Tree plantations as a cost-effective tool for reforestation of abandoned pastures in Amazonian Ecuador

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Las plantaciones de árboles como herramienta eficaz para la reforestación de pastos abandonados en el Ecuador amazónico

Una causa importante de la deforestación de las selvas tropicales en Sudamérica es su transformación en pastos. El uso ganadero de zonas previamente forestales no es sostenible y conduce a la degradación por medio del lixiviado de nutrientes, la compactación del suelo, la competencia, cambios en el microclima y la escasez de propágulos. Si la degradación es severa, la sucesión puede detenerse y el terreno permanece desarbolado incluso si cesa el uso ganadero. El presente estudio considera el uso de las plantaciones forestales como catalizadores de la reforestación; dichas plantaciones sortean las barreras a la sucesión y facilitan en su sotobosque la regeneración de las especies forestales nativas. Se cuantificó la regeneración de especies leñosas en plantaciones forestales en la estación biológica Jatun Sacha en el este de Ecuador. Se evaluaron la abundancia y la riqueza específica de las especies en regeneración en tres tipos diferentes de plantaciones, y se compararon con las de pastos control y abandonados. Las plantaciones dominadas por dos especies del género Inga (I. ilta *e* I. edulis) *fueron similares entre sí en la composición de especies en regeneración y tuvieron el mayor número de especies e individuos en regeneración de todos los tipos de plantaciones examinados. Las plantaciones mixtas de árboles mostraron la menor cantidad de individuos y especies en regeneración. Las parcelas control mostraron valores intermedios. La riqueza específica y la abundancia de las especies en regeneración estuvieron negativamente correlacionadas con la cobertura de vegetación basal y de gramíneas. La capacidad de las plantaciones de Inga para acumular especies en regeneración se atribuye a la estructura de su dosel, que sombrea y elimina con éxito la vegetación basal competidora. La disponibilidad de semillas no parece ser un factor limitante de la riqueza específica o de la abundancia de las especies en regeneración de dichas plantaciones en este estado.*

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Abstract

Conversion to pastures is an important cause of deforestation of rainforests in South America. Cattle-grazing on previously forested land is unsustainable and leads to degradation through nutrient leakage, soil compaction, competition, changes in microclimate and lack of propagules. If the degradation is severe, succession may be arrested and the land remains open even if the grazing ceases. This study considers tree plantations as catalysts for reforestation, by breaking the barriers to succession and facilitating regeneration of native forest species in their understories.

Woody regeneration in plantations was measured at Jatun Sacha biological field station in eastern Ecuador. Abundance and species richness of the regeneration in three different types of plantations were evaluated and compared to a control on abandoned pasture. Plantations dominated by two species of the genus Inga *(*I. ilta *and* I. edulis*) were similar in the composition of their regeneration and had most species and individuals in the regeneration of the sampled plantation types. Plantations of mixed tree species had least abundant and species-rich regeneration, and the controls were in between. Species richness and abundance of the regeneration were negatively correlated with ground vegetation and with grass cover in ground vegetation. The ability of the* Inga *plantations to accumulate regeneration is ascribed to the structure of their canopy, which successfully eliminates competing ground vegetation by shading. Seed availability does not appear to be a limiting factor for species richness or abundance of the regeneration in these plantations at this stage.*

Introduction

One of the most serious environmental threats worldwide is deforestation. The case is especially serious regarding the tropical moist forest, which is considered the home of more than half of the world's species. Between the years 1990 and 2000, 14.2 million hectares of tropical natural forest disappeared annually, corresponding to 0.9 % of the total forest cover (FAO 2001). For Ecuador, this figure is 1.2-1.6 percent annually (WRI 2003, FAO 2001), the second highest in South America. The most important cause of deforestation in Latin America is conversion to other landuse, predominantly cultivation and pastures. Other causes include fuelwood gathering, commercial logging, oil and mineral extraction and infrastructure development (Rowe et al. 1992). This development is a cause of serious concern, as forests provide many goods and services that humans are dependent on. Loss of biodiversity, flooding, watershed degradation, carbon release to the atmosphere and loss of resource base for indigenous people and rural poor are among the consequences of deforestation (Rowe et al. 1992).

The use of land for agricultural or grazing activities often leads to degradation. The poor nutrient retention capacity of rain forest soils is well known. Soils loose their nutrients fast when the forest cover is gone and the productivity of the land decreases after only a few years (Jordan 1987, Reiners et al. 1994). Soil compaction and decreasing soil organic matter also lead to reduced productivity of the land and subsequent abandonment. The opening of land leads to changes in microclimate towards higher and more fluctuating soil and air temperature and lower humidity (Bazzaz 1991). The vegetation on deforested land is often dominated by herbaceous vegetation like grasses and ferns (Lugo 1988). These conditions inhibit establishment of woody plants and make pastures more fireprone than forests (Uhl et al. 1988, Nepstad et al. 1991). Many seed dispersers are restricted to forests, resulting in a decrease in recruitment of animal dispersed seeds. There is also evidence for a higher level of seed predation in open land than in forests (Parrotta 1993, Uhl et al. 1988).

The result of this land use is thus a severely degraded ecosystem with persistent chemical, physical and biological barriers to natural succession. Forest recovery on abandoned pasture sites is much slower than recovery following other disturbance types (Aide et al. 1995). Evidence exist for ecosystem shifts to savanna-like vegetation (Cavelier et al. 1998, Ashton et al. 1997). The impact on succession is mainly determined by the degree of degradation (Nepstad et al. 1991, Uhl et al. 1988).

A parallel development to deforestation is the establishment of monospecific plantations in the tropics to supply the need of timber, firewood or other valuable products such as latex (Hartley 2002). Plantations could reduce the pressure on natural forest, if the harvest obtained from the plantation is replacing exploitation of the forest. In terms of biodiversity conservation they are generally viewed as a poor substitute for natural forest. However, in terms of a functioning natural community, plantations compare favourably to many other intensive industrial land uses such as annual crop agriculture or human developments (Moore and Allen 1999, in Hartley 2002). Many of the environmental services provided by forests, such as carbon storage, climate amelioration and water regulation could be provided by plantations. Plantations can also benefit landscape composition by buffering edges between natural forests and non-forest lands, and by acting as corridors and thus improve connectivity among forest patches (Norton 1998, in Hartley 2002).

Compared with natural forest systems, secondary forests, degraded lands and other human-impacted areas have received little attention from researchers (Clüsener Godt & Hadley 1993). However, recent studies have revealed the potential of tree plantations to act as catalysts for forest regeneration on severely degraded sites with arrested succession. Plantations accumulate species-rich, native vegetation in their understories and host part of the diversity found in mature tropical forests (e.g. Lugo 1988, 1992, Parrotta 1993, Fimbel & Fimbel 1996). Establishing plantations could thus be a cost-effective way to rehabilitate native forest vegetation.

A plantation can be a tool for reversing degradation processes and facilitate changes in a number of factors crucial for the recruitment, survival and growth of native trees. The planting of trees improves microclimate and soil conditions, for example by reducing temperature fluctuations, increasing organic matter content and available nutrients, and reducing erosion rates (Lugo 1988). The plantation constitutes a habitat for wildlife which act as seed dispersers from neighbouring native forests (Parrotta et al. 1997). Maybe the most important feature of the plantation is that it shades out grasses and ferns, thereby reducing competition, which is a serious barrier for seedling establishment and survival of woody species (Aide et al. 1995).

When the aim of the plantation is to increase succession rate in order to rehabilitate degraded land, some factors are important to consider. Composition of the plantation overstory affects the quantity and quality of understory woody regeneration (e.g. Guariguata et al. 1995, Powers et al. 1997, Parrotta & Knowles 2001). Thus choice of plantation species, density and management matters. If the site to be reforested is severely degraded, the choice of species is limited to those that can tolerate the harsh conditions. In many cases exotic species have been used for this reason (Lugo 1988). Nitrogen-fixing legume species can have a dramatic effect on soil fertility through their production of readily decomposable, nutrient-rich litter (Montagnini & Sancho 1990). Many authors propose the use of native species, preferably in mixed plantations (e.g. Guariguata et al. 1995, Hartley 2002, Leopold et al. 2001, Lamb 1998). To facilitate dispersion of seeds by animals, fruit-bearing species can be included to attract birds and bats (Wunderle Jr 1997, Parrotta 1993).

Plantations accumulate species with time; age of the plantation has been shown to be an important factor (Keenan et al. 1997, Lugo et al. 1993).

Distance to seed sources has an impact on the number and type of species that establishes on a deforested site. Studies from Puerto Rico and Brazil have shown distance to older forest to influence spontaneous succession on former agricultural lands (Chinea 2002) and in plantations (Parrotta 1993, Parrotta & Knowles 2001).

The plantation tree species might be chosen exclusively as a tool to rehabilitate native forest cover, in which case it can be left and with time replaced by the regenerating trees. However, the plantation is often expected to give a direct economic outcome. In that case, the planted species will be chosen for the production of some demanded product; such as timber, forage, fruits or medicines. The extraction of the plantation species could then aim to leave the regenerating forest as intact as possible, to combine the economic return of the planted species with the benefit of a restored forest cover. It is not well known how plantation harvest would affect the regeneration. Harvest is generally associated with severe damage to remaining trees. Contrarily, according to one study (Duncan & Chapman 2003) forest succession accelerated after harvest - despite the killing of many stems – through more favourable conditions for seedlings.

Rehabilitation projects are typically very expensive. In a situation where land is a scarce resource, however, the cost of non-productive land is also high. Hence rehabilitation may in the long run be a necessary measure. Studies have shown that tropical ecosystems can and do recover from human impact, and that the costs involved are usually associated with time, (Lugo 1988, Uhl et al. 1988) i.e. the period during which the land is not usable. To minimise the costs of rehabilitation, natural processes should be used as much as possible for plant dispersal or soil restoration (Lugo, 1988). If there are opportunities to get an economic return, rehabilitation projects are more likely to get started.

The aim of this study is to investigate the impact of plantations of native trees on woody regeneration in abandoned pastures. The effectiveness of different plantation designs in rehabilitating forest cover on degraded land is evaluated. The abundance and species richness of the regeneration is compared between plantations dominated by one species, plantations comprised of several species and controls on abandoned pasture. This work is focused on the influence of overstory structure and understory light conditions on the regeneration.

Site description

Jatun Sacha Biological Station is located on the south bank of the upper Napo River in Napo province, Ecuador, about 40 km east of the Andes, at 400 m elevation (01°04'S, 77°36'W). Mean annual rainfall is 3800 mm, distributed relatively evenly throughout the year. Mean annual temperature is about 24°C, with little annual variation. This area is one of the most rich in plant species in the world, with 246 tree species recorded in a one-hectare plot (Neill & Palacios unpublished). Jatun Sacha Biological Station is owned and administered by Fundación Jatun Sacha, a private, non-profit Ecuadorian foundation. The station is a centre for biological research, environmental education and conservation. It includes a forest reserve, which was established 1986 and presently comprises around 2000 hectares. A major part (80 %) of the reserve consists of primary forest. It is growing continually as new land is being purchased (see map, appendix 1).

The area surrounding the reserve is typical of many areas of lowland wet tropics. The region has been colonised in the past few decades by indigenous groups from the Sierra, the Quichuas, who began cultivating the land. The Quichuas are cultivating maize, manioc and plantains for subsistence, and coffee and cacao as cash crops (Cleuren 2000). A quite recent practice is the breeding of cattle for beef production.(This is a highly unsustainable land-use form, for reasons stated above.) The cultivation and grazing activities have led to a severe deforestation in the area; the reserve is left as a forested island in a sea of open land.

Conservation work at Jatun Sacha has focused on the development of more sustainable forms of land-use and on reforestation of pastures. Plantations of different types have been established, both for rehabilitation and as trials with various crops. Where the main purpose is rehabilitation, a mix of large seeded forest species has been used, such as *Parkia multijuga*. Crop cultivation is conducted either as agroforestry trials with a tree shelter (e g coffee) or as tree crops in monospecific plantations (e g *Croton* "sangre de drago", used for medicinal purposes, or *Bixa* "achiote", used as a pigment).

This study was conducted in plantations on the lands of Cabañas Aliñahui, just outside the borders of the reserve. The site where these plantations are established was deforested in the early 1970's and grazed by cattle for about 20 years. The pasture was abandoned in 1994, a few months before establishment of the first plantations. The soil has been classified as oxic dystropept; highly acidic, low in nutrients and high in aluminium. Vegetation at the site prior to planting consisted of the introduced African grass *Brachiaria decumbens* Stapf. (Neill & Revelo unpublished). Some remnant trees of the genera *Ceiba*, *Acacia*, *Apeiba*, *Otoba*, *Sterculia*, *Terminalia*, *Simira*, *Cordia*, *Guarea*, *Cabralea*, *Chorysia*, *Chisolobium* and some Melastomataceas and Sapindaceas (N. Revelo, pers. comm.) were present at the site. Three different types of plantations and one control were studied (table 1).

Table 1.
Plantation species, age, spacing, plantation size and distance from potential seed source. (l) = leguminous species.

Plantation type	Species	Year of establishment	Spacing (m)	Area (m^2)	Distance to primary forest (m)
1	Inga edulis (l) Swietenia macrophylla	1994	4x4	2500	1400
	Inga edulis (l) Swietenia macrophylla	1994	4x4	2500	1450
	Inga edulis (l) Swietenia macrophylla	1994	4x4	2500	1600
2	Inga ilta (l) Swietenia macrophylla	1994	4x4	2500	1400
	Inga ilta (l) Swietenia macrophylla	1994	4x4	2500	1500
	Inga ilta (l) Swietenia macrophylla	1994	4x4	2500	1600
3	Parkia multijuga (l), Gyranthera sp., Swietenia macrophylla	1995	4x4	1200	1250
	Parkia multijuga (l), Pleurothyrium insigne, Swietenia macrophylla	1995	4x4	1200	1300
	Apeiba aspera, Dussia tessmanni (l), Virola duckei, Hymenea oblongifolia (l), Huertea glandulosa, Bauhinia brachycalyx (l)	1995	3x3	1800	2600
	Inga edulis (l), Sterculia colombiana, Pleurothyrium insigne, Swietenia macrophylla	1995	5x5	3650	2500
control	Control (Swietenia macrophylla)	1994	8x8	2500	1450
	Control (Swietenia macrophylla)	1994	8x8	2500	1500
	Control (Swietenia macrophylla)	1994	8x8	2500	1550

The plantations with *Inga* and *Swietenia* were planted to test the possibility of growing mahogany (*Swietenia*) together with a nitrogen-fixing species (*Inga*), to provide vegetative cover and enrich the soil with nitrogen and organic matter. Many monospecific planting trials with mahogany have failed due to attacks by the shoot-borer *Hypsipyla grandella*, a moth larva. The interplanting with *Inga* also aims at "hiding" the mahogany plants to the herbivore. The *Ingas* themselves are used as firewood, and they produce protein-rich, edible fruits (Neill, unpublished). Four times as many *Inga* as *Swietenia* were planted (Neill & Revelo unpublished) and *Inga* totally dominated these sites, at the time being about two times as high as the *Swietenia*. These sites will hereafter be referred to as *Inga* plantations.

The maintenance of these plantations consisted of removal of grass around each plant at 3 month intervals until the plants were above the level of the grass. Regenerating woody vegetation was removed at 6 month intervals until crown closure was attained (Neill unpublished). In 1999 *Inga* were thinned to allow a higher light penetration for better growth of *Swietenia*. About 40 % of *Inga ilta* were felled, a little fewer of *I. edulis*. (N. Revelo, pers. comm.).

The control of the *Inga-Swietenia* trial was planted with only *Swietenia*. At the time of this study, more than 90 % of *Swietenia* had died (N. Revelo, pers. comm.). These sites were therefore used as control plots, as the soil conditions and the landuse history were similar to the other plantations.

The mixed-species plantations were established with the sole purpose to reforest the degraded pasture. Planted trees are native, large-seeded forest species, both legumes and non-legumes. The goal for these plantations is to maximise tree species diversity and they were designed to be similar in structure and composition to the mature forest of the region (Neill unpublished). Maintenance of these plantations involved grass removal around the plants until they were above the level of the grass (A. Alvarado, pers. comm.).

Methods

Sampling was conducted in three different types of plantations; (1) *Inga edulis* and *Swietenia macrophylla,* (2) *Inga ilta* and *Swietenia macrophylla* and (3) mixed species plantations, and one control. Three different sites were sampled for each plantation type and control, except for the mixed species plantations where four sites were sampled. The plantations differ in the planted species and in distance from primary forest. They are located on similar soil and are of almost the same age (table 1).

Six sample plots of 25 m^2 were randomly distributed in each plantation site - corresponding to a total sampling area of 150 m^2 per site. No plots were placed in a buffer zone of 5 meters from the edges of the plantations, to avoid a potential edge effect. Within the plots all regenerating woody vegetation of more than one-meter height was measured and samples were collected. Species, growth form, height and number of individuals of the plants were recorded. Occurrence of specimens of more than 2,5 cm diameter in breast height was noted. The plant samples were identified at the National Herbarium in Quito.

Parameters hypothesised to influence regeneration were measured from the middle of each plot. Vegetation cover in three layers (1-4 metres, 4-10 metres and 10-30 metres) was estimated in percentages to the nearest ten percent. Ground vegetation cover was estimated in percentages, totally and for different families, to the nearest ten percent. Volume of standing wood in the plantations was measured by means of a relascope. Remnant trees were recorded separately in the relascope measurements. A camera was used to record canopy cover with photos taken at one-meter height. These pictures were later analysed in Imagetool to get percentage canopy cover.

As the data were not normally distributed, Kruskal-Wallis ANOVA was used to compare abundance and species richness of the regeneration, canopy cover, basal area and ground vegetation among plantation types and control. Mann-Whitney U-test was used to find significant differences between treatments. Correlations were run using Spearman coefficients.

A similarity matrix of Bray-Curtis coefficients based on to what extent the sites shared the same species was constructed for a multidimensional scaling (MDS) analysis. The MDS analysis was used to find similarities in species composition among sites.

Results

A total of 1818 individuals were recorded. Of these, 1742 were identified to at least family level and in most cases species level. They represented 180 species of 39 families. Of these, 105 (58 %) were trees, 18 (11 %) were shrubs, 6 (3 %) were either shrubs or trees and 51 (28 %) were lianas. 77 of the species (43 %) were only present in one sample. An additional 28 (16 %) were present in two samples. It was not possible to identify 76 individuals.

The tree species represented in the regeneration were mainly short-lived pioneers (like *Cecropia, Solanum*) and long-lived pioneers (*Cordia, Jacaranda, Ficus, Vochysia, Vismia*).

Piperaceae was by far the most abundant family, with 606 individuals – almost five times as much as the second most abundant family, Euphorbiaceae. Piperaceae was most abundant in all plantation types. None of the planted species was found regenerating.

Abundance (mean number of individuals per sample plot) and species richness (mean number of species per sample plot) of the regeneration show a consistent pattern, with the *Inga* plantations highest, the mixed plantations lowest and the control in between. Significant differences between the plantation types were found for species richness (Kruskal-Wallis $p<0.001$, $n=78$) where the *Inga* plantations differ significantly from the mixed species plantations (Mann-Whitney U-test: $p<0.001$) (Fig. 1). Abundance also differs significantly between the plantation types (Kruskal-Wallis $p<0.001$, $n=78$) again with *Inga* differing from the mixed plantations (Mann-Whitney U-test: $p<0.001$) (Fig. 2).

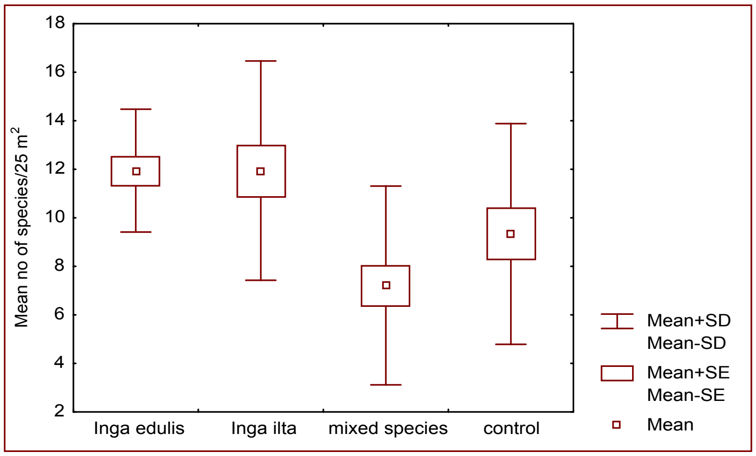

Figure 1. Differences among plantation types in species richness of the regeneration. P<0.001, n=78.

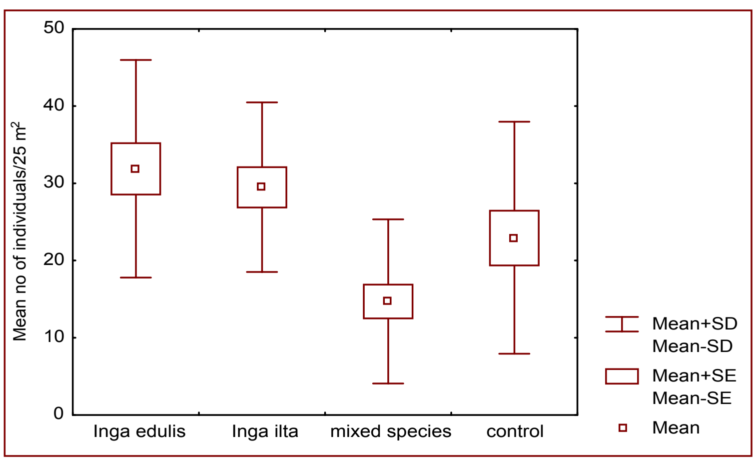

Figure 2. Differences among plantation types in abundance of the regeneration. P<0.001, n=78.

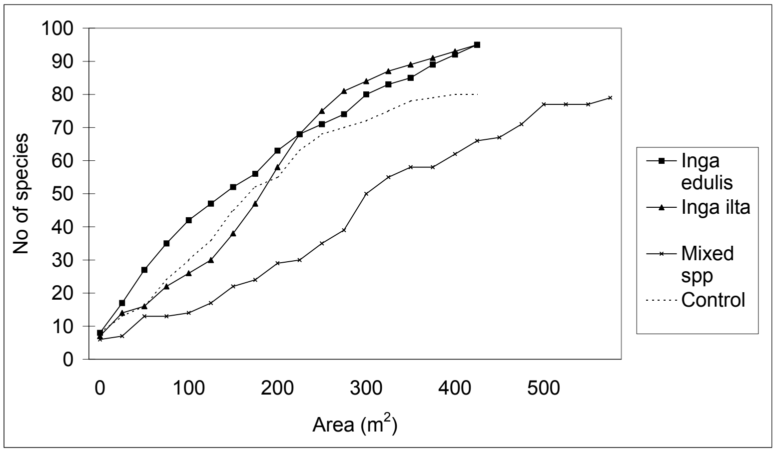

Figure 3. Cumulative number of species with increased sampling area in the different plantation types.

The *Inga* plantations and the controls accumulate species at a similar rate until a sampled area of approximately 300 m^2. At larger areas the control group shows a tendency to reach an asymptote. The mixed plantations have a considerably slower species accumulation rate (Fig. 3).

Trees were the most species rich growth form among all plantation types. The results show significant differences in the abundance of trees, where the *Inga* plantations had more trees than the mixed plantations (Mann-Whitney U-test: $p<0.001$) and the controls ($p=0.014$). The *Inga* plantations also had more shrubs than both the mixed plantations (Mann-Whitney U-test: $p<0.001$) and the controls ($p=0.005$) (Fig. 4). The species richness also differ; the *Inga* plantations had significantly more shrub species (Mann-Whitney U-test: $p<0.001$) and tree species ($p<0.001$) than the mixed plantations, and more tree species than the controls (Mann-Whitney U-test: $p=0.002$) (Fig. 5). No differences were found for lianas.

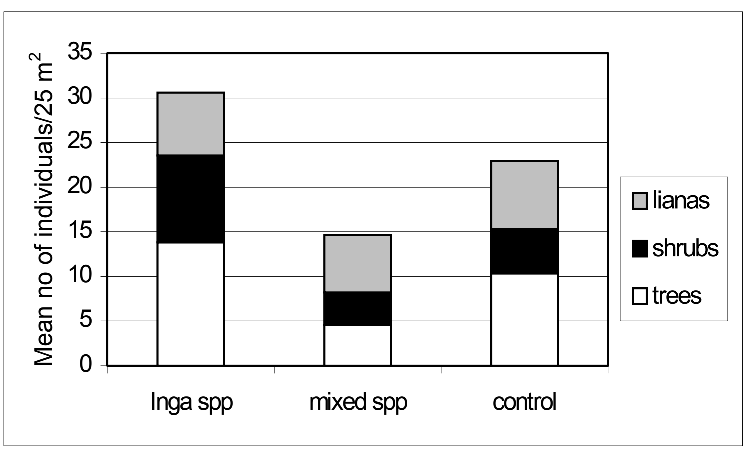

Figure 4. Relations between number of individuals of different growth forms in the regeneration among the plantation types.

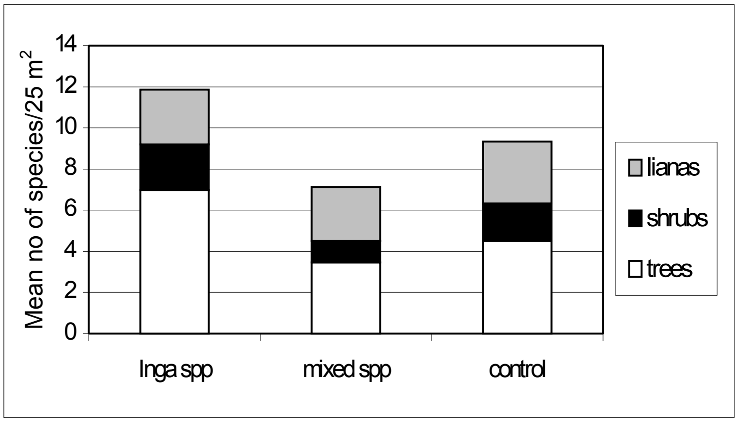

Figure 5. Relations between number of species of different growth forms in the regeneration among the plantation types.

The exposure of the site seems to have a strong negative effect on both species richness and abundance. The most exposed sites (i.e. with least trees around them) of each plantation type (except the *Inga edulis*, that was not represented by any exposed site) and control were also the most poor in species and individuals, respectively, in the regeneration. One of the control sites was surrounded by *Inga* plantations on three sides, i.e. not exposed at all, and was also the highest in species and abundance among the controls.

The results from the MDS ordination show that the *Inga* sites are similar in species composition (Fig. 6, stress: 0.120). They form a group together with two of the control sites (CO 1 and CO 2) and one of the mixed sites (MIX 3). Three of the mixed sites form a group which clearly differs from the first group. The most exposed control site differs from all the other sites in species composition (CO 3). Note the difference in species composition within the control group.

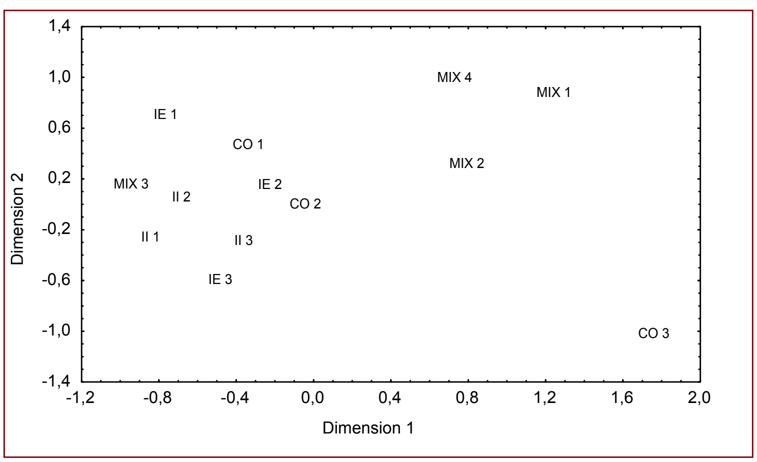

Figure 6. MDS ordination of samples in two dimensions, based on Bray-Curtis similarities between samples. Stress: 0.120. IE = *Inga edulis* plantations, II = *Inga ilta* plantations, MIX = mixed species plantations and CO = control.

Canopy cover differed between the plantations, with the *Inga* plantations highest, the mixed species plantations in between and the controls with least canopy cover (Kruskal-Wallis p=0.015, n=77). The *Inga ilta* plantations were significantly separated from both the controls (Mann-Whitney U-test: p=0.002) and the mixed plantations (p=0.049). The variation in canopy cover was much higher in the controls and mixed species plantations. Basal area differed with the *Inga* plantations having significantly larger basal area than the controls (Mann-Whitney U-test, p=0.006). The *Inga* plantations had significantly less ground vegetation than both the mixed species plantations (Mann-Whitney U-test: p<0.001) and the controls (p=0.025). Grasses (Poaceae) was the most dominant family in the ground vegetation, accounting for more than 50 % of the cover in 23 % of the sample plots.

Species richness was barely correlated with canopy cover (Spearman R=0.2194, p=0.055, n=78). Abundance was not correlated with canopy cover. Negative correlations were found between species richness and ground vegetation (Spearman R=-0.4145, p<0.001, n=78) (Fig. 7) and abundance and ground vegetation (R=-0.5294, p<0,001, n=78) (Fig. 8). The amount of grass in the ground vegetation was also negatively correlated with species richness (Spearman R=-0.4305, p<0.001, n=77) (Fig. 9) and abundance (R=-0.4906, p<0.001, n=77) (Fig. 10). Basal area was weakly correlated with species richness (Spearman R=0.3401, p=0.002, n=78) and abundance (R=0.2333, p=0.040, n=78). No correlation was found between species richness and distance from primary forest.

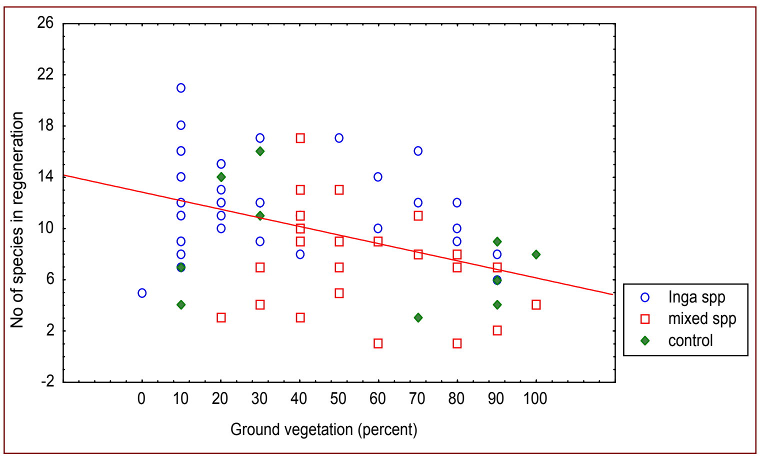

Figure 7. Correlation between species richness of the regeneration and ground vegetation cover. Spearman R=-0.4145, p<0.001, n=78.

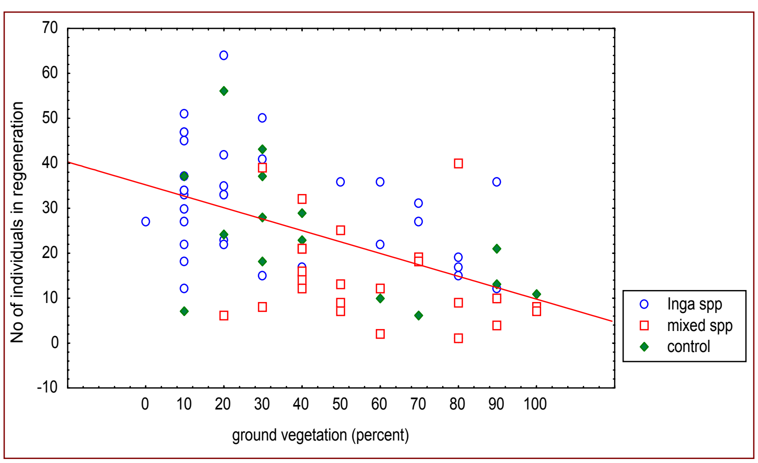

Figure 8. Correlation between abundance of the regeneration and ground vegetation cover. Spearman R=-0.5294, p<0.001, n=78.

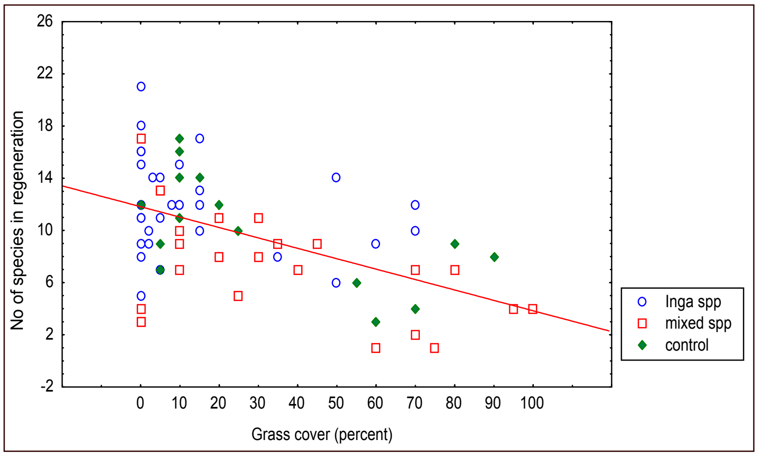

Figure 9. Correlation between species richness of the regeneration and grass cover in ground vegetation. Spearman R=-0.4305, p<0.001, n=77.

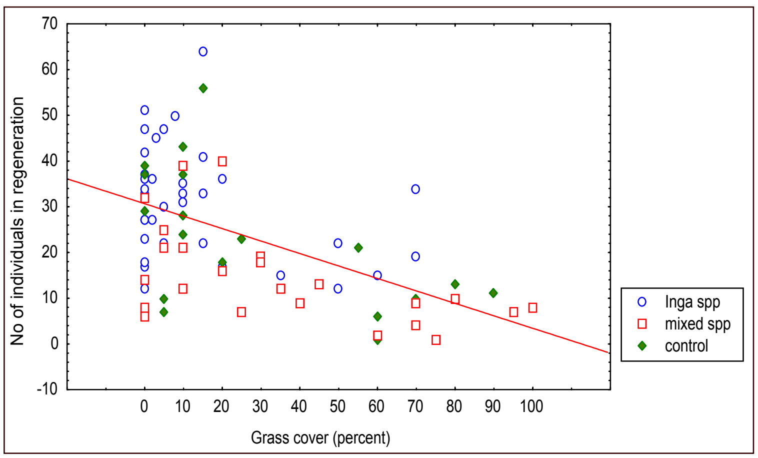

Figure 10. Correlation between abundance of the regeneration and grass cover in ground vegetation. Spearman R=-0.4906, p<0,001, n=77.

The pattern of vertical layering of the vegetation differs between the plantation types (Fig. 11). The lowest layer (1-4 meters) represents the regeneration. It is most dominant in the *Inga* plantations and the control. The middle layer (4-10 meters) is most dominant in the mixed plantations, where it is composed mainly of the planted trees. In the *Inga* plantations and the control it consists of the regenerating trees and the mahoganies. In the highest layer (10-30 meters) less than 10 % is covered by vegetation in the controls and mixed plantations. In the *Inga* plantations, this layer represents the crowns of *Inga*.

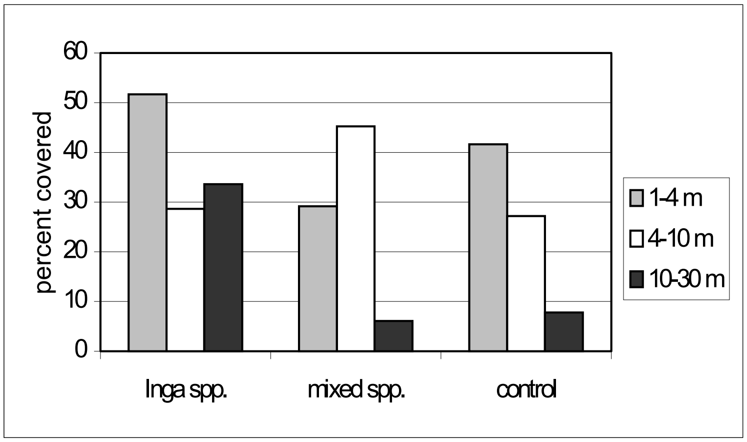

Figure 11. Differences in vertical layering of vegetation among the plantation types.

The results are summarised in Table 2. The *Inga* plantations had most individuals and species in their regeneration, and were significantly separated from the mixed plantations, but not from the controls. The controls had less basal area than the *Inga* plantations. There was a difference between the *Inga ilta* and *I. edulis* plantations in the amount of canopy cover; *I. ilta* had more canopy cover than both the controls and the mixed plantations, whereas *I. edulis* did not differ significantly from any of them. The *Inga* plantations together differed significantly from both controls and mixed plantations in canopy cover. The *Inga* plantations had less ground vegetation than the mixed plantations, and *I. ilta* had less ground vegetation than the controls.

Table 2.
Mean abundance, species richness, basal area, canopy cover and ground vegetation for different plantation types and control. Standard deviations in parentheses. Differences among plantation types are statistically significant when the standard error is followed by different letters ($p<0.05$).

	No of individuals /sampling plot	No of species /sampling plot	Basal area m^2/ha	Canopy cover %	Ground vegetation %
1. Inga edulis (n=18)	31.9 (14.1)a	11.9 (2.5)a	9.0 (1.7)a	90.6 (5.4)ab	36.1 (25.7)ab
2. Inga ilta (n=18)	29.5 (11.0)a	11.9 (4.5)a	9.5 (3.3)a	92.1 (8.0)a	28.9 (29.9)a
3. Mixed species (n=24)	14.7 (10.6)b	7.2 (4.1)b	7.9 (3.5)ab	84.0 (16.1)b	58.3 (23.2)c
4. Control (n=18)	22.9 (15.0)ab	9.3 (4.6)ab	7.2 (2.1)b	79.9 (16.7)b	48.3 (30.4)bc

Discussion

The regeneration in the *Inga* plantations is richer in individuals and species than the mixed plantations, which were established for reforestation. A very surprising result is that the mixed plantations have less regeneration than the controls too, although not significantly. These results are thus contradictory to the widely held opinion that mixed plantations are preferable when the aim is to rehabilitate forest. A rationale for promoting mixed plantations is that they create a wider variability of habitat conditions for seed dispersers, which renders possible a greater diversity of plant species in the regeneration (Carnevale & Montagnini 2001). The regeneration in the plantations in this study is probably not limited by seed availability, as shown by the non-existing relationship between distance to primary forest and regeneration abundance and species richness.

Many studies (e. g. Guevara et al. 1992, Elmqvist et al. 2002) have shown remnant trees to be important as nuclei in succession, attracting seed dispersers like bats and birds. Many of the species found regenerating in this study are also represented as remnants in the study area - like *Cordia*, *Simira*, *Guarea* and *Cabralea* – suggesting that they are important as seed sources. However, more remnants were recorded in the mixed plantations (28) compared with the *Inga* plantations (6) and the controls (0). Even though the relascope method involves uncertainties in these figures, as the same tree may have been counted more than once, they are sufficiently different to conclude that the mixed plantations have more remnant trees. The remnants are thus not an important factor affecting succession at this site, another reason to believe that seed availability is not a limiting factor.

Instead it appears like the amount of ground vegetation, and especially the amount of grass, is the most important factor regulating woody regeneration. The amount of ground vegetation is linked to the amount of canopy cover; increased canopy cover means decreased ground vegetation cover. A dense canopy shades out grass and thereby reduces competition and allows regeneration of woody species. However, the link is not that simple in this case, as the mixed plantations have more canopy cover than the controls coupled with more ground vegetation. The failure of the mixed plantations to accumulate woody regeneration is probably due to the structure of the canopy. As the trees are of different species, they have different growth rates and develop different crown shapes. As the canopy is not continuous, these plantations allow much light to reach the ground and thus fail to shade out the grass.

The *Inga* are fast-growing, and as they are of the same species and the same age, have developed a dense and even canopy and successfully shaded out the ground vegetation, at some places completely. An even-aged, monospecific stand of trees is of course an anomaly in these regions, and does not appear as something to strive for in a rehabilitation context. According to these results, however, the herbaceous ground vegetation is the most serious barrier to succession. The *Inga* plantations are most effectively overcoming that barrier.

Another explanation for the advanced regeneration in the *Inga* plantations could be that the *Ingas* have a markedly more positive effect on the soil, and thus have enhanced the germination of seeds and the establishment of seedlings. As no soil measurements were made, no such conclusions can be drawn.

The plantations are fairly small, all but one of the mixed plantations being less than 3000 m^2. It is likely that the surroundings have a considerable impact on the conditions in such small areas. Although no measurements of site exposure were made, a general impression is that the amount of trees standing around the sites has a strong influence. The sites with the lowest figures for species richness and abundance in the regeneration of *Inga ilta*, mixed plantations and controls, respectively, are also the most exposed sites of each group.

Exposure has strong effects on the microclimate of the site, with more pronounced temperature fluctuations and differences in humidity and water availability (Bazzaz 1991). This must be regarded the normal state for pastures, thus the most exposed control site probably represents the most true value for the control group. In contrast, the other two control sites are bordering or surrounded by *Inga* plantations. The low amount of ground vegetation in these sites is probably due to impact from *Inga*. This circumstance could be responsible for the high regeneration in these sites, with them grouping together with *Inga* in the MDS ordination. They must be regarded as not representative. If all of the control sites had been as exposed as the most representative (most exposed) site, it is likely that their regeneration would have been poorer than in the mixed plantations.

No explanation has been found for the differences in species composition within the mixed plantations group, with one of the plantations clearly separating from the other three.

There were no differences in abundance or species richness of lianas among the groups, in contrast to significant differences in trees and shrubs. Lianas were thus proportionally more abundant in mixed plantations and pastures. Lianas are considered an element of early succession, occurring in high numbers in light environments such as riverbanks, fragmented forests and gaps (Schnitzer & Bonger 2002, Whitmore 1991). The relatively lower importance of lianas in the *Inga* plantations suggests that these sites have "skipped a step" in succession towards dominance of trees.

Contrary to the common advice that plantations with mixed species is preferable for reforestation, these results show that *Inga* is better suited as plantation species for fast accumulation of woody regeneration in their understories. However, the quality of this regeneration can be discussed. Most of the species found are from typical pioneer genera, e.g. *Piper, Cecropia, Vismia, Pavonia,* and *Solanum.* The composition of the future forest will thus be different from primary forests in the area. It appears likely that it could take a long time before late-successional primary forest species get established in the plantations. That was also the rationale for choosing these species in the reforestation (i.e. mixed) plantations. Primary forest species are generally large-seeded and have poor capacities for dispersal (Whitmore 1991). Studies from Brazil show that large-seeded tree species (Parrotta & Knowles 2001) and the animals who disperse them (Parrotta et al. 1997) are under-represented in plantations. Limitations in the seed availability of these species in the study area could be an important factor influencing diversity at a later successional stage. If the initial barriers to seedling establishment are overcome, mixed plantations are probably more effective in accumulating species in their regeneration, as suggested in previous studies. Possibly the diversity of seeds arriving to these plantations are higher than in the *Inga* plantations, although they cannot germinate under the prevailing conditions. Seed rain in the area will be the subject of investigation later.

Primary species are also characterized by shade tolerance and slow growth (Whitmore 1991). They are the first to disappear in disturbed environments. An approach to future rehabilitation could be to use *Inga* initially, to enrich the soil and shade out the grass, and later enhance the recruitment of late-successional species by planting mature forest species under the canopy of *Inga*. This strategy would also probably reduce the costs of establishment and improve the survival of the mature forest species. As they are not very competitive in open environments, they require quite a lot of management.

The performance of the *Inga* plantations clearly shows that tree plantations can be a successful tool to catalyze succession on degraded land. The cost of establishing these plantations is limited to the cost of the seedlings and the time used for planting and weeding. As mentioned in the introduction, forest-covered land has a number of ecological advantages over open land, such as carbon storage, water regulation, biodiversity conservation and improved landscape connectivity. Forests also have a number of advantages over degraded pasture for the landowner, as they produce commodities, marketable as well as non-marketable. Apart from the planted species in this case, the regeneration includes many useful species; for timber, fruits and medicines for example. The landowner could thus have a viable production of commodities to a limited cost and effort, in an ecologically sound production system.

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Appendix 1.

Map of Jatun Sacha reserve with the study area at Cabañas Aliñahui marked (Instituto Geografico Militar 1988). The squares are 1 km^2.

Appendix 2.

Presence of families in regeneration in the plantation sites. Ie=Inga edulis, Ii=Inga ilta, Mix=mixed species, Con=control.

Site	Ie 1	Ie 2	Ie 3	Ii 1	Ii 2	Ii 3	Mix 1	Mix 2	Mix 3	Mix 4	Con 1	Con 2	Con 3	Total
Acantaceae	0	39	0	0	0	0	0	0	0	0	0	0	0	39
Annonaceae	1	2	0	1	1	1	0	0	1	0	2	0	0	9
Apocynaceae	0	1	3	1	1	7	0	3	3	0	0	0	3	22
Araceae	5	0	8	1	17	2	1	8	1	25	7	24	0	99
Araliaceae	2	1	0	0	1	0	0	1	2	0	0	0	0	7
Arecaceae	0	1	0	5	1	0	0	0	4	0	1	1	0	13
Asteraceae	2	5	0	4	0	0	5	9	0	3	2	6	3	39
Bignoniaceae	4	0	13	20	20	5	1	1	12	19	8	1	7	111
Bombacaceae	0	0	0	0	0	1	0	0	0	1	1	0	0	3
Boraginaceae	4	3	0	0	10	3	0	2	3	2	1	3	1	32
Clusiaceae	4	3	0	0	1	3	0	1	0	2	3	0	1	18
Combretaceae	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Convolvulaceae	0	0	0	0	0	0	0	3	2	0	17	0	0	22
Cucurbitaceae	3	2	5	6	5	4	6	0	1	4	3	3	0	42
Euphorbiaceae	6	5	36	1	4	17	0	1	1	2	10	2	40	125
Fabaceae	1	5	10	4	12	3	4	4	11	8	13	2	7	84
Flacourtiaceae	2	1	1	2	4	1	0	1	1	0	0	0	0	13
Gesneriaceae	0	1	2	0	0	0	0	0	0	0	1	0	0	4
Lauraceae	0	7	1	0	0	0	0	0	0	0	0	0	0	8
Lecytidaceae	0	4	0	0	0	0	0	0	0	0	0	0	0	4
Malpighiaceae	0	0	0	0	0	0	2	0	0	0	0	0	0	2
Malvaceae	3	3	8	0	6	6	0	0	1	0	5	2	0	34
Melastomataceae	1	18	2	0	7	1	1	5	3	2	4	3	1	48
Meliaceae	3	5	5	3	2	5	0	0	0	2	2	0	0	27
Monimiaceae	2	0	0	0	1	0	0	0	0	0	0	0	0	3
Moraceae	8	11	5	5	22	6	1	7	8	1	5	6	1	86
Myristicaceae	0	6	0	1	3	0	0	1	0	0	0	0	0	12
Myrtaceae	1	4	0	2	12	10	0	2	0	5	1	10	1	39
Passifloraceae	0	0	0	0	0	0	1	0	0	0	1	0	0	2
Piperaceae	33	54	109	50	82	91	4	20	34	11	75	41	2	606
Rubiaceae	30	1	5	6	4	2	0	1	2	3	13	3	2	72
Rutaceae	0	0	2	0	1	0	0	0	0	0	0	0	0	3
Sapindaceae	0	1	15	0	3	3	3	0	18	0	2	1	0	46
Sapotaceae	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Solanaceae	6	5	0	1	1	9	0	2	0	1	1	1	1	28
Tiliaceae	1	0	0	0	0	1	0	2	0	0	5	0	0	9
Urticaceae	6	6	0	8	0	0	0	0	0	0	2	1	0	23
Verbenaceae	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Vochysiaceae	0	0	0	0	0	0	1	0	1	0	1	1	0	4