). In this thesis, the term edge effect is used as a collective name for all of the changes that occur when a closed forest becomes fragmented. Due to the perimeter/area relationship, small forest fragments have more edge in relation to the area than larger fragments, and thus are more influenced by the edge effect (Saunders et al. 1991).

Soil

Most of the nutrients in a tropical rainforests are bound in in the living biomass, so that when forests are logged the nutrients in the timber are removed from the ecosystem (Buschbacher et al. 1988;

Uhl 1988). One example comes from a Malaysian forest, a single cutting was estimated to remove more than 200 years of the natural formation and accumulation of exchangeable calcium (Nykvist 2000). After a forest fire, ash is easily blown or washed away, which reduces the nutrients available to new trees (Harcombe 1977). Studies in eastern Madagascar have shown that 95-98 percent of the carbon and nitrogen fixed in the biomass and 22-24 percent fixed by the soil are lost by burning (Brand & Pfund 1998). As much as 96 percent of the pre-fire, above-ground nitrogen and carbon and 56 percent of phosphate were lost as a result of agricultural fires in one neotropical dry forest (Kauffman et al. 1993). The carbon content of the soil increases the first year after a forest is burned, due to increased charcoal deposits . However, charcoal is quickly washed away and carbon levels found after 7 to 11 years are lower than the carbon found in forest soils (Garcia-Oliva et al. 1994). In a study from Colombia, the soil in pastures converted from rain forest continued to degrade more than 9 years after conversion (Martínes & Zinck 2004).

Micro-climate

Temperatures are typically lower, while humidity is typically higher in a forest interior than in an open area (Saunders et al. 1991; Murica 1995). When a forest is fragmented, wind and light penetration will increase the temperature and lower the humidity.

Changes in micro-climate as a result of the edge effect can reach deep into a forest. One study in Brazil showed an increase in forest air temperatures could be measured 100 meters from a burnt forest edge (Didham & Lawton 1999).

Isolation

The open areas between forest fragments isolate animals and plants in the fragments (Saunders et al. 1991). Individual animals or plants may be separated from others of their species, or from resources and other species they depend on for food, dispersal or pollination. The further apart the fragments are, the stronger is isolation's effect. The impact of isolation is dependent on the structure of the open area surrounding the fragments and if it allows movement through the open areas.

Cascading effects of fragmentation

Fragments may suffer several serious consequences as a result of the edge effect. We have so far discussed effects such as changes in temperature, moisture and isolation. However, there can be a series of more intricate, cascading effects that can occur in forest fragments that could lead to a downward-spiral of biodiversity loss.

One such effect can result when the lowered number of trees in a fragment leads to a lack of food for some animals, which may then disappear from the fragment. Some of the animals that might disappear may be pollinators and/or fruit eaters, which then lowers the probability that trees will be able to set or disperse their seeds. This in turn reduces a tree's ability to regenerate in the fragments, so as a consequence, these trees might disappear leaving fewer remaining trees in the fragment. And so the cycle can perpetuate itself in a downward spiral that leads to an increasingly impoverished forest.

A study of a fragmented forest, in Oregon, USA (Tallmon et al. 2003), showed that large predators needed large ranges, so that they disappeared from the smaller fragments. This lack of predators led to an increased in the herbivores in the fragments, resulting in greater seed predation in the fragment than in the forest. The study also showed that the herbivore in question, a small mouse, had unrestricted movement between the fragments and forest, while predators were restricted to the forest.

Tropical trees may often suffer from inbreeding depression if the population becomes too small (Alvarez Buylla et al. 1996). One study showed a decrease in the number of seeds per fruit from a tree in a fragment compared to to the number of seeds per fruit, from the same species, in a closed forest (Griffin 1990). Another study showed that seeds produced in fragments did not have inferior seed quality and that seeds from fragments were just as successful in germination as seeds produced in closed forest (Gigord et al. 1999).

Challenges in reforestation of grasslands

There has been a substantial increase in the study of the restoration of tropical forests converted to grassland (Holl 2002). This thesis focuses on the mechanisms for the establishment of trees in a grassland. A schematic figure, adopted from Holl *et al* (2000) and Holl (2002), of the factors assumed to limit tree establishment is presented in Fig. 1. Tropical America has experienced a large scale conversion of forests to grassland in the last 150 years (Posada et al. 2000). Many of these grasslands have subsequently been abandoned, and studies show that reforestation is difficult (Uhl et al. 1988; Holl 1999; Zahawi & Augspurger 1999; Zimmerman et al. 2000). Studies of succession in forests converted to grassland in mainland Africa also show that establishing trees is difficult in Africa (King et al. 1997; Chapman & Chapman 1999; Duncan & Duncan 2000). Few studies have been conducted in Madagascar, however, a study of the grassland/forest ecotone with the use of aerial-photos in the south-west of Madagascar found several examples where the forest edge had advanced into the grassland (Morat 1973). A study of the forest-grassland ecotone in Ambohitantely (Radimbison 1990) showed that some forest species had been established in the grassland, although in their numbers were limited.

Sward

The sward of perennial grasses can become too dense to allow tree seed germination and seedling development (Holl 2002) (Fig 1). However, some studies show that grasses increase the survival

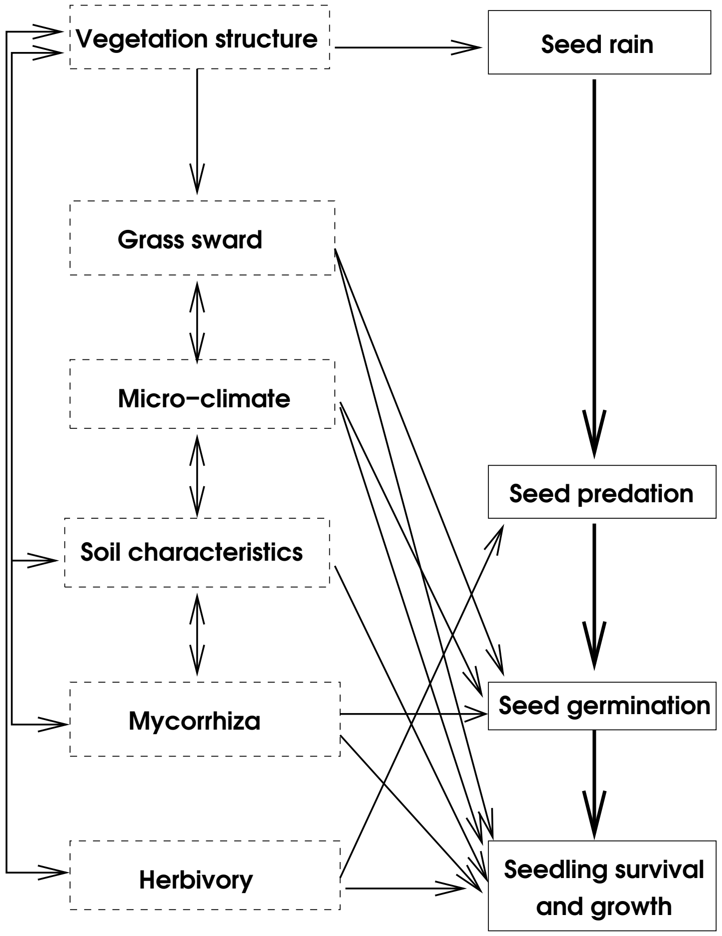

Figure 1: Factors limiting establishment of trees in a grassland. Processes influencing seedling establishment are shown in solid boxes, factors affecting the magnitudes of these factors are shown in dashed boxes. Adapted from Holl *et al* (2000) & Holl (2002).

of tree seedlings in severely dry seasons (Holl 2002). A study from Costa Rica reported five times the species richness and cover of broad-leaved species when areas were cleared for pasture grasses (Holl et al. 2000). In Australia survival and growth of a pioneer tree was found to be higher when the dominant grass was removed from the plots (Sun & Dickinson 1996). However, an experiment on the establishment of trees seedlings in Puerto Rico where the vegetation was removed did not find any effect from the removal of the grass sward (Zimmerman et al. 2000).

Micro-climate

There are sharp contrasts between the micro-climate in the grassland and the forest, which might influence tree establishment in the grassland (Fig 1). Light levels, and air and soil temperatures are typically higher in the grassland than in the forest (Uhl 1988; Nepstad et al. 1996; Holl 1999). As the forest edge is a transitional zone from the micro-climate in the grassland to the micro-climate in the forest, the micro-climate close to the forest is though to be more similar to the forest than the micro-climate further away. In a study in Northern Thailand tree seedlings were damaged by elevated light intensities in open areas (Hardwick et al. 1997). A study of the survival of tree seedlings in Costa Rica showed high mortality, especially in the first dry season (Gerhardt 1993). It has been demonstrated that the soil in adjacent grasslands is dryer than forest soil, which might impede the establishment of trees in grass-dominated vegetation (Uhl 1988). Shading reduces the light influx and reduces air and soil temperatures, along with evaporation. In an experiment on seedling survival in a tropical forest in Jamaica, partial shading was shown to have a positive effect on tree seedling survival (McLaren & McDonald 2003).

Soil

Some studies have shown that low nutrient levels inhibit the establishment of forest tree species in grasslands (Holl 2002) (Fig 1). The loss of nutrients from the ecosystem after logging and burning must be replaced in any successful reforestation scheme. Addition of chemical fertilizer is one way to replace some of the nutrients lost. However, this can pose a risk of overfeeding the ecosystem, which may lead to a weed-dominated ecosystem. In Costa Rica the herb *Phytolacca rivinoides* out-competed tree seedlings after nutrients were applied (Harcombe 1977). Many tropical rain forest soils are nutrient poor. However, some of the more species rich tropical forests are found on nutrient rich soil (Gentry 1988).

Tropical forest tree species often depend on mycorrhiza for their mineral nutrient uptake (Janos 1980). A study from Brazil (Siqueira et al. 1998) shows that pioneer tree species rely heavily on mycorrhiza and on a good nutrient supply to successfully establish themselves in a new site. Late successional tree species did not show the same dependencies (Siqueira et al. 1998).

Soil seed bank

Studies have shown that tropical forests typically contain a viable seed bank (Swaine & Hall 1983; Garwood 1989; Skoglund 1992). However, when the forest is converted to grassland the soil seed bank may be reduced or disappear and many studies show a lack of seeds from forest species in grassland soil seed banks (Uhl 1987; Nepstad et al. 1996; Wijdeven & Kuzee 2000; Zimmerman et al. 2000; Holl 2002). Any forest species that will establish itself in the grassland thus must be dispersed from the forest in the grassland.

Dispersal

Seed dispersal seems to be a problematic bottleneck in forest restoration. Animal-dispersed trees are particularly plagued with problems in dispersal to a grassland (Holl & Kappelle 1999). Most rain forest tree species are animal-dispersed, in Amazonia 85% of the tree species have fruits that are associated with animal dispersal (Uhl 1988). The percentage of animal dispersed species in Ambohitantely is uncertain. The frugivorous brown lemur (*Eulemur fulvus fulvus*) is the main disperser of seeds in the dry forests of Madagascar (Ganzhorn et al. 1999). One study indicates that the brown lemur disperses the seeds of at least 21 tree species (Rakotoson 2001). In addition some tree species seem to have an increased rate of germination after passing through the digestive tract of the lemurs (Rakotoson 2001). The frugivorous bats and birds that also live in the dry forest were found to be less important for the seed dispersal (Ganzhorn et al. 1999). In a study of seed dispersal from mature forest into abandoned pastures in eastern Amazonas (Nepstad et al. 1996), 46 seeds m^{-2} were dispersed into open pasture, in contrast to 990 seeds m^{-2} beneath trees in one year. A study in Florida showed the same pattern (McClanahan 1986), with on average 340 seeds found beneath bird perches and average of just two seeds in open areas. From these studies it was interpreted that the greatest impediment to reforestation was scarcity of seeds.

Herbivory

Herbivory may in some in some sites limiting forest recovery (Holl 2002). However, there have been few studies on the effect of herbivory on forest succession in tropical ecosystems. In an experiment in Costa Rica, 64 percent of the stems of tree seedlings were cut by rabbits in the first two years after germination (Holl & Quiros-Nietzen 1999).

Deflected succession

When an ecosystem has been disturbed for a long time the trajectory of succession may be altered and the succession becomes deflected (Godwin 1929; Gibson & Brown 1992). This deflected succession can lead to alternative stable states for the ecosystem, where a return to the original course of succession needs assistance and a change in the disturbance pattern (Suding et al. 2004). Disturbance, in this thesis, is defined as "any process or condition external from the physiology of living organisms that results in the sudden mortality of biomass in a community on a time scale significantly shorter than that of the accumulated biomass" (Huston 1994). It is important to understand the effect of deflected succession and how this creates stable states (Suding et al. 2004) when trying to re-establish vegetation that predated the disturbance regime.

Aims

The main aim of this thesis is to give an overview of the results from a number of sub-studies undertaken to explain the lack of forest regeneration in the grasslands surrounding the Ambohitantely forests in the highlands of Madagascar. More specifically, the following research questions have been posed:

- **Is the grass sward a barrier for shrub and tree establishment?** Does removal of the grass sward increase the number of shrubs and trees?

- **Is the grasslands micro-climate suitable for tree establishment?** Does shading increase tree establishment in the grassland? Is there effect of distance from the forest on seedling establishment? Do forest tree species sown in the grassland germinate and develop into seedlings?

- **Do grassland soil properties limit tree establishment?** Are there differences between forest and grassland soil properties? Does the use of chemical fertilizer increase tree establishment? Does augmenting grassland with forest soil increase the tree species establishment?

- **Is there a lack of tree seeds in the grassland?** If the dispersal of forest seeds is spatially limited, are there more (abundance and number of species) shrubs and trees closer to the forest than further away ? Does moving forest soil and its associated seed bank, into the grassland lead to establishment of shrubs and trees in the grassland?

- **What characterize succession after fire at the forest edge?** What are the characteristics of the fire's succession and are there differences between grassland and forest succession?

- **Is there continuing forest fragmentation in the Ambohitantely forest?** Has there been a change in forest fragmentation in Ambohitantely from 1949 to 1992?

- **Does forest fragmentation influence tree reproduction?** Do small fragments have fewer tree seedlings than larger fragments ?

Study area

Madagascar

Madagascar has a high level of endemism. More than 50 percent of bird species, 90 percent of plant species, and more than 98 percent of the amphibian, reptile and mammals species found in Madagascar are endemic (Ganzhorn et al. 2001). Most of the endemic species are confined to the forest (Koechlin 1972; Gade 1996). Due to the high level of endemism, Madagascar has been identified as one of the three most important biodiversity hot-spots in the world, along with the Philippines and Sundaland (Myers et al. 2000).

Grasslands dominate the highlands of Madagascar (Koechlin 1972; White 1983). The highlands of Madagascar have probably always been a mosaic of forest and grassland (Burney 1987). However, paleo-ecological studies show that the extent of grassland greatly increased 1500 years ago, probably as human use intensified (Burney 1987; Burney 1997). The grasslands in Madagascar are species poor, and the low number of endemic grassland species might be attributed to the short time the grasslands have been dominant (Koechlin 1993). One example of such a species poor grassland in Madagascar is the "Tampoketsa" grassland type, found in the highlands, and consisting of only 34 plant species (White 1983).

Fire has been an important agro-pastoral tool for farmers in Madagascar and still is. It is used for a multitude of purposes such as clearing grasslands to produce green fodder for cattle and to eradicate pests around rice fields (Kull 2000*a*). Fire is also used to eliminate shrubs that compete with the important *Uapaca bojeri* in the tapia woodland, which provides food for Madagascar silkworms (Gade 1985). These grass fires often spread beyond their intended limits and over large areas, damaging forest remnants far from the original fire. To stop this perceived destruction of the highland forests, all use of fire in grasslands and forest has been outlawed. However, this has not stopped all fires; grass and forest fires remains a great threat to biodiversity in Madagascar (Teholy 2002).

For the purpose of this thesis we have chosen the Ambohitantely forest as study area. The forest is situated in the highlands of Madagascar (Fig. 1)

Ambohitantely

One of the last natural forests on the highland of Madagascar is the Ambohitantely forest at an altitude of 1300 to 1650 m a.s.l. The forest covers approx. 2500 ha, divided among 378 fragments (Hanssen 2002). Of the 378 fragments, 77 fragments, covering a total of 1585 ha of forest, are protected as part of the Ambohitantely Forest Reserve (Reserve Spécial d'Ambohitantely), including the largest fragment covering 1250 ha (Hanssen 2002). Biodiversity studies from Ambohitantely show that species richness is lower in the smaller fragments than in the larger fragments among birds (Langrand 1995), amphibians (Vallan 2000) mammals (Rakotondravony & Goodman 2000) and plants (Lundberg 2000).

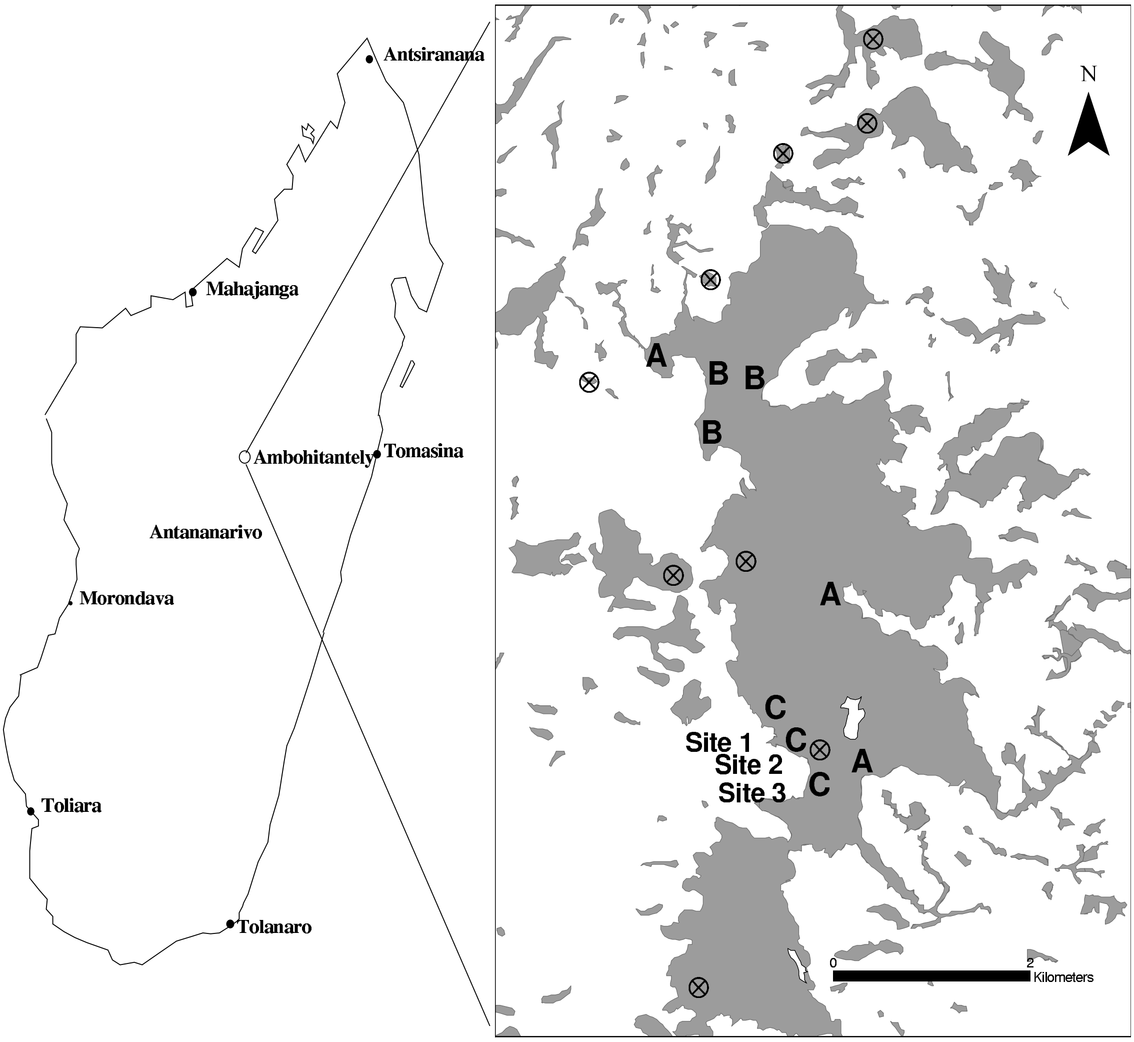

Figure 2: Madagascar and the locality of the Ambohitantely forest. The Ambohitantely Forest Reserve is shown to the right. Sites 1-3 are the 3 experimental sites in the grassland. A: Succession stage 1 (edges burnt in 1999); B: Succession stage 2 (edges burnt in 1991); C: Succession stage 3 (edges burnt in 1981 or earlier). ⊗ indicates the fragments used in the fragmentation study.

The Ambohitantely forest belongs to the sub humid forests of Madagascar (Cornet 1974). The mean annual precipitation is 1823 mm divided over 114 days. January is the wettest month with an average of 387 mm and June/July are the driest with 14 mm. The mean annual temperature is 16.5°C. November is the month with the highest average temperature of 23.7°C and August has the lowest average temperature of 13.5°C. There are five months from May to September that are cold and dry and seven months from October to April that are warm and wet. The bedrock in this part of the highland is acidic granite overlaid by red laterite soil with a high clay content (Roederer 1972), which can be classified as an oxisol (Ross 1993).

In 1951 the Ambohitantely forest was set aside as a part of the Manankazo Forestry Reserve. The Manankazo Forestry Reserve covered an area of 15000 ha. *Eucalyptus robusta* and *Pinus patula* were planted in several plantations inside the reserve from 1958 onwards (Bastian 1964). In 1982, 5600 hectares of the forestry reserve were set apart as the Ambohitantely Special Forest Reserve. This special reserve contains about 50 percent forest and 35 percent grassland, with the remaining 15 percent covered by non-native tree plantations. In 1988, it was decided that the ESSA-Forêt (Dèpartment des Eaux et Forêts de l'ESSA, University of Antananarivo) would be allowed to use the forest reserve as a research area. Beginning in 1990, ANGAP (*Association Nationale pour Gestion des Aires Protégées*) took responsibility for the reserve and in 1996 ANGAP established a permanent camp in the reserve (Ratsirarson & Goodman 2000). The reserve was divided into three parts, each with different management objectives. One area was set aside as a nature reserve with that would be free of human intervention, one area was set aside for eco-tourism and scientific studies, and the last area, consisting mostly of grassland and small forest fragments, was intended for sustainable use by the local people.

There is no indication in Ambohitantely Special Reserve that native species have established themselves in the plantations of exotic species, but *Pinus* spp. and *Eucalyptus* spp. have been observed at the edge of the native forest (pers. obs.). It is possible that the plantations of exotic species in Ambohitantely make the soil in the plantations unsuitable for native species.

Koechlin (1972) described the grassland in the highland of Madagascar as a pseudo-steppe to distinguish them from African savannas and South-Sahara steppes. White (1983) divided the grasslands into "Tanety" and "Tampoketsa" grassland, depending on the dominant species and altitude. In this thesis the collective name "grasslands" is used for the grasslands in Ambohitantely, as they have traits from both the Tanety and Tampoketsa grassland types. The grass species that dominate the study sites are presented in Table 2. The three most common grass species are regarded as a part of the Tampoketsa grassland type, while *Hyparrhenia rufa* is regarded as a part of the "Tanety" grassland type (White 1983).

It is believed that the Ambohitantely forest has been gradually reduced in size as a result of the continuing burning of the adjacent grasslands (Battistini & Verin 1972). In the Ambohitantely Forest Reserve 18 fires were reported between 1996 and 1999 (Ranarisoa, pers. comm.). These fires burned about 180 ha of grassland, but some of the fires encroached on the forest fragments. However, other areas of Ambohitantely have not burnt since 1983 (Radimbison 1990).

Table 1: Geographic distribution and abundance of the five most common grasses found at the study sites.

Species	Geographical distribution	Cover (in %) *Site 1*	*2*	*3*
Trachypogon spicatus Kuntze.	Pantropic	70	70	35
Loudetia simplex Hubb.	Africa	20	25	55
Aristida similis Steud.	Madagascar	10	0	10
Panicum glanduliferum Schum.	Madagascar	0	5	0
Hyparrhenia rufa Stapf.	Africa	0	5	0

Selection of study sites

The largest forest fragment and the adjacent grassland were chosen for all experiments (Sites 1,2 and 3 in Fig. 1), except for the study of the effect of fragmentation on the seedling density, where we needed several fragments of varying size (⊗ in Fig. 1). For the grassland experiments, 3 sites were selected that had been fire-free for the last 18 years. Ecological characteristics for each of these three sites are presented in Table 1. For the fire succession study nine areas were chosen, with the sites partitioned into three groups according to their fire history (A, B and C in Fig. 1).

Table 2: Major ecological features of Sites 1, 2 and 3.

	Site 1	*Site 2*	*Site 3*
Topography	Hill slope	Hill slope	Hill top
Slope	15%	10%	0%
Aspect	270°	135°	Flat
Mean grass height	48 cm	52 cm	70 cm
Mean litter depth	35 cm	39 cm	37 cm
Soil depth above hardpan	15 cm	15 cm	10 cm

Selection of species used in the experiments

It is often difficult to choose native species for use in a reforestation scheme. The ecological requirements and ecological responses for most of the species found in tropical forests remain unknown. There are, however, several non-native tree species whose ecological requirements, growth rate and yield are known. These species are often used in forest plantations instead of local tree species with their greater uncertainty of growth rate and yield. However, in an experiment comparing the forestry values of native and exotic species, at the La Selva biological station in Costa Rica, a more complex relationship was discovered. Non-native species had more rapid elongation than the local species, but the wood-volume for exotic and native species was the same (Butterfield 1995). Other studies have shown that rapid growing, high yielding species are not automatically suited for reforestation of degraded soils, as they may have a low survival rate in unsuitable environmental conditions (Butterfield 1995; Fimbel & Fimbel 1996).

In a study in Costa Rica (Fisher 1995), *Pinus teunumanii* significantly reduced the soil pH when planted in a degraded rain forest soil. It has also been demonstrated that *Eucalyptus* outside of its natural distribution area can degrade the soil and make it even less suitable for natural regeneration (Bargali et al. 1993). In *Eucalyptus* forests in Ghana ,the litter contains fewer nutrients than the litter found in the native forest (Lisanework & Michelsen 1994).

An example of an exotic species used in Madagascar is the exotic plant *Acacia dealbata* Linn. (Fabaceae). This species was planted as a nitrogen-fixing plant in the *Eucalyptus* plantations around the Ambohitantely Special Reserve, and these shrubs are still found in great numbers in the plantations today. However, any exotic species can become an invasive species and threaten the native biodiversity and should thus be avoided in conservation work (Wittenberg & Cock 2001; Binggeli 2003).

Native species were used in the research in this thesis. The choice was based primarily on the fact that exotic species may become invasive, but also on the uncertainty of the long term effect on soil characteristics, as well as the unknown stability of exotic species in forest restoration.

The tree species used in the experiments are both pioneer and non-pioneer species. Pioneer species "can only germinate in the forest canopy open to the sky and in which full sunlight impinges at ground level for at least part of the day" (Swaine & Whitmore 1988), and non-pioneers species can germinate in shade. However, the knowledge of fruiting (Razakanirina & Andrianjaka 1993) and germination of the local tree species was limited, and we had to rely on observation of seedlings that were found inside the forest and at the edge to decide if the species were pioneers or not. Another difficulty was collecting the seeds, especially seeds from trees with fleshy fruits, like *Ilex mitis*, as they were eaten by birds and lemurs before we could pick the fruits.

The species used in the experimental studies are presented in Table 3.

Table 3: Local tree species that were planted as seedlings, and the species sown as seeds in the grassland

Seedlings	Seeds	Species (Family)
	x	*Anthocleista madagascariensis* Baker (Loganiaceae)
x	x	*Dodonaea madagascariensis* Radlk. (Sapindaceae)
x		*Filicium decipiens* Thw. (Sapindaceae)
	x	*Harungana madagascariensis* Lam. ex Poir.(Clusiaceae)
x	x	*Olea lancea* Lam. (Oleaceae)
x		*Podocarpus madagascariensis* Baker (Podocarpaceae)
x		*Rhus taratana H.Perrier* (Anacardiaceae)
	x	*Trema orientalis* (L.) Blume (Ulmaceae)

The sub-studies

What follows is a presentation of the sub-studies used to answer the principal research questions posed in this thesis.

Table 4: The number of establishments per m^2 in the plots where the grass sward was intact or removed.

Species	Grass sward intact	removed
Clerodendrum sp.	0.04	
Helichrysum bracteiferum	0.01	1.0
Macaranga alinifolia	0.05	
Melastomataceae *sp.*		0.13
Philippia floribunda	0.09	
Vaccinium emirnense	0.01	
Vernonia garnieriana		0.13
Weinmannia rutenbergii	0.05	
Total	0.25	1.25

The grass sward as a barrier to tree establishment

If the sward is a barrier to tree and shrub establishment in Ambohitantely, there should be a difference in the number of shrubs and trees established in plots where the sward have been removed as compared to plots were the sward is intact. This question was addressed by combining two different studies, which explains discrepancies in the methodology. Two transects were placed perpendicular to the forest edge at Site 1 and 2. All shrub and tree species that were established in undisturbed 4x4 m plots placed at 0 and 40 m from the forest along the transects were recorded after 30 months (Pareliussen et al. 2004*c*). In another study of establishment in plots without the sward, we removed the grass sward from two 1 m^2 plots placed at 10 and 50 meters from the forest edge between the two transects. The number of established shrubs and trees was recorded after 30 months.

The number of shrubs and trees that had been established was greater in the plots with the sward removed (Table 4). In the 128 m^2 where the grass sward was undisturbed, only 32 shrub and tree individuals established themselves in the 30 months. Thus, there were 0.25 establishments per square meter. The total area with grass removed was 8 m^2, with 10shrub and tree individuals established, giving a density of 1.25 individuals per square meter.

Two of the three species in the plots where the sward were removed was not found in plots with intact sward. The density of *Helichrysum bracteiferum* increased when the grass sward was removed (Table 4).The area where the grass sward was removed was much smaller than the area left intact, and thus the total number of species could not be compared. The findings indicate that the grass sward is a barrier to establishment of some trees and shrub species. Removing the grass sward is a potentially easy way to increase the establishment of shrubs and trees in the grassland.

Micro-climate

The effect of shading on species establishment

As shades can lower the soil and air temperatures, the micro-climate underneath the shade should be more similar to the forest where the canopy creates a natural shade. Thus, one would expect a positive effect on survival and growth from shading. The effect of shading on the survival and growth was tested by shading of seedlings of five local tree species (Table 3) with bamboo screens (Pareliussen et al. 2004*a*; Pareliussen et al. 2004*b*).

Shading had little impact in survival and growth in this study. Shading reduced the survival of *Dodonaea madagascariensis* (Pareliussen et al. 2004*b*). There were only marginal positive effects on the growth of *Olea lancea* when shaded (Pareliussen et al. 2004*a*). The management implication are clear: shading does not justify its cost.

The effect of distance on establishment

If the micro-climate in the grassland is different closer to the forest than further away, there should be difference in growth and survival of forest tree seedlings at different distances from the forest edge. The effect of distance from the forest edge on the survival and growth of the seedlings of five local tree species (Table 3) was studied by planting the seedlings in the grassland at different distances from the forest (10 or 50 m) (Pareliussen et al. 2004*b*; Pareliussen et al. 2004*a*).

In a pooled analysis, all species showed lower survival 50 m from the forest than 10 m (Pareliussen et al. 2004*b*). *Olea lancea* had higher growth 10 m from the forest than 50 m (Pareliussen et al. 2004*a*).

The effect of distance can be an indication that the micro-climate closer to the forest is more beneficial for seedlings than conditions further from the forest edge. However, micro-climate is not the only factor that differs between these two areas. Soil characteristics can often be different at the forest edge as compared to the grassland further away from the forest. It is impossible in this study,however, to unravel the contribution of soil characteristics from the micro-climate. However, the lesson from a management perspective is that reforestation measures should be focused at the forest edges of the grassland, due to the greater survival of tree seedlings.

Do forest tree seeds germinate and develop in the grassland?

If the micro-climate is hostile in the grassland seeds from local tree species would have problems germinating and developing there. Seedlings from five local tree species (Table 3) were planted in the grassland at the 3 study sites (Pareliussen et al. 2004*a*; Pareliussen et al. 2004*b*). Survival and growth were measured 15 months after planting.

Seeds of the five species were sown March 1999. The total number of seed sown was 960, divided into 24 1 m^2 plots. The grass sward was removed from the plots and the soil was worked to a depth of 60 cm. In December 1999, 7 seedlings of *Olea* and 20 seedlings of *Harungana* had developed, but during January 2000 a torrential rain destroyed the shading over the seedlings and the *Olea* seedlings died. In February 2000, 5 seedlings of *Dodonaea* developed. However, in the first dry season the seedlings of *Harungana* and *Dodonaea* died.

Three of the five species germinated, but subsequently died. This indicates that the first dry season after germination is a critical bottleneck for the establishment of the seedlings.

Soil factors

Differences between forest and grassland soils

If there are differences in the soil properties of the forest and the grassland, these difference could pose a barrier for tree establishment. Soil samples from the forest, the forest edge and the grassland were collected and the chemical and biological properties were analyzed
(Olsson & Pareliussen manuscript).

We collected soil inside the forest, at the forest edge, and in the grassland, at each of the three sites to study soil chemical composition (Olsson & Pareliussen manuscript). In addition we studied the micro-biological composition, of these soils with the use of PFLA-chromatograms
(Olsson & Pareliussen manuscript).

The grassland soil differed from forest soil with respect all to the chemical properties we studied; that is, in loss on ignition, pH, NO_3-N, NH_4-N, PO_4-P, K, Na, Ca and Mg (Olsson & Pareliussen manuscript). The pattern of soil properties in the forest edge, however, did not differ from either the grassland or the forest. All properties were intercorrelated except the two nitrogen fractions (NO_3-N and NH_4-N). There were some significant differences between the sites, reflecting environmental variation. The micro-biological groups (algae, protozoa, cyanobacteria, bacteria, fungi, vesicular-arbuscular mycorrhiza (VAM) and ecto-mycorrhiza) showed a similar pattern as the soil chemical properties, with significant differences between grassland and forest (Olsson & Pareliussen manuscript). The only exception was in the VAM which showed significantly lover levels of mycorrhiza in the grassland soil than in the soil from the forest edge, which in turn had lower levels than the forest soil.

It is clear that the chemistry and biological properties of the grassland soils were poorer than the forest soils. It is impossible to discern from this study, however, if these lower levels in the grassland pose a barrier for tree establishment.

Use of chemical fertilizers

We studied the survival and growth of tree seedlings when treated with chemical fertilizer. Seedlings from five local tree species (Table 3) were planted in the grassland at the tree study sites (Pareliussen et al. 2004*a*; Pareliussen et al. 2004*b*) and studied when chemical fertilizer (NPK: 20N + 4.3P + 16.3K) was added. Survival and growth were both measured 15 months after planting.

Chemical fertilizer reduced the survival for *Filicium decipience*, *Olea lancea* and *Podocarpus madagascariensis* (Pareliussen et al. 2004*b*), mainly because it increased the competition from naturally establishing shrubs. Chemical fertilizer increased the growth of *Rhus taratana* and *Dodonaea madagascariensis* (Pareliussen et al. 2004*a*).

The effect of chemical fertilizers was largely negative due to competing weedy shrubs that colonized the plots. Thus, even if some species had increased growth, the lower survival along with the cost of chemical fertilizers indicate that the restoration benefits might be low.

Application of soil from the forest

The project also analyzed the survival and growth of tree seedlings when soil from the forest was applied in the experimental plots.

There was no effect on seedling survival when soil from the forest was added to the plots (Pareliussen et al. 2004*b*). *Filicium decipience* had marginally higher growth when it was treated with forest soil and shaded at the same time (Pareliussen et al. 2004*a*).

The effect of forest soil was limited, and the marginal effect on the growth of *Filicium decipience* did not justify the destructive use of a limited resource.

Lack of tree seeds in the grassland

Spatial limits on seed dispersal

Seed dispersal is related to dispersal vectors and distance from seed source. One would thus expect a larger number of trees closer to the forest than further away. Five transects were placed perpendicular to the forest edge at the three study sites and all shrub and tree species growing in 4x4 m plots, placed at 0, 40 and 80 meters from the forest along the transects, were recorded (Pareliussen et al. 2004*c*). The species composition at the different distances was compared to the species in the forest, both close to the forest edge and in the forest interior (Pareliussen et al. 2004*c*).

The number of individual trees and shrubs was higher close to the forest than further away (Table 5), and the number of species was also higher close to the forest than further into the grassland. The species found in the grassland were different from the species found inside the forest edge.

Fully 71 percent of the species in the grassland were not dispersed by animals, in contrasting to 36 percent at the forest edge and 25 percent inside the forest (Pareliussen et al. 2004*c*).

There are a greater number of shrub and tree species and a greater number of individuals closer to the forest than further away, which may be caused by a lack of dispersal of shrubs and trees from the forest. The shift from animal-dispersed species inside the forest to non-animal dispersed species in the grassland may indicate that animals have difficulty dispersing seeds outside the forest.

Table 5: The number of individuals found in the grassland, all transects pooled at each of the three sites.

		Site 1			Site 2			Site 3		
Species	Family	0	40	80	0	40	80	0	40	80m
Anthocleista sp.	Gentianaceae							2		
Clerodendrum sp.	Verbenaceae	6			27			10		
Harungana madagascariensis Poir.	Clusiaceae							1		
Helichrysum bracteiferum Humbert	Asteraceae	1			33			9	1	
Macaranga alinifolia Baker	Euphorbiaceae	10								
Fabaceae sp.	Fabaceae							5		
Nuxia capitata Baker	Buddlejaceae	4			1					
Philippia cauliflora Hochr.	Ericaceae								44	
Philippia floribunda Benth.	Ericaceae	35	40		34	20	83	38	15	5
Philippia parkerii Baker	Ericaceae		1			16	7	2		
Psorospermum sp.	Clusiaceae							3		
Senecio faujasioides Baker	Asteraceae				1			2		
Vaccinium emirnense Hook.	Ericaceae	4	1	1	6	8	4	12	5	9
Vernonia garnieriana Klatt.	Asteraceae	3			2	0	4	23	17	
Weinmannia rutenbergii Engl.	Cunoniaceae	8			26			8	5	

The effects of moving soil as an amendment from the forest to the grassland

If the there is a lack of seeds in the grassland soil seed bank, with a large forest soil seed bank, moving soil from the forest to the grassland should increase species establishment. This question was addressed by combining three different studies, which in turn explains discrepancies in methodology. Ten 1 m^2 plots were placed 10 m from the forest and another 10 plots were placed 50 m from the forest at Sites 1 and 2. The grass sward was removed and the soil worked to a depth of 60 cm. In all plots approx. 3 l of forest soil from the forest was mixed with the top-soil in the plots. The number of seedlings of shrubs and trees that had established in the plots after 39 months was recorded. This study did not allow us to distinguish between the seedlings that germinated from the forest seed banks and the seedlings that dispersed into the plots. However, if there are species not found in the undisturbed grassland (Table 5) or in the grassland plots with the sward removed (Table 4), this suggests that these species originated from the soil seed bank.

The species that were established in the plots treated with forest soil are presented in Table 6. Three species had not been recorded in the forest earlier: *Helichrysum cordifolia, Solanum mauritanium*

Table 6: The number of seedling establishments per m^2 in the plots treated with forest soil at 10 and 50 m from the forest.

	Distance	
Species	10 m	50 m
Clerodendrum sp.	0.1	
Harungana madagascariensis		0.1
Helichrysum cordifolia	0.3	0.1
Helichrysum bracteiferum	0.1	
Macaranga alinifolia	0.1	
Solanum mauritanium	0.1	
Trema orientalis	0.2	0.2
Total	0.9	0.4

and *Trema orientalis*. The *Helichrysum cordifolia* is not animal dispersed, while the two others are animal dispersed. *Solanum mauritanium* and *Trema orientalis* were found in the 2- and 10-year-old fire successions areas in the forest (Wehn et al. 2004, Table: 4). *Solanum mauritanium* is an exotic species introduced at around 1900 from South America, and as an exotic is not suitable for reforestation purposes.

There are indications that the *Helichrysum cordifolia, Solanum mauritanium* and *Trema orientalis* are pioneer species confined to the forest edge. The two animal dispersed species could be limited by dispersal vectors. As a pioneer species, *Trema orientalis* is planted around coffee and thee plantations in Madagascar (Samyn 1999), and might be a candidate for reforestation in Ambohitantely.

Fire succession

Characteristics of succession after a forest fire

If the characteristics and the species composition at different successional stages after forest fires are different from the characteristics in the grassland 18 years after the grassland burnt, the grassland succession may have become deflected. We studied nine forest edges that had burned either 2, 10 or 18 years ago (2 years A, 10 years B and 18 years ago C in Fig. 1), and compared them to the un-burnt forest interior (Wehn et al. 2004). Control plots 1, 2 and 3 were placed parallel to the forest edge, at least 50 meters inside the forest. We studied seedlings, saplings and trees of 38 species in 20 m^2 plots, 10 at each edge and 10 in each forest interior, making a total of 3600 m^2 studied.

Two of the three species dominating the edges burnt two years ago were exotic and non-woody species (Table 4). The juveniles of the plants dominating the edges burnt two years ago were not found in the edges that were burnt 10 years ago. The species dominating the edges burnt 10 years ago were native trees and shrubs. In the edges burnt more than 18 years ago, there is greater establishment of native shrub and tree species. However, there were differences between the controls in the forest interior as well. This indicates that there is heterogeneity in the species composition inside the forest (Wehn et al. 2004, Table: 4). However, it seem that even if the succession in the edges burnt two years ago is dominated by exotic species, the succession in the edges burnt 10 and more than 18 years ago are both dominated by forest tree species.

Comparing the species composition in the grassland (Table 5) with the species composition in the fire succession stages (Table 4), only six species that are found both in the grassland and in the successional stages 10 and 18 years after burning. However, none of the six species dominates either site or succession. In the grassland *Philippia spp.* dominates, and in the 10-year-old successional stage *Filicium decipience* and *Macaranga sp.* dominate. In the 18-year-old successional stage the *Dodonaea madagascariensis* and *Psorospermum sp.* dominate.

Even if the species dominating the succession after 2 years are exotic species, the 10 and 18 year successional stages are dominated by native tree species. The difference in species composition between the grassland and forest edges may indicate that the succession trajectory differs, but only long time study of the actual succession can prove that this is the case.

Is there continuing fragmentation of Ambohitantely forest?

To study the change in forest fragmentation a comparison of aerial photos from 1949 and 1992 of the Ambohitantely forest was conducted (Hanssen 2002).

In the areas outside the forest reserve the forested area has been reduced by 28.3 percent from 1949 to 1992 (Hanssen 2002). Inside the forest reserve only 9.2 percent of the forested area has been deforested. In 1949 the forest was composed of 402 fragments, and in 1992 it was composed of 378 fragments. Most of the fragments that disappeared were less than 4 ha (Hanssen 2002).

There is a continuing reduction in number of fragments and forested area from 1949 to 1992. The reduction was stronger in the non-protected area and for the small fragments.

Forest fragmentation and its effect on tree reproduction

One way to detect the effect of forest fragmentation on reproduction is to look at the recruitment of seedlings in relation to fragment size. A study of the influence of fragment size on the density of tree seedlings was conducted by studying 12 forest tree species in six fragments. The fragments size varied from 0.3 to 52 ha. Ten plots of 2x10 m were studied in each fragment and all individuals from seedlings to mature trees of the 12 species were recorded (Lundberg 2000).

The number of tree species was lower and the density of seedlings was lower in smaller fragments than larger fragments (Lundberg 2000), with the exception of *Rhus taratana,* which did not show an effect from fragments size. The number of tree species was also lower as the distance between the fragments increased (Lundberg 2000).

The reduction in the number of seedlings in smaller fragments, as well as the lower number of tree species, may indicate that the smaller fragments have a problem with recruitment.

Table 7: Species distribution, grouped in succession- and control classes based on percent of total individuals registered of each species in the different classes.

Species [1]	Succession stage 1	Succession stage 2	Succession stage 3	Control 1	Control 2	Control 3	Total
Buddleia mad.	**100**	0	0	0	0	0	360
Phytolacca dode.	**100**	0	0	0	0	0	2708
Solanum maur.	**100**	0	0	0	0	0	2424
Filicium decipience	0	**94**	4	0	2	0	52
Macaranga sp	0	**91**	7	0	2	0	43
Psiadia sp	14	**86**	0	1	0	0	166
Harungana mad.	17	**77**	5	1	0	0	155
Trema orientalis	30	**70**	0	0	0	0	160
Croton oreades	11	**65**	11	7	0	5	220
Dichaetanthera sp	17	**59**	24	0	0	0	63
Nuxia capitata	4	**49**	17	9	9	13	397
Macaranga alinifolia	10	**42**	14	20	6	7	1496
Rhus tarantara	3	**38**	7	27	23	4	541
Dodonaea mad.	0	7	**93**	0	0	0	14
Psorospermum sp	10	12	**65**	8	5	1	1957
Weinmannia ruten.	8	17	**64**	5	2	6	200
Vernonia garn.	13	4	**59**	15	0	9	138
Kaliphora mad.	8	23	**48**	18	3	0	120
Rhus thouarsii	1	5	**39**	12	19	24	136
Uapaca densifolia	7	2	4	**61**	25	0	2835
Leptolaena pauc.	12	2	9	**53**	23	1	242
Vepris pilosa	3	8	7	**38**	34	10	996
Pandanus mad.	0	9	0	7	**58**	26	137
Sarcolena multiflora	5	10	0	30	**54**	0	237
Podocarpus ambo.	0	0	3	17	**51**	28	497
Carissa obovata	0	6	2	8	**50**	34	165
Dilobeia sp	0	0	0	18	**42**	39	33
Dracaena spp.	1	18	11	26	**26**	19	729
Olea lancea	0	3	3	19	22	**54**	638
Vepris macrophylla	8	0	0	19	14	**59**	37
Ravenea mad.	0	3	16	8	4	**68**	73
Pandanus vandami	1	1	4	9	17	**69**	162
Erythroxylum spha.	0	0	0	2	0	**98**	2726
Dypsis oropedonis	0	0	0	0	0	**100**	10

[1] Species with less than 10 individuals were excluded from this table.

Main findings

It is our hope that the main findings from this thesis can be used as a starting point for a successful reforestation of the grasslands around the forest fragments in Ambohitantely Forest Reserve.

The REMOVAL OF GRASS SWARD increased the establishment of some shrub and tree species. The shrub *Helichrysum bracteiferum* most increased its density. The areas where sward was removed in this study were small, and pilot studies should thus be conducted to ensure that the successful results from our study can be transfered to a larger scale. If such pilot studies are successful, sward removal can be quickly done with tractors to plow the grasslands.

SHADING of tree seedlings reduced the survival of the pioneer species *Dodonaea madagascariensis*, and the only positive effect was a marginal increase in growth for *Olea lancea*. Thus, shading did not justify its cost. The experiment of planting tree seedlings at different DISTANCES FROM THE FOREST EDGE showed that all planted species had higher survival closer to the forest and *Olea* had marginally higher growth closer to the forest. Three of the five tree species SOWN IN THE GRASSLAND did germinate, but did not survive the first year.

GRASSLAND SOIL differed from the forest soil. CHEMICAL FERTILIZER lowered the survival for three of the five tree species studied, and two species showed increased growth. Fertilization increased the number of small, weedy-shrubs and herbs, and thus impaired tree and shrub establishment. Application of SOIL FROM THE FOREST did not affect the survival or growth of the species sufficiently to justify the use of the limited resource of forest soil.

The greater abundance in species and individuals close to the forest suggests that there are spatial limitation on SEED DISPERSAL. The species in the grassland are mainly non-animal dispersed species, while the species inside the forest are animal-dispersed. When soil was moved from the forest to the grassland, several new species were established. One explanation is that there are animal-dispersed pioneer species in the forest, such as *Trema orientalis*, that can not be dispersed into the grassland without human intervention.

Even if the FIRE SUCCESSION in the edges is dominated by exotic species 2 years after fire, the successional stages 10 and 18 years are dominated by native species. The species composition in the grassland burnt more than 18 years ago indicates that the trajectory for the GRASSLAND SUCCESSION may differ from the fire succession in the forest edge.

Deforestation and FRAGMENTATION has been more evident outside the reserve, but even inside the reserve there has been reduction in forested area. Decreasing the size of forest fragments decreases the DENSITY OF SEEDLINGS in the fragment.

Future management

The Ambohitantely Forest Reserve is an important component of the natural forests of Madagascar. Implementing some of the suggestions from this thesis should provide excellent opportunities to protect the biodiversity of the forest for future generations.

Fire protection must be paramount in all management plans to preserve the Ambohitantely forest. The disruptive force of annual fires should not be underestimated. The fires threatening the Ambohitantely forest are most likely linked to cattle herders in the area (Réau et al. in Press). The main interest of the villagers is not the forest per se, but the fodder quality of the grassland adjacent to the forest. They need to burn the grassland to improve fodder quality for their cattle. The law banning grass fires has not had the desired effect; instead of controlling fires, people now flee to escape prosecution (Réau et al. in Press). Thus, easing the law and ensuring co-operation with the local people is important to get fire under control, and to limit burned areas (Kull 2002).

Removing the grass sward from the grassland seems to offer a possible way to improve shrub and tree establishment. However, few of the species that were established in the plots where the sward was removed were forest tree species. Raising seedlings in a nursery and planting them in the grassland, was shown in this study to be successful as a reforestation measure. Based on the result from this thesis, the following species are recommended: *Dodonaea madagascariensis, Olea lancea* and *Rhus taratana.* Another species worth mentioning, even if it did not germinate when sown in the grassland, is *Trema orientalis.* It has nitrogen fixing capabilities (Samyn 1999), and was able to be established in the forest soil transplants in the grassland.

All forest fragments, as inherent parts of the forest system, are important and must be protected (Laurance & Bierregaard 1997). In 1992, approx. 750-1000 ha, or 30-40 percent, of the forest lay outside the protected area (Hanssen 2002). It is important to increase the reserve to protect all remaining fragments of the Ambohitantely forest. Due to the planting of exotic species around Ambohitantely in the 1950s, the new reserve would contain some *Eucalyptus spp.* and *Pinus spp.* plantations, which would have to be controlled to prevent them from becoming invasive.

Future studies

The studies covered in this thesis have contributed to an understanding of the shrub and tree establishment in Ambohitantely. There are, however, areas where more in depth studies are needed to arrive at a better understanding of this system and how to successfully reforest the grasslands.

Trema orientalis, a native species from Ambohitantely, is known to fix nitrogen (Samyn 1999). However, there might be other native species able to fix nitrogen. A search of the TROPICOS database at the Missouri Botanical Garden for plants from the Fabaceae (legume family) from Ambohitantely turned up two species (*Mundulea laxiflora* and *Vaughania perrieri*; Zachary Rogers, pers. comm.). These species should be checked for their nitrogen-fixing capabilities to see if they could be suitable for use along with *Trema orientalis* in future reforestation projects in Ambohitantely.

Differences in the characteristics between the grassland and forest soils mean that it would be interesting to observe soil changes after forest trees are established in the grassland. Of particular interest would be to follow changes in levels of mycorrhiza as the forest tree species are established in the grassland.

One way to introduce trees in the grassland is by planting twigs cuttings. In a study in Malaysia (Itho et al. 2002) 66 percent of species planted as twig cuttings rooted, with an overall rooting success of 38 percent. Rapidly growing, small trees rooted more readily than slow-growing, late-maturing, trees. However, other studies (Ray & Brown 1995) show that cuttings can have higher mortality than seedlings raised from seeds in a nursery. From our work in Ambohitantely we have observed that a branch of *Buddleia madagascariensis* that was used as a pole actually rooted and started to grow in the grassland. *Uapaca densifolia* might be another candidate as it spreads via ramets. As we only have anecdotal observations of twigs rooting from Ambohitantely, a study of the effectiveness of twig cuttings in reforestation would be valuable as a way to find easy, low-cost and rapid reforestation methods.

Literature Cited

Alvarez Buylla, E., Garcia Barrios, R., Lara Moreno, C., & Martinez Ramos, M., 1996. Demographic and genetic models in conservation biology: applications and perspectives for tropical rain forest tree species, Annual Review of Ecology and Systematics 27:387–421.

Bargali, S., Singh, R., & Joshi, M., 1993. Changes in soil characteristics in *Eucalyptus* plantations replacing natural broad-leaved forests, Journal of Vegetation Science 4:25–28.

Bastian, G., 1964. La foret d‘Ambohitantely, Madagascar revue de geographie 5:1–42.

Battistini, R., & Verin, P., 1972. Man and the environment in Madagascar, in Biogeography and Ecology of Madagascar, Battistini, R., & Richard-Vindard, G., editors, pages 311–338, Dr. W. Junk B.V., The Hague.

Bierregaard, R., Lovejoy, T., Kapos, V., Dossantos, A., & Hutchings, R., 1992. The biological dynamics of tropical rain-forest fragments, Bioscience 42:859–866.

Binggeli, P., 2003. Introduced and invasive plants, in The Natural History of Madagascar, Goodman, S., & Benstead, J., editors, University of Chicago Press.

Brand, J., & Pfund, J., 1998. Site and watershed-level assessment of nutrient dynamics under shifting cultivation in eastern Madagascar, Agriculture Ecosystems & Environment 71:169–183.

Burney, D., 1987. Late quaternary stratigraphic charcoal records from Madagascar, Quaternary Research 28:274–280.

Burney, D., 1997. Tropical islands as paleoecological laboratories: Gauging the consequences of human arrival, Human Ecology 25:437–457.

Buschbacher, R., C.Uhl, & Serrão, E., 1988. Abandoned pastures in eastern Amazonia. II: Nutrient stocks in soil and vegetation, Journal of Ecology 76:682–699.

Butterfield, R., 1995. Promoting biodiversity - advances in evaluating native species for reforestation, Forest Ecology and Management 75:111–121.

Chapman, C. A., & Chapman, L. J., 1999. Forest restoration in abandoned agricultural land: a case study from East Africa, Conservation biology 13:1301–1311.

Cochrane, M., Alencar, A., Schulze, M., Jr., C. S., Nepstad, D., Lefebvre, P., & Davidson, E., 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests, Science 284:1832–1835.

Cornet, A., 1974. Essai de cartographie bioclimatique à Madagascar, Notice explicative ORSTOM 55.

Didham, R., & Lawton, J., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments, Biotropica 31:17–30.

Duncan, R., & Duncan, V., 2000. Forest succession and distance from forest edge in an afro-tropical grassland, Biotropica 32:33–41.

FAO, 2001. State of the World's forest, Food and Agriculture Organization of the United Nations, Rome.

Fimbel, R., & Fimbel, C., 1996. The role of exotic conifer plantations in rehabilitating degraded tropical forest lands: a case study from the Kibale forest in Uganda, Forest Ecology and Management 81:215–226.

Fisher, R., 1995. Amelioration of degraded rain-forest soils by plantations of native species, Soil Science Society of America Journal 59:544–549.

Freidenburg, L., 1998. Physical effects of habitat fragmentation, in Conservation Biology, Fiedler, P., & Kareiva, P., editors, Chapman & Hall, New York.

Gade, D., 1985. Savanna woodland, fire, protein and silk in highland Madagascar, Journal of Ethnobiology 5:109–122.

Gade, D., 1996. Deforestation and its effects in highland Madagascar, Mountain Research and Development 16:101–116.

Ganzhorn, J., Fietz, J., Rakotovao, E., Schwab, D., & Zinner, D., 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar, Conservation Biology 13:794–804.

Ganzhorn, J., Lowery II, P., Schatz, G., & Sommer, S., 2001. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out, Oryx 35:346–348.

Garcia-Oliva, F., Casar, I., Morales, P., & Maass, J., 1994. Forest-to-pasture conversion influences on soil organic-carbon dynamics in a tropical deciduous forest, Oecologia 99:392–396.

Garwood, N., 1989. Tropical soil seed banks: a review, in Ecology of Soil Seed banks, Leck, M., Parker, V., & Simpson, R., editors, pages 149–209, Academic press, San Diego.

Gentry, A., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients, Annals of the Missouri Botanical Garden 75:1–34.

Gerhardt, K., 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica, Journal of Vegetation Science 4:95–102.

Gibson, C., & Brown, V., 1992. Grazing and vegetation change: deflected or modified succession?, Journal of Applied Ecology 29:120–131.

Gigord, L., Picot, F., & Shykoff, J., 1999. Effects of habitat fragmentation on *Dombeya acutangula* (Sterculiaceae), a native tree on la Reunion (Indian ocean), Biological Conservation 88:43–51.

Ginsberg, J., 1998. Perspectives on wildfire in the humid tropics, Conservation Biology 12:942–943.

Godwin, H., 1929. The sub-climax and deflected succession, Journal of Ecology 17:144–147.

Griffin, R., 1990. Effects of inbreeding on growth of forest trees and implications for management of seed supplies for plantation programmes, in Reproductive Ecology of Tropical Forest Plants, Bawa, K., & Hadley, M., editors, pages 355–374, The Parthenon Publishing Group, Paris.

Hanssen, S., 2002. The Ambohitantely Special Reserve in Central High Land Madagascar - Forest change and forest occurrence, Masters thesis: Norwegian University of Science and Technology, Trondheim, Norway.

Harcombe, P., 1977. The influence of fertilization on some aspects of succession in a humid tropical forest, Ecology 58:1375–1383.

Harcourt, C., Jenkins, M., Langrand, O., Stone, D., & Lowry, P., 1992. Madagascar, chapter 26, pages 221–229, Macmillian.

Hardwick, K., Healey, J., Elliott, S., Garwood, N., & Anusarnsunthorn, V., 1997. Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand, Forest Ecology and Management 99:203–214.

Holl, K., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate and soil, Biotropica 31:229–242.

Holl, K., 2002. Tropical moist forest, in Handbook of Ecological Restoration, Restoration in Practice, Perrow, M., & Davy, A., editors, volume 2, chapter 23, pages 539–558, Cambridge University press, Cambridge,UK.

Holl, K., & Kappelle, M., 1999. Tropical forest recovery and restoration, Trends in Ecology and Evolution 14:378–379.

Holl, K., Loik, M., Lin, E., & Samuels, I., 2000. Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment, Restoration Ecology 8:339–349.

Holl, K., & Quiros-Nietzen, E., 1999. The effect of rabbit herbivory on reforestation of abandoned pasture in southern Costa Rica, Biological Conservation 87:391–395.

Huston, M., 1994. Biological Diversity, Cambridge University Press, Cambridge.

Itho, A., Yamakura, T., Ohkubo, T., Palmiotto, P., LaFrankie, J., Kendawang, J., & Lee, H., 2002. Rooting ability of cuttings relates to phylogeny, habitat preference and growth characteristics of tropical rainforest trees, Forest Ecology and Management 168:275–287.

Janos, D., 1980. Mychorrhizae influence on tropical succession, Biotropica 12:56–64.

Jarosz, L., 1996. Defining deforestation in Madagascar., in Liberation Ecologies: Environment, Development, Social Movements, Peet, R., & Watts, M., editors, pages 144–164, Routledge.

Kauffman, J., Sandford, R., Cummings, D., Salcedo, I., & Sampaio, E., 1993. Biomass and nutrient dynamics associated with slash fires in a neotropical forest, Ecology 74:140–151.

King, J., Moutsinga, J., & Doufoulon, G., 1997. Conversion of anthropogenic savanna to production forest through fire-protection of the forest-savanna edge in Gabon, central Africa, Forest Ecology and Management 94:233–247.

Koechlin, J., 1972. Flora and vegetation of Madagascar, in Biogeography and ecology in Madagascar, Battistini, R., & Richard-Vindard, G., editors, pages 145–190, Dr.W.Junk B.V., Den Hague.

Koechlin, J., 1993. Grasslands of Madagascar, in Natural Grasslands., Coupland, R., editor, volume 8B of *Ecosystems of the World*, pages 291–301, Elsevier, Amsterdam.

Kull, C., 2000*a*. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar, Environment and History 6:423–450.

Kull, C., 2000*b*. Isle of Fire: the political ecology of grassland and woodland burning in highland Madagascar, Ph.D. Thesis from the University of California, Berkeley.

Kull, C., 2002. Empowering pyromaniacs in Madagascar: ideology and legitimacy in community-based natural resource management, Development and Change 33:57–78.

Langrand, O., 1995. The effects of forest fragmentation on bird species in Madagascar: a case study from Ambohitantely Forest Reserve on the central high plateau, Masters thesis: University of Natal, South Africa.

Laurance, W., & Bierregaard, R., 1997. Tropical forest remnants. Ecology, Management, and Conservation of fragmented commmunities, The University of Chicago press, Chicago.

Lisanework, N., & Michelsen, A., 1994. Litterfall and nutrient release by decomposition in three plantations compared with a natural forest in the Ethiopian highlands, Forest Ecology and Management 65:149–164.

Lundberg, M., 2000. Effects of fragmentation on forest regeneration in central highland Madagascar, Masters thesis, Norwegian University of Science and Technology,, Trondheim, Norway.

Martínes, L., & Zinck, J., 2004. Temporal variation of soil compaction and deterioration of soil quality in pasture areas of Colombian Amazonia, Soil and Tillage Research 75:3–17.

McClanahan, T., 1986. The effect of a seed source on primary succession in a forest ecosystem, Vegetatio 655:175–178.

McLaren, K., & McDonald, M., 2003. The effects of moisture and shade on seed germination and seedling survival in a tropical dry forest in Jamaica, Forest Ecology and Management 183:61–75.

Morat, P., 1973. Les savanes du sud-ouest de Madagascar, volume 68 of *Mémoires orstom*, ORSTOM, Paris.

Murica, C., 1995. Edge effects in fragmented forests – implications for conservation, Trends in Ecology and Evolution 10:58–62.

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G., & Kent, J., 2000. Biodiversity hotspots for conservation priorities, Nature 403:853–858.

Nepstad, D., Uhl, C., Pereira, C., & Cardoso da Silva, J., 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia, OIKOS 76:25–39.

Nykvist, N., 2000. Tropical forests can suffer from a serious deficiency of calcium after logging, AMBIO 29:310–313.

Olsson, E., & Pareliussen, I., manuscript. Soil property changes along tropical forest-grassland gradients in Ambohitantely Forest Reserve, central highlands of Madagascar, Unpublished manuscript.

Pareliussen, I., Armbruster, W., Olsson, E., & Edwards, M., 2004*a*. Factors limiting the growth of native tree seedlings at the edges of forest fragments in upland Madagascar, Ph.D. thesis, NTNU.

Pareliussen, I., Olsson, E., & Armbruster, W., 2004*b*. Factors limiting the survival of native tree seedlings used in a experimental reforestation effort at the edges of forest fragments in upland Madagascar, Ph.D. thesis, NTNU.

Pareliussen, I., Olsson, E., & Wehn, S., 2004*c*. Natural establishment of trees in the grasslands between forest fragments in upland Madagascar, Ph.D. thesis, NTNU.

Posada, J., Aide, T., & Cavelier, J., 2000. Cattle and weedy shrubs as restoration tools of tropical montane rainforests, Restoration Ecology 8:370–379.

Radimbison, A., 1990. Les différents types de lisière de la forêt d'Ambohitantely, Thèse de Doctorat 3ème cycle de Sciences Biologiques Appliquées. Etablissement d'Enseignement Supérieur des Sciences. Université d'Antananarivo.

Rajaonah, H., 2000. Consummation de bois plus de 100000 tonnes par an dans les grandes villes, Midi Madagasikara (19/mai/2000) .

Rakotondravony, D., & Goodman, S., 2000. Les effects de la fragmentation forestiére et l'isolement sur les communautés des mammifères (lipotyphla) dans le haut plateau central de Madagascar, in Monographie de la forêt d'Ambohitantely, Goodman, J. R. S., editor, pages 57–69, Cidst, Antananarivo.

Rakotoson, S., 2001. Contribution a L'etude du role d'*Eulemur fulvus fulvus* dans la dissemination et la regenration des especes forestieres dans la reserve special D'Ambohitantely(Ankazobe), Mémoire de fin d'études. Universitet D'Antananarivo, Ecole superiure des Science & Agronomiques, Departement des Eaux et Forets.

Ratsirarson, J., & Goodman, S., 2000. Monographie de la forêt d'Ambohitantely, volume 16 of *Série Sciences Biologiques*, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.

Ray, G., & Brown, B., 1995. Restoring Caribbean dry forest – Evaluation of tree propagation techniques, Restoration Ecology 3:86–94.

Razakanirina, D., & Andrianjaka, M., 1993. Les résultats des observations phénologiques dans le forêt d'Ambohitantely, Akon'ny Ala 11:19–31.

Réau, B., Tsaboto, J., Razafiarison, S., & Andriantsheno, D., in Press. Stratégies territoriales et identitaires des acreurs locaux et plan de gestion des ressources naturelles à Madagascar: l'example de la réserve forestère spéciale d'Ambohitantely (Province de l'Imerina), Series A, volume 7, (A)cta Geographica, Trondheim, Department of Geography, NTNU, Trondheim.

Roederer, P., 1972. Les sols de Madagascar, in Biogeography and Ecology in Madagascar, Battistini, R., & Richard-Vindard, G., editors, pages 201–226, Dr.W.Junk B.V., The Hague.

Ross, S., 1993. Organic matter in tropical soils: current conditions, concerns and prospects for conservation., Progress in Physical Geography 17:265–305.

Samyn, J., 1999. Plantes utilies des hautes terres de Madagascar, intercooperation, Antananarivo.

Sanford, R., Saldarringa, J., Clark, K., Uhl, C., & Herrera, R., 1985. Amazon rain-forest fires, Science 227:53–55.

Saunders, D., Hobbs, R., & Margules, C., 1991. Biological consequences of ecosystem fragmentation - a review, Conservation Biology 5:18–32.

Siqueira, J., Carneiro, M., Curi, N., Rosado, S., & Davide, A., 1998. Mycorrhizal colonization and mycotrophic growth of native woody species as related to successional groups in southeastern Brazil, Forest Ecology and Management 107:241–252.

Sizer, N., & Plouvier, D., 2000. Increased investment and trade by transnational logging companies in Africa, the Caribbean and the Pacific, Joint report of the World Wide fund for Nature-Belgium, World Resources Institute and WWF-international.

Skoglund, J., 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems, Journal of Vegetation Science 3:357–360.

Suding, K., Gross, K., & Houseman, G., 2004. Alternative states and positive feedbacks in restoration ecology, Trends in Ecology and Evolution 19:46–53.

Sun, D., & Dickinson, G., 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.

Swaine, M., & Hall, J., 1983. Early succession on cleared forest land in Ghana, Journal of Ecology 71:601–627.

Swaine, M., & Whitmore, T., 1988. On the definition of ecological species groups in tropical rain forests, Vegetatio 75:81–86.

Tallmon, D., Jules, E., Radke, N., & Mills, L., 2003. Of mice and men and *Trillium*: cascading effects of forest fragmentation, Ecological Applications 13:1193–1203.

Teholy, M., 2002. Gestion des ressources forestières, L'Express Madagascar (3/Oct/2002) .

Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia, Journal of Ecology 75:377–407.

Uhl, C., 1988. Restoration of degraded lands in the Amazon basin., chapter 37, pages 326–332, National Academy of Sciences and Smithsonian Institute, Washington, D.C.

Uhl, C., 1998. Perspectives on wild fire in the humid tropics, Conservation Biology 12:942–943.

Uhl, C., Buschbacher, R., & Serrão, E., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession, Journal of Ecology 76:663–681.

Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar, Biological Conservation 96:31–43.

Wehn, S., Olsson, G., & Pareliussen, I., 2004. Natural recovery of trees after fire in the edges of forest fragments in Ambohitantely forest, upland Madagascar., Ph.D. thesis, NTNU.

White, F., 1983. The Vegetation of Africa, Unesco, Paris.

Wijdeven, S., & Kuzee, M., 2000. Seed availability as a limiting factor in forest recovery in Costa Rica, Ecological Restoration 8:414–424.

Wittenberg, R., & Cock, M., 2001. Alien species: A toolkit of best prevention and management practices, CAB international, Wallingford, Oxon, UK.

Zahawi, R., & Augspurger, C., 1999. Early succession in abandoned pastures in Ecuador, Biotropica 31:540–552.

Zimmerman, J., Pascarella, J., & Aide, T., 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico, Restoration Ecology 8:350–360.

Paper I

The grassland and the forest in Ambohitantely

Natural establishment of trees in the grasslands between forest fragments in upland Madagascar

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Abstract: The grasslands between forest fragments in Ambohitantely Forest Reserve show little establishment of trees and shrubs. Even areas that have been free of fire for more than 18 years have almost no establishment of shrub and tree species. To quantify and document the succession rate we studied shrub and tree species and their abundances along grassland-forest transects at 3 sites. Fifteen transects were placed perpendicular to the forest and the abundance of each shrub and tree species, along with the height of each individual, were registered. Changes were recorded after 14 and 30 months in 6 of the transects. All 15 tree and shrub species found in the grassland were native to Madagascar and 8 were endemic. Tree and shrub species in the grassland were different from both the species in mature forest and in the forest edge. Animal-dispersed species dominated the forest while non-animal-dispersed species dominated in the grassland. The most abundant species in the grassland, *Philippia floribunda*, is associated with mountain scrub-land and fire influenced forests. It appears that succession in the grassland ecosystem has been deflected. A change in the disturbance regime of the grasslands may be necessary to establish more trees and shrubs.

Keywords: Forest fragmentation,tropical forest, succession, establishment, growth rate, fire, mountain grasslands, Madagascar

Introduction

The highland forests of Madagascar were once perceived as the remnants of a large forest, that covered the whole island, but was destroyed by humans (Humbert 1927). However, paleo-ecological studies have shown that a mosaic of grasslands and forests was present in the highlands even before human settlement (Burney 1997). The increase of charcoal deposited in lakes 1500-2000 years ago shows an increase in number of fires. The upsurge of fires is thought to have resulted from an increase in agriculture and forest clearing, leading to a more fragmented forest (Burney 1997).

Fire remains an important agro-pastoral tool for farmers in Madagascar today. In the highland it is used to produce green shoots in the grassland as fodder for cattle and to eradicate pests (Kull 2000*a*). Grass fires often spread over larger areas, damaging forest remnants far away from the fire source. To stop the destruction of the highland forests all use of fire has been outlawed in both the grasslands and the forest. The law did not stop all fires; grasslands fires are still a problem in Madagascar (Teholy 2002).

The Ambohitantely Forest Reserve consists of one large forest fragment and several smaller fragments interspersed with grasslands. The grasslands around the reserve burn frequently, and 18 fires were recorded inside the reserve between 1996 and 1999 (Ranarisoa, pers. comm.). These fires burned about 180 ha of grasslands, but some of the fires also invaded the forest. This fragmentation has several serious effects on the plant and animal life in the forest (Langrand 1995; Lundberg 2000; Rakotondravony & Goodman 2000; Vallan 2000). The detrimental effects of fragmentation generally are well known (Saunders et al. 1991; Murica 1995). Due to fire-breaks and other conservation efforts, some grasslands in the Ambohitantely Special Reserve have been free from fire for the last 18 years, but even un these areas, little or no establishment of trees can be observed. The soil in the burnt grasslands has been considered too degraded to allow natural reforestation: “These soils are in fact so degraded that it is doubtful if natural re-afforestation would be possible.” (Koechlin 1972). Some studies have been conducted on forest regeneration dynamics in the Ambohitantely Forest Reserve (Radimbison 1990; Rajoelison 1990; Ratsinjomanana 2000), however, the methods used makes these findings difficult to incorporate in this study.

The aim of this study is to investigate the extent and rate of tree and shrub establishment in the grasslands surrounding the Ambohitantely forest fragments. Further, we wish to relate the species that have been established in the grassland to the species growing in the forest with respect to dispersal modes and species composition.

Study area

The Ambohitantely Forest Reserve is located between 1300 and 1650 m.a.s.l. and contains some of the last highland forests in Madagascar. The Ambohitantely reserve contains approx. 5600 ha of mixed vegetation; about 1700 ha is covered by forest and the remaining area is dominated by grasslands with scattered trees and shrubs (Ratsirarson & Goodman 2000). The forested area compromises 378 fragments of approx. 2 ha to 1250 ha (Hanssen 2002). The forest fragments edges are very distinct, with an abrupt transition from ten meter tall trees to bracken (*Pteridium aquilinum*) and grassland vegetation. The grasslands of Ambohitantely are dominated by few grasses (*Trachypogon spicatus, Loudetia simplex* and *Aristida similis*), and are a part of the Tampoketsa grassland, described by White (1983). According to White (1983), *Trachypogon spicatus* is associated with gentle slopes and *Aristida similis* with steeper slopes and on degraded soils.

Methods

Selection of sites

Sites 1, 2 and Sites a, b were chosen for the study in Oct. 1998 (Fig. 1), but Sites a and b burned in Nov. 1999, and had to be excluded from the study. A new site, Site 3, was added in Jan. 2000 to replace the two burned sites. The three sites used in this study have not been burnt since 1983.

At each site, five 80-meters-long transects, were located perpendicular to the forest edge, with a distance of 40m between the different transects (Fig. 2). The first transect in each site was located at random, but the four remaining were placed in a predetermined pattern with respect to the first transect. In each of these transects three 4x4m plots were located 0, 40 and 80 meters from the forest (Fig. 2). Shrub and tree species, along with the height of each individual, were recorded in each quadrat. Two transects at each site were chosen to be permanent and all individuals were marked with a unique tag to follow growth and survival of individuals. The transects were recorded in Nov. 1998 (Site 1 and 2), Jan. 2000 (Site 1, 2 and 3) and in May 2001 (Site 1, 2 and 3). Two time periods are used in this study, with the first time period lasting 30 months the second lasting 16 months. The first time period has been used when pooling or comparing Site 1 and 2. The second time period has been used when all three sites are pooled or compared. Data collected May 2001 are used for species abundance.

From a separate study on fire succession (Wehn et al. 2004) the abundance of 40 tree and shrub species was recorded in 10 randomly chosen plots in a transect running along the forest edge at Site 1, 2 and 3 (Fig. 2). In addition the 40 species were recorded in 10 parallel plots in the forest interior. These plots were incorporated in this study and thus the present study comprises records along transects from grasslands at 80, 40, and 0 m from the forest edge, and from the forest at the same site at the forest edge (0-3 m inside the forest) and forest interior (>50 m, Fig. 2). The area examined in the fire succession study is 1200 m^2, compared to 720 m^2 in the grassland.

Species and dispersal modes

Shrub and tree species were identified by staff at ESSA-Forêt at the University of Antananarivo. Information on life form and fruit type are drawn from several sources (Anonymous 1996; Mabberley 1997; Samyn 1999; Schatz 2001; Solemon URL). The data on seed dispersal were based on the description of fruits and seeds in Schatz (2001). Dehiscent fruits with small seeds were determined to be non-animal-dispersed or dispersed by wind or gravity. Examples of this

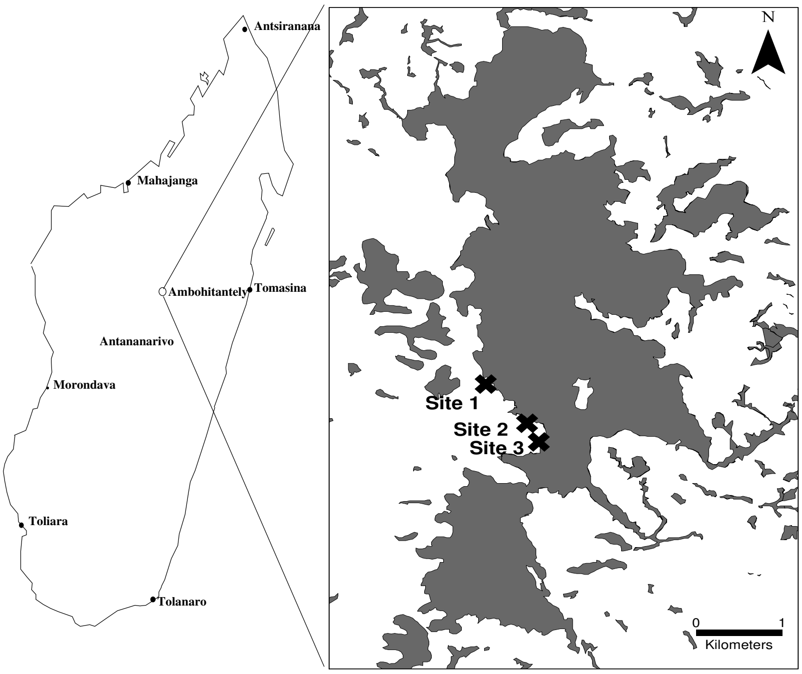

Figure 1: The Ambohitantely forest and the location of the three study sites

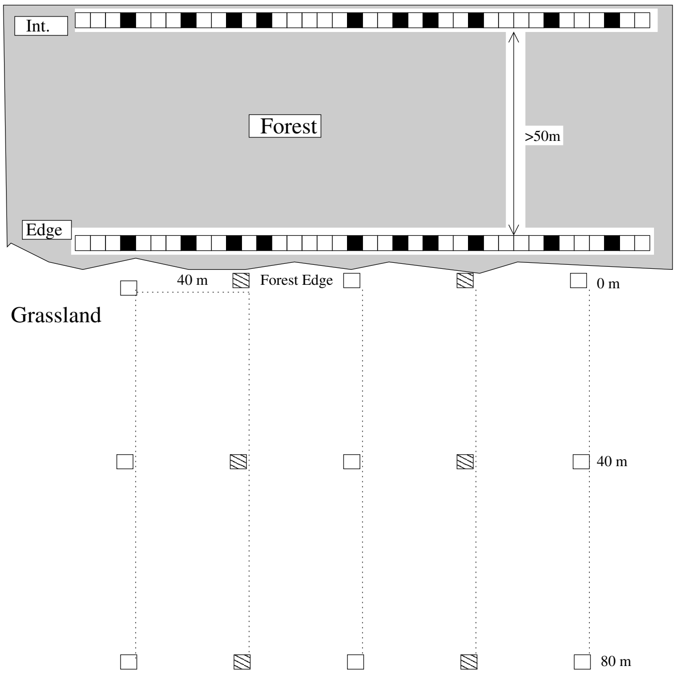

Figure 2: Design and location of the grassland transects in relation to each other and the forest succession plots in the forest. Permanent transects marked with hatched lines. Black squares marks the randomly chosen plots used in the forest succession study.

kind of fruit are capsules, and achenes. Fleshy, indehiscent fruits with larger seeds were determined to be animal-dispersed. Examples includes drupes and berries. There are some species that have dry dehiscent fruits, but have fleshy seed coats or arils for facilitating animal dispersal. *Podocarpus madagascariensis*, a gymnosperm, has a fleshy seed coat, which led us to include the species in the animal-dispersed group. *Leptolaena pauciflora* was also included in the animal-dispersed group as it has a fleshy involucre surrounding the dry capsule. We may have underestimated the animal dispersed group, as dry, dehiscent fruits may also be passively dispersed by animals (Stiles 2000). Animal-dispersed seeds could not be further partitioned by disperser type (bird, lemur or bat) because of insufficient data.

Statistical considerations

The data were analyzed by a GLM ANOVA procedure. A Levenes test was used to check for heterogeneity in the variance between the factors in the ANOVA analysis. The sites were pooled when there was no difference in the effect of sites. To determine if the number of new individuals was equal to the number of dead, henceforth called turnover, all were species pooled, and a paired Wilcox rank sum was used. A paired Wilcox rank sum test was also used to examine the turnover at different distances from the forest. To test turnover it is important to use the longest possible time span, and thus only data from Site 1 and 2 were used. All statistical tests were performed using S-Plus 6.0 for Linux.

Results

Species abundance and composition

The species found in the grassland and in the forest are presented in Table 1. Only six of the 15 species found in the grassland were found in the forest. The most numerous species in the grassland do not correspond with the most numerous species at the forest edge or in the forest interior.

Table 1: The abundance of shrub and tree species and their life form, fruit type and dispersal vector at the 3 study sites. The abundance represents the total number of individuals found in each site regardless of differences in the sampling methods in the grassland and in the forest. See methods for further information.

					Grassland abundance*			Forest edge ab.			Forest interior ab.		
Species	Family		Dispersal	Fruit	Site 1	2	3	Site 1	2	3	Site 1	2	3
Anthocleista sp.	Gentianaceae	tree	Animal	berry			2						
Clerodendrum sp.†	Verbenaceae	shrub	Animal	drupe	6	27	10						
Harungana madagascariensis Lam. ex Poir.	Clusiaceae	tree	Animal	drupe			1	24	9				
Helichrysum bracteiferum (DC.) Humbert †	Asteraceae	shrub	Non-animal	achene	1	33	10						
Macaranga alinifolia Baker	Euphorbiaceae	tree	Non-animal	capsule	10			6	4	4	8	98	2
Fabaceae sp. †	Fabaceae	shrub	?	pod			4						
Nuxia capitata Baker	Buddlejaceae	tree	Non-animal	capsule	4	1		2	1	8		1	5
Philippia cauliflora Hochr.	Ericaceae	shrub	Non-animal	capsule			44						
Philippia floribunda Benth.	Ericaceae	shrub	Non-animal	capsule	74	137	58						
Philippia parkerii Baker	Ericaceae	shrub	Non-animal	capsule	1	25	48						
Psorospermum sp.	Clusiaceae	shrub	Animal	berry			3	184	300	683	3	3	8
Senecio faujasioides Baker†	Asteraceae	shrub	Non-animal	achene	0	1	2						
Vaccinium emirnense Hook.†	Ericaceae	tree	Animal	berry	6	18	26						
Vernonia garnieriana Klatt.	Asteraceae	tree	Non-animal	achene	3	6	40		6	33			2
Weinmannia rutenbergii Engl.	Cunoniaceae	tree	Non-animal	capsule	8	26	13	13	15	12			2
Carissa obovata Markgr.	Apocynaceae	shrub	Animal	berry				2		1	6	22	26
Croton oreades Leandri	Euphorbiaceae	tree	Non-animal	capsule				2		2		8	
Dichaetanthera sp.	Melastomataceae	tree	Non-animal	capsule				1		1			
Dodonaea mad. Radlk.	Sapindaceae	tree	Non-animal	capsule				23	16	13			
Dracaena spp.	Convallariaceae	tree	Animal	berry				1		1	57	9	26
Filicium decipience Thw.	Sapindaceae	tree	Animal	berry				1		4			
Kaliphora mad. Hook.	Kaliphoraceae	tree	Animal	drupe					8				
Leptolaena pauciflora Thouars.	Sarcolaenaceae	tree	Animal	capsule††						1			
Macaranga sp. (acutifolia)	Euphorbiaceae	tree	Non-animal	capsule				123	42	34			
Olea lancea Lam.	Oleaceae	tree	Animal	drupe				1		2	83	126	85
Podocarpus mad. Baker	Podocarpaceae	tree	Animal	seed coat				1		2			
Ravenea mad. Becc.	Arecaceae	tree	Animal	drupe				1	3		5	2	4
Rhus taratana H.Perrier	Anacardiaceae	tree	Animal	drupe				16	1	6		2	1
Rhus thouarsii H.Perrier	Anacardiaceae	tree	Animal	drupe				30	9	3	4		1
Uapaca densifolia Baker	Euphorbiaceae	tree	Animal	drupe					60	1		1	2
Vepris pilosa I.Verd.	Rutaceae	tree	Animal	drupe				21	26	16	17	54	33
Dilobeia thouarsii Roem. & Schult.	Protaceae	tree	Animal	drupe							3	1	
Dypsis oropedionis Beentje	Arecaceae	tree	Animal	drupe									2
Erythroxylum sphaeranthum H.Perrier	Erythroxylaceae	tree	Animal	drupe							643	1359	522
Pandanus sp. (madagascariensis)	Pandaceae	shrub	Animal	drupe								16	18
Pandanus vandamii Martelli & Pic. Serm.	Pandanacea	tree	Animal	drupe							5	8	

*All distances pooled.†Not recorded in the forest. ††Capsule surrounded by a fleshy involucre.

All sites had a fringe of bracken (*Pteridium aquilinum*) at the outer forest edge. The grass height was significantly different among the sites (Df 2, F=6.6, p=0.003). Site 1 had the lowest grass height and Site 3 had the highest. No significant difference was found between the sites for grass cover, litter depth or litter cover, or for bracken height or cover.

A total of 15 species of trees and shrubs were found in the grassland at the forest edge; at 40 meters from the forest edge, seven species were found; and at 80 meters from the forest only five species were found. All tree and shrub species found in the grassland are native to Madagascar, and eight are endemic to the island: *Helichrysum bracteiferum., Nuxia capitata, Philippia cauliflora, Philippia parkerii, Senecio faujasioides, Vaccinium emirnense, Vernonia garnieriana* and *Weinmannia rutenbergii*. Five species were found only at one site, one species was found at two sites and nine species were found at all three sites. Seven of the species were only found at the forest edge. *Philippia cauliflora* was only found 40 m from the forest in the grassland.

Philippia floribunda was the most abundant species in the grassland at all sites (Table 1). *Philippia floribunda* was not found in the forest and there are no significant differences in its abundance among the different distances from the forest (Fig. 3). Nine of the 15 species found in the grassland were only found close to the forest edge. Six species grew inside the forest as well as in the grassland (Fig. 3).

There are no significant effects from distance on the number individuals that were established in the grassland (Df 43, F-value=3.56, p=0.066).

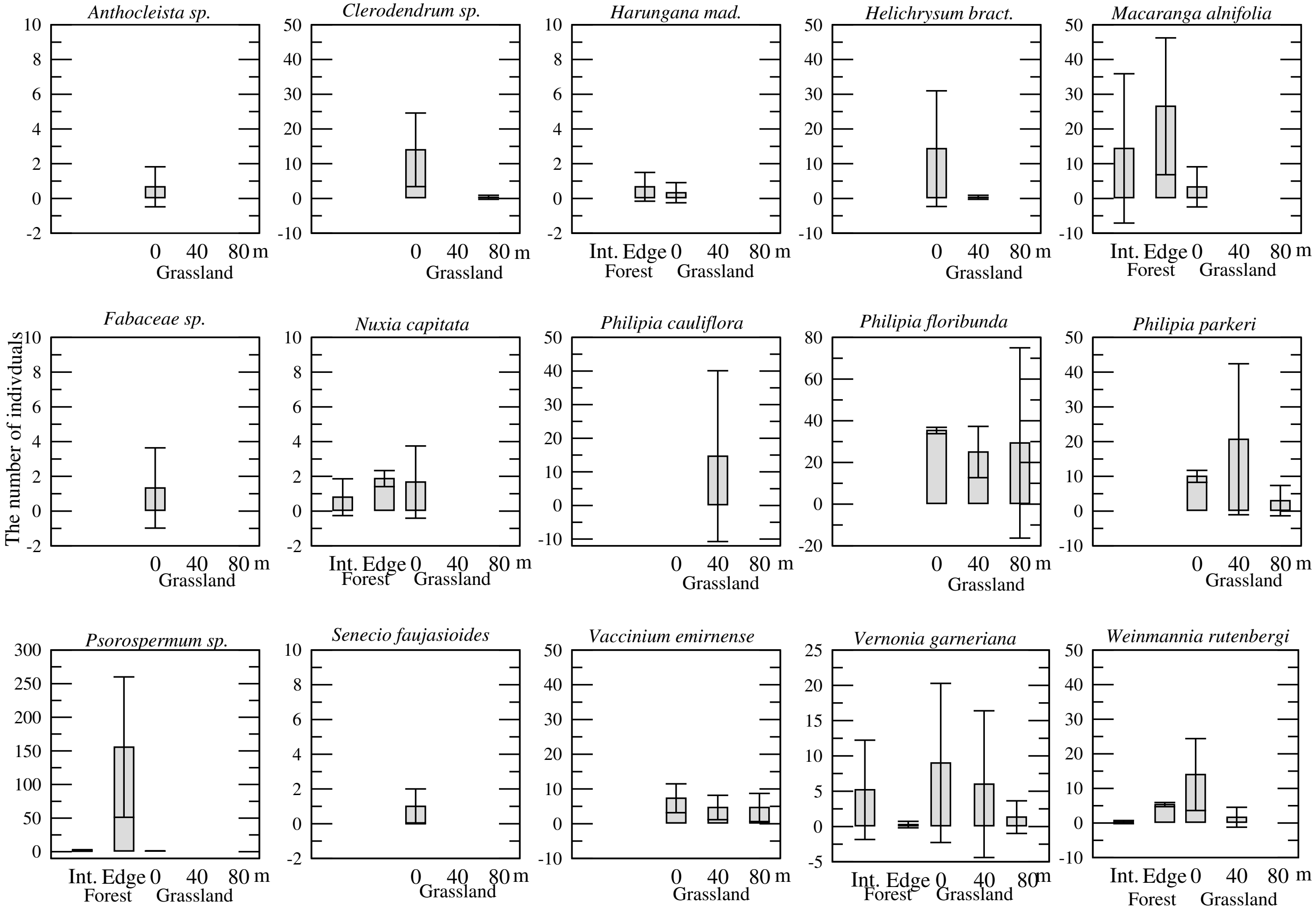

Figure 3: The number of individuals, all sites pooled, of each species found at different distances in the grassland and in the forest. Standard deviations are given for each bar.

Comparing the grassland with the forest

We found few shrub and tree species in the grassland, only 15 species in the 720 m^2 studied. The total numbers of individuals were also low, with only 693 individuals in 720 m^2. The density of trees and shrubs was thus only 0.9 individuals per m^2. In comparison, the density of the 40 species examined in the forest was 4.45 individuals per m^2 at the forest edge and 8.45 individuals per m^2 50 m in the forest interior. However, if the 2524 seedlings of *Erythroxylum sphaeranthum* are removed from the analysis, the number of individuals in the forest interior was only 1.27 per m^2.

In the grassland four species (29%) were animal dispersed, while 10 species (71%) were not. At the forest edge, 14 species (64%) were animal dispersed, while eight species (36%) were not. Fifty meters inside the forest, 15 species (75%) were animal dispersed, while five species (25%) were not.

Six species were found both in the forest and in the grassland (Fig. 3). *Psorospermum sp.* and *Harungana* are animal-dispersed (Table 1), but the four other species are not. *Psorospermum sp.* had a very large number of individuals in the forest edge, but was poorly established in the grassland (Fig. 3). *Philippia floribunda, Philippia parkerii, Vaccinium emirnense* and *Vernonia garnieriana* were represented at all distances in the grasslands, and *Vernonia garnieriana* also grew at both distances inside the forest (Fig. 3).

Turnover

There were significantly more shrubs and trees established in the grassland than died in the grassland in the 30 months that the study ran (Z=2.633, p=0.0085), suggesting that the abundance of shrubs and trees is slowly increasing (Table 2). 63% of the new establishments were *Philippia floribunda.* There were too few individuals of each species to examine differences in turnover between the species. The data from Site 3 is presented in Table 3, but there were too few individuals to perform statistical tests on the data.

At Site 1 and 2 there were significantly more new individuals established than died at 40 meters from the forest (Z=2.329, p=0.0198). 95% of the new establishment was composed of *Philippia floribunda* found at site 2. At 0 and 80 meters there was no significant turnover.

Growth

The average growth rate for all 115 individuals at Sites 1 and 2 was 13.1±8.9mm per month. Species growth rates varied from -2,9±11.2mm (*Fabaceae sp.*) to 16.2±9.2mm per month (*Helichrysum bracteiferum*) (Tables 4 and 5). At Sites 1 and 2, *Philippia floribunda* was the only species with enough individuals to test for differences in growth response at different distances from the forest. There was no significant difference in growth of *Philippia floribunda* at the different distances from the forest (Table 4). At Site 3, even *Philippia floribunda* was insufficiently represented to allow a statistical test for forest distance effects (Table 5).

Distance from the forest	0			40			80		
	new	alive	dead	new	alive	dead	new	alive	dead
Clerodendrum sp.	29	52	19						
Philippia floribunda	3	86	11	40	5		70	21	9
Helichrysum bracteiferum	17	77	6						
Macaranga alinifolia	84	8	8						
Vaccinium emirnense	33	64		33	67		50	50	
Vernonia garnieriana		100						100	

Table 2: The percentage of new, alive and dead individuals for Sites 1 and 2 over the 30 month period.

Distance from the forest	0			40			80		
	new	alive	dead	new	alive	dead	new	alive	dead
Clerodendrum sp.		90	10						
Philippia floribunda	9	64	27			100	67		33
Harungana mad.		100							
Fabaceae sp.		75	25						
Senecio faujasioides	20		80						
Vaccinium emirnense				50	50				
Vernonia garnieriana		83	17		100				

Table 3: The percentage of new, alive and dead individuals for all sites over the 16 month period at Site 3.

Distance from the forest	0			40			80		
	mean	SD	N	mean	SD	N	mean	SD	N
Clerodendrum sp.	4.4	8.8	21						
Philippia floribunda	15.2	10.8	37	13.6	5.9	45	15.9	5.6	33
Helichrysum bracteiferum	16.2	9.8	29						
Macaranga alinifolia	3.0	2.5	11						
Vaccinium emirnense	5.0	1.7	3	4.9	5.4	3	5.0	4.2	2
Vernonia garnieriana	7.9	9.1	5				7.8	1.2	2

Table 4: Site 1 and site 2. The monthly growth rate is shown in mm, over 30 months and at three distances from the forest.

Distance from the forest	0			40			80		
	mean	SD	N	mean	SD	N	mean	SD	N
Clerodendrum sp.	2.0	6.5	10						
Philippia floribunda	9.1	14.5	11	0	-	1	39.1	4.9	3
Harungana mad.	6.9	-	1						
Fabaceae sp.	-2.9	11.2	4						
Senecio faujasioides	52.5	-	1						
Vaccinium emirnense				12.5	15.9	2			
Vernonia garnieriana	9.9	11.7	6	5.6	3.2	3			

Table 5: Site3. The monthly growth rate is shown in mm, over 16 months and at three distances from the forest.

Discussion

The grassland has few shrub and tree species, with relatively few individuals in each species. A third of the species were found only at one site. Half of the species were only found at the forest edge. Non-animal-dispersed species tend to dominate in the grassland compared to inside the forest, suggesting that animal-dispersal is difficult in the grassland. This observation is also strengthened by the fact that *Psorospermum sp.*, an animal dispersed species, had only 3 individuals recorded in the grassland, compared to 1167 individuals recorded inside the forest edge. A number of other studies show that seed dispersal is a bottleneck in the reforestation of grasslands (Gorchov et al. 1993; Zahawi & Augspurger 1999; Holl 1999).

A subset of the true species diversity in the forest was examined, with a study inside the forest including only 40 species (Wehn et al. 2004). To give an example of the tree diversity in Ambohitantely, one study of trees with dbh larger than 10 cm in a 1 ha plot in the largest remaining forest fragment identified 104 tree species (Birkinshaw et al. 2000). If we had included all the existing species in the forest at our study site, the difference between the grassland and the forest would been even more pronounced.

This study shows that the density of tree and shrubs in the grassland is lower than at the forest edge which in turn is lower than in the forest interior. Other studies show comparable results; however, the great variability in results suggests that other factors, such as land use history, soil, and seed sources influences the establishment rate in grasslands. Two savannas in Gabon were studied (King et al. 1997); one savanna burned every year and the other burned every 3-5 years. After protection from fire for 3 years the most frequently burnt savanna had only 0.25 trees per m^2 near the forest edge. The less frequently burnt savanna had an average of 1.25 trees m^2 near forest edge (King et al. 1997). In eastern Amazonas a study (Uhl et al. 1988) was done on the number of trees in abandoned pastures with different utilization histories (pasture, weed control, burn rate etc) . The number of trees established varied greatly between sites with low, moderate and high use intensity. The highest number of trees was found in moderately used pasture, abandoned 4 years before the study, with 4.78 trees per square meter. Intensively used pasture, abandoned eight years before the study, had the lowest number of trees, with only 0.05 trees per square meter (Uhl et al. 1988).

Our study showed greater establishment of shrubs and trees in the grassland than individuals deaths in the 30 month period. The species *Philippia floribunda* made for most of the newly established individuals. Additionally more individuals established than died at Site 2, 40 meters from the forest. However, other sites at different distances showed no significant turnover. The number of individuals of each species was insufficient to detect any shift in the species composition that could indicate a succession.

More shrub and tree species were found closer to the forest than further from it; however, no significant effect of distance was revealed in the number of individuals that were established in the grassland. A study in Kibale National Park, Uganda, found a similar lack of significant effect from forest distance on tree density (Duncan & Duncan 2000).

The length of time it will take for the grasslands of the Ambohitantely reserve to be reforested cannot be estimated from this study. However, it is possible to compare the advance of succession found in Ambohitantely with forest succession reported in other studies. A study of abandoned slash and burn plots in the Amazonas, Brazil, estimated a 200-year recovery time before the original vegetation was restored (Uhl 1988). In other studies where forest disturbance was more limited, forest recovery was faster: A five-year study in Ghana showed rapid re-growth of species and abundance after forest clearing (Swaine & Hall 1983). A 30-year-long study of succession after a tropical storm in 1932 in Puerto Rico showed recovery after 18 years (Crow 1980). Another study in Puerto Rico (Aide et al. 1995) compared 12 former pastures that had been abandoned for 0 to 60 years, and found few tree and shrub species arrived during the first 10 years. However, species accumulated rapidly during the subsequent 15 years. Most of the forest succession studies show long recovery time for disturbed sites, but most studies show more succession after 18 years since the last disturbance than this study shows.

The most abundant species in the grassland was *Philippia floribunda,* and the second most abundant species was *Philippia parkerii.* These species were observed at forest edges in Ambohitantely, that had been burned repeatedly, but were never found inside the mature forest. These species are well known from the shrub layer in the tapia (*Uapaca bojeri*) forest (Humbert 1927; Koechlin 1972; White 1983). The tapia forests are economically important forest in Madagascar (Gade 1985), dominated by the *Uapaca bojeri,* which are adapted to fires (Kull 2000*a*). The tapia forests are homogenous and species poor (Gade 1985), and are burned frequently by local inhabitants as a part of tapia forest management (Kull 2000*a*). It is unclear from the literature whether *Philippia* species are adapted to fire or not. Some studies report that they are easily killed by fire (Gade 1996), while others reports that it is partially resistant to fires and forms dense thickets in previously burned areas (Schatz 2001). Our observations of the *Philippia* species in Ambohitantely suggest that it is easily killed by fire, but that its seeds germinate freely afterwards (Pareliussen. pers. obs.). Even if the role that *Philippia* species play in forest succession is uncertain, it seem possible that the species relies on a seed-bank as a fire adaption and if the fire frequency is low it may become dominant, at least in the shrub layer. However, it is still unknown if *Philippia* facilitates further forest recovery, when the fire frequency is extremely low.

When an ecosystem has been disturbed for a long time the trajectory for the succession may be altered and the succession becomes deflected (Godwin 1929; Gibson & Brown 1992). This deflected succession can lead to alternative stable states of the ecosystem (Suding et al. 2004), where a return to the original course of succession needs assistance and a change in the disturbance pattern. The low/non congruence in species composition between the grassland and forest after 18 years and the slow establishment of forest shrub and tree species in the grassland, along with the dominance of *Philippia floribunda*, indicates that the grasslands in the Ambohitantely Special Reserve reflect a deflected succession created by repeated disturbance by fire. These ecosystem changes are also illustrated by the differences in the soil properties in the forest and in the grassland (Olsson & Pareliussen manuscript).

Conclusions

The number of tree and shrub species established in the grasslands of the Ambohitantely Forest Reserve that have been fire-free for 18 years is low. The species in the grassland differ from the species found in the areas of fire succession at the forest edges. Non-animal dispersed species dominate in the grassland while animal-dispersed trees dominate in the forest.

The number of established species of trees and shrubs is largest close to the forest. The most common species, *Philippia floribunda,* is a species confined to the grassland, and to fire-influenced tapia forests in Madagascar.

There are reasons to believe that the disturbance regime of frequent fires in the grasslands has deflected succession. Removing the disturbance of fire, however, has not provided the desired result; even after more than 18 years post-fire, the establishment of shrubs and trees remains low. Additional management changes of the grasslands are probably necessary to facilitate establishment of forest trees in the grasslands.

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Literature Cited

Aide, T., Zimmerman, J., Herrera, L., Rosario, M., & Serrano, M., 1995. Forest recovery in abandoned tropical pastures in Puerto Rico, Forest Ecology and Management 77:77–86.

Anonymous, 1996. Inventaire ecologique forestier national. Recueil botanique de 200 espèces forestières, Direction des Eaux et Forêts, Antananarivo, Madagascar.

Birkinshaw, C., Ralimanana, H., Ranaivojaona, R., Randrianaivo, R., & Ravololonanahary, H., 2000. Flore et structure de la foret de la Reserve Speciale d'Ambohitantely, chapter 2, pages 7–23, Cidst, Antananarivo.

Burney, D., 1997. Tropical islands as paleoecological laboratories: Gauging the consequences of human arrival, Human Ecology 25:437–457.

Crow, T., 1980. A rainforest chronicle: A 30-year record of change in structure and composition at El Verde, Puerto Rico, Biotropica 12:42–55.

Duncan, R., & Duncan, V., 2000. Forest succession and distance from forest edge in an afro-tropical grassland, Biotropica 32:33–41.

Gade, D., 1985. Savanna woodland, fire, protein and silk in highland Madagascar, Journal of Ethnobiology 5:109–122.

Gade, D., 1996. Deforestation and its effects in highland Madagascar, Mountain Research and Development 16:101–116.

Gibson, C., & Brown, V., 1992. Grazing and vegetation change: deflected or modified succession?, Journal of Applied Ecology 29:120–131.

Godwin, H., 1929. The sub-climax and deflected succession, Journal of Ecology 17:144–147.

Gorchov, D., Cornejo, F., Ascorra, C., & Jaramillo, M., 1993. The role of seed dispersal in the natural regeneration of rain-forest after strip-cutting in the Peruvian Amazon, Vegetatio 108:339–349.

Hanssen, S., 2002. The Ambohitantely Special Reserve in Central High Land Madagascar - Forest change and forest occurrence, Masters thesis: Norwegian University of Science and Technology, Trondheim, Norway.

Holl, K., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate and soil, Biotropica 31:229–242.

Humbert, H., 1927. La destruction d'une flore insulaire par le feu. Principaux aspects de la végétation à Madagascar, Mémoire Acadademie Malgache 5:1–78.

King, J., Moutsinga, J., & Doufoulon, G., 1997. Conversion of anthropogenic savanna to production forest through fire-protection of the forest-savanna edge in Gabon, central Africa, Forest Ecology and Management 94:233–247.

Koechlin, J., 1972. Flora and vegetation of Madagascar, in Biogeography and ecology in Madagascar, Battistini, R., & Richard-Vindard, G., editors, pages 145–190, Dr.W.Junk B.V., Den Hague.

Kull, C., 2000*a*. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar, Environment and History 6:423–450.

Langrand, O., 1995. The effects of forest fragmentation on bird species in Madagascar: a case study from Ambohitantely Forest Reserve on the central high plateau, Masters thesis: University of Natal, South Africa.

Lundberg, M., 2000. Effects of fragmentation on forest regeneration in central highland Madagascar, Masters thesis, Norwegian University of Science and Technology,, Trondheim, Norway.

Mabberley, D., 1997. The plant book, Cambridge University Press, Cambridge, UK.

Murica, C., 1995. Edge effects in fragmented forests – implications for conservation, Trends in Ecology and Evolution 10:58–62.

Olsson, E., & Pareliussen, I., manuscript. Soil property changes along tropical forest-grassland gradients in Ambohitantely Forest Reserve, central highlands of Madagascar, Unpublished manuscript.

Radimbison, A., 1990. Les différents types de lisière de la forêt d'Ambohitantely, Thèse de Doctorat 3ème cycle de Sciences Biologiques Appliquées. Etablissement d'Enseignement Supérieur des Sciences. Université d'Antananarivo.

Rajoelison, L., 1990. Analyse sylvicole d'une foret naturelle des Hauts-plateaux Malagaches, Mémoire de Fin d'études ESSA: Département des Eaux et Forêts. Université d'Antananarivo, Madagascar.

Rakotondravony, D., & Goodman, S., 2000. Les effects de la fragmentation forestiére et l'isolement sur les communautés des mammifères (lipotyphla) dans le haut plateau central de Madagascar, in Monographie de la forêt d'Ambohitantely, Goodman, J. R. S., editor, pages 57–69, Cidst, Antananarivo.

Ratsinjomanana, K., 2000. Etude de la dynamique d'une foret naturelle des hautes-plateaux a travers la regenerastion Naturelle., Mémoire de Fin d'études ESSA: Département des Eaux et Forêts. Université d'Antananarivo, Madagascar.

Ratsirarson, J., & Goodman, S., 2000. Monographie de la forêt d'Ambohitantely, volume 16 of *Série Sciences Biologiques*, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.

Samyn, J., 1999. Plantes utilies des hautes terres de Madagascar, intercooperation, Antananarivo.

Saunders, D., Hobbs, R., & Margules, C., 1991. Biological consequences of ecosystem fragmentation - a review, Conservation Biology 5:18–32.

Schatz, G., 2001. Generic tree flora of Madagascar, Royal Botanical Gardens, Kew & Missouri Botanical Garden.

Solemon, J., URL. W3tropicos: online herbarium/nomenclature database for Missouri botanical garden., http://mobot.mobot.org/W3T/Search/vast.html .

Stiles, E., 2000. Animals as seed dispersers, in Seeds, the ecology of regeneration in plant communities, Fenner, M., editor, pages 111–124, CABI publishing, New York, USA.

Suding, K., Gross, K., & Houseman, G., 2004. Alternative states and positive feedbacks in restoration ecology, Trends in Ecology and Evolution 19:46–53.

Swaine, M., & Hall, J., 1983. Early succession on cleared forest land in Ghana, Journal of Ecology 71:601–627.

Teholy, M., 2002. Gestion des ressources forestières, L'Express Madagascar (3/Oct/2002) .

Uhl, C., 1988. Restoration of degraded lands in the Amazon basin., chapter 37, pages 326–332, National Academy of Sciences and Smithsonian Institute, Washington, D.C.

Uhl, C., Buschbacher, R., & Serrão, E., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession, Journal of Ecology 76:663–681.

Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar, Biological Conservation 96:31–43.

Wehn, S., Olsson, G., & Pareliussen, I., 2004. Natural recovery of trees after fire in the edges of forest fragments in Ambohitantely forest, upland Madagascar., Ph.D. thesis, NTNU.

White, F., 1983. The Vegetation of Africa, Unesco, Paris.

Zahawi, R., & Augspurger, C., 1999. Early succession in abandoned pastures in Ecuador, Biotropica 31:540–552.

Paper II

The experimental plots for planting seedlings, at Site 3

Factors limiting the survival of native tree seedlings used in experimental reforestation at the edges of forest fragments in upland Madagascar

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Abstract: *We performed experimental reforestation of fire-damaged tropical forest fragments in upland Madagascar. This paper reports a study of factors limiting survival of native trees in the grasslands surrounding forest fragments. We conducted a full-factorial experiment on the survival of transplanted seedlings of five local tree species in grassland plots adjacent to the forest fragments in Ambohitantely Forest Reserve. The species were* Dodonaea madagascariensis*,* Filicium decipiens*,* Olea lancea*,* Podocarpus madagascariensis *and* Rhus taratana*. The factors examined were: distance from the forest, application of forest soil, application of chemical fertilizers, experimental shading of plots, and shrub cover. Distance from the forest had a significant negative effect. Mixing soil from the forest had no effect. Fertilization had a surprisingly strong negative effect on survival. This might be partly explained by competition from naturally establishing shrubs adapted to exploit high nitrogen levels. Shading reduced the survival of Dodonaea madagascariensis, and had no positive effects on survival for any species. We conclude that the results from this study can be used for reforestation projects with the aim of extending small forest fragments.*

Keywords: Tropical forest, forest fragments, grassland, tree seedling survival, fire, reforestation, native species, Madagascar

Introduction

As is true for many forests around the globe (Holl 2002), the forests of Madagascar have experienced serious reduction. In 1950 the east coast of Madagascar had 7.6 million ha of rainforest;

by 1985 only 3.8 million ha remained. In only 35 years, half the rainforest on the east coast had disappeared (Sussman et al. 1994). The highlands of Madagascar, however, are dominated by grasslands, with some small pockets of native forest. This has been the case for at least the last 110 years (Landmark 1889). The expanse of the highland forest before human arrival is unknown, but most researchers agree that it was greater in former times (Sussman et al. 1994; Jarosz 1996; Kull 2000*a*). Why extensive forest disappeared is uncertain, but charcoal in cave sediments indicates burning; most probably by the early human settlers (Burney et al. 1997). Today there are strict laws prohibiting vegetation burning, but grassland fires continue (Teholy 2002). Most damage to upland forest is caused by wildfire traveling over the grassland and entering the forest fragments. Grass fires are part of a local pastoral management scheme, providing green grass for the cattle. Some authors mention other reasons, such as hiding evidence of cattle theft, political protests, and accidents (Kull 2000*b*). In this light it is understandable that conservation efforts in Madagascar have been targeted towards preservation the remaining forest rather than restoration. Considering the fire frequency causing damages in forest fragments and the decreasing numbers of fragments in the uplands, it is obvious that restoration of fire damaged forests is important as one conservation measure of the unique forest biodiversity. Madagascar has an unique flora and fauna as most animal and plant species are endemic. For example, 96% of the 4220 species of trees and large shrubs of Madagascar are endemic (Schatz 2001). Facilitating the natural succession processes by planting native tree species could be a conservation measure.

In the Ambohitantely forest reserve there is no natural establishment of trees in the grassland adjacent to the forest fragments even after 18 years since the last fire (Ratsirarson et al. 2003). Similar observations of difficulties of tree establishment in severely disturbed tropical sites have been made elsewhere; e.g. in a study in Amazonia a comparison was made of the establishment of trees in forest gaps, forest understory and in abandoned pastures over a two year period. The largest number of establishments occurred in the forest gaps (up to 17 individuals m^{-2}) and lowest in the abandoned pastures (0.3 individuals m^{-2}). This was explained by a lack of seed dispersal and greater seed predation in the pastures (Nepstad et al. 1996).

This paper presents the results of experimental reforestation along forest fragments borders in the highland of Madagascar. We address the survival of tree seedlings during the first 15 months after planting one year old seedlings, raised in a nursery, in the grassland. We also explore the effects of five experimental treatments on the survival of these seedlings.

Methods

Study area

The Ambohitantely reserve is located in the central highland of Madagascar at the altitude of 1300 to 1650 m.a.s.l., and consists of 5600 ha of which 1700 ha is forest and the remaining area is dominated by grassland with scattered trees and shrubs (Ratsirarson & Goodman 2000). The forested

Table 1: Major ecological features of the study sites.

	site 1	*site 2*	*site 3*
Topography	Hill slope	Hill slope	Hill top
Slope	15%	10%	0%
Aspect	270°	135°	Flat
Mean grass height	48 cm	52 cm	48 cm
Mean litter depth	35 cm	39 cm	37 cm
Soil depth above hardpan	15 cm	15 cm	10 cm

area comprises 378 fragments ranging from approx. 2 to approx. 1250 ha in size (Hanssen 2002). Studies in biodiversity show that species richness is lower in the smaller fragments than in the larger fragments (Langrand 1995, birds) (Vallan 2000, amphibians)(Lundberg 2000, plants).

The Ambohitantely forest was set aside in 1982 as a botanical reserve to be exempt from exploitation and protected from fire (Ratsirarson & Goodman 2000). In 1988, it was decided that the Ecole Supérieure de Sciences Agronomiques, Département des Eaux et Forêts, Université d'Antananarivo (ESSA-Forêts) would be allowed to use the forest reserve as a research area. In 1990, the control and management of the forest reserve was given to the governmental organization for protected areas, ANGAP (Agence National pour le Gestion des Aires Protégées) (Ratsirarson & Goodman 2000). In 1998, the Department of Botany at Norwegian University of Science and Technology (NTNU) along with ESSA-Forêts started a joint research project on several aspects of forest fragmentation in Ambohitantely (Ratsirarson et al. 2003).

The grassland around the reserve burns frequently, and 18 fires were reported inside the reserve between 1996 and 1999 (Ranarisoa, pers comm.). These fires burned about 180 ha of grassland, and some encroached the forest fragments. However, some parts of the reserve have been protected from fire for more than 18 years.

Selection of sites

Three grassland sites along the forest-grassland boundary of the largest forest fragment were selected for the experiment (Fig. 1). Ecological characteristics for each site are presented in Table 1. The five most common grass species and their respective cover at the three experiment sites are presented in Table 2. All sites have good fire protection today and the last time the sites burned was prior to 1983 (Radimbison 1990, Ranarisoa, pers. comm.).

Selection of tree species

The tree species chosen for this experiment were common species found in the Ambohitantely forest reserve. The local ESSA-Forêt staff were familiar with the species and the germination requirements were known (Table 3). Most seeds were collected from forest fragments close to the reserve, but some were also collected inside the reserve. *Olea* and *Podocarpus* seeds were

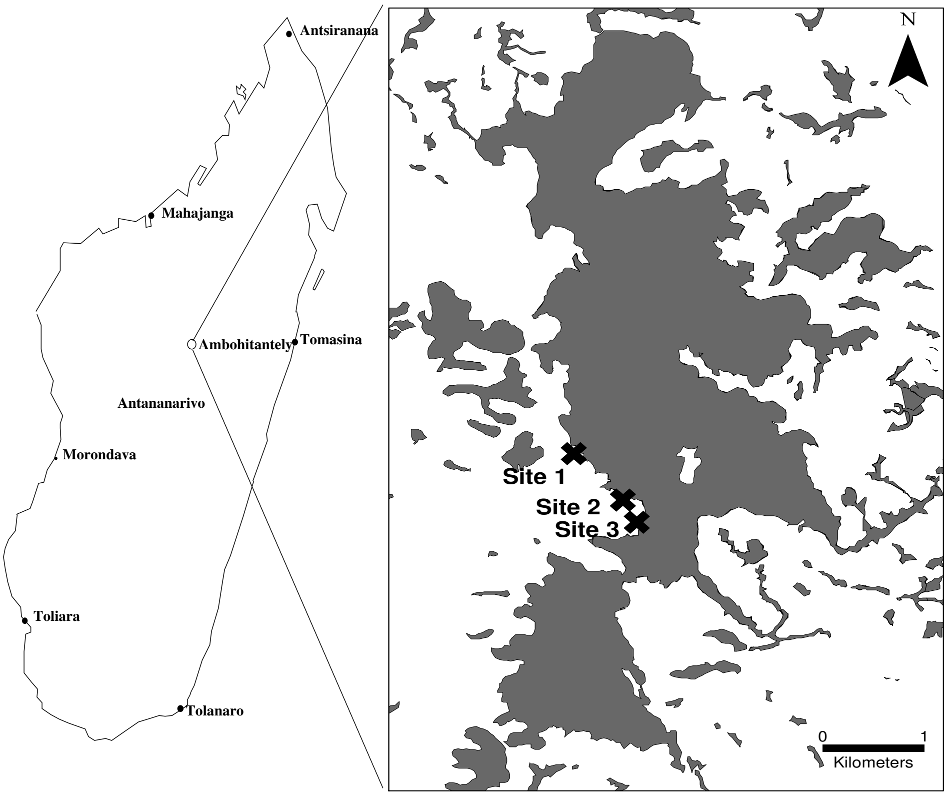

Figure 1: Map of Madagascar, and the Ambohitantely forest reserve (shaded), showing the location of the three study sites.

Table 2: Geographic distribution and abundance of the five most common grasses found at the study sites.

Species	Geographical distribution	Cover (in %) *site 1*	*2*	*3*
Trachypogon spicatus Kuntze.	Pantropic	70	70	35
Loudetia simplex Hubb.	Africa	20	25	55
Aristida similis Steud.	Madagascar	10	0	10
Panicum glanduliferum Schum.	Madagascar	0	5	0
Hyparrhenia rufa Stapf.	Africa	0	5	0

Table 3: The tree species used in the study and their germination success.

Species (Family)	Germination
Dodonaea madagascariensis Radlk. (Sapindaceae)	25%
Filicium decipiens Thw. (Sapindaceae)	25%
Olea lancea Lam. (Oleaceae)	70%
Podocarpus madagascariensis Baker (Podocarpaceae)	60%
Rhus taratana H.Perrier (Anacardiaceae)	30%

Table 4: The experimental treatments and their execution.

Treatment	Execution
Distance from the forest	Plots placed at 10 or 50 m from the forest.
Soil from the forest	Mixed 3 l soil, collected at least 15m inside the forest, in each plot.
Soil from the forest	Applied 20 gr per plot of NPK. (20N+4.3P+16.3K)
Shading	Applied 1 sq.m of reed shade screen on 1 m. tall bamboo rods.

collected on the ground, the seeds for the other species were collected still attached to the tree. The germination time was between 1 and 8 months, and germination success varied between 25 and 70 % (Table 3). The seedlings were raised in the plant nursery at the ESSA-Forêt field station at Ambohitantely by Mr J.J. Rasolofonirina .

Execution of experiments

The number of experimental factors to be manipulated was limited by the supply of seedlings of each species. Thus the experimental treatments were chosen based on careful ecological consideration. The experimental treatments used in this experiments are presented in Table 3.

The layout of the experiment is presented in Figure 2. The experiments were started in February 2000 and ended fifteen months later in May 2001. This is a short time to study survival of trees, but the most precarious time for a tree seedling appears to be the first dry season. One experiment in Costa Rica found that 15-70% of the seedlings planted in an abandoned pasture died during the first dry season (Gerhardt 1993). The seedlings size were recorded at the beginning and at the end of the experiment. Forty-eight experimental plots (50-by-50 cm) were stripped of vegetation, and the soil was worked to a depth of 60 cm. In addition, the vegetation on all sides was removed out to at least 25 cm from the experimental plots, making a clearing of at least 1 m^2. A grid was placed inside each plot. The seedlings were then randomly assigned a place inside the grid. The random assignment inside the grid ensured that any remaining interaction was randomly distributed among the plots. After fifteen months we measured the cover of the naturally established herbs, grass and shrubs, along with the cover of the planted seedlings in the experimental plots. Among the measured vegetation variables the cover of natural establishing shrubs was the only factor that had a detectable effect on the planted seedlings and was therefore included in the statistical models. We use the term natural establishing shrubs only as a distinction from the experimental planted seedlings.

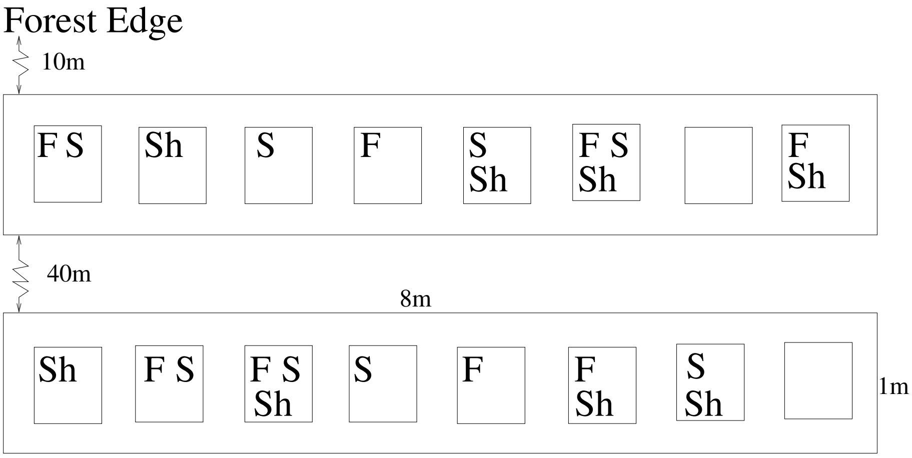

Figure 2: The experimental layout at each site. The letters signify the treatment. F= Fertilized, S = Soil from the forest and Sh = Shaded. Treatments were randomly assigned, and thus varied between the sites. Two individuals of each species were planted in each plot.

Statistical analysis

The statistical analyses were performed with SPlus 6.1 on Linux. All factors were fixed orthogonally, except for the factor site. Site was found to interact with the other treatments in a mixed model ANOVA, therefore the data from each site were analyzed separately. The influence each treatment had on survival was tested using a logistic regression with chi-square test (Venables & Ripley 1999). When doing repeated measurements, the likelihood of random error increases, in this case a significance level 0.01 is comparable to the group-wise significance level of 0.05 (Sokal & Rohlf 1998, Dunn-Šidák method: $\alpha' = 1-(1-\alpha)^{1/k}$; k= independent significance test = 5, α=group-wise significance =0.05, α'=adjusted experiment-wise significance$\approx$ 0.01). Abbreviation used in the text and figures: df is the degrees of freedom for a factor, dev is the deviation removed by adding the factor to the model, R.dev is the residual deviation, not explained by the model and R.df is the residual degrees of freedom. The relation between the fertilizer and shrub cover and the survival was examined in an path analysis based on a Spearman correlation matrix, adjusted for the indirect effects of fertilizer.

Results

The effect of site

The survival for the different species and sites is presented in table 5. The survival differed significantly among the three sites when all species were pooled (Table 5). At sites 1 and 2 there were interaction between species and the experimental treatments, and the data from each species were analyzed separately. At site 3, however, there were no interactions between the experimental treatments and species (Table 6), and this allowed the examination of the experimental treatments on all species pooled.

Table 5: The percentage of seedlings that survived the first 15 months after planting in the grassland.

Species	*site 1*	*site 2*	*site 3*	all sites
Olea	47%	47%	59%	51%
Dodonaea	78%	75%	16%	40%
Filicium	53%	38%	19%	41%
Rhus	66%	44%	19%	42%
Podocarpus	63%	41%	16%	40%
All species	61%*	49%*	26%*	46%

*df:2, dev:39.04, R.df: 445, R.dev:579.43, p-value=3e^{-9}

Table 6: The survival at site 3, all species (df=Degrees of freedom, dev=deviation, R.df=Residual Degrees of freedom, R.dev=Residual deviation). Treatments added sequentially.

	df	dev	R.df	R.dev	p-value
Species	4	21.2	139	145.0	0.0003
Distance	1	6.3	138	138.8	0.0123
Fertilizer	1	9.0	137	129.7	0.0026

Seedling survival differed significantly among the species at site 3 (Tables 5 & 6). *Olea* had the highest survival and *Dodonaea* and *Podocarpus* had the lowest. Distance from the forest significantly lowered the survival of all species from 35%, at 10m from the forest, to 18%, at 50m from the forest, at site 3. Fertilization significantly lowered the survival from 36% to 17% fertilized (Table 6).

The effect of the experimental treatments

Shading significantly lowered the survival of *Dodonae*a from 93%to 63% at site 1 (df: 1, dev: 4.96, R.df:28.65, R.dev:30, p-value=0.025).

Fertilization lowered the survival of *Filicium* from 81% to 25% at site 1 (df:1, dev:10.8, R.df:30, R.dev:33.4, p-value=0.001). Fertilizer significantly lowered the survival of *Filicium* from 75% to 0% at site 2 (df:1, dev:12.2, R.df:14, R.dev:8.99, p-value=0.0004). Fertilizer significantly lowered the survival of *Olea* from 81% to 13% at sites 1 and 2 (Table 7). Fertilizer significantly lowered

Table 7: The survival of \emph{Olea lancea} at site 1 and 2 (df=Degrees of freedom, dev=deviation, R.df=Residual Degrees of freedom, R.dev=Residual deviation). Treatments added sequentially.

		df.	dev	R.df.	R.dev	p-value
	Fertilizer	1	16.7	30	27.5	0.00004
	Distance	2	0.24	29	27.6	0.624
	Fert:Distance	1	7.7	28	19.6	0.0056
site 2:	Fertilizer	1	16.7	30	27.5	0.00004

the survival of *Podocarpus* from 75% to 6,25% at site 2 (df:1, dev:17.9, R.df:30, R.dev:25.5, p-value=0.00002). Fertilizer significantly lowered the survival for all species pooled from 36% to 17% at site 3 (df:1, dev:7,13, R.df:142, R.dev:159,0, p-value=0,0075).

Distance from the forest and fertilizer had a significant interaction for *Olea* at site 1. At 10m from the forest the survival was 25% with fertilizer and 63% without fertilizer. At 50 meters from the forest the survival was 0% with fertilizer and 100% without fertilizer (Table 7).

Distance from the forest significantly lowered the survival of *Rhus* from 88% at 10m from the forest to 44% at 50m from the forest at site 1 (df:1, dev:7.19, R.df:30, R.dev:33.98, p-value=0.007). Distance from the forest significantly lowered survival for all species pooled from 35% at 10m from the forest to 18% at 50m from the forest at site 3 (Table 6). There was no significant effect on the survival of seedlings by mixing soil from the forest in the plots.

The effect of the cover of the naturally establishing shrubs

The main naturally establishing shrub in plots with chemical fertilizer was *Helichrysum fulvecens* D.C (Asteraceae), a small shrub that rarely exceeds 50 cm in height. The fertilized plots also contained several slow-growing species of shrubs, but they could not be determined to species due to their small size.

Site 2 had the largest cover of naturally establishing shrubs and site 3 had lowest. Chemical fertilizers increased the shrub cover: Site 2 had a 50% increase in shrub cover when fertilized, Site 1 had a 28% increase, and site 3 had a 9% increase in shrub cover.

At site 1 the shrub cover was 46% less at 50m than at 10 meters from the forest edge. At site 2 the shrub cover was 7% less at 50m than at 10 meters from the forest edge. At site 3 distance from forest had no effect on the shrub cover.

The response of the cover of naturally establishing shrubs to the interaction between distance from the forest and fertilizer varied among sites. Fertilization increased the shrub cover both at 10m and 50m from the forest at sites 1 and 2. Fertilization significantly lowered the shrub cover at 50 meters from the forest at site 3.

At sites 1 and 2, shading had a positive effect on the cover of naturally establishing shrub and fertilizers reduced the effect of shading. Site 3 had a larger cover of naturally establishing shrubs when fertilized; shading gave a positive effect when the plots were fertilized, but had no effect without fertilization.

One explanation for the reduced survival of seedlings with fertilization is that fertilizer may increase the shrub cover, and the shrubs in turn compete with the planted seedlings thus lowering their survival. In order to examine such an indirect effect we used path analysis based on Spearman correlations. The path analysis allowed us to show both the direct and indirect effect of fertilizer (Figs. 3, 4 & 5). Sites 1 and 2, fertilizer increased the shrub cover and lowered survival of the seedlings. However, there was still a direct negative effect of fertilizer that could not be explained

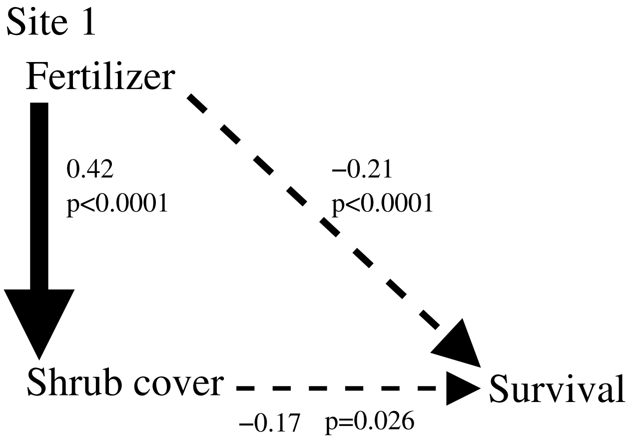

Figure 3: The direct and indirect effect of fertilizer on seedling survival at site 1. Dashed arrows indicate negative effects and solid arrows indicate positive effects. Path coefficient and significance are presented at each arrow

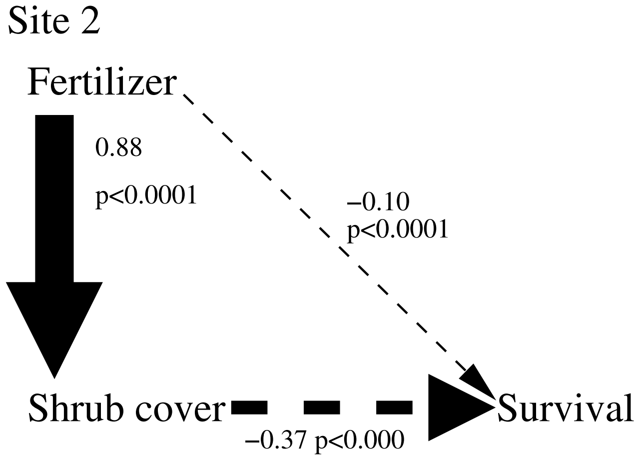

Figure 4: The direct and indirect effect of fertilizer on seedling survival at site 2. Dashed arrows indicate negative effects and solid arrows indicate positive effects. Path coefficient and significance are presented at each arrow.

by the increase in shrub cover (Figs. 3 & 4). At site 3 fertilization increased shrub cover, but no significant effect was found of the increased shrub cover. However, there was apparently still a direct negative effect of fertilizer (Fig. 5).

Discussion

Distance from the forest

An increased distance from the forest lowered survival of all species at site 3, and of *Rhus* at site 1. A possible interpretation is a change of microclimate and/or soil condition further away from the

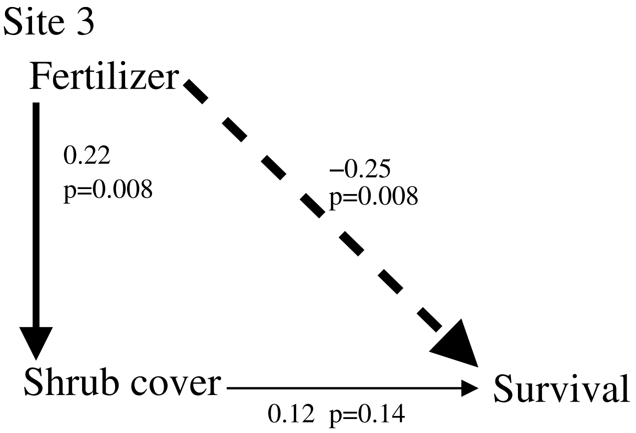

Figure 5: The direct and indirect effect of fertilizer on seedling survival at site 3. Dashed arrows indicate negative effects and solid arrows indicate positive effects. Path coefficient and significance are presented at each arrow.

forest. It is believed that the Ambohitantely forest has been gradually reduced in size by continual burning of the adjacent grasslands (Battistini & Verin 1972). The areas close to the forest would therefore have soil that is more similar to the forest soil than areas further away from the forest. This result suggests that distance from the forest should be considered in reforestation efforts in upland Madagascar and perhaps elsewhere.

Analysis of the grassland and forest soils indicates that the levels of soil organic matter, potassium, sodium, phosphorus, and magnesium were lower in the forest edge than in the interior and were even lower 50 m into the grassland (Olsson et al. unpubl. data). This confirms that soil in the grassland is different from the soil in the forest. This difference in soil nutrients in forest and adjacent grasslands have been confirmed by other studies from Mexico and Costa Rica (Garcia-Oliva et al. 1994; Reiners et al. 1994; Holl 1999). The distance from existing forest must be taken into consideration when planning reforestation of tropical ecosystems, the success rate will be higher close to forest fragments than further away. Reducing fragmentation by straightening forest edges and joining forest fragments close by one another is more likely to yield success than reforestation of large expanses of open areas.

Application of soil from the forest

The reason for the lack of significant effect of mixing soil from the forest in the experimental plots may be technical. The amount of soil might have been too low to detect any effect of soil from the forest, but soil is a limited commodity, and moving a large amount of soil would not be defendable in a large scale conservation effort.

Fertilization

Fertilization lowered survival of *Filicium* and *Olea* at site 1 and 2. Fertilization lowered survival for *Podocarpus* at Site 2. Fertilization lowered survival for all species pooled at site 3. At site 1 and 2 some of the decrease in survival was probably caused by competition from naturally establishing shrubs, which increased with fertilizing. The increase in weedy species, as a result of fertilizing, seen in this study is also documented in other studies. For example, in Costa Rica the weedy herb *Phytolacca rivinoides* dominated forest regeneration after chemical fertilizer was applied, and delayed the establishment of tree seedlings (Harcombe 1977). In future studies weeding out the naturally establishing shrubs would be one way to increase the survival of the seedlings. However, our study shows a direct link between fertilization and lowered survival, and this should be considered in future restoration projects.

Shading

The only measurable effect of shading was the lowered survival of *Dodonaea* at site 1. The lowered survival for *Dodonaea* is probably due to the fact that it is light demanding. *Dodonaea* usually grows at the forest edge and colonizes burnt forest. All the seedling used in the experiment had been acclimatized to high light intensities in the nursery. This may explain the lack of any positive effect of shading on seedling survival. Thus shading is probably not needed in upland Madagascar when the seedlings have been acclimatized to high light intensities in the nursery.

Soil moisture

In other studies researchers have found that soil moisture is significantly lower in open areas than in closed forest and forests gaps (Nepstad et al. 1996; Yohannes 1999; Uhl 1988). Thus, differences in soil moisture may have influenced the survival of seedlings used in this experiment. It was not logistically possible to water our plots, although manipulating this variable would have been desirable and may have resulted in higher survival.

Importance of site

Seedlings at site 1 and 2 had similar survival rates and responded similarly to the treatments. Seedlings at site 3, however, differed with lower survival for most species except *Olea lancea*. It is our experience that hill top sites usually have shallower soil and greater water stress than sites located on slopes or in valleys. In a forest inventory of a one hectare plot in the largest forest fragment in Ambohitantely (Birkinshaw et al. 2000), *Olea lancea* occurred both at hill tops and on the slopes.

Conclusion

The survival of the tree seedlings in this study varied greatly among species and among study sites. However, *Dodonaea madagascariensis* had over 70% survival at two of the sites. *Olea lancea* had reasonably high survival (56%) at site 3 and could probably be used in reforestation on hill tops.

Even with the limited knowledge we have today, it may be possible to implement small scale reforestation projects. Examples might be straightening the configuration of fragment borders to reduce the edge effect, or establishing small patches of forests in the vicinity of existing fragments, thus facilitating migration for dispersal vectors like insects, birds and mammals for pollination and fruit/seed dispersal.

Acknowledgments

This study was undertaken under a collaborative memorandum of agreement between the Forestry Department at ESSA of the University of Antananarivo and the Departments of Botany and Geography of the University of Science and Technology at Trondheim in Norway. We would like to thank our key collaborator at ESSA Dr. J. Ratsirarson. We are grateful to the Tripartite Commission and ANGAP for granting permission to work in the Réserve Spécial d'Ambohitantely. Special thanks are due to Mr. R. Ranarisoa at ANGAP and the "Agent de Conservation et d'Education" (ACE) at ANGAP, as well as Mr. J. J. Rasolofonirina at ESSA field-station in Ambohitantely, for their invaluable help and assistance in the field. We would like to thank the Norwegian masters students Ms. M. Lundberg and Ms. S. Wehn for help and company in the field. Thanks goes to S. Hanssen, who made the map of our study area in Ambohitantely. We are grateful for the valuable comments Dr. Mary Edwards gave on the manuscript. The Norwegian Research Council (NFR) financially supported this project by a grant to Dr. G.A. Olsson (project nr. 12/579/720). This paper was written in LyX.

Literature Cited

Battistini, R., & Verin, P., 1972. Man and the environment in Madagascar, in Biogeography and Ecology of Madagascar, Battistini, R., & Richard-Vindard, G., editors, pages 311–338, Dr. W. Junk B.V., The Hague.

Birkinshaw, C., Ralimanana, H., Ranaivojaona, R., Randrianaivo, R., & Ravololonanahary, H., 2000. Flore et structure de la foret de la Reserve Speciale d'Ambohitantely, chapter 2, pages 7–23, Cidst, Antananarivo.

Burney, D., James, H., Grady, F., Rafamantanantsoa, J., Ramilisonina, Wright, H., & Cowart, J., 1997. Environmental change, extinction and human activity: evidence from caves in NW Madagascar, Journal of Biogeography 24:755–767.

Garcia-Oliva, F., Casar, I., Morales, P., & Maass, J., 1994. Forest-to-pasture conversion influences on soil organic-carbon dynamics in a tropical deciduous forest, Oecologia 99:392–396.

Gerhardt, K., 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica, Journal of Vegetation Science 4:95–102.

Hanssen, S., 2002. The Ambohitantely Special Reserve in Central High Land Madagascar - Forest change and forest occurrence, Masters thesis: Norwegian University of Science and Technology, Trondheim, Norway.

Harcombe, P., 1977. The influence of fertilization on some aspects of succession in a humid tropical forest, Ecology 58:1375–1383.

Holl, K., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate and soil, Biotropica 31:229–242.

Holl, K., 2002. Tropical moist forest, in Handbook of Ecological Restoration, Restoration in Practice, Perrow, M., & Davy, A., editors, volume 2, chapter 23, pages 539–558, Cambridge University press, Cambridge,UK.

Jarosz, L., 1996. Defining deforestation in Madagascar., in Liberation Ecologies: Environment, Development, Social Movements, Peet, R., & Watts, M., editors, pages 144–164, Routledge.

Kull, C., 2000*a*. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar, Environment and History 6:423–450.

Kull, C., 2000*b*. Isle of Fire: the political ecology of grassland and woodland burning in highland Madagascar, Ph.D. Thesis from the University of California, Berkeley.

Landmark, N., 1889. Det Norske missjonsselskab, dets oprindelse og historiske udvikling, dets arbeidsmarker og dets arbeider, Det Norske misjonselskaps Forlag, Kristiania.

Langrand, O., 1995. The effects of forest fragmentation on bird species in Madagascar: a case study from Ambohitantely Forest Reserve on the central high plateau, Masters thesis: University of Natal, South Africa.

Lundberg, M., 2000. Effects of fragmentation on forest regeneration in central highland Madagascar, Masters thesis, Norwegian University of Science and Technology,, Trondheim, Norway.

Nepstad, D., Uhl, C., Pereira, C., & Cardoso da Silva, J., 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia, OIKOS 76:25–39.

Radimbison, A., 1990. Les différents types de lisière de la forêt d'Ambohitantely, Thèse de Doctorat 3ème cycle de Sciences Biologiques Appliquées. Etablissement d'Enseignement Supérieur des Sciences. Université d'Antananarivo.

Ratsirarson, J., Edwards, M. E., Olsson, E. G. A., Armbruster, W. S., Pareliussen, I., Réau, B., & Baudouin, A., 2003. Forest restoration and biodiversity conservation in the central highlands: the case of the Réserve Spéciale d'Ambohitantely, in The Natural History of Madagascar, Goodman, S., & Benstead, J., editors, The University of Chicago Press, Illinois, USA.

Ratsirarson, J., & Goodman, S., 2000. Monographie de la forêt d'Ambohitantely, volume 16 of *Série Sciences Biologiques*, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.

Reiners, W., Bouwman, A., Parsons, W., & Keller, M., 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties, Ecological Applications 4:363–377.

Schatz, G., 2001. Generic tree flora of Madagascar, Royal Botanical Gardens, Kew & Missouri Botanical Garden.

Sokal, R., & Rohlf, F., 1998. Biometry, the principles and practice of statistics in bilogical research, W.H. Freeman and company, New York.

Sussman, R., Green, G., & Sussman, L., 1994. Satellite imagery, human-ecology, anthropology, and deforestation in Madagascar, Human Ecology 22:333–354.

Teholy, M., 2002. Gestion des ressources forestières, L'Express Madagascar (3/Oct/2002) .

Uhl, C., 1988. Restoration of degraded lands in the Amazon basin., chapter 37, pages 326–332, National Academy of Sciences and Smithsonian Institute, Washington, D.C.

Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar, Biological Conservation 96:31–43.

Venables, W., & Ripley, B., 1999. Modern applied statistics with SPlus, Statistics and Computing, Springer Verlag, New York, third edition.

Yohannes, F., 1999. Improvement of water application efficiency by moisture conservation methods for establishment of planted tree seedlings, Communications in soil science and plant analysis 30:1119–1125.

Paper III

Dodonaea madgascariensis in the seedling planting experiment

Factors limiting the growth of native tree seedlings at the edges of forest fragments in upland Madagascar

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Abstract: *In a study of ecologically relevant and sustainable conservation measures for reforestation of fire-damaged tropical forests in upland Madagascar, we investigated selected species for suitability in reforestation efforts, along with the factors that limit or enhance growth of native species in the grassland surrounding forest fragments. We conducted a full-factorial experiment on the growth of transplanted seedlings of five local tree species in grassland plots adjacent to forest fragments in Ambohitantely Forest Reserve. The species were* Dodonaea madagascariensis*,* Filicium decipiens*,* Olea lancea, Podocarpus madagascariensis *and* Rhus taratana. *The factors examined were distance from the forest, application of forest soil, application of chemical fertilizers, experimental shading of plots, and shrub cover. Survival and growth were better on gentle slopes than on hilltops.* Dodonaea madagascariensis *had the greatest height-growth.* Olea lancea *and* Rhus taratana *grew better close to the forest than farther away. It is concluded that tree planting for forest restoration should be focused on the areas close to forest fragments to reduce the edge effect and to build forest corridors between forest fragments.*

Keywords: Forest fragmentation, tropical forest, tree seedlings, growth rate, fire, mountain grasslands, Madagascar

Introduction

Madagascar has one of the highest levels of endemism in the world, yet has very little remaining primary vegetation (Myers et al. 2000). One of the most threatened ecosystems in the island is the forest on the central highlands of Madagascar (Ganzhorn et al. 2001).

The highlands of Madagascar are dominated by species-poor grasslands. Paleo-ecological studies of lake sediments show an increase in grasslands and forest fires from about 1500-2000 year ago (Burney 1997). It is believed that these changes resulted from agricultural activities.

Fire is still an important agro-pastoral tool in Madagascar for modern-day farmers. It is used to produce green shoots in the grassland as fodder for cattle and to eradicate pests (Kull 2000*a*). Fire is also used to remove competing shrubs in the important tapia woodland, which provides food for Madagascar silkworms (Gade 1985; Kull 2000*a*). Grass fires often spread over large areas, damaging forest remnants far away from the fire source. To stop the destruction of highland forests, all use of fire in grasslands and forest, has been outlawed. The law did not stop all fires, however, and fires are still perceived as a large problem in Madagascar (Teholy 2002). The Ambohitantely forest in the Ankazobe district is one of a handful forests found on the highland. It was set aside in 1982 as a botanical reserve to be exempt from exploitation and protected from fire (Ratsirarson & Goodman 2000). The forest is divided into many forest fragments of varying size. Conservation efforts have been reasonably effective in reducing fire frequency in the Ambohitantely Special Forest Reserve. Some areas in the Ambohitantely reserve have been free from fire for the last 18 years. However, even in grasslands that have been fire-free for more than 18 years, little or no establishment of trees can be observed (Pareliussen et al. 2004*c*).

This observation suggests that effective reforestation of the grasslands must be based on active measures. To examine if experimental planting of tree seedlings could be used for reforestation of fire-damaged grasslands, we manipulated 4 factors in a full-factorial experiment to determine if these factors affected seedling growth in the first 15 months after transplantation. Growth was measured in height and in the number of new leaves per month. The pattern of seedling survival in the study is presented in a separate paper (Pareliussen et al. 2004*b*).

Methods

Study area

The Ambohitantely reserve is located in the central highlands of Madagascar at an altitude of 1300 to 1650 m a.s.l. It covers 5600 ha, of which 1700 ha is forested. The remaining area is dominated by grassland with scattered trees and shrubs (Ratsirarson & Goodman 2000). The forested area comprises 378 fragments ranging from roughly 2 to 1250 ha in size (Hanssen 2002). Biodiversity studies from Ambohitantely show that species richness for birds (Langrand 1995), amphibians (Vallan 2000) mammals (Rakotondravony & Goodman 2000) and plants (Lundberg 2000) is lower in smaller fragments than in larger fragments.

The grassland around the reserve burns frequently, and 18 fires were reported inside the reserve between 1996 and 1999 (Ranarisoa, pers comm.). These fires burned about 180 ha of grassland, but some of the fires encroached on the forest fragments.

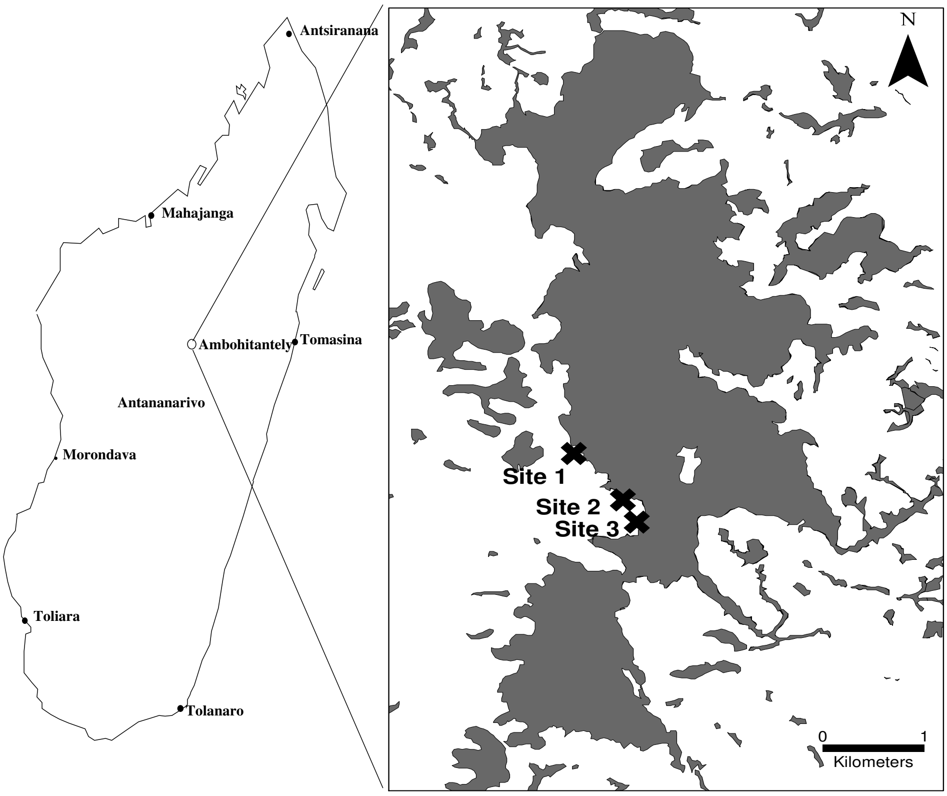

Figure 1: Map of Madagascar, and the Ambohitantely Forest Reserve (shaded), showing the location of the three study sites.

Site selection

Three grassland sites along the forest-grassland boundary of the largest forest fragment were selected for the experiment (Fig.1). Ecological characteristics for each site are presented in Table 1. The five most common grass species and their cover, measured in a 10 m^2 plot, at each of the three experiment sites are presented in Table 2. All sites are well protected from fire today, with the last fires prior to 1983 (Radimbison 1990, Ranarisoa, pers. comm.).

Table 1: Major ecological features of the study sites.

	Site 1	*Site 2*	*Site 3*
Topography	Hill slope	Hill slope	Hill top
Slope	15%	10%	0%
Aspect	270°	135°	Flat
Mean grass height	48 cm	52 cm	48 cm
Mean litter depth	35 cm	39 cm	37 cm
Soil depth above hardpan	15 cm	15 cm	10 cm

Table 2: Abundance of the five most common grasses found at the study sites

	Cover (in %)		
Species	*Site 1*	*2*	*3*
Trachypogon spicatus Kuntze.	70	70	35
Loudetia simplex Hubb.	20	25	55
Aristida similis Steud.	10	0	10
Panicum glanduliferum Schum.	0	5	0
Hyparrhenia rufa Stapf.	0	5	0

Table 3: Experimental treatments and execution

Treatment	Execution
Distance from the forest	Plots placed at 10 or 50 m from the forest.
Soil from the forest	Mixed 3 l soil, collected at least 15m inside the forest, in each plot.
Soil from the forest	Applied 20 gr per plot of NPK. (20N+4.3P+16.3K)
Shading	Applied 1 sq.m of reed shade screen on 1 m. tall bamboo rods.

Tree species used in the experiment

The tree species chosen for this experiment were common species found in the Ambohitantely Forest Reserve. The local ESSA-Forêt staff were familiar with the species and germination requirements were known. The selected species were from different stages of forest succession. The species were *Dodonaea madagascariensis* Radlk. (Sapindaceae), *Filicium decipiens* Thw. (Sapindaceae), *Olea lancea* Lam. (Oleaceae), *Rhus taratana* H.Perrier (Anacardiaceae) and *Podocarpus madagascariensis* Baker (Podocarpaceae). *Dodonaea* is an early colonizer after fire. *Filicium* dominates successions after ten years, and the others are late-successional species (Wehn et al. 2004). Most seeds were collected from forest fragments close to the reserve, but some were also collected inside the reserve. *Olea* and *Podocarpus* seeds were collected on the ground, and seeds for the other species were collected while still attached to the tree. The seedlings were raised in the plant nursery at the ESSA-Forêt Field Station at Ambohitantely. The germination time was between 1 and 8 months, and germination success varied between 25 and 70%.

The experimental factors

The number of experimental factors was limited by the seedling supply, and thus the experimental factors were chosen after careful ecological consideration. The factors manipulated in this experiments are presented in Table 3.

Distance from the forest. It is believed that the Ambohitantely forest has been gradually reduced in size by continuous burning of the adjacent grasslands (Battistini & Verin 1972). The areas close to the forest would therefore have soil that is more similar to the forest soil than areas further away from the forest. In addition the micro-climate would be more similar to the forest close to the forest than further away. We thus decided to study the growth of seedlings at 10 and 50 m from the forest edge.

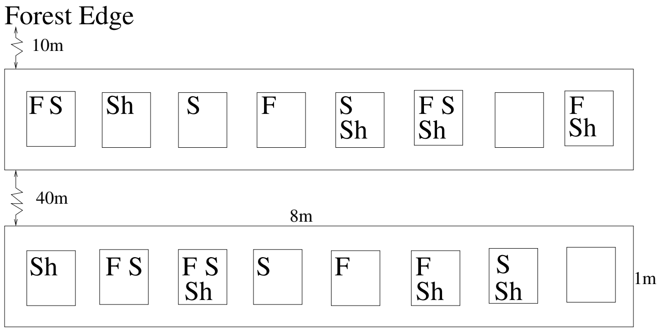

Figure 2: The experimental layout at each site. Letters signify the treatment, with F= fertilized, S = soil from the forest and Sh = shaded. Two individuals of each species were planted in each plot

Soil from the forest. The abundance of soil microbes in the grassland in Ambohitantely is different from the forest soil (Olsson & Pareliussen manuscript). Other studies have shown that mycorrhiza play an important role in the establishment of tropical tree seedlings (Janos 1983). We moved forest soil to the grassland plots to inoculate the grassland soil with forest soil fungi and bacteria.

Chemical fertilizer. As the nutrients levels were generally lower in the grassland than in the forest (Olsson & Pareliussen manuscript), we decided to add chemical fertilizer to study the effect of nutrient levels on seedling growth.

Shading. The humidity and soil-moisture levels are reduced in open areas as compared to closed forest (Williams-Linera et al. 1998; Holl 2002). Shading the seedlings is the easiest way to reduce water stress, by reducing the light intensity and thus reducing soil and air temperature.

Execution of experiments

The experiments were started in February 2000 and ended fifteen months later in May 2001. The layout of the experiment is presented in Fig. 2. In all 480 seedlings were planted. The seedlings were measured at the beginning and at the end of the experiment. Growth was measured as the increase in height and the number of new leaves over the period of the experiment. Forty-eight experimental plots (50-by-50 cm) were stripped of vegetation, and the soil was worked to a depth of 60 cm. In addition, the vegetation on all sides was removed at least 25 cm away from the experimental plots, making a clearing of at least 1 m^2. The seedlings were placed randomly inside a predetermined matrix. After fifteen months it was clear that other plants in addition to the planted seedlings had established in the plots. Therefore we measured the naturally established herb, grass and shrub cover, along with the amount of cover of the planted seedlings in the experimental plots. The shrub cover was the only factor that had a detectable effect on the planted seedlings and was therefore the only vegetation variable included in subsequent statistical models.

Statistical analysis

All factors were orthogonal and fixed, except for the site factor. Site as a factor was found to have interactions with the other factors in a mixed model ANOVA. Therefore the data from each site were partitioned and all the subsequent tests were conducted separately. We used an ANOVA model, with site as the random factor, to estimate the site effect. To test other experimental factors, a two way GLM ANOVA procedure was used. When doing repeated measurements, the likelihood of random error increases, in this case a significance level 0.01 is comparable to the group-wise significance level of 0.05 (Sokal & Rohlf 1998, Dunn-Šidák method: $\alpha' = 1 - (1 - \alpha)^{1/k}$; k= independent significance test = 5, α=group-wise significance =0.05, α'=adjusted experiment-wise significance$\approx$ 0.01). Statistical analyses were performed with SPlus 6.1 on Linux. The species were treated separately, as there was a significant species effect. The height-growth was calculated and transformed as log((final height - initial height/duration of the experiment)+1). The number of new leaves was calculated in the same manner. The effect of experimental factors on seedling growth was tested using a generalized linear model, adjusted for an unbalanced design. The imbalance was caused by the loss of seedlings that died over the course of the experiment. The survival of *Dodonaea* in Site 3 was too low to perform any analysis of treatment effect. *Filicium* showed no significant site effect and thus data from all sites were pooled for all analyses involving growth in height and number of new leaves.

Results

Sites

Rates of growth, as measured by height and the number of new leaves, significantly differed among sites for all species, with the exception of new leaves for *Filicium* and *Podocarpus* (Fig. 3 & 4). Plants at Site 1 had the greatest increase in height and in number of new leaves, and Site 3 the lowest, with the exception that *Olea* had the highest number of new leaves at Site 2 and *Filicium* had the highest growth at Site 2.

Species

Dodonaea had a significantly higher height-growth rate than all other species at Sites 1 and 2, and higher than *Olea, Rhus* and *Podocarpus* at Site 3 (Fig. 3 & Table 4). *Olea* and *Rhus* had significantly higher height-growth rate than *Filicium* and *Podocarpus* at Site 1. *Olea* and *Filicium* had significant higher height-growth rates than *Podocarpus* at Site 2. *Dodonaea* had a significantly higher height-growth rate than *Olea, Rhus* and *Podocarpus*, and *Olea* had significant higher height-growth rate than *Podocarpus* at Site 3.

Dodonaea had a significantly larger number of new leaves than all other species at Sites 1 and 2. *Olea* had significantly larger number of new leaves than *Filicium* and *Podocarpus* at Site 1

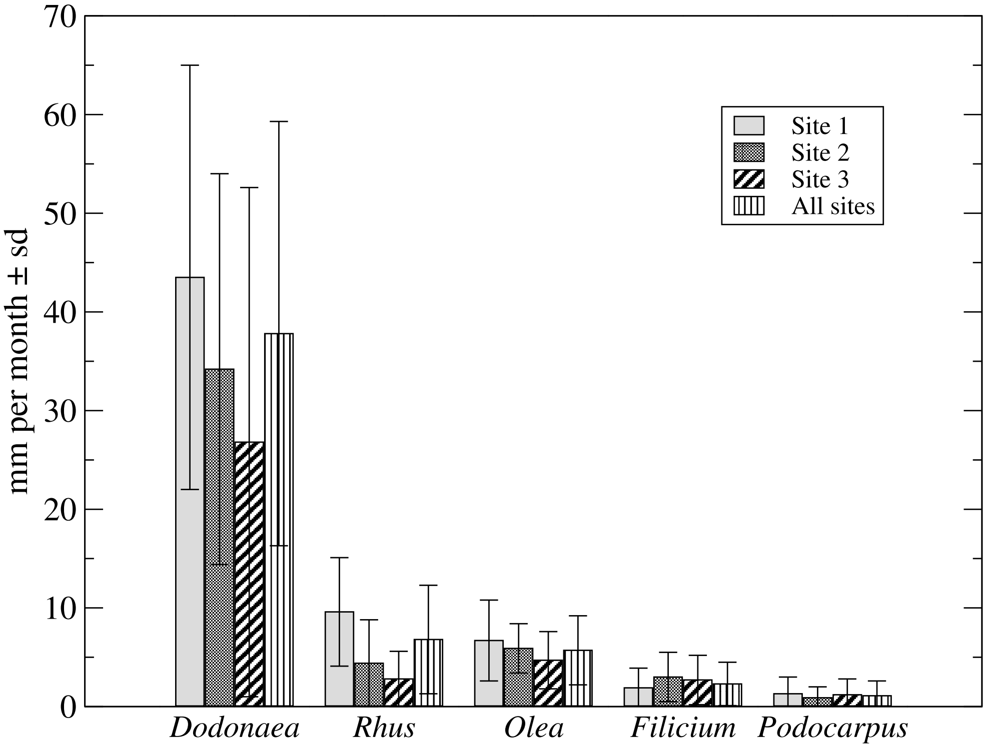

Figure 3: The mean height-growth for all species.

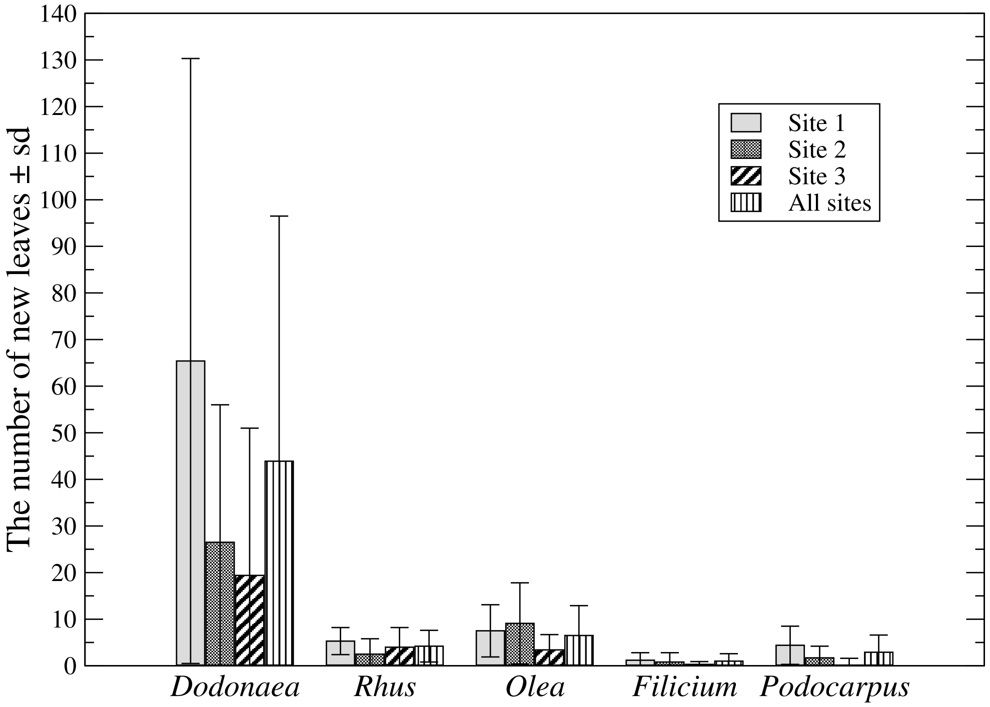

Figure 4: The mean number of new leaves for all species.

Table 4: Statistical analysis of height-growth for the different species. p-value: *<0.001, **<0.01, *<0.05.**

	Species	df	F-value	p-values
Site1	*Dodonaea>Olea*	1/38	60.8	***
	Dodonaea>Filicium	1/40	115.1	***
	Dodonaea>Rhus	1/44	59.1	***
	Dodonaea>Podocarpus	1/43	146.6	***
	Olea>Filicium	1/30	18.1	***
	Olea>Podocarpus	1/33	31.0	***
	Rhus>Filicium	1/36	35.0	***
	Rhus>Podocarpus	1/25	8.7	***
Site 2	*Dodonaea>Olea*	1/28	26.8	***
	Dodonaea>Filicium	1/37	45.4	***
	Dodonaea>Rhus	1/36	50.3	***
	Dodonaea>Podocarpus	1/35	75.3	***
	Filicium>Podocarpus	1/17	6.9	*
	Olea>Podocarpus	1/26	28.1	***
Site 3	*Dodonaea>Olea*	1/22	19.4	***
	Dodonaea>Rhus	1/9	8.7	*
	Dodonaea>Podocarpus	1/8	9.4	*
	Olea>Podocarpus	1/22	7.8	*

(Fig. 4 & Table 5). *Olea* had a significantly larger number of new leaves than *Rhus, Filicium* and *Podocarpus* at Site 2. *Olea* had a larger number of new leaves than *Filicium* and *Podocarpus*, and *Rhus* had larger number of new leaves than *Filicium* and *Podocarpus* at Site 3.

Distance

Distance from the forest edge had a significant effect on the growth rates of *Olea*. *Olea* had a higher height-growth rate 10 m from the forest than 50 m from the forest at Site 1 (df 1/13, F-value 7.27, p=0.018). *Olea* had a significantly larger number of new leaves 10 m from the forest compared to 50 m from the forest at Site 3 (df 1/17, F-value 4.97, p-value=0.039). The interaction between distance from the forest and shading was significant for height-growth in *Olea* at all sites (Table 6).

Forest soil

Shading and soil interacted significantly in affecting the number of new *Filicium* leaves at Site 1 (df 1/13, F-value 7.46 p-value=0.017): The fewest new leaves were found in unshaded plots with forest soil (-0.2±0.18), where there were more leaves lost than gained. There were more new leaves in shaded plots not treated with forest soil (-0.05±0.15). There were even more new leaves

Table 5: Statistical analysis of number of new leaves for the different species . p-value: *<0.001, **<0.01, *<0.05.**

	Species	df	F-value	p-value
Site 1	*Dodonaea>Olea*	1/38	20.7	***
	Dodonaea>Filicium	1/40	47.5	***
	Dodonaea>Rhus	1/44	35.2	***
	Dodonaea>Podocarpus	1/43	46.9	***
	Olea>Filicium	1/33	29.7	***
	Olea>Podocarpus	1/33	12.1	**
Site 2	*Dodonaea>Olea*	1/37	5.9	*
	Dodonaea>Filicium	1/28	13.2	**
	Dodonaea>Rhus	1/36	18.9	***
	Dodonaea>Podocarpus	1/35	24.3	***
	Olea>Filicium	1/19	13.0	**
	Olea>Podocarpus	1/26	12.2	**
	Olea>Rhus	1/27	10.1	**
Site 3	*Olea>Filicium*	1/20	6.75	*
	Olea>Podocarpus	1/22	8.25	**
	Rhus>Filicium	1/7	10.3	*
	Rhus>Podocarpus	1/9	7.6	*

Table 6: Height-growth in mm per month of *Olea lancea* ± st-dev. NA =none available.

	Site 1*		Site 2*		Site 3*	
	Shading		Shading		Shading	
Distance	0	1	0	1	0	1
10 m	0.4±0.25	0.8±0.18	0.6±0.21	0.3±0.18	0.4±0.12	0.3±0.21
50 m	0.2±0.19	0.4±0.10	0.5±0.30	0.3±0.14	0.4±0.22	0.2±0.07

*Significance level for the interactions: Site1: df 1,11, F-value 7.27, p-value=0.021; Site2: df 1,11, F-value 6.26, p-value=0.029; Site3: df 1,15, F-value 5.26, p-value=0.036

in unshaded plots that were not treated with forest soil (0.04±0.13). But the largest number of new leaves was found in shaded plots treated with forest soil (0.05±0.07).

Fertilizer

Dodonaea and *Rhus* were the only species that responded to chemical fertilizers. *Dodonaea* had a significant increase in height-growth (df 1, 22, F-value 18.83, p-value=0.0003) and a significant increase in the number of new leaves (df 1/, 22, F-value 9.54, p-value=0.005) when fertilized at Site 2. *Rhus* had a significantly higher height-growth rate when fertilized at Site 1 (df 1/19, F-value 5.56, p=0.029).

Shading

Distance from the forest and shading interacted significantly to affect height-growth for *Olea* (Table 6).

The naturally establishing shrub cover

Both the number of new leaves and height-growth of *Dodonaea* were positively affected by naturally establishing shrubs in Site 2 (Height: df 1/22, F-value 16.34, p-value=0.0005; Leaves: df 1/22, F-value 6.54, p-value=0.018). However, the partitioning of height-growth into fertilized and un-fertilized plots resulted in the plots with low shrub cover being unfertilized and the plots with high shrub cover being fertilized (Fig. 5a). This makes it impossible to separate the effect of fertilizer from the effect of shrub cover.

Rhus had increased height-growth when associated with greater cover from naturally establishing shrubs at plots near the forest at Site 2. However, at 50 m from the forest there was a small decrease in height-growth rate with greater shrub cover. The interactions between the naturally establishing shrub cover and treatments are shown in Fig. 5.

Discussion

Main findings

Site 1 had plants with the highest growth rate and Site 3 had plants with the lowest growth rate. *Dodonaea* showed the greatest amount of growth as measured both in number of new leaves and height at all sites. *Olea* had the next strongest growth response in both number of leaves and height, with the exception of height-growth at Site 1 and number of new leaves at Site 3, where *Rhus* exceeded it. *Olea* and *Rhus* had higher growth rates closer to the forest than 50 m from the forest.

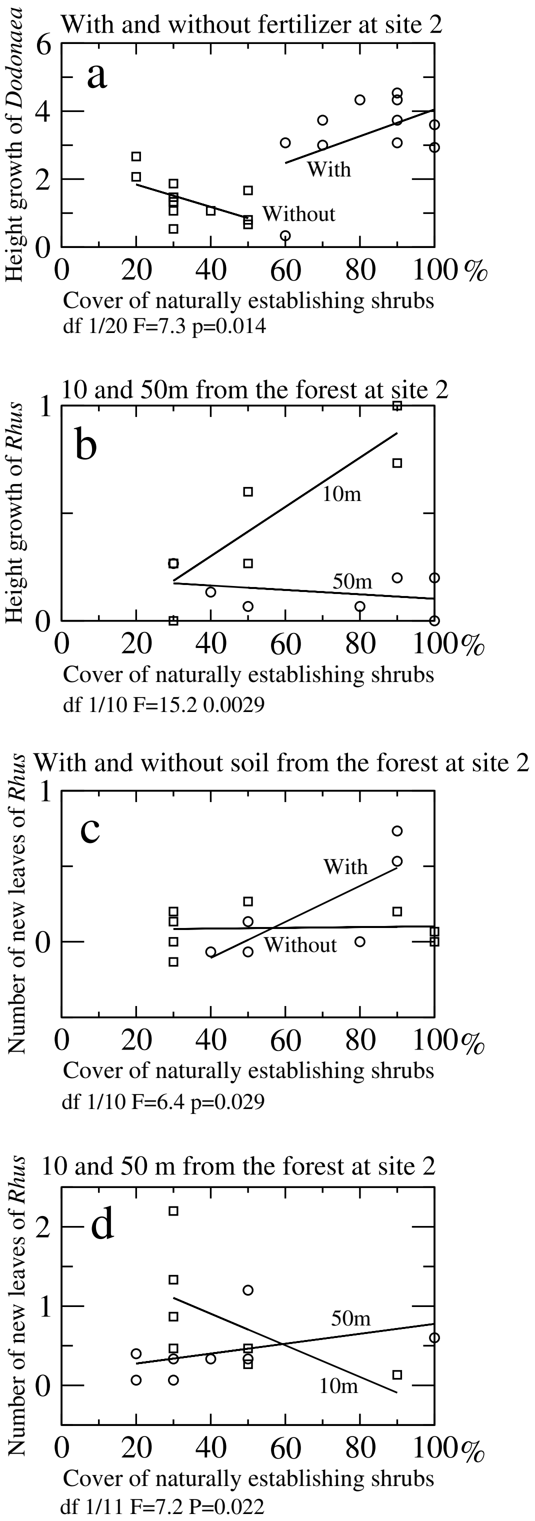

Figure 5: Regressions for naturally established shrubs and height-growth of the planted seedlings, showing treatment interactions. Only significant interactions are shown.

Filicium growing in shaded plots at Site 1 had more new leaves when forest soil was added to the plot. However, *Filicium* had fewer new leaves when forest soil was added to unshaded plots. It seems that increasing the soil nutrients and planting the seedlings close to the forest gave *Dodonaea* and *Rhus* a better opportunity to compete with the naturally establishing shrubs. However, the present data makes it impossible to determine which factor promoted the growth response. It should be noted that experimental shading did not give the same effect as naturally established shrub cover, indicating a complex response.

Comparison of growth and survival patterns

In developing management plans both growth and survival of seedlings must be considered. Some of the most important patterns detected in survival rate from a the previous study (Pareliussen et al. 2004*b*) and the growth in this study were: The survival of *Dodonaea* was high at Sites 1 and 2 (approx 75%), but at Site 3, survival dropped to only 16%. The growth of *Dodonaea* was high in all 3 sites. *Olea* had the highest survival at Site 3 (Pareliussen et al. 2004*b*), the growth for *Olea* in Site 3, however, was lower than *Dodonaea* and *Rhus*. All species had higher survival close by the forest than 50 m from the forest at Site 3, while *Rhus* also showed this pattern at Site 1 (Pareliussen et al. 2004*b*). *Olea* had greater height growth close to the forest than 50 m from the forest. Fertilization led to lower survival overall, both in direct terms, but also indirectly by increasing the amount of cover of naturally establishing shrubs (Pareliussen et al. 2004*b*). Fertilizer did increase the growth for *Dodonaea* and *Rhus*.

The factors

Dodonaea is usually found growing in gaps of newly burned forest, where it grows rapidly to a height of 4 to 8 m (pers. obs.). *Dodonaea* is probably the species that establishes most rapidly, as it is a fast-growing, short-lived tree, and it is a prime candidate to use in a reforestation project. *Rhus* and *Olea* are also fast-growing trees that are more long-lived, and might also be good candidates for planting. *Olea* is a prime candidate for reforestation on hill tops, as it had high survival and the growth was good at Site 3. In a forest inventory of a one-hectare plot in the largest forest fragment in Ambohitantely *Olea* occurred both on hill tops and on slopes (Birkinshaw et al. 2000).

All species had a higher survival rate close to the forest, and *Olea* had a higher growth rate close to the forest. A possible interpretation of this pattern is a difference of microclimate and/or soil properties (nutrients and microbes) further away from the forest. In a study of soils in the grassland, forest edge and forest of Ambohitantely, however, there were only limited differences between the soil characteristics of the grassland soil and the forest edge (Olsson & Pareliussen manuscript). The soil study shows, however, significantly differences between the soils of the grassland and the forest. Studies from Mexico (Garcia-Oliva et al. 1994) and Costa Rica (Reiners et al. 1994; Holl 1999) showed similar differences.

Due to the higher survival for all species close to the forest, the distance from the existing forest must be taken into consideration when planning reforestation of tropical forests. Reducing fragmentation by straightening forest edges and joining forest fragments that are close to one another is more likely to yield success than the reforestation of large expanses of open areas. The significance levels for the effect of distance on survival and growth are above 0.01, and there are a possibility that these findings might be caused by chance. However, even if these finding should be caused by chance the logic of starting reforestation close by existing forest to reduce the effect of fragmentation is still valid.

The lack of significant effect from the application of forest soil might be due to the small amount of soil applied. The grassland soil might also have been too inhospitable for forest fungi and bacteria to live in. Another explanation could be that the seedlings were grown in local, untreated soils at the plant-nursery, and thus already were inoculated with local fungi and bacteria. As forest soil is a finite and valuable resource, our results do not justify the use of forest soil.

The increase in growth when treated with fertilizer is surprisingly low. This may due to the fertilizers itself, which was a slow-release type, which was mixed with the soil in the plot. This may have limited effect of chemical fertilizer below our ability to detect its effect in the limited time of this study. The link between the cover of naturally establishing shrubs and chemical fertilizer implies that fertilizer probably should be used sparingly, if at all. In light of the large negative impact that naturally establishing shrubs have on the survival of the tree seedlings it might be advisable to weed out the naturally establishing shrubs in reforestation projects. It should be noted that even if most studies find weeding to be beneficial for tree establishment (Holl 2002), some studies show a reduction in establishment by weeding (Chapman et al. 2002). Considering the reduced survival and the relatively small increase in growth found in all fertilized seedlings, it is hard to defend the expense of chemical fertilizers.

Our results with respect to the effect of shading were inconclusive. The difference in shading effect between sites could be due to the variability in slope steepness among the sites, which would vary the effectiveness of shading. However, the lack of replication precludes statistical assessment of this hypothesis. The time and monetary cost of shading is not trivial, and based on our limited results, it makes sense not to use shading in reforestation projects involving these species.

The effect of moisture

Other studies have shown that soil moisture is significantly lower in open areas than in closed forest and in forests gaps (Nepstad et al. 1996; Yohannes 1999; Uhl 1988). Thus, a difference in soil moisture may have influenced the survival and growth of seedlings used in this experiment. It was not logistically possible to water our plots, although manipulating this variable would have been desirable. Variation in soil moisture and nutrients may have influenced root-to-shoot allocation. Thus it is possible that our treatments have influenced below-ground growth more than height-growth and number of new leaves. Therefore we may have missed the response to our treatments by not measuring below-ground parts.

Conclusion

This study shows encouraging results for using seedling transplants to promote establishment of trees in the grassland surrounding the Ambohitantely Forest Reserve. *Dodonaea* showed the most growth of all the species we tested. And, as an early successional species, it is probably the best candidate for starting reforestation, especially when the soil is not too poor. *Olea* and *Rhus* are larger tree species that survive and grow well. *Olea* had the highest survival and growth at the hilltop site and is probably the best species to use here.

In this study tree seedlings survived better close to the forest. Fertilizer, however, led to decreased survival but increased growth. Shading and adding forest soil did not produce enough of a positive effect to justify the time and money invested.

Reducing fragmentation by straightening forest edges and joining forest fragments that are close to one another is probably the most practical way to enhance the conservation of the Ambohitantely forest.

Acknowledgments

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Literature Cited

Battistini, R., & Verin, P., 1972. Man and the environment in Madagascar, in Biogeography and Ecology of Madagascar, Battistini, R., & Richard-Vindard, G., editors, pages 311–338, Dr. W. Junk B.V., The Hague.

Birkinshaw, C., Ralimanana, H., Ranaivojaona, R., Randrianaivo, R., & Ravololonanahary, H., 2000. Flore et structure de la foret de la Reserve Speciale d'Ambohitantely, chapter 2, pages 7–23, Cidst, Antananarivo.

Burney, D., 1997. Tropical islands as paleoecological laboratories: Gauging the consequences of human arrival, Human Ecology 25:437–457.

Chapman, C., Chapman, L., Zanne, A., & Burgess, M., 2002. Does weeding promote regeneration of indigenous tree comunity in felled pine plantations in Uganda, Restoration Ecology 10:408–415.

Gade, D., 1985. Savanna woodland, fire, protein and silk in highland Madagascar, Journal of Ethnobiology 5:109–122.

Ganzhorn, J., Lowery II, P., Schatz, G., & Sommer, S., 2001. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out, Oryx 35:346–348.

Garcia-Oliva, F., Casar, I., Morales, P., & Maass, J., 1994. Forest-to-pasture conversion influences on soil organic-carbon dynamics in a tropical deciduous forest, Oecologia 99:392–396.

Hanssen, S., 2002. The Ambohitantely Special Reserve in Central High Land Madagascar - Forest change and forest occurrence, Masters thesis: Norwegian University of Science and Technology, Trondheim, Norway.

Holl, K., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate and soil, Biotropica 31:229–242.

Holl, K., 2002. Tropical moist forest, in Handbook of Ecological Restoration, Restoration in Practice, Perrow, M., & Davy, A., editors, volume 2, chapter 23, pages 539–558, Cambridge University press, Cambridge,UK.

Janos, D., 1983. Tropical mychorrhizas, nutrient cycles and plant growth, in Tropical rain forest: Ecology and management, Sutton, S., Whitmore, T., & Chadwick, A., editors, Blackwell Oxford.

Kull, C., 2000*a*. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar, Environment and History 6:423–450.

Langrand, O., 1995. The effects of forest fragmentation on bird species in Madagascar: a case study from Ambohitantely Forest Reserve on the central high plateau, Masters thesis: University of Natal, South Africa.

Lundberg, M., 2000. Effects of fragmentation on forest regeneration in central highland Madagascar, Masters thesis, Norwegian University of Science and Technology,, Trondheim, Norway.

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G., & Kent, J., 2000. Biodiversity hotspots for conservation priorities, Nature 403:853–858.

Nepstad, D., Uhl, C., Pereira, C., & Cardoso da Silva, J., 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia, OIKOS 76:25–39.

Olsson, E., & Pareliussen, I., manuscript. Soil property changes along tropical forest-grassland gradients in Ambohitantely Forest Reserve, central highlands of Madagascar, Unpublished manuscript.

Pareliussen, I., Olsson, E., & Armbruster, W., 2004*b*. Factors limiting the survival of native tree seedlings used in a experimental reforestation effort at the edges of forest fragments in upland Madagascar, Ph.D. thesis, NTNU.

Pareliussen, I., Olsson, E., & Wehn, S., 2004*c*. Natural establishment of trees in the grasslands between forest fragments in upland Madagascar, Ph.D. thesis, NTNU.

Radimbison, A., 1990. Les différents types de lisière de la forêt d'Ambohitantely, Thèse de Doctorat 3ème cycle de Sciences Biologiques Appliquées. Etablissement d'Enseignement Supérieur des Sciences. Université d'Antananarivo.

Rakotondravony, D., & Goodman, S., 2000. Les effects de la fragmentation forestiére et l'isolement sur les communautés des mammifères (lipotyphla) dans le haut plateau central de Madagascar, in Monographie de la forêt d'Ambohitantely, Goodman, J. R. S., editor, pages 57–69, Cidst, Antananarivo.

Ratsirarson, J., & Goodman, S., 2000. Monographie de la forêt d'Ambohitantely, volume 16 of *Série Sciences Biologiques*, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.

Reiners, W., Bouwman, A., Parsons, W., & Keller, M., 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties, Ecological Applications 4:363–377.

Sokal, R., & Rohlf, F., 1998. Biometry, the principles and practice of statistics in bilogical research, W.H. Freeman and company, New York.

Teholy, M., 2002. Gestion des ressources forestières, L'Express Madagascar (3/Oct/2002) .

Uhl, C., 1988. Restoration of degraded lands in the Amazon basin., chapter 37, pages 326–332, National Academy of Sciences and Smithsonian Institute, Washington, D.C.

Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar, Biological Conservation 96:31–43.

Wehn, S., Olsson, G., & Pareliussen, I., 2004. Natural recovery of trees after fire in the edges of forest fragments in Ambohitantely forest, upland Madagascar., Ph.D. thesis, NTNU.

Williams-Linera, G., Dominguez-Gastelu, V., & Garcia-Zurita, M., 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest, Conservation Biology 12:1091–1102.

Yohannes, F., 1999. Improvement of water application efficiency by moisture conservation methods for establishment of planted tree seedlings, Communications in soil science and plant analysis 30:1119–1125.

Paper IV

Forest edge burnt 2 years ago

Natural recovery of trees after fire in the edges of forest fragments in Ambohitantely forest, upland Madagascar.

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Abstract:*Forest fragments on the high land of Madagascar are under constant threat due to human induced fire. This study examines forest succession after grassland fires that penetrated edges of the natural forest in Ambohitantely Special Reserve. Three fire histories were identified in the study sites: Sites burnt two years ago, ten years ago or more than 18 years ago. Edges with dissimilar fire histories were compared and the burnt edge plots were compared with parallel unburnt interior plots used as controls. The composition and abundance of 40 predetermined species were recorded. The first species to establish after fire were large non-native non-woody plant species. However, in the plots burnt 10 years ago, there was no new establishment of these species, and native tree species dominated. 18 years after a fire the forest consisted of only native species with species diversity indices comparable to the control sites. However, the assemblage of species differed from the control sites. Future forest management of this area must improve prevention of fire events in the forest-edges. The native species that established in the early phases of the fire succession might be suitable for forest restoration in the upland region. In order to maintain the forest the human induced fires encroaching the forest have to come to an end. Therefore there is a need to involve the local rural populations in the management of both the forest and the surrounding grasslands. Further, the forest has to be seen as one component of the local agro-ecosystem where grasslands and rice paddies are other components.*

Keywords: Tropical forest, fire succession, recovery of diversity, fire management

Introduction

Fire

Human induced fire is among the most serious threats to tropical forests (Goldammer 1999; Dawson 2001), but little is known about the succession after fire in tropical forests. This might be due to the earlier interpretation that tropical forests had not been influenced by fire. It was assumed in the 1970s that tropical forests were resistant to fire because the forest under story has high air moisture (relative humidity > 90%) (Hammond & ter Steege 1998; Uhl 1998). When charcoal remains in tropical forest soil where found in different regions of the world in the late 70's and early 80's, it was discovered that forest fires are important in tropical forests, although in low frequencies and usually in relation to other natural disturbances. Studies from the Amazon revealed that forest fires had occurred in correspondence to dramatic weather incidences and the shortest time span between successive fires was 150 years (Sanford et al. 1985; Clark & Uhl 1987; Meggars 1994). In New Zealand volcanic eruptions set the forest on fire, although the fire frequency recorded in one site was approximately 2000 years (Ogden et al. 1998).

Fire has been used by humans as an agricultural management tool for a long time (Gowlett et al. 1981; Gade & Perkins-Belgram 1986; Kauffman et al. 1993; Burney 1997; Cochrane et al. 1999; Kull 2000*a*). Increased human populations in the tropics have increased the forest fire frequency in order to create arable fields and pasture land (Burney 1997; Ogden et al. 1998; Laurance & Williamson 2001). When the fire frequency becomes high enough the forest does not manage to recover between the fires. This can change the vegetation and the forest become fragmented, which leads to greater vulnerability to fire than for larger blocks of forest (Laurance & Williamson 2001). The species composition after a fire will include many herbs, vines, and short lived shrubs (Pinnard et al. 1999). These can provide fuel for future forest fires, and increase the fire intensity (Cochrane et al. 1999; Cochrane & Shulze 1999; Roberts 2001). After extensive fires in Indonesia in 1997, more dead and damaged trees were observed in previously burnt plots compared with previously unburnt plots (Kinnear & C.G.Gray 1999). This increases the amount of ignitable fuel and thus contributes to the inflammability and increases the risk of repeated fires. The high frequency of human induced fires in tropical forests is regarded as one of the major forces of the transformation of forest to grassland (Goldammer 1999).

Forests have been shown to recover from large-scale fires but the recovery time is much longer than after small disturbances. In order to manage and restore disturbed forest, knowledge about the natural recovery process is necessary. Recovery times of abandoned farm plots created by slash and burn in Amazonian forest is at least 200 years (Uhl 1988). Since Amazonian forest has a history of relatively frequent large-scale disturbances, many Amazonian tree species have adapted traits to survive fire, such as resprouting and large soil seed banks (Uhl 1988). In New Zealand however, no such traits have been developed in the native trees which might be an indication of low tolerance to fire (Ogden et al. 1998). There are no previous extensive studies on the fire adaption of the tree flora in Madagascar.

Madagascar

Natural fires occurred in the highlands of Madagascar before human settlement (Burney 1997; Burney et al. 1997), but some 2000 years ago there was an increase in the charcoal deposits in lakes in Madagascar. This is assumed to indicate the start of human inhabitation in Madagascar (Burney 1997; Burney et al. 1997). There were further rises of charcoal deposits in the sediments 1000-500 years ago, which are assumed to be caused by an increase in agricultural areas caused by the growing human population. Fire has been and still is used as an agricultural tool in Madagascar to clear forest, regenerate grassland and keep pests and disease at bay (Kull 2000*a*). In Madagascar the human induced fire frequency is high and it might be too high to allow natural forest regeneration. From Landsat satellite images it has been estimated that the natural forests of Madagascar covered 3,8 million hectares in 1985, and that 1/3 of the original forest had been converted to grassland. The annual deforestation rate was estimated to 111.000 hectares (Green & Sussman 1990).

In the central highlands of Madagascar forest fragments exist in the extensive grasslands. The grasslands are frequently put on fire and the fires often enter the forest fragments. The Ambohitantely Forest Reserve includes a big tract of forest, many forest fragments and grasslands. The aim of the present study is to investigate forest succession after fire in the forest edges of the highland forest of Ambohitantely. More to the point we wish to investigate the influence of the time since the fire on species composition, number of species and diversity in the early phases of forest succession. The succession stages of the studied plots were 2, 10 and 18 years after fire.

Methods

Study area

Ambohitantely Forest is located on the highland of Madagascar, 140 km NW of Antananarivo, at 18°09´S, 47° 16´E. The altitude varies between 1300 and 1650 m a s l. The total area of forest fragments and grassland is 5.600 ha. The cold and dry season is from May to September and the wet and warm season between October and April. Precipitation varies from 387 mm in January to 7,1 mm in June and mean annual precipitation is 1740 mm. The mean temperature varies from 21,5°C in December to 15,9°C in July (Radimbison 1990). The bedrock of the area is of the type magmatic granites (Bastian 1964) and the soil is acid and nutrient poor red laterite except in the valleys, where deep humus layers and yellow ferralitic, hydromorfic soil can be found (Ratsirarson & Goodman 2000). The forest is semi-evergreen (Langrand 1995) and the surrounding grasslands are species poor (Ratsirarson & Goodman 2000) with few grass and herbs species.

In 1951 Ambohitantely Forest and the surrounding areas were protected as part of the 15.000 ha reserve of the Station Forestiére de Manankazo (Bastian 1964). In 1980 5.600 ha of this

Table 1: The burnt forest edge plots and parallel unburnt, forest interior, control plots.

Sites	Years since last fire	Succession stage	Control group
1-3	2	1	1
4-6	10	2	2
7-9	>18	3	3

area was separated and given the status as special reserve. In 1987 ESSA/Forêts (Universite d'Antananarivo, Madagacsar) and DEF (Direction des Eaux et Forêts) established the Reserve as a research site. In 1990 a management agency for all reserves and parks in Madagascar was formed, ANGAP (Association Nationale pour la Gestion des Aires Protégées), which was given the responsibility for management of Ambohitantely Special Reserve (Ratsirarson and Goodman, 2000). In spite of ANGAP's work with establishing fire breaks and patrolling the reserves edges, uncontrolled anthropogenic grassland fires have penetrated some of the forest edges in the reserve. Between 1996 and 1999, 18 fires burned inside the reserve (Ranarisoa pers. comm.). In 1992 the Special Reserve included 77 fragments and the areas of these had shrunk from 1949 by 4,6% (Hanssen 2002).

Field investigations

Selection of study sites was based on the fire history of the forest edges. Nine sites with three fire histories (three parallels in each), were selected in the main forest of Ambohitantely Forest (Fig. 1). The information about the fire history was obtained from interviews and written sources (Rasolofonirina pers. comm., Desiré pers. comm., Ranarisoa pers. comm. Radimbison 1990). The exposition differed among sites since the fire history of sites was given first priority. This confounds the fire history with exposition, but could not be rectified without experimental burning, which is prohibited. In each site two plots were located, one in the burnt edges and one control plot parallel to the edge plot at least 50 m inside the forest (Fig. 1). Care was taken to place the control plot in similar topography to the edge plot. The control plots were assumed to be unburnt and to have no edge effects. We classified the edge plots in three succession stages based on fire history, Succession stage 1: edge plots burnt in 1999, Succession stage 2: edge plots burnt in 1991, Succession stage 3: edge plots burnt in 1981 or earlier. The control plots parallel to the replicates of each succession stage are hereafter called Control 1, 2, and 3 respectively (Table 1). Inside each edge plot, ten quadrates of 20m2 were located randomly. In the control plots, ten quadrates were placed parallel to the quadrates in the edge plot (Fig. 1).

There are several hundred species of trees and large shrubs in Ambohitantely. Within the time available for this study, it was not possible to learn and distinguish all these species. We decided to work with a subset of species and formed a list of 38 common woody species and two common non-woody species (Table 2). The species chosen were easily recognizable even in the seedling state, and predominant in the plots. Two of the selected species are non-woody species (*Phytolacca dodecandra* and *Solanum mauritianum*). They were included since they dominated Succession stage 1.

Table 2: The a priori species list, and their estimated adult diameter at breast height (dbh) (Mr. J. Rasolofonirina, pers. comm)

Family	Species	dbh
Anacardiaceae	*Rhus taratana*	8
Anacardiaceae	*Rhus thouarsii*	10
Apocynaceae	*Carissa obovata*	10
Asteraceae	*Psiadia sp*	10
Asteraceae	*Vernonia garnieriana*	10
Bignoniacaea	*Phyllarthron madagascariensis*	5
Bignoniaceae	*Phyllarthron bojeranum*	10
Cunoniaceae	*Weinmannia rutenbergii*	7-10
Dracaenaceae	*Dracaena spp*	7
Erythroxylacea	*Erythroxylum corymbosum*	7
Erythroxylacea	*Erythroxylum sphaeranthum*	7
Euphorbiaceae	*Croton oreades*	7
Euphorbiaceae	*Macaranga sp*	7
Euphorbiaceae	*Macaranga alnifolia*	8
Euphorbiaceae	*Uapaca densifolia*	8
Guttiferae	*Harungana madagacariensis*	8
Guttiferae	*Psorospermum sp*	3
Kaliphoraceae	*Kaliphora madagascariensis*	4
Loganiaceae	*Buddleja madagascariensis*	1)
Loganiaceae	*Nuxia capitata*	8
Loginaceae	*Antocleista madagscariensis*	10
Loginaceae	*Antocleista sp*	10
Melastomataceae	*Dichaetanthera sp*	8
Oleaceae	*Olea lancea*	10
Palmaceae	*Dypsis decipiens*	10
Palmaceae	*Dypsis oropedionis*	10
Palmaceae	*Ravenea madagascariensis*	10
Pandanaceae	*Pandanus madagascariensis*	6
Pandanaceae	*Pandanus vandamii*	10
Phyttolaccaceae	*Phytolacca dodecandra*	1)
Podocarpaceae	*Podocarpus amohitantelensis*	6
Proteaceae	*Dilobeia sp*	10
Rutaceae	*Vepris macrophylla*	2
Rutaceae	*Vepris pilosa*	2
Sapindaceae	*Dodonea madagascariensis*	4
Sapindaceae	*Filicium decipiens*	10
Sarcolaenaceae	*Leptolaena pauciflora*	7
Sarcolaenaceae	*Sarcolaena multiflora*	10
Solanaceae	*Solanum mauritianum*	1)
Ulmaceae	*Trema orientalis*	4

1) Non-woody plants, counted as adult when observed flowering.

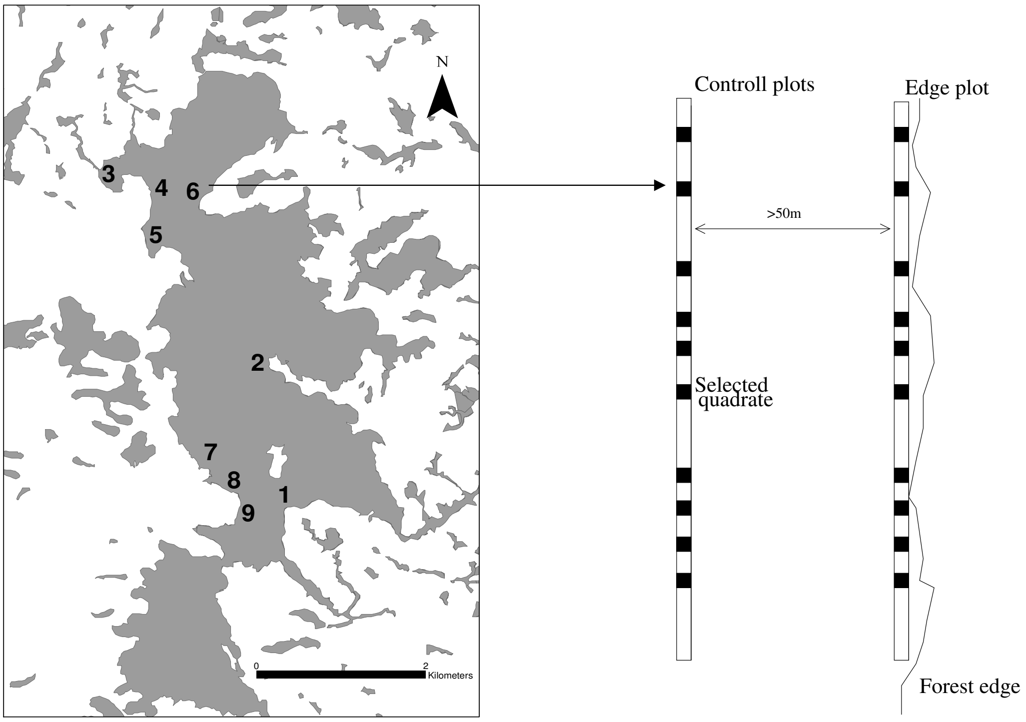

Figure 1: The selected study sites in Ambohitantely Forest. 1-3: edges burnt in 1999, 4-6: edges burnt in 1991, 7-9: edges burnt in 1981 or earlier. The map is from Hanssen (2002).

In each quadrate the number of individuals per species was recorded. Adults within a distance of 10 m around the quadrates were also recorded. The life strategy of the different species make them flower at different ages and at different sizes. We consider individuals higher than 160 cm and exceeding the estimated adult diameter at breast height (dbh) as adults. The estimated adult dbh was obtained from ESSA's site manager of Ambohitantely Forest Field Station, Mr. J.J. Rasolofonirina (Rasolofonirina, pers comm, Table 2). The number of juveniles was of special interest when analysing the re-establishment of tree species. Individuals less than 160 cm of height were defined as juveniles. Exposition and altitude were registered in each site, soil depth was registered in each plot and slope was registered in each quadrate (Table 3).

Statistical analysis

The number of species was defined as the total number of tree species in each quadrate. Shannon's index (base: log 2) was calculated for each quadrate as an estimate of species diversity. It was assumed that the environmental variables were more similar between edges and their parallel control plots than among edges and among control plots, respectively. In order to test the effect of fire, the number of species and diversity of species between the edge replicates and the parallel control replicates were compared with paired t-tests (Underwood 1997; Løvås 1999). Levenes test ($\leq$ 0,05) (Kinnear & C.G.Gray 1999) was used to test for homogeneity of variances. Whether the number of species increased with the time since the fire in the edges was investigated by a

Table 3: Exposition, altitude, soil depth and slope at each site. Slope is graded from 0 (flat) to 6 (steep)

Site	Exposition	Altitude (m a.s.l)	Soil depth, edge (cm)	Soil depth, control (cm)	Slope, edge. (μ+/-SE, n=10)	Slope, contr. (μ+/-SE, n=10)
1	NE	1581	10	19	0,7 +/- 0,21	0,9 +/- 0,23
2	N	1586	21	>30	0,6 +/- 0,16	1,6 +/- 0,34
3	SE	1569	30	17	0,1 +/- 0,01	0,0 +/- 0,00
4	W	1547	20	18	0,0 +/- 0,00	0,7 +/- 0,15
5	W	1547	>30	27	2,0 +/- 0,42	0,5 +/- 0,17
6	E	1551	20	33	0,3 +/- 0,15	0,8 +/- 0,20
7	WS	1550	43	24	0,7 +/- 0,15	0,8 +/- 0,29
8	W	1585	34	23	0,8 +/- 0,25	1,1 +/- 0,23
9	NW	1589	15	20	0,2 +/- 0,13	2,5 +/- 0,17

Pearson correlation test. A Spearman correlation test (Kinnear and Grey, 1999) was used to investigate the same for species diversity. ANOVA analysis (Underwood 1997) on the species number and Kruskal Wallis Chi-Square tests (Løvås 1999) on the species diversity were applied to test if Control 1, 2 and 3 had equal species diversity. Cluster analysis was used to group species into species assemblages. The clustering strategy unweighted-pFair group method (UPGMA) (van Tongeren 1995) was used and the relationship between the species based on Sørensen's binary similarity coefficient (Waite 2000) was calculated. Species re-establishment was investigated, using a Detrended Correspondence Analysis (DCA) (Gauch Jr. 1994; ter Braak 1995) performed on species in the juvenile class in each quadrate. The analysis were performed with SPSS for Windows, version 10.0, MVSP, version 3.13c, and CANOCO for Windows, version 4.0 (ter Braak & Smilauer 1998).

Results

Environmental variables that might affect the variables investigated

As fire history was the most important factor in the selection of the study sites, there are differences in other environmental factors (Table 3). The sites burnt two years ago face east, while the other sites face westwards. Soil depth varied among the sites. The soil in the sites of Succession stage 3 was darker brown and moister compared to the soil in the earlier succession stages. This might indicate a higher content of organic material in the older succession stages. Most quadrates were more or less flat, but the quadrates in Control 3 were more sloped than quadrates in the other controls and succession stages.

Succession after fire

The species dominating Succession stage 1, were *Solanum mauritianum* and *Phytolacca dodecandra* (Table 4). These two species are non-native non-woody plants. In those plots juveniles of

Table 4: The species distribution, grouped in succession- and control classes based on percent of total individuals registered of each species in the different classes.

Species [1]	Succession stage 1	S. stage 2	S. stage 3	Control 1	Ctrl 2	Ctrl 3	Total
Buddleja	**100**	0	0	0	0	0	360
Phytolacca	**100**	0	0	0	0	0	2708
Solanum	**100**	0	0	0	0	0	2424
Filicium	0	**94**	4	0	2	0	52
Macaranga ac	0	**91**	7	0	2	0	43
Psiadia	14	**86**	0	1	0	0	166
Harungana	17	**77**	5	1	0	0	155
Trema	30	**70**	0	0	0	0	160
Croton	11	**65**	11	7	0	5	220
Dichaetanthera	17	**59**	24	0	0	0	63
Nuxia	4	**49**	17	9	9	13	397
Macaranga al	10	**42**	14	20	6	7	1496
Rhus ta	3	**38**	7	27	23	4	541
Dodonaea	0	7	**93**	0	0	0	14
Psoropermum	10	12	**65**	8	5	1	1957
Weinmannia	8	17	**64**	5	2	6	200
Vernonia	13	4	**59**	15	0	9	138
Kaliphora	8	23	**48**	18	3	0	120
Rhus th	1	5	**39**	12	19	24	136
Uapaca	7	2	4	**61**	25	0	2835
Leptolaena	12	2	9	**53**	23	1	242
Vepris p	3	8	7	**38**	34	10	996
Pandanus m	0	9	0	7	**58**	26	137
Sarcolena	5	10	0	30	**54**	0	237
Podocarpus	0	0	3	17	**51**	28	497
Carissa	0	6	2	8	**50**	34	165
Dilobeia	0	0	0	18	**42**	39	33
Dracaena	1	18	11	26	**26**	19	729
Olea	0	3	3	19	22	**54**	638
Vepris m	8	0	0	19	14	**59**	37
Ravenea	0	3	16	8	4	**68**	73
Pandanus v	1	1	4	9	17	**69**	162
Erythroxylm s	0	0	0	2	0	**98**	2726
Dypsis	0	0	0	0	0	**100**	10

[1] Species with less than 10 individuals was excluded from this table.

Buddleja madagascariensis, *Psiadia sp*, *Harungana madagascariensis* and *Trema orientali*s are also found in lower abundances. The species dominating Succession stage 1 were not found as juveniles in Succession stage 2. In Succession stage 2, *Macaranga alnifolia, Psorospermum sp., Rhus taratana, Croton oreades,* and *Nuxia capitata* dominated. Psorospermum sp. was present in all plots, but dominated in Succession stage 3. In Succession stage 3 *Weinmannia rutenbergii, Vernonia garnieriana, Kaliphora madagascariensis,* and *Rhus thourasii* were more frequent than in other succession stages. There were differences in species registered in the three unburnt control groups as well. *Uapaca densifolia* dominated the plots in Control 1. The number of individuals registered Uapaca densifolia is somewhat misleading since it has vegetative dispersal and the number registered is hence the number of ramets, not gamets. The species dominating Control 2 was *Podocarpus ambohitantensis*, and in Control 3, *Erythroxylum sphaeranthum* and *Olea lancea* dominated. Some species had more or less equal distribution in the different control groups such as *Dracaena sp.* and *Vepris pilosa.*

The dendrogram from the cluster analysis, illustrates that the widespread species are divided into two groups with similarities less than 15% (Fig. 2 and Table 4). When combining the classification in Table 4 with the classification in the cluster analysis, we find that species in the Group I are the most abundant species in Control 1, 2 & 3, Succession stage 3 and partly in Succession stage 2. Subgroup IA consist of a small number of edge species that is showing similarities with the rest at about 30%. Subgroup IA and IB have similarities of 40%. Subgroup IB can be divided into two Sub-subgroups with *Leptolena pauciflora, Uapaca densifolia and Sarcolena multiflor*a in one group as species dominating in the Control plots and the other sub-subgroup consisting of species from Succession stage 2.The species in subgroup IC are most numerous in Control 2 and Control 3. In Group II, Subgroup IIA and IIB have similarities of less than 20%. Species dominating Succession stage 1 are found in Group IIA and in Group IIB the species from Succession stage 2 are found.

Re-establishment

An ordination diagram based on quad2rate scores from the juvenile size class, shows that there is a gradient along the first axis from the Control 3, 2, and 1 to Succession stages 3, 2, 1 (Fig. 3). Along the second axis there is separation of the edge and controls (Fig. 3). Succession stage 1 are grouped in the right end of the first axis. These scores are more than 4 SD from the scores of some of the quadrates from the control plots. This means that there is a complete turnover of species between these quadrates . Even if the scores of the quadrates in Succession stage 3 are close to the scores of the control quadrates, the species in Succession stage 3 are different from the species composition found in the controls. The ordination diagram also shows that species juvenile composition is not equal among the controls.

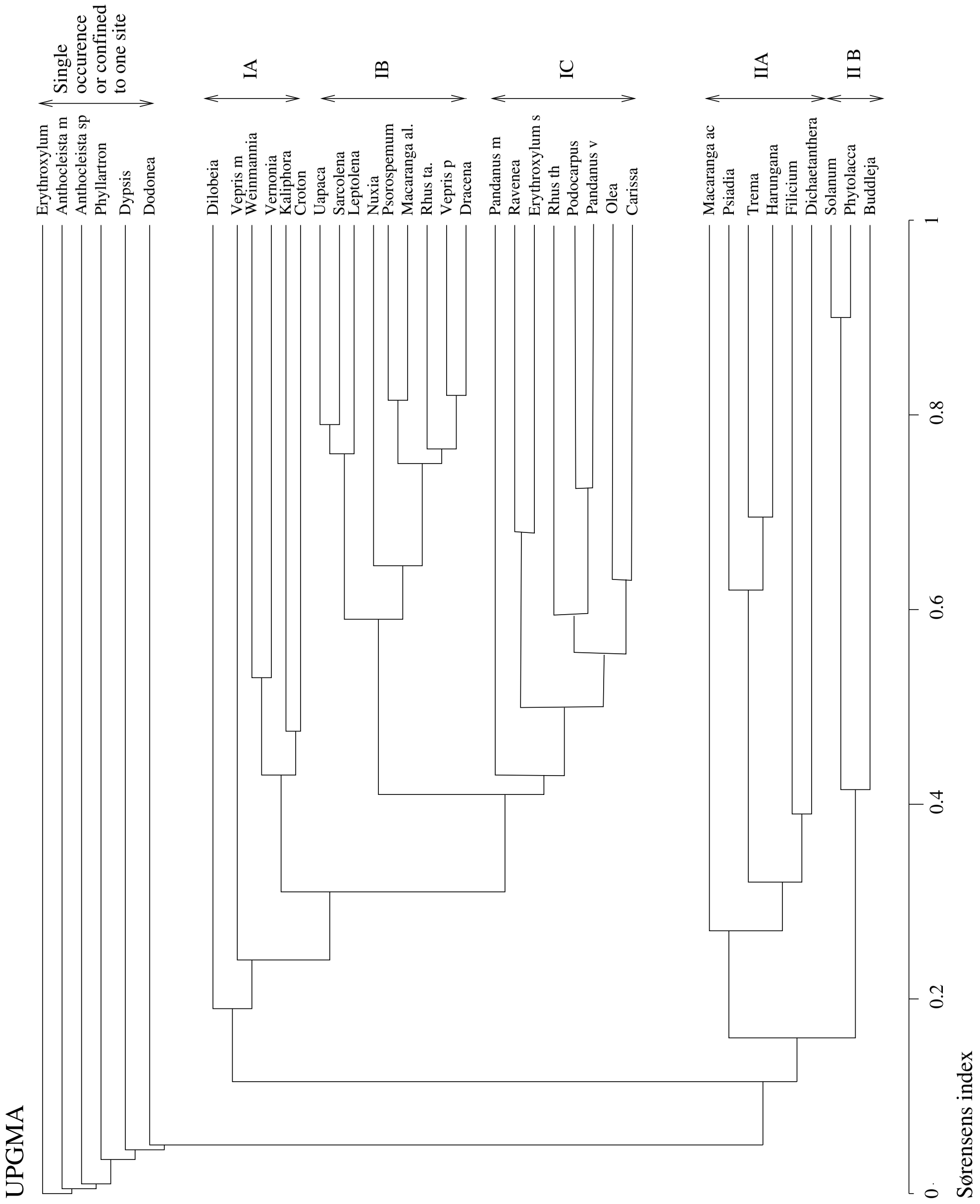

Figure 2: Classification groups of the species from a cluster analysis (method: unweighted-pair group (UPGMA), similarity coefficient: Sørensens). Similarities are based on presence/absence of data for each species, all size classes together.

Classification group	Sub group	Species in:
I	A	Succession stage 3
	B	Succession stage 2 and 3, Control 1
	C	Control 2 and 3
II	A	Succession stage 2
	B	Succession stage 1

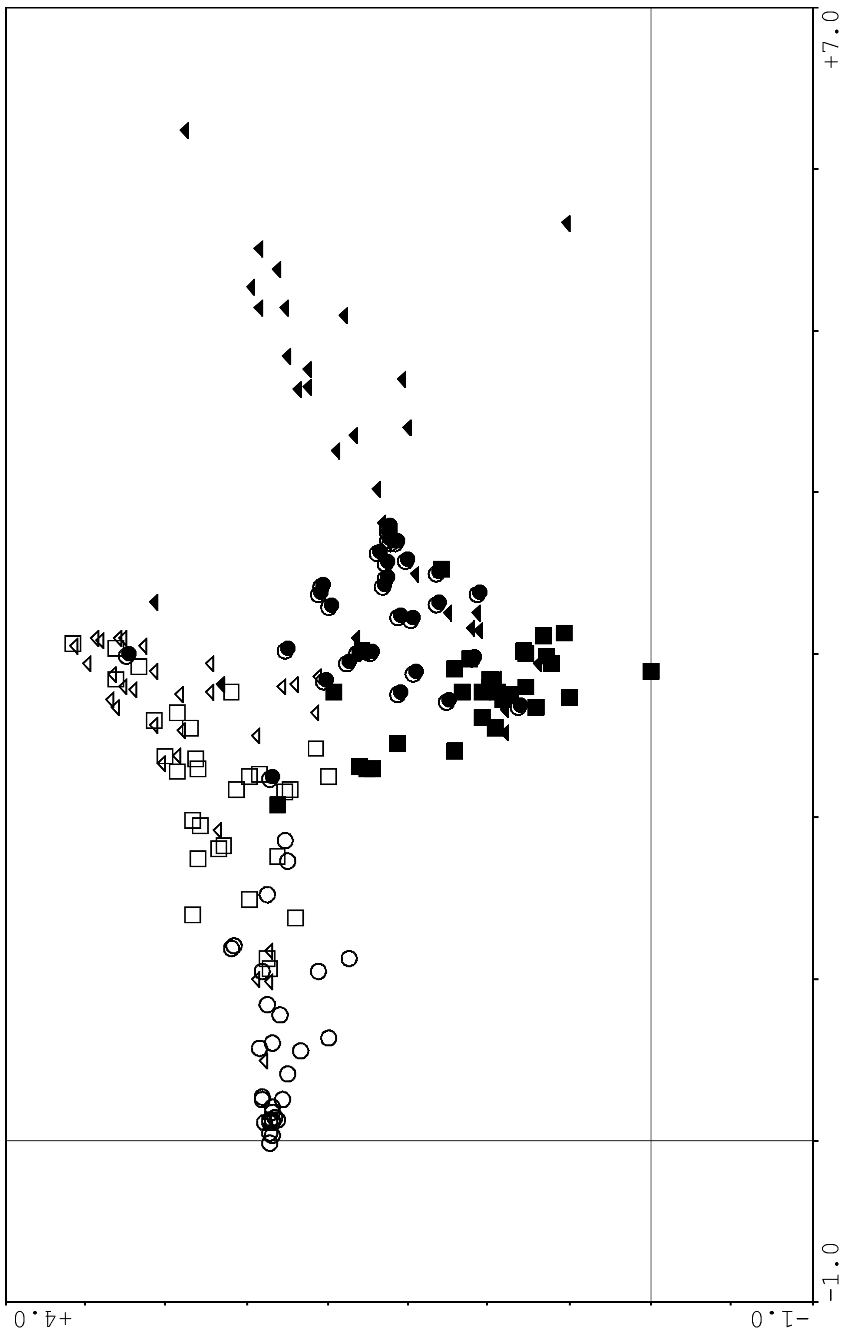

Figure 3: Quadrate scores of tree species plotted on the two first detrended correspondence analysis (DCA) axes that described most of the variation in the data. Scores are based on abundance data for each species in the juvenile stage. Black symbols represent quadrates in edge and white symbols represent control quadrates. ▲: Fire in the edges in 1999, ■: Fire in the edges in 1991, •: Fire in the edges in 1981 or earlier.

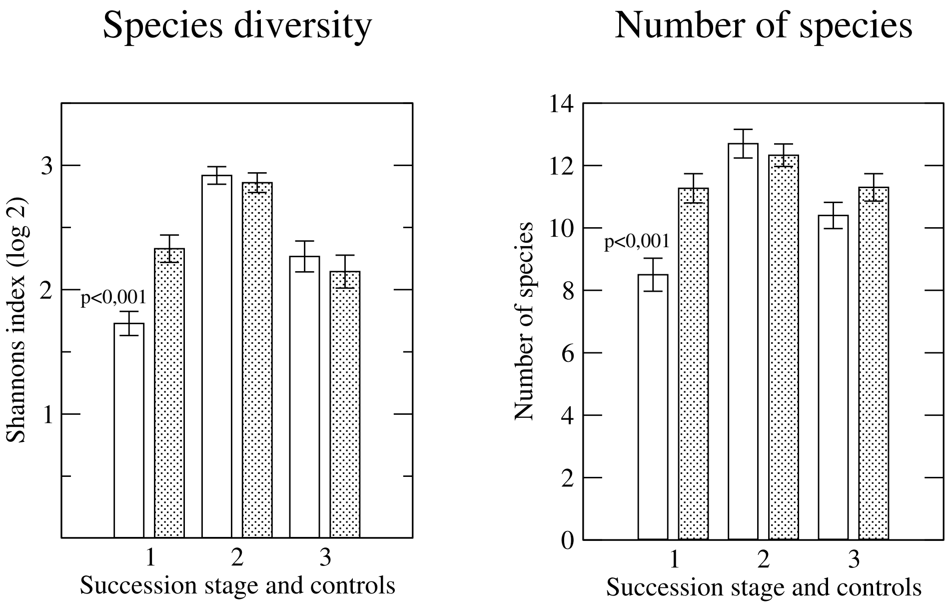

Figure 4: Mean and SE of number of species and species diversity (Shannons index, log 2) in the different replicates. Black bars represent edge replicates and white control replicates.

Recovery of number of species and diversity

The number of species and diversity index in the burnt edge plots reached the same magnitudes as the number species and diversity index in the parallel control plots already after ten years (Fig. 4). In Succession stage 2 compared with Control 2 and Succession stage 3 compared with Control 3, neither number of species nor species diversity differed significantly. In Succession stage 1, however, the number of species and diversity index were significantly lower compared with their unburnt control plots (Control 1) (number of species: $t = -5.147$, $p < 0.01$, Shannon's index: $t = -5.143$, $p < 0.01$, Fig. 4). In the burnt edges number of species and species diversity increased with the time after fire (number of species: Pearson correlation coefficient = 0.22, $p = 0.037$, Shannon's index: Spearman correlation coefficient = 0.289, $p < 0.01$). ANOVA analysis showed no significant differences among number of species in the control groups ($F = 2.022$, $p = 0.139$). However Kruskal Wallis Chi-Square test on Shannon's index did show differences among the control groups (Kruskal Wallis Chi-Square = 19.307, $p < 0.01$).

Discussion

Succession after fire

The species composition two years after fire is characterised by non-woody plant species, but after ten years there has been a succession towards dominance of tree species. This result is in accordance with the general models of secondary succession that state that in early stages there is a turnover from a community dominated by short lived, low-statured plant species to a community dominated by long lived, large species (Crawley 1997; Morin 1999). A requirement for re-establishment of plants after fire is available seeds or resprouting from stumps. Seed sources can be soil seed banks and/or fertile mother trees from where seeds are dispersed to the burnt areas. In neo-tropical forests soil seed banks consist mostly of seeds from short lived pioneer species (Finegan 1996). The existence or composition of the soil seed bank in Ambohitantely is unknown. Pareliussen did in another experiment transplant soil from the forest out into the grassland and a number of native tree species germinated in the transplanted soil. This supports the existence of a soil seed bank in Ambohitantely. Seeds are either passively dispersed by gravity, explosive dehiscence or bristle contraction, abiotically dispersed with water or wind or animal dispersed (Howe & Westley 1997). In Ambohitantely Forest the most important vectors for dispersal into burnt areas are probably animals and wind since the waterways are small and scarce.

The species dominating the edges burnt two years ago are *Phytolacca dodecandra*, and *Solanum mauritianum*. From field observation it is clear that these two species occur only in edges recently burnt. The fruits of *Phytolacca dodecandra, and Solanum mauritianum* are fleshy berries that do not disperse easily by wind. Thus it seems that they are either present in the soil seed bank or that animals disperses them from other recently burnt areas.

Seedling establishment from seed dispersal by animals depends on whether the area is attractive for animals or not. Attraction depends on available perches, structural complexity and availability of trees with fruits (Wunderle Jr. 1997). The seed-rain is higher under tree canopies (Wunderle Jr. 1997; Elmquist et al. 2001). In some of the recently burnt areas along the edges of Ambohitantely most of the tree crowns were killed. Even though birds can use these dead crowns as resting sites, there are no fruits to harvest, which indicate the importance of a soil seed bank.

The species dominating Succession stage 2, could be present in the soil seed bank, or they have been recently dispersed after fire. Unfavourable micro-climate (light, wind, and drought), soil conditions and/or competition from the species dominating Succession stage 1 could have inhibited the seedlings dominating Succession stage 2 in Succession stage 1.

The results show that the post-fire environment does not favour establishment or survival of native tree species, but already after ten years the introduced non-woody plant species are succeeded by native tree species (Table 4 and Fig. 2). Juveniles of native species were found in recently burnt edges, but as the growth rate of these tree species are slower than the growth rate of the non-woody *Phytolacca dodecandra,* and *Solanum mauritianum*, they need a longer time to become dominant. This supports the Initial Floristic Composition hypothesis of Egler (1952) which states that many of the species dominating in later stages in succession are present in early stages but dominance is a function of differential life histories (Egler 1952; Smith 1987; Pickett et al. 1987).

Even if there is a dominance of non-woody species in the first years after fire, some tree species survived the fires. *Weinmannia rutenbergii* and *Nuxia capitata* the canopies were killed by the fire, but they re-sprouted from the trunk. This trait accelerates the recovery rate of species composition.

Soil in tropical forests is often nutrient poor and much of the nutrients are accumulated in the standing vegetation (Cox & More 1998). Fire releases nutrients to the soil (Uhl & Jordan 1984; Crawley 1997). In experimental reforestation in Ambohitantely *Phytolacca dodecandra* grew profusely in fertilised plots in the grassland (Pareliussen, unpublished). Native tree seedlings had lower survival in the fertilised plots, this may be attributed to the competition from a small shrub *(Helichrysum fulvecens* D.C.). In Costa Rica the weedy herb *Phytolacca rivinoides* dominated the forest regeneration after chemical fertiliser was applied, and delayed the regeneration of tree seedlings (Harcombe 1977). Even if the native tree species can grow in this nutrient rich soil they are competitively inferior compared with *Phytolacca dodecandra* and the other two species dominating the areas of recent fire. In a study in Amazon, Uhl and Jordan (1984) showed that already after two years the nutrient concentration in burnt sites already equaled the concentration in control sites. The nutrient release after fire in Ambohitantely Forest is also probably washed out after a couple of rainy seasons. This could explain the short time period of dominance for *Phytolacca dodecandra*.

Native species establish in Succession stage 2 and 3, but neither the species composition neither in Succession stage 2 nor in Succession stage 3, equals the composition in the Controls. The species composition in the edges is influenced by the edge effect i.e. different abiotic conditions compared to the conditions in the interior of the forest.

We have not investigated effect or interactions of mycorrhizae or herbivores (Walker & and 1987; Pickett & McDonnel 1989). If the fires have been intense and/or with high frequencies, the mycorrhizae, which several tree species might be dependent upon, could have been destroyed, and this would be detrimental to their establishment. Seed predation might impede the establishment of some species. This is true for the endemic palm *Dypsis decipiens*, which is native to Ambohitantely forest reserve. Introduced wild boar (*Potamocherus larvatus*) eat the fruit and seeds of the palm and thus reduce regeneration to a minimum (Ratsirarson 2000).

The number of species and diversity index recovered within 10 years after fire as our results show when comparing with the unburnt controls (Fig. 4). However, the species composition recovers slower than the number of species and diversity index. This pattern is in line with earlier studies (Finegan 1996). Time for recovery of tropical forest after fire has been estimated to be as long as 200 years (Uhl 1988; Cochrane & Shulze 1999). In this context 18 years , the time span of this study, is too short to gauge the recovery time for the Ambohitantely forest. However, it is evident that 18 years after the fire, the forest is able to recover to a forest dominated by native species, even if the species composition is different from the controls in the forest interior.

Explanations for the differences in diversity index and species composition in the controls

Both species diversity and species composition differed among the controls (Fig. 2, Fig. 3 and Table 4). Traditionally, edge effects were thought to affect the forest at a distance of 2 times the height of the trees from the edge (Noss and Csuti, 1997). In this study 50 meters was used and this would be more than double this estimate (2 × 10m. tall trees = 20m.). However, later studies have shown that in fragmented forests the edge effects could be measured up to 150 m into the forest (Laurance, 2000) and in the case of burnt forest edges, it could be measured even deeper into the forest (Didham and Lawton, 1999). In the cluster analysis *Leptolaena pauciflora, Uapaca densifolia,* and *Sarcolaena multiflora* were classified together with edge species in Subgroup IB (Fig. 2, Table 4). Since these species are abundant in Control 1, this might imply that fire has caused edge effects also in these assumed undisturbed plots.

Another explanation for the differences between the species composition in the controls could be an effect of species clumping. In tropical forests many of the species have an aggregated distribution (Armesto et al. 1986; Sterner et al. 1986; He & Lafrankie 1997). The seed rain decreases with distance to the mother tree and thus the seedlings have a higher probability of establishing close to the mother tree than elsewhere in the forest. Thus the species composition in each site is an effect of the random distribution of mother trees. A third explanation could be the effect of different environmental conditions between the plots, such as the exposition and slope (Table 3). In Control 3, the topography is steeper than in the other controls. In Ambohitantely Forest the species composition was different on the hilltops compared to the slopes (Birkinshaw et al. 2000). Indeed, trees are taller on the slopes, which decreases light intensity reaching the forest floor and this could influence the survival of the tree seedlings and change the species composition.

The role of introduced species in the succession

In the edges burnt two years ago, two out of the three most abundant species, *Phytolacca dodecandra* and *Solanum mauritianum*, are introduced species. *Solanum mauritianum* originally from South America, was introduced to Madagascar around 1900 (Binggeli 2003). It is not known when the introduction of *Phytolacca dodecandra* native to the African mainland occurred. The dominance of non-native species can be explained by a lack of native species adapted to high fire frequency.

Introduced species were considered as a threat only in human disturbed habitats in Madagascar (Koechlin et al. 1974). However, now some have vocalized their belief that introduced species could act as a threat to native vegetation as well (Rauh 1995; Rauh 1998). Will these two introduced species be a threat to the natural forest succession in the Highlands? Studies in Puerto Rico showed that for re-establishment of native tree species in abandoned agricultural land, introduced species that were inferior competitors in late succession, acted as facilitators for tree establishment (Aide et al. 2000). *Solanum mauritianum* has been considered to be an invasive species in Madagascar (Binggeli 2003). Invasive species prevent regeneration of native species (Stram 1999). However, our results indicate that the introduced species (*Phytolacca dodecandra* and *Solanum maurutianum*) do not prevent succession of native species in Ambohitantely Forest. Already ten years after fire, these introduced species have almost disappeared in the succession and are replaced by mainly endemic tree species.

Even if the introduced species do not prevent native species from establishing, these non-woody plant species could be fuel sources for recurrent fires. These species are short lived and the dead, dry biomass they leave behind, is excellent fuel for subsequent fires. This implies that fires are more likely to occur due to the dry fuel and that the next fire will have higher intensities than the first fire. This could lead to a vicious cycle and thus alter the succession.

Forest management in a context of local agro-ecosystems

A number of rural villages are located in the valleys around the reserve area. The majority of the population in these villages immigrated after the middle of the 19. century from other parts of Madagascar (Merina, Betsileo, Betsimiraka) (Edwards et al. 2002; Kalland 2003). This diversity of social groups is the background to the diverging interests of the local peoples with different traditions, economic outlook and social status. Agriculture in the area is based on rice cultivation and cattle herding. Grassland fires are traditionally set as a mean to rejuvenate the grassland biomass and thus improve the fodder quality. These fires often get out of control and enter the forest fragments. Due to the harmful effects on biological diversity, this fire activity is forbidden by law except from in occasions where the authorities gives special permissions (Kull 2002). In the reserve all these activities are prohibited and the control of compliance with this prohibition is observed by ANGAP. ANGAP guards the reserve against wild fires and maintains the fire breaks. In spite of their effort, numerous wild fires enter the forest. The total denial of access to the forest for the local populations creates tension. Most of the social groups express little interest in the forest. although some small scale collection and harvest of non-timber products are carried out (Kalland 2003). The management plan for the reserve, did not take those needs of the local population groups sufficiently into account (Kalland 2003). An other example of such neglected interests is the prohibition of grassland fires. Allowing the local populations to burn their grazing land, would lead to better grassland fire management with the active involvement of local populations. This would imply less likelihood for the fires to penetrate the forest.

Provided successful fire management future forest management could include forest restoration and replanting of forest tree species in the grassland in order to restore previously forested areas. Species in the Classification group II from the cluster analysis (Fig. 3 and Table 4) might be suitable species for this purpose. These species are able to establish in burnt areas and might also be suitable for planting in the grassland for restoration purposes. However, further investigations must be done to increase the knowledge about possible effects of the introduced non-woody species.

Conclusions

Although the earliest succession stage was dominated by introduced non-woody species there was no regeneration of those species the plots ten years after fire. Tree species number and tree species diversity index recovered and equalled the species number and diversity in control plots ten years after fire. The species composition is still different from the composition in the forest interior 18 years after fire. In order to maintain the forest the human induced fires encroaching the forest have to come to an end. Therefore there is a need to involve the local rural populations in the management of both the forest and the surrounding grasslands. Further, the forest has to be seen as one component of the local agro-ecosystem where grasslands and rice paddies are other components.

Acknowledgments

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Literature Cited

Aide, T., Zimmerman, J., Pascarella, J., Rivera, L., & Marcano-Vega, H., 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology, Restoration Ecology 8:328–338.

Armesto, J., Mitchell, J., & Villagran, C., 1986. A comparison of spatial patterns of trees in some tropical and temperate forests, Biotropica 18:1–11.

Bastian, G., 1964. La foret d‘Ambohitantely, Madagascar revue de geographie 5:1–42.

Binggeli, P., 2003. Introduced and invasive plants, in The Natural History of Madagascar, Goodman, S., & Benstead, J., editors, University of Chicago Press.

Birkinshaw, C., Ralimanana, H., Ranaivojaona, R., Randrianaivo, R., & Ravololonanahary, H., 2000. Flore et structure de la foret de la Reserve Speciale d'Ambohitantely, chapter 2, pages 7–23, Cidst, Antananarivo.

Burney, D., 1997. Tropical islands as paleoecological laboratories: Gauging the consequences of human arrival, Human Ecology 25:437–457.

Burney, D., James, H., Grady, F., Rafamantanantsoa, J., Ramilisonina, Wright, H., & Cowart, J., 1997. Environmental change, extinction and human activity: evidence from caves in NW Madagascar, Journal of Biogeography 24:755–767.

Clark, K., & Uhl, C., 1987. Farming, fishing, and fire in the history of the Upper Rio Negro region of Venezuela, Human Ecology 15.

Cochrane, M., Alencar, A., Schulze, M., Jr., C. S., Nepstad, D., Lefebvre, P., & Davidson, E., 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests, Science 284:1832–1835.

Cochrane, M., & Shulze, M., 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition, Biotropica 31:2–16.

Cox, C., & More, P., 1998. Biogeography an ecological and evolutionary approach., Blackwell Science, Oxford.

Crawley, M., 1997. Life history and environment, in Plant Ecology, pages 73–132, Blackwell Science, Oxford.

Crawley, M., 1997. Structure of plant communities, in Plant ecology, Crawley, M., editor, Blackwell Oxford.

Dawson, T., 2001. Impact of forest fires on biodiversity in asean, ASEAN Biodiversity 1:15–17.

Edwards, M., Armbruster, W., Blaikie, S., Kalland, I., Klein, J., Lein, H., Olsson, E., Pareliussen, I., & Reau, B., 2002. I hver sin verden. Skogforvalting på Madagaskar høyland, in Tverrfagelige forskningsprosjekter ved NTNU, pages 81–98, Tapir Trykk, Trondheim.

Egler, F., 1952. Vegetation science consepts. 1. Initial floristics composition a factor in old-field vegetation development, Vegatatio 4:412–417.

Elmquist, T., Wall, M., Berggren, A., Fritioff, Å., & Rinman, U., 2001. Tropical forest reorganization after cyclone and fire disturbance in Samoa: remnant tree as biological legacies, Conservation Ecology 5:10.

Finegan, B., 1996. Pattern and process in neotropical secondary rain forest: the first 100 years of succession, Trends in Ecology and Evolution 11:119–124.

Gade, D., & Perkins-Belgram, A., 1986. Woodfuels, reforestation, and ecodevelopment in higland Madagascar, GeoJournal 12.4:365–374.

Gauch Jr., H., 1994. Multivariate analysis in community ecology, Cambridge University Press, Cambridge.

Goldammer, J., 1999. Forest on fire, Science 284:1782–1783.

Gowlett, J., Walton, J. H. D., & Wood, B., 1981. Early archeological sites, hominid remains and traces of fire from Chesowanja, Kenya, Nature 294:125–129.

Green, G., & Sussman, R., 1990. Deforestation history of the eastern rain forest of Madagascar from satellite images, SCIENCE 248:212–215.

Hammond, D., & ter Steege, H., 1998. Propensity for fire in Guinanan rainforest, Conservation Biology 12:944–947.

Hanssen, S., 2002. The Ambohitantely Special Reserve in Central High Land Madagascar - Forest change and forest occurrence, Masters thesis: Norwegian University of Science and Technology, Trondheim, Norway.

Harcombe, P., 1977. The influence of fertilization on some aspects of succession in a humid tropical forest, Ecology 58:1375–1383.

He, F., & Lafrankie, J., 1997. Distribution patterns of tree species in a Malaysian tropical rain forest, Journal of Vegetation Science 8:105–114.

Howe, H., & Westley, L., 1997. Ecology of pollination and seed dispersal, in Plant ecology, pages 262–284, Blackwell Science, Oxford.

Kalland, I., 2003. Klemt mellom brennende skog og bare trær. Ambohitantelys lokal befolking og globale naturvernere på Madagaskar, Masterthesis: Institute of Geography, Norwegian University of Science and Technology, Trondheim, Norway.

Kauffman, J., Sandford, R., Cummings, D., Salcedo, I., & Sampaio, E., 1993. Biomass and nutrient dynamics associated with slash fires in a neotropical forest, Ecology 74:140–151.

Kinnear, P., & C.G.Gray, 1999. SPSS for Windows made simple, Psychology Press, East Sussex.

Koechlin, J., Guillaumet, J., & Morat, P., 1974. Flore et végétation de Madagascar, J.Cramer, Vaduz.

Kull, C., 2000*a*. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar, Environment and History 6:423–450.

Kull, C., 2002. Empowering pyromaniacs in Madagascar: ideology and legitimacy in community-based natural resource management, Development and Change 33:57–78.

Langrand, O., 1995. The effects of forest fragmentation on bird species in Madagascar: a case study from Ambohitantely Forest Reserve on the central high plateau, Masters thesis: University of Natal, South Africa.

Laurance, W., & Williamson, G., 2001. Positive feedback among forest fragmentation, drought, and climate change in the Amazon, Conservation Biology 15:1529–1538.

Løvås, G., 1999. Statistikk - for universiter og høgskoler, Universitetsforlaget, Oslo.

Meggars, B., 1994. Archaeological evidence for the impact of mega Niñjo events on Amazonia during the past two millennia, Climate Change 28:321–338.

Morin, P., 1999. Community ecology, Blackwell Science, Malden Massachusetts.

Ogden, J., Basher, L., & McGlone, M., 1998. Fire, forest regeneration and links with early human habitation: evidence from New Zealand, Annual review of Botany (London) 81:687–696.

Pickett, S., Collins, S., & Armesto, J., 1987. Models, mechanisms and pathways of succession, Botanical review 53:335–371.

Pickett, S., & McDonnel, M., 1989. Changing perspectives in community dynamics: a theory of successional forces, Trends in Ecology and Evolution 4.

Pinnard, M., Putz, F., & Licona, J., 1999. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia, Forest Ecology and Management 116:247–252.

Radimbison, A., 1990. Les différents types de lisière de la forêt d'Ambohitantely, Thèse de Doctorat 3ème cycle de Sciences Biologiques Appliquées. Etablissement d'Enseignement Supérieur des Sciences. Université d'Antananarivo.

Ratsirarson, J., 2000. Les palmiers d'Ambohitantely, in Monograpie de la forêt d'Ambohitantely, Ratsirarson, J., & Goodman, S., editors, chapter II, pages 53–56, Cidst and WWF, Antananarivo.

Ratsirarson, J., & Goodman, S., 2000. Généralités sur la forêt d'Ambohitantely, in Monographie de la forêt d'Ambohitantely, Cidst and WWF, Antananarivo.

Rauh, W., 1995. Succulent and xerophytic plants of Madagascar. Volume one, Strawberry Press, Mill Valley.

Rauh, W., 1998. Succulent and xerophytic plants of Madagascar. Volume two, Strawberry Press, Mill Valley.

Roberts, S., 2001. Tropical fire ecology, Progress in Physical Geography 25:286–291.

Sanford, R., Saldarringa, J., Clark, K., Uhl, C., & Herrera, R., 1985. Amazon rain-forest fires, Science 227:53–55.

Smith, M. H. T., 1987. Plant succession: Life history and competetion, American Naturalist 93:168–198.

Sterner, R., Ribic, C., & Schatz, G., 1986. Testing for life historical changes in spatial patterns of four tropical tree species, Journal of Ecology 74.

Stram, W., 1999. Invasive species in Mauritius: examining the past and charting the future, in Invasive species and biodiversity management, Sandlund, O., Sche, P., & Viken, Å., editors, pages 325–349, Kluwer Academic Publishers, Dordrecht.

ter Braak, C., 1995. Ordination, in Data analysis in community and landscape ecology, Jongman, R., ter Braak, C., & van Tongeren, O., editors, pages 91–174, Cambridge University Press, Cambridge.

ter Braak, C., & Smilauer, P., 1998. CANOCO reference manual user's guide to CANOCO for Windows: software for canonical community ordination (version 4), Microcomputer power, Ithaca.

Uhl, C., 1988. Restoration of degraded lands in the Amazon basin., chapter 37, pages 326–332, National Academy of Sciences and Smithsonian Institute, Washington, D.C.

Uhl, C., 1998. Perspectives on wild fire in the humid tropics, Conservation Biology 12:942–943.

Uhl, C., & Jordan, C., 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia, Ecology 65:1476–1490.

Underwood, A., 1997. Experiments in ecology, Cambridge University Press, Cambridge.

van Tongeren, O., 1995. Cluster analysis, in Data analysis in community and landscape ecology, Jongman, R., ter Braak, C., & van Tongeren, O., editors, pages 174–213, Cambridge University Press, Cambridge.

Waite, S., 2000. Statistical ecology in practice, Prentice Hall, New Jersey.

Walker, L., & and, F. C., 1987. Interactions among processes controlling successional change, OIKOS 50:131–135.

Wunderle Jr., J., 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands, Forest Ecology and Management 99:223–235.

Doctoral theses in Biology

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1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
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Year	Name	Degree	Title
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.

Year	Name	Degree	Title
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. - A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco* : An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.

Year	Name	Degree	Title
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus* , *Hylocomium splendens* , *Plagiochila asplenigides* , *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Salvesen, Ingrid	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race

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2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Hilmo, Olga	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronical constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth

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2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway - Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation - an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)