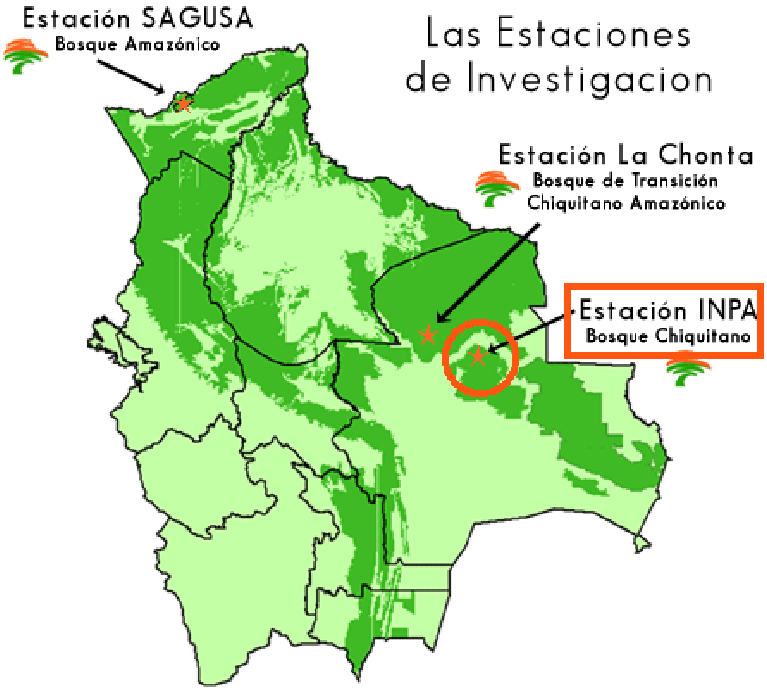
Thesis Forest Ecology and Management

Fire and logging in a Bolivian dry forest: their effects on natural regeneration



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Supervisors:
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Summary

Forest fire and logging have increased in spread, frequency and intensity in Bolivian forests. However the impact of these phenomena on stand development and regeneration is not fully known and therefore it is hard to make management decisions. Most timber species in dry deciduous forest are light-demanding, and have a relatively poor regeneration. It is thought that their regeneration can be enhanced by large scale disturbances, such as logging and especially fire. The objective of this study was to compare consequences of fire and logging in the dry deciduous forest of the private property of Inpa, two years after fire and logging.
The study looked at the effect of fire and microsites on abiotic factors, cover of life forms and regeneration (resprouts or seedlings, shade tolerance classes and commercial species). Three different microsites were sampled in burned and unburned areas. The microsites included the undisturbed forest understory, and logging gaps, which were subdivided in the trunk zone (where the tree stump of the logged tree was left) and the crown zone (where the crown of the logged tree was left). In all the 6 different treatment combinations 15 regeneration plots of 1x5 m were established. Therefore in total 90 plots were measured (2 fire treatments x 3 microsites x 15 plots per treatment combination).

After fire I found an increase in ash cover and charring height, pH became higher, and there was more mineral soil cover and a higher canopy openness. On the other hand, soil bulk density decreased. All these changes are indicative of higher resource availability and better growing conditions. Also forbs cover increased, while tree cover and cover of ground bromeliads decreased. After fire there were more pioneers, and there was an increase in abundance of two commercial species (*Anadenanthera columbrina* and *Tabebuia spp.*). But there was also a decrease in total number of tree regeneration (both seedlings and resprouts), a decrease in number of species and a decrease of abundance of 5 woody species of which one was a commercial species. The decrease in amount of regeneration was probably due to burned advanced regeneration, seed predation, low seed viability and high seedling mortality during the dry season.

In trunk-sites there was the highest density of tree regeneration, species number, number of resprouts, number of pioneers tree stems and a higher abundance of three woody species of which one was a commercial species (*Tabebuia spp.*). In the crown sites I found more ash cover than in the understory sites, highest charring height, highest pH and highest cover of woody debris. In the understory sites highest water infiltration rate and highest litter cover were found. In the trunk- and crown sites the highest cover of trees and climbers was found.
All treatment combinations showed a J-shaped size structure of woody plant regeneration, indication continuous regeneration.

Fire, logging and their combination all increase opportunity for regeneration of trees and other live forms. And all show a structure that suggest sufficient and continuous woody regeneration. But there is also an increase of climber abundance which can form a threat if the abundance is high enough negatively affect the regeneration of tree species. If fire frequency and intensity are too high, then the vegetation will not get the change to regrow. If logging intensity is too high, no seed and shelter trees will be left for regeneration. But gaps both caused by fire and logging should be large enough to stimulate the regeneration of light- demanding commercial species. Apparently for managing this type of forest is necessary to found an adequate combination of logging intensity and fire intensity and frequency that would allow benefiting from the positive effects of these disturbance on regeneration without overexploiting the forest.

Resumen

Los incendios forestales y el aprovechamiento forestal han aumentado en extensión, frecuencia e intensidad en los bosques de Bolivia. Sin embargo, no se conoce completamente el impacto de estos fenómenos en el desarrollo del rodal y en la regeneración, y por lo tanto, es difícil tomar decisiones de manejo. La mayoría de las especies comerciales de los bosques secos bolivianos son especies demandantes de luz, que tienen problemas de regeneración. Se piensa que la regeneración de estas especies depende de perturbaciones de gran escala, como ser incendios forestales y aprovechamiento. El objetivo de este estudio fue comparar las consecuencias del fuego y el aprovechamiento en un área del bosque seco de la propiedad privada Inpa, dos años después del fuego y del aprovechamiento. El estudio evaluó el efecto del fuego y micrositios en factores abióticos, cobertura de formas de vida y regeneración (rebrotes o plantines a partir de semillas, gremios ecológicos, y especies comerciales). Se muestreo tres diferentes tipos de micrositios en áreas quemadas y no quemadas. Los micrositios fueron el sotobosque no perturbado y claros de aprovechamiento, los cuales fueron subdivididos en la zona del tronco (donde se dejo el tocón del árbol aprovechado) y zona de la copa (área donde quedo la copa del arbole aprovechado). En todas las 6 combinaciones de tratamientos se establecieron 15 parcelas de 1x5 m. Por lo tanto, en total se midieron 90 parcelas (2 tratamientos del fuego x 3 micrositos x 15 parcelas por combinación del tratamiento)

Después del fuego se encontró un incremento en la cobertura de ceniza, altura de carbonización, pH, cobertura de suelo mineral y apertura del dosel. Por otro lado, la compactación del suelo disminuyo. Todos estos factores indican una mayor disponibilidad de recursos y mejores condiciones de desarrollo para las plantas. También la cobertura de hierbas aumentó, y disminuyó la cobertura de árboles y bromelias. Después del fuego, se encontraron más plantas pioneras y una mayor abundancia de dos especies comerciales (*Anadenanthera columbrina* and *Tabebuia spp.*). Pero también hubo una disminución en la abundancia total de la regeneración de especies arbóreas (tanto de plantines de semillas como de rebrotes), en el numero de especies y una disminución en la abundancia de 5 especies maderables, entre ellas una especie comercial. La disminución en la abundancia de la regeneración se debe probablemente a que la quema de la regeneracion avanzada, predación de semillas, baja producción de semillas y una alta tasa de mortalidad de plantines durante la época seca.

En las áreas del tronco se encontró una mayor densidad de regeneración de especies arbóreas, mayor numero de especies, mayor cantidad de rebrotes, mayor abundancia de especies pioneras, y la mayor abundancia de tres especies arbóreas, siendo una de ellas comercial (*Tabebuia spp.*). En las áreas de la copa se encontró una mayor cobertura de ceniza que en el sotobosque, la mayor altura de carbonización, el pH más alto y la mayor cobertura de material leñoso. En el sotobosque se encontró mayor grado de infiltración y mayor cobertura de hojarasca. En las zonas del tronco y de la copa se encontró una mayor cobertura de árboles y bejucos. Todas las combinaciones de tratamientos mostraron una estructura J-invertida de la regeneración de las especies leñosas, sugiriendo una regeneración continua.

Los incendios forestales, el aprovechamiento forestal y las combinaciones mostraron una estructura de población que sugiere una regeneración continua y adecuada de especies arbóreas. Sin embargo, también se evidencio un aumento de la abundancia de bejucos, los cuales pueden ser una amenaza si su abundancia llega a incrementar y a afectar a la regeneración natural. Si la frecuencia y la intensidad del fuego es demasiado alta, la vegetación no tendrá chance de recuperarse. Si la intensidad de aprovechamiento es demasiado alta, habrá pocos árboles semilleros y árboles remanentes para promover la regeneración de especies comerciales. Por otro lado, los claros producidos por el fuego o por el aprovechamiento deben ser lo suficientemente grandes como para estimular la regeneración de especies comerciales demandantes de luz. Aparentemente para manejar este tipo de bosques es necesario encontrar una combinación adecuada de intensidad de aprovechamiento e intensidad y frecuencia de fuego que permita beneficiarse del efecto positivo que tienen estos disturbios en la regeneración de especies comerciales sin sobreexplotar el bosque.

1. Introduction

The forest sector in Bolivia generates an annual income of 130 million dollar by export and a direct employment for 50 thousand people (IBIF, 2006). Forest fires causes damage to commercial trees and may reduce the quality of standing timber. This affects the economical and social benefits that can be derived from the forest. Decrease in economic value will likely result in an increase in exploitation intensity, because more trees should be logged to gain the same income as before, and with an increase in deforestation other land use options become more profitable (IBIF, 2006).

Not only is fire economically important, it has also a lot of other effects like changing composition and structure of a forest (Cochrane, 1999; Grayson, 2001; Kennard et al., 2002), reducing seed availability (Van Nieuwstadt et al., 2001), affecting animals because of habitat destruction and forest patch isolation (Steininger et al., 2001) and therefore changing distribution and number of animals (Grayson, 2001). Fire also causes emission of greenhouse gasses (Gillet, 2004) and people can lose their homes because of it. There are also concerns about human health because of the emission of smoke (Pyne et al., 1996; Cochrane, 2003: Bradley, and Millington, 2006). In Bolivia near Santa Cruz, Cobija and Trinidad for example, respiration diseases are more and more frequent (IBIF, 2006).

Forest fires are initiated because of human or natural causes (Di Bella et al., 2006; IBIF, 2006). During the last decades forest fires are occurring more frequently in the tropics. In Bolivia for example the number of forest fires raised from 5000 in 1999 to 28000 in 2004. This increase in forest fires is also due increased population pressure, because Bolivian forest dwellers use fire to clear the forest and make the area suitable for agriculture (IBIF, 2006). When doing this, there is a chance that fire will escape into the surrounding forest (Pinard et al., 1999; McDaniel et al., 2005; Cochrane, 2003; Otterstrom et al., 2006). Slash and burn for logging can because of these escapes cause uncontrolled fire.

Not only slash and burn increases fire susceptibility. Logging is one of the main causes for a forest to become more susceptible to fire (Uhl and Kauffman, 1990). In Bolivia most timber is obtained from natural forests (Fredericksen et al., 2003). Logging can be done in different intensities, but even selective extraction of timber with low impact techniques causes damage (Pinard et al., 1999b). Logging opens up the canopy allowing sunlight to reach the forest floor where it dries out the organic debris created by logging. In addition there is a higher amount of combustible material on the floor (IBIF 2006; Nepstad et al. 1999; Cochrane, 2003; Gerwing, 2002; Nepstad, 1998; Blate, 2005). Logged forests can enter into a positive feedback loop where an initial forest fire increases the chance of more intense forest fires (Cochrane et al. 1999; IBIF, 2006). Logged forests are not only more susceptible to fire, but fires in logged forests are more severe because of the extra combustible material (logging waist) on the forest floor (Blate, 2005 and Uhl and Kauffman, 1990).

Areas with logging and agriculture will therefore play a significant role in forest degradation (Gerwing, 2002), but drought itself also adds its bit. During the past decades el Niño events have also become more frequent because of global warming (Timmermann et al., 1999). These droughts will cause dryer conditions in the forest, which becomes more susceptible to fire (Nepstad et al., 1999; Siegert et al. 2001; Cochrane, 2003; Goldammer, 1999; McDaniel et al., 2005).

In Bolivia there is little information about fire ecology and how it effects forest ecosystems (Mostacedo and Fredericksen, 1999). Fires may even favour regeneration of (commercial) species (Kennard, 2002), but how this works in Bolivia is still not fully understood (IBIF, 2006). Forest managers need an understanding of how fire affects the dynamics of the forest if they want to produce a steady supply of timber. The same can be said for logging; sustainability of logging in the tropical forest of Bolivia for the establishment of commercial tree regeneration is a focus for concern (Fredericksen and Mostacedo, 2000). Not only knowledge about tree damage and mortality is needed, also knowledge on environmental conditions that effect regeneration is necessary (Pinard et al., 1999). Applying information from other forest from around the world directly to Bolivia without validating its relevance for the local site conditions will lead to possible failures in prevention plans (IBIF, 2006; Fredericksen et al., 2003), because each forest has its own ecological characteristics and may react in a different way than forests from other parts of the world (Mostacedo et al., 2001).

In 2005 the Bolivian Forest Research Institute (IBIF), in cooperation with the Forest Service of the United States, started to investigate the ecology of forest fires. The main objectives are to learn more about fire ecology in Bolivian forests, to evaluate the fire impact and behaviour in the Chiquitano dry forest and the transition of the Chiquitano-Amazonian forest and to determine the influence of fire in the dynamics of the forest. The results of these studies will be used in campaigns and prevention management in rural communities and will integrate technical and commercial knowledge on fires to stimulate the wise use, and prevent the misuse of fire (IBIF, 2006).

This research institute not only investigates ecology of forest fires but also evaluates the impact of logging on the dynamics and yield of the forest. In this way foresters can make adjustments to guarantee the sustainability of the forest. IBIF monitors experimental parcels for costs and benefits of logging treatments to find the best combination for yield and maintenance of biodiversity and conservation of the forest (IBIF, 2006).

2. Theoretical framework

2.1. Influence of forest fires and logging on abiotic factors

Logging and fire both remove trees from the canopy and therefore creates gaps resulting in a more open canopy (Woods, 1989; Fredericksen and Mostacedo, 2000). Closed-canopy forest are protected from wind (Cochrane, 2003) and fire intensity and spread are kept low by the high moisture content of combustible materials (Kennard and Gholz, 2001). If gaps are created in the canopy, sunlight can reach the forest floor creating a dryer and warmer atmosphere and desiccates combustible material on the forest floors more rapidly (IBIF 2006; Nepstad et al. 1999; Cochrane, 2003; Woods, 1989; Kennard and Putz, 2005; Park et al., 2005; Denslow et al., 1998). Removing trees also reduces biomass (Gould et al., 2002; Gerwing, 2002). Even in a low intensity fire 38% of the living trees can be killed and the majority of saplings and climbers will be lost (Gerwing, 2002; Cochrane and Schulze, 1999).

Fire has also a strong impact on other abiotic factors. During fire, the soils is heated and ash is being deposited (Kennard and Gholz, 2001). Ash increases the nutrient availability and enhances soil pH. After logging there is a deposit of a large mass of fresh litter under the fallen crown which increases nutrient availability (Denslow, et al. 1998; Vitousek and Sanford, 1986). Fires with a soil temperature above 450^{o}C on the other hand reduces soil organic matter content (Hosking, 1938 cited by Kennard and Gholz, 2001). Due to decomposing of fine roots of incoming vegetation the latter effect may be diminished within two years (Kennard and Gholz, 2001). Soil compaction increases during the first year after fire , and this is likely to be caused by a reduction soil organic matter. After a high intensity forest fire ash and soil minerals would fill up the pores left in the soil, contributing to the compaction and increasing bulk density. Logging increases bulk density, because of the used machinery (Guariguata and Dupuy, 1997; Malmer and Grip, 1990; Pinard et al., 1996). Soil compaction reduces water infiltration and the soil structure can take months to years to recover (Kennard and Gholz, 2001).

2.2. Effect of fire and logging on life form distribution

Logging and fire both decrease tree cover (Gerwing, 2002; Otterstrom et al., 2006; Woods, 1989; Uhl and Kauffman, 1990). Logging of 8 trees per hectare for instance can cause a 35% reduction of canopy (Uhl and Kauffman, 1990). But not only trees are influenced by fire and logging, there are also other live forms. Large climbers for example are reduced significantly by fire (Cochrane and Schulze, 1999; Gerwing 2002). Small climbers where to be found in all areas but far more abundant in burned or logged areas, because they can colonize quickly after disturbance (Gerwing, 2002; Fredericksen and Mostacedo, 2000; Woods, 1989). 14 months after logging the climber cover in logging gaps can even be 2,5 times higher than in undisturbed forest understory (Fredericksen and Mostacedo, 2000). Also grasses invade the burned areas (Cochrane and Schulze, 1999; Woods, 1989). Climbers and grasses can increase the amount of combustible material in the forest because they grow very quickly (Cochrane and Schulze, 1999; Woods, 1989) while at the same time impeding regeneration of other plants (Pinnard et al,. 1999; Gould et al., 2002).

Grasses and forbs are most frequent seen as dominant vegetation in logging gaps (Frederickson and Pariona, 2002). And also after fire abundance of forbs increases (kutt and Woinarski, 2007; Sawadogo et al., 2005). Succulents consists of epiphytes (plants growing or attached to other living plants [Townsend et al., 2000]) and ground bromeliads. Ground bromeliads have a intermediate shade tolerance (Francis, 2007). They are very sensitive to fire, and recover slowly (Francis, 2007; Heuberger et al., 2002). Soil disturbance caused by logging also results in a decrease in ground bromeliads (Fredericksen and Mostacedo, 2000).

2.3. Woody regeneration after fire and logging

2.3.1. Regeneration intensity and number of species

In many Bolivian tropical forests, natural regeneration of commercial tree species is very poor (Mostacedo and Fredericksen, 1999). If a gap is created in the canopy, this will lead to an enhanced irradiance and tree regeneration at the forest floor (Whitmore, 1985 cited by Woods, 1989). In logged areas more regeneration is observed (Magnusson et al., 19999; Horne and Mackowski, 1987) as well as in burned areas (Gould et al., 2002). Species richness is positively related to intensity of logging damage (Magnusson et al., 1999). Fire, on the other hand, results in a high mortality and has a negative effect on species richness (Woods, 1989; Saha and Howe, 2003) especially high intensity or high frequency fires (Cochrane and Schulze).

2.3.2. Resprouts and seedlings

There are three major strategies for dry forest trees to respond to forest fires (Otterstrom et al., 2006); to be resistant, resprout, or recruit. In forests that have been exposed to low intensity fires, trees can adjust to the fire damage and will not die. After fire resprouts will grow out of latent buds on the roots or stem base (Otterstrom et al., 2006; Pyne et al., 1996). If they are small, they are mostly killed in the next forest fire. Recruiters use either wind dispersed seed or seeds in serotinous cones (cones that will not open before a fire has passed). Wind-dispersed seeds belong mostly to pioneer species. There are also plants adapted or even depending on fire. These plants will be the first to start growing in burned places together with pioneer species (Pyne et al., 1996).

After a forest fire pioneers are the first species to colonize the area (Gerwing, 2002; Cochrane and Schulze, 1999). With a higher intensity of fire more pioneers are emerging (Cochrane, 2003). Seed dispersal is a very important regeneration mechanism for those species which are not able to resprout (Otterstrom et al, 2006).

Abundance of seedlings is higher than abundant of resprouts in burned and unburned forest (Gould et al, 2002). In logging gaps 89% of all saplings where found to be resprouts (Pariona et al., 2003). Seedling are taller in burned areas than in unburned areas (Kennard and Gholz, 2001; Gould et al., 2002), but tend to be smaller than resprouts (Kennard and Putz, 2005; Gould et al., 2002; Miller and Kauffman, 1998). Resprouts can grow really fast because of large amount available recourses from the mother plant (Pyne et al., 1996)

Seedlings that establish soon after fire benefit from greater nutrient and light availability (Kennard and Gholz, 2001). Seedlings, establishing in the following years may not be as good, because nutrient availability and soil structure tend to decline afterwards.

2.3.3. Shade tolerance classes

Different ecological groups show a different responds to fire and logging. Jardim et al. (2003), Mostacedo et al. (2003), Justiniano et al. (2004), and Markesteijn et al., (2007) classified tree species into groups based on their shade-tolerance. They divided tree species into short-lived pioneer, long-lived pioneers, partial shade-tolerant species and shade-tolerant species. Short-lived pioneers need high light to establish and grow, and have a life span of up to 30 years. Long-lived pioneers need intermediate light to establish. This group grows to the high light environment of the canopy and has a life span longer than 30 years. Partial shade-tolerant species can establish in shaded understory, but need more light in later stage of their lifecycle to reach their maximum stature in the high light of the canopy. Shade-tolerant species can complete their whole lifecycle in shade.

If a gap appears in the canopy, regeneration takes place in response (Whitmore, 1985 cited by Woods, 1989). A small gap will enhance the grow of shade-tolerant species that were already established on the forest floor. Larger gaps (caused by logging or multiple treefall) are usually dominated by newly geminated pioneer species which suppresses the shade-tolerant seedlings. Logging opens up the canopy and allows more sunlight to reach the forest floor (IBIF, 2006; Nepstad et al., 1999; Cochrane, 2003; Gerwing, 2002, Nepstad, 1998). Therefore majority of regeneration in logging gaps are pioneers (Park, 2005). A study of Gerwin (2002) in a evergreen forest showed that in extreme cases 97,7 % of all saplings where pioneers. Fire reduces living biomass (Cochrane and Schulze, 1999; Gould et al., 2002; Gerwing, 2002) which increasing light availability and this stimulates pioneers. These light demanding species grow fast and form a new canopy under which they are unable to regenerate. The light-demanding species will eventually be replaced by shade-tolerant species germinating from seeds produced by neighbouring trees.

2.3.4. Commercial species

Many Bolivian commercial tree species regenerate poorly in managed forests (Mostacedo and Fredericksen 1999). Most species need some kind of site preparation of the forest before regeneration will occur. Logging gaps for example create a better environment for commercial tree regeneration than undisturbed areas (Fredericksen and Mostacedo, 2000; Magnusson et al., 1999). Mostacedo and Fredericksen (1999) studied 68 valuable Bolivian tree species. 66% was valuable for timber, the rest was valuable for non timber products or is playing an important ecological role. They found that 24 of 68 species are shade intolerant, and 31 partial shade tolerant. Most of these commercial species are thus shade intolerant (Mostacedo and Fredericksen, 1999). 22% of the 68 species would easily regenerate in large gaps, or clearings the others needed more site preparation.

In the 1990's Bolivian forest managers also identified prescribed fire as a potential management option to increase regeneration of shade-intolerant commercial species (Kennard, 2004). A recent study of Kennard (2004) shows the highest density of commercial tree regeneration can be found in areas that have been exposed to high-intensity fires sometimes even tree times as much as in the low-fire and non fire plots. The control plot had lowest density of the commercial species. Unfortunately management interventions such as cleaning, prescribed burning and liberation are expensive and currently not considered to be economically feasible in Bolivia (Mostacedo and Fredericksen, 1999).

3. Research objective and research questions

3.1. Research objective

Forest fires and logging are common phenomena in Bolivian forests. The impact of forest fires however is not fully known and may vary with forest type and logging intensity. Without this knowledge it is not possible to make the correct management decisions. Information about how fire, logging and their combination can change the forest structure and diversity of a forest can help the foresters to manage their forests in a more sustainable way.

The main objective of this study is to compare the consequences of fire and logging in a Bolivian dry forest, two years after fire and logging. To evaluate the effect of logging three microsites are compared: the undisturbed forest understory, the trunk zone in logging gaps where the tree stump of the logged tree was left, and the crown zone in logging gaps where the crown of the tree after logging had fallen and was left.

3.2. Research questions

1. How do fire and microsites affect abiotic factors such as light and soil characteristics
2. How do fire and microsites affect cover of different life forms
3. How do fire and microsites affect the mode of woody regeneration (resprouts or seedlings), the type of regeneration (shade tolerance classes) and the regeneration of commercial tree species

3.3. Hypotheses

Abiotic factors

A fire burns the forest vegetation, and therefore two years after the fire the canopy will be more open, on the forest floor there will be ash cover, and trees will be charred. There will be less cover of woody debris and less litter cover, because most combustible material will be burned. There will also be less bare mineral soil because of fast regrowth of vegetation due to an increased light and nutrients availability. Bulk density will be higher, because ash parts will have filled up pores in the soil and as a result of the higher bulk density water infiltration rate will be lower in burned areas.

In the trunk - and crown sites bulk density will be highest because of soil compaction by the logging machinery, and therefore these plots will have a low water infiltration rate as well. In trunk- and crown micro-sites there will also be more woody debris compared to the forest understory because of logging waste and a higher canopy openness because of removed trees. Furthermore less litter cover will be found in these plots because of removal of trees. There will also be less bare mineral soil due to the regrowth stimulated by high light availability after logging.

In the burned crown plots more ash cover and tall charring height will be found because there the highest fire intensity took place due to the large amount of combustible materials left after logging.

Life forms

After fire there will be an increase in cover of climbers, forbs and grasses, because of more available light and nutrients. There will be a decrease in trees and succulent plants, because these are burned and will not have fully recovered two years after the burn.

In the understory sites there will be highest abundance of ground bromeliads, because these are intermediate shade-tolerant. In the trunk- and crown sites highest cover of climbers, forbs and grasses will be seen, because of the available light and disturbed soil.

In the burned crown sites there will be the lowest tree cover, because most of the advanced regeneration will have been burned by the high fire intensity found here due to the high amount of combustible materials left after logging. There will be less tree cover in trunk- and crown plots, because the tree is harvested.

Woody regeneration

After fire there will be a higher density of tree regeneration of seedlings and pioneers. This is because of more available nutrients and light. Most commercial species are considered to be pioneers, therefore they will also be more abundant in the burned area. Species richness will be reduced after fire, due to high mortality of advanced regeneration because of the fire.

In the understory sites most shade-tolerant species will be found, because these areas will be more shaded. In trunk- and crown sites there will be the highest species richness, regeneration density, seedling abundance, resprout abundance, pioneer abundance, and density of commercial species. This will also be because of the disturbance and increased available light caused by logging.

Resprouts will be taller than seedlings in the disturbed areas, because they have the advantage of a large root system and hence, a larger pool of carbohydrate reserves.

4. Methodology

4.1. Study region and site

The Inpa forest is a dry deciduous forest in the lowlands of eastern Bolivia (Killeen, 1998). The forest is classified as dry deciduous (Markesteijn et al., 2007), and is located in the province Ñuflo de Chávez (16°6'S, 61°42'W) of the department of Santa Cruz (IBIF, 2006). The annual average temperature in Conception ca 40 km from the study site is 24,3 °C but can be as low as 8 °C when cold winds from Argentina arrive during the dry time. The annual average precipitation is 1.160 mm with a dry period from April till October (100 mm rainfall per month) (Markesteijn, et al., 2007). Between May and October, the potential evapotranspiration exceeds the mean rainfall in these months and this can result in a water deficit (Figure1). During the dry period 95% of the canopy species lose their leafs (IBIF, 2006).

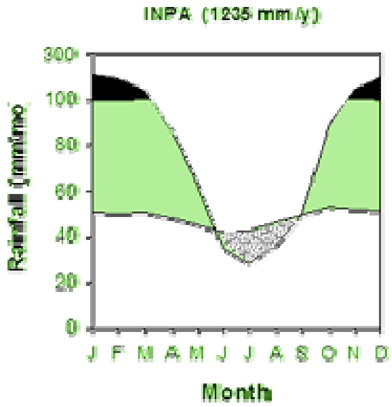


Figure 1
Amount of rainfall in mm/month in Inpa with a total of 1235 mm per year (more accurate data is used in the text).

The study area has a mean altitude of 458 m and is located on the Precambrian Brazilian shield (Markesteijn et al., 2007). The soils are oxisols and are poor in nutrients. The topography varies from slightly flat till undulated.

The canopy is quite open and will reach a height of 22 m with emergent trees op to 30 m (Markesteijn et al., 2007). The density of individuals with a diameter bigger than 10 cm is 437 per ha and the basal area is 19,7 m^2 per ha with a species richness of 34 per ha. 115 tree species with a diameter at breast height of more than 10 cm have been identified. Lianas are very common in the forest (IBIF, 2006). Around 60% of the trees with a diameter < 10 cm has some degree of infection of lianas. The understory is very dense with a large abundance of shrubs and lianas.

At the moment all the area of property Inpa is under forest management. A short rotation cycle of 30 years has been defined and a minimum diameter felling limit of 40 cm is applied. The annual exploited area is approximately 900 ha. The rest of the 30000 ha has the destination of protected area. The forest is being exploited since the 1970-80s (IBIF, 2006). The company INPA parket LTDA, which owns the forest since 2001, considers that 17 of the 115 identified species are commercial. But only nine of these species are being extracted in significant volumes. The forest has received a Forest Stewardship Council (FSC) certification in 1999.

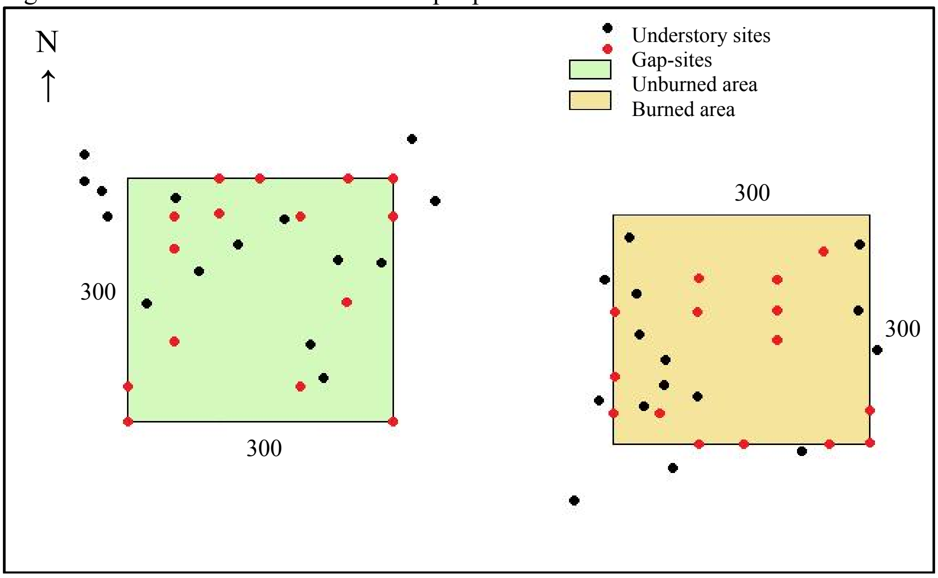
4.2. Experimental design and treatments

To learn more about the different effects of fire and logging in a dry forest in Bolivia, a comparative study has been done in the Inpa forest, two years after an experimental forest fire (the fire has burned in September 2005) in which part of the forest was set to fire and two years after logging (logging took place in December 2004). The logging was normal intensity logging (5 trees/ha) and the trees had to have a diameter of minimal 40 cm to be logged (IBIF, 2006). It has been evaluated how fire and logging effect a-biotic factors, cover of life forms and regeneration. Regeneration will be evaluated in terms of its mode (seedling or resprout), shade tolerance class (shade-tolerant, partial shade-tolerant, long-lived pioneer and short-lived pioneer) and economic value (yes/no). The effect of logging was evaluated using three different microsites; forest understory and two microstes in a logging gap; the trunk zone where the tree stump of the logged tree was left, and crown zone where the crown of the tree had fallen after logging and was left. Unburned understory served as a control.

Between September and December 2007 30 plots of 1 x 5 m were established in each of the three microsites. For each type of microsite 15 pots were placed in the burned area and 15 in the unburned area, providing a total of 90 plots. Understory-plots were randomly selected from the 49 pole locations in the 300 by 300 m selected area both in logged burned and logged unburned area. The selected areas are used for research and had a pole every 50 meter north and every 50 m east until an area of 300 by 300 meter was established. The starting point for the understory plots was first five meter to the east of the pole and then the plot was established 5 meter to the south and one m to the east covering 5 m^2. On the southern border the plots were established in the northern direction. On the eastern border the starting point from the pole was established five meter to the west.

In the logging gaps GPS data were used. The trunk- and crown sites should be considered to be paired, because they were established in the same logging gap. The trunk-plots were established with the stump of the logged tree as the centre. Crown-plots were placed with the first left crown-parts to be found from the trunk, in the centre. Plots were established 2,5 meter north and 2,5 meter south and one meter east from the trunk or crown.

Figure 2 Schematic overview of the sample plots.



Forest with burned (orange) and unburned (green) area (300mx300m) with underbrush-sites (red dots) and gap-sites (black dots) in which the trunk- and crown plots are located. Understory plots were established 1m to the east and 5m to the south, each 5m east of one randomly selected 50m boundary pole. In case of trunk- and crown, plots were established 2,5m north 2,5 m south and 1m to the east from the tree stump or crown left over.

The same methodology was used as in a research of Carlos Pinto, a researcher of IBIF who has evaluated the effect of forest fires in two other forest types in Bolivia (C. Pinto, unpublished report). This includes the following aspects;

- Exact plot location or GPS point of the plots in trunk- and crown-plots were determined.
- The cover of litter (%), woody debris (%) and mineral soil (%) were estimated in the 5 m^2 plot with an eye estimation in whole percentages up to one percentage precise.
- Canopy openness (%) was measured with a densitometer (Forestry suppliers Spherical Crown Densiometers- Concave- model C, Jackson Mississippi) at the height of 1 m as an indicator of light availability. The canopy openness was measured in the middle of all four sides of the plot in northern, eastern, southern and western direction. That gives in total 16 measurements per plot. Later these measurements were combined to one overall percentage for canopy openness.
- The percentage of surface covered by ash was estimated in the 5 m^2 plot by eye in whole percentages up to one percentage precise.
- Charring height (cm) on trees was measured in the plot from the base of the stem vertically upwards with a measuring-tape. If the plot does not contain any trees it was measured on trees within a distance of maximum 10 m from the plot.
- A soil sample was used to measure soil pH. This was done with demineralised-water and pH-paper (Nahita, UNIVERSAL INDICATOR PAPER, Réf: 80910040 **pH 1-14** Batch: 2239-4-384) . Demineralised-water was added to a soil sample from the centre of the plot, and a pH-paper was put in this substance for one second. Then the paper was compared with a reference colour chart. pH belonging to the colour closest to the colour of the pH paper was considered to be the soil pH, and was given in whole numbers.
- Soil compaction was measured with a soil sample taken with a 135 ml volume can (a tomato can) out of the centre of the plot. Soil samples were put in paper envelopes weighted before and after they dried in the oven for three and a half days at 87 ^{0}C. Bulk density (g/cm^3 = g/ml) was then calculated by dividing the weight of the dry sample by the volume of the can, 135 ml.
- Water infiltration rates (in ml/cm^3/s) were measured in every plot using the method of Kennard and Gholz (2001). The centre of the plot was cleared from surface litter and a graduated PCV cylinder (1,57 cm diameter) was inserted in the soil for 5 cm. The cylinder was filled to a certain point and the time the water needed to drop 10 cm was noted. With this the infiltration rates (ml/cm^3/s) was calculated by dividing the surface of the cylinder by the radius and to divide that by the time in seconds which was needed for the water to drop the 10 cm.
- The plants were subdivide into the following life forms; trees, palms, bamboos, climbers (all climbing plants), herbs (forbs and ferns), grasses, ground bromeliads and succulent epiphytes (Appendix 1). The percentage cover of these life forms was estimated in the 5 m^2 plot by eye estimation in whole percentages up to one percentage precise. For a better analysis of regeneration of climbers, woody and herbaceous climbers, was grouped together.
- All tree regeneration from 3 cm and more were counted and identified to species name with help from a tree-spotter. The height (cm) was measured

with use of a measuring-tape or height measurement tool from the forest floor vertically up until the growing point. In case of grown trees (trees larger than 500 cm), basal outline at DBH (diameter breast height; 1,30 m) was also measured (in cm). If plants could not be identified in the field, a herbarium was made to take these plants with us for later identification.

- The mode of regeneration (seedling or resprout) of woody plants was determined using an experienced tree-spotter and if necessary after digging to see if the plant was a seedling or a resprout.
- Woody plants were subdivided into 4 ecological groups; short-lived pioneer, long-lived pioneers, partial shade-tolerant species and shade-tolerant species. Short-lived pioneers need high light to establish and grow, and have a life span of up to 30 years. Long-lived pioneers need intermediate light to establish. This group grows to the high light environment of the canopy and has a life span longer than 30 years. Partial shade-tolerant species can establish in shaded understory, but need more light in later stage of their lifecycle to reach their maximum stature in the high light of the canopy. Shade-tolerant species can complete their whole lifecycle in shade. Trees were divide into these groups based on data from Jardim et al. (2003), Mostacedo et al. (2003), Justiniano et al. (2004), and Markesteijn et al., (2007). If a particular specie was not mentioned in the data that specie was classified as UK (Un Known). Also a shade successional index was made for the different treatment combinations. This was accomplished by making a mean index per plot based on all available woody plants in this plot. The plants were classified as 1 if they were shade-tolerant, 2 if it was a partial shade-tolerant, 3 for long live pioneers and 4 if it was a short live pioneers. The sum of the classification was divided by the number of plants in the particular plot and the result was the succesional index per plot. The shade succesional index per treatment combination is the mean of the succesional index of the 15 plots of one treatment.
- Identified tree species were categorized in commercial and non commercial valuable species based on data from IBIF. Species considered to be of commercial value are; *Piptadenia viridiflora* (Cari Cari Colorado), *Anadenanthera colubrina* (Curupau), *Aspidosperma tomentosum (*Jichituriqui amarillo*)*, *Aspidosperma subincanum (*Jichituriqui Blanco*), Sweetia fruticosa* (Mani), *Caesalpinia pluviosa* (Momoqui), *Machaerium acutifolium* (Moradillo), *Machearium scleroxylon* (Morado), S*pondias mombin* (Azucaro or Ocorosillo), *Hymenaea courbaril* (Paqujo), *Pogonopus tubulosus* (Quina), *Guibourtia chodatiana* (Sirari), *Tabebuia serratifolia* (Tajibo Amarillo), *Tabebuia impetiginosa* (Tajibo Negro), *Centrolobium microchaete* (Tarara Amarilla), *Platymiscium ulei* (Tarara Colorada) and *Machaerium villosum* (Tipa).

4.3. Data analysis

For the statistical analyses the plot is the unit of replication. There are 90 plots in total (2 fire treatments x 3 microsites x 15 replicates per treatment combination). The influence of fire and microsite on abiotic factors, cover of different life forms and regeneration was evaluated using a two-way ANOVA. A Tuckey post-hoc test was performed to show differences between al 6 treatment combinations. For those variables with unequal variances a non-parametric Kruskall-Wallis was used. The results of the non-parametric Kruskal-Wallis tests were consistent with the results of the ANOVAs. This means that the unequal variances did not confound the results to a significant extend, and therefore also for these variables the results of the ANOVAs are reported. This was done because the ANOVA is more powerful, and then also an evaluation can be made to determine if there is a significant interaction between logging and fire. To determine the difference between the height of seedling and resprouts an independent-samples t-test was used. In this t-test only seedlings and resprouts from the burned plots were used, to make sure that the regeneration was not older than two years. In this test the plants were the units of replication. Furthermore a X^2 test was used to distinguish the regeneration of the most abundant tree species between fire - no fire and between microsites. For this test I only considered those species (10 in total) with an abundance of at least 10 trees in all treatment combinations combined. With the X^2 test I tested if the distribution of these regeneration trees was significantly different between fire and no fire areas. The same was done for distribution in different microsites. For all tests differences were considered statistically significant at $P \leq 0,05$.

5. Results

Table 1
Two way ANOVA with the effect of fire treatment and microsite on abiotic factors, life form cover and woody regeneration. F values (F), the significant differences (P), coefficient of determination (R^2) and number of plots used in the statistical test (N) are given. Significant difference is accepted if $p \leq 0.05$ and is described in bold. Fire treatment consists of no fire and fire. Microsite consists of understory, trunk and crown. $_1$= log transformation, $_2$= square root transformation $_3$= arcsin transformation 1 df (degree of freedom) for fire, 2 df for microsites and 2 df for interaction.

	Fire		Microsites		Interaction		R^2	N
	F	P	F	P	F	P		
Abiotic factors								
pH	42.15	**<0.001**	3.97	**0.022**	0.04	0.964	0.37	90
Water infiltration rate$_2$ (ml/cm^3/s)	<0.001	0.995	5.63	**0.005**	2.81	0.066	0.17	90
Ash cover (%)	13.99	**<0.001**	3.55	**0.033**	3.55	**0.033**	0.25	90
Charing height$_2$ (cm)	124.45	**<0.001**	12.78	**<0.001**	12.78	**<0.001**	0.68	90
Litter cover$_3$ (%)	1.71	0.194	46.35	**<0.001**	3.81	**0.004**	0.56	90
Woody debris$_1$ (%)	0.42	0.521	4.58	**0.013**	8.82	**<0.001**	0.25	90
Minsoilcover$_1$ (%)	23.67	**<0.001**	0.14	0.869	8.78	**<0.001**	0.33	90
Canopy cover$_3$ (%)	31.20	**<0.001**	9.03	**<0.001**	6.08	**0.003**	0.42	90
Canopy openness$_1$ (%)	23.00	**<0.001**	9.52	**<0.001**	5.71	**0.005**	0.39	90
Bulk density$_2$ (g/cm^3)	5.19	**0.025**	4.52	**0.014**	1.02	0.366	0.16	90
Life form cover								
Trees$_1$ (%)	7.73	**0.007**	7.23	**0.001**	6.89	**0.002**	0.30	90
Climbers (%)	3.13	0.081	4.08	**0.020**	2.40	0.097	0.16	90
Forbs$_2$ (%)	14.81	**<0.001**	2.02	0.138	0.51	0.604	0.19	90
Groundbromeliads$_1$ (%)	13.09	**0.001**	0.92	0.401	1.76	0.178	0.18	90
Woody regeneration								
Economic trees (nr/m^2)	3.13	0.080	1.35	0.266	0.03	0.973	0.07	90
Economic regeneration (nr/m^2)	2.28	0.134	1.38	0.258	0.01	0.994	0.06	90
(Partial) Shade-tolerant (nr/m^2)	16.80	**<0.001**	3.44	**0.037**	1.01	0.338	0.19	90
Pioneers (nr/m^2)	7.15	**0.009**	3.46	**0.036**	3.39	**0.038**	0.15	90

Table 1 continued
Two way ANOVA with the effect of fire treatment and microsite on abiotic factors, life form cover and woody regeneration. F values (F), the significant differences (P), coefficient of determination (R^2) and number of plots used in the statistical test (N) are given. Significant difference is accepted if p≤0.05 and is described in bold. Fire treatment consists of no fire and fire. Microsite consists of understory, trunk and crown. $_1$= log transformation, $_2$= square root transformation $_3$= arcsin transformation
1 df (degree of freedom) for fire, 2 df for microsites and 2 df for interaction.

	Fire		Microsites		Interaction		R^2	N
	F	P	F	P	F	P		
Woody regeneration								
Shade tolerant (nr/m^2)	16.55	**<0.001**	5.08	**0.008**	1.41	0.249	0.27	90
Partial shade tolerant (nr/m^2)	3.38	0.070	0.34	0.711	0.22	0.806	0.05	90
Long live pioneer (nr/m^2)	5.69	**0.019**	3.47	**0.036**	3.29	**0.042**	0.19	90
Short live pioneer (nr/m^2)	2.00	0.161	0.50	0.608	0.50	0.608	0.05	90
Successional index	7.08	**0.010**	2.11	0.129	2.50	0.089	0.18	90
Seedlings (nr/m^2)	12.50	**0.001**	1.93	0.152	0.53	0.593	0.17	90
Resprouts genets$_2$ (nr/m^2)	5.13	**0.026**	24.66	**<0.001**	2.84	0.064	0.42	90
Resprouts ramets$_2$ (nr/m^2)	0.69	0.410	16.51	**<0.001**	1.23	0.299	0.30	90
Species (nr/5m^2)	12.03	**0.001**	5.08	**0.008**	0.39	0.680	0.22	90
Regeneration (nr/m^2)	14.37	**<0.001**	4.57	**0.013**	0.82	0.444	0.23	90
Total regeneration$_1$ (nr/m^2)	4.39	**0.039**	11.32	**<0.001**	0.40	0.671	0.25	90
Seedlings (%)	0.20	0.654	5.18	**0.008**	1.35	0.265	0.15	84
Resprouts genets (%)	0.20	0.654	5.18	**0.008**	1.35	0.265	0.15	84
Seedlings of reprouts ramets (%)	4.51	**0.037**	8.59	**<0.001**	1.48	0.233	0.26	84
Resprouts ramets (%)	4.51	**0.037**	9.59	**<0.001**	1.48	0.233	0.26	84
Regeneration (0-50 cm)	7.47	**0.008**	2.59	0.081	0.41	0.664	0.14	90
Regeneration (51-100 cm)	14.54	**<0.001**	6.13	**0.003**	1.07	0.347	0.26	90
Regeneration$_2$ (101-150 cm)	0.22	0.641	0.79	0.458	1.11	0.335	0.05	90
Regeneration (151-200 cm)	0.52	0.473	2.07	0.132	0.13	0.879	0.06	90
Regeneration (> 200 cm)	0.21	0.659	3.34	**0.040**	2.72	0.072	0.13	90

5.1. Abiotic factors

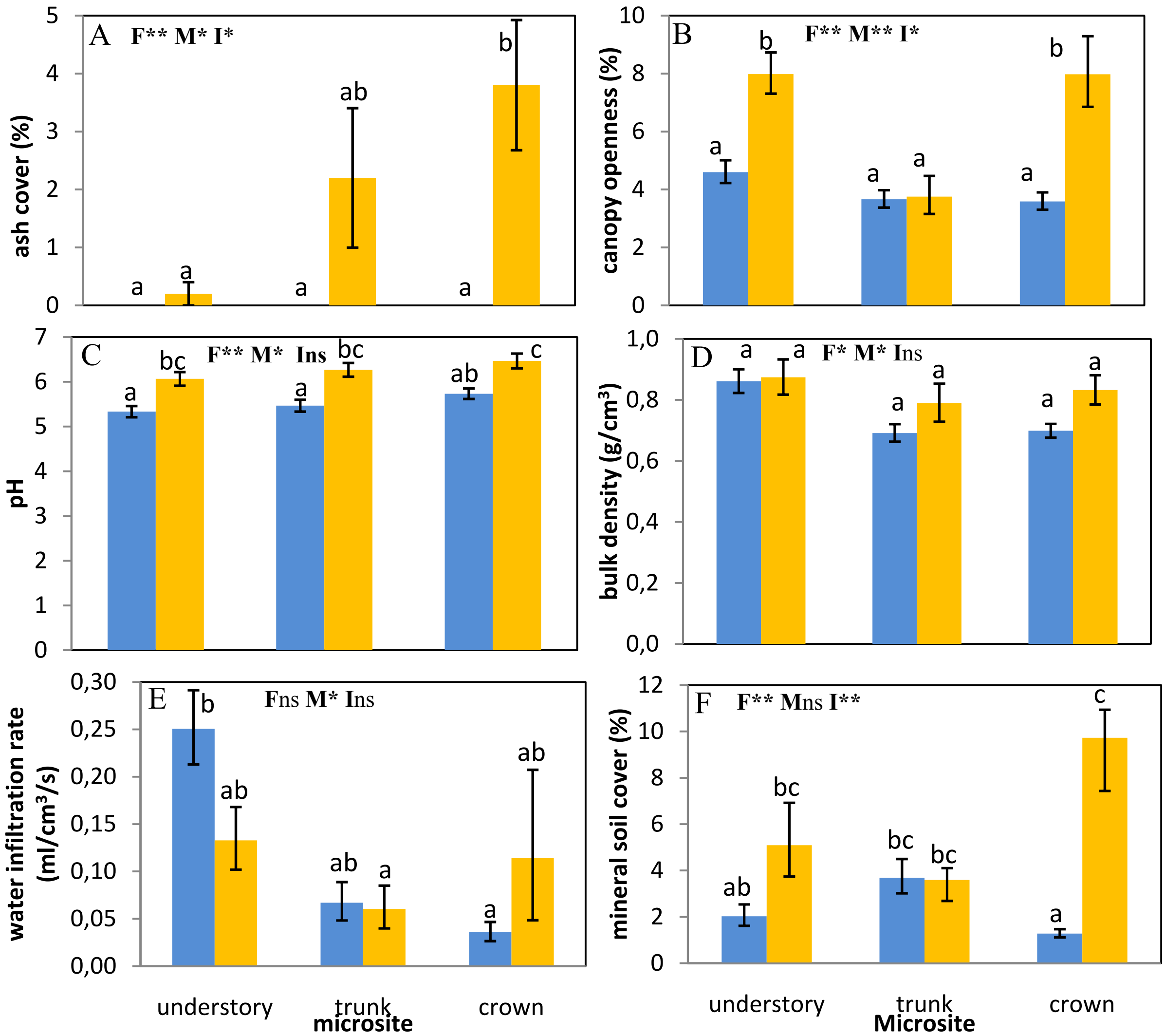


Figure 3
The effect of fire (blue bars no fire, orange bars fire) and microsite (understory, trunk and crown) on A) Ash cover (%), B) Canopy openness (%), C) pH, D) Bulk density (g/cm^3), E) Water infiltration rate (ml/cm^3/s) and F) Mineral soil cover (%). Back transformed means and standard errors are shown. Bars accompanied by a different letter are significantly different at p≤0.05 (Tuckey PostHoc test). F=Fire M=Microsite I=Interaction *p≤0.05**p≤0.001 ns = not significant (ANOVA).

In unburned sites I did not find any signs of ash cover (Figure 3A) or charring (Table 1). Only after fire I found an increase in ash cover ($p < 0.001$) and charring height ($p < 0.001$). There was a significant interaction between fire and microsites ($p = 0.033$); burned trunk- and crown sites had the highest ash cover. The same can be said for charring height (interaction $p <$ 0.001) here crown sites had the tallest charring height (appendix 2C).
Canopy openness increased after fire ($p < 0.001$), but was also affected by microsites ($p <$ 0.001) (Table 1). Fire enhanced canopy openness, especially in the understory and crown sites (interaction $p = 0.005$) (Figure 3B).
Fire had no significant overall effect on woody debris ($p = 0.521$) although there was an interaction ($p < 0.001$) with microsite: fire had a slightly negative effect on woody debris in the crown-plot and a slightly positive effect in the understory sites (Table 1). Highest woody debris cover was found in crown sites ($p = 0.013$) (Appendix 2A).

Fire had a positive effect on pH ($p < 0.001$) (Table 1). pH varied with microsites ($p = 0.022$), in which the highest pH was found in the crown sites (Figure 3C).
Bulk density increased after fire ($p = 0.025$) (Table 1), and varied with microsite: trunk - and crown sites showed lower bulk density than understory sites ($p = 0.014$) (Figure 3D).
Fire did not have a significant effect on water infiltration rate ($p = 0.995$) (Table 1). Highest water infiltration rate was found in understory sites ($p = 0.005$) (Figure 3E).
Highest litter cover is found in understory sites ($p < 0.001$) (Table 1). Fire had a positive effect on litter cover in the trunk-sites (interaction $p = 0.004$) (Appendix 2D).
Highest bare mineral soil cover was found in burned sites ($p < 0.001$) (Table 1). Microsites did not differ significantly ($p = 0.869$). The effect of fire was strongest in the crown sites (interaction $p < 0.001$) (Figure 3F).

5.2. Life forms

Fire did not have a significant effect on climber cover ($p = 0.081$) (Table 1). Highest climber cover was found in trunk- and crown sites ($p = 0.02$) (Figure 4A).
Forb cover increased after fire ($p < 0.001$) (Table 1), but microsite did not have a significant effect ($p = 0.138$) (Figure 4C).

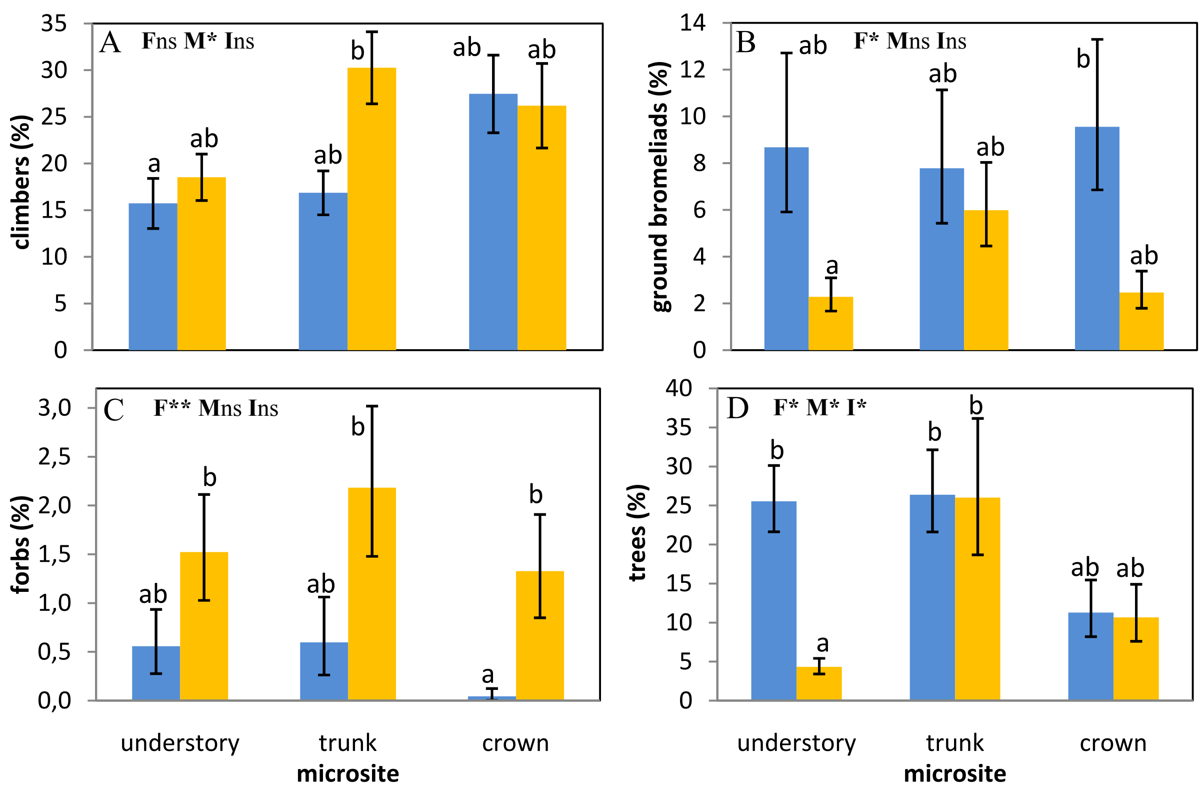


Figure 4
The effect of fire (blue bars no fire, orange bars fire) and microsite (understory, trunk and crown) on A) climbers cover (%), B) Ground bromeliads cover (%), C) Forb cover (%) and D) Tree cover (%). Back transformed means and standard errors are shown. Bars accompanied by a different letter are significantly different at p≤0.05 (Tuckey PostHoc test). F=Fire M=Microsite I=Interaction *p≤0.05**p≤0.001 ns = not significant (ANOVA).

Fire decreased tree cover ($p = 0.007$) (Table 1), but this effect was only seen because of the effect in the understory sites (interaction $p < 0.002$). Highest tree cover was found in trunk- and crown sites ($p = 0.001$) (Figure 4D).
Fire decreased cover of ground bromeliads ($p = 0.001$) (Table 1), whereas microsites did not have a significant effect ($p = 0.401$) (Figure 4B).

There were not enough succulent epiphytes, grasses, bamboos, palms and ferns to do any statistical tests.

5.3. Woody regeneration

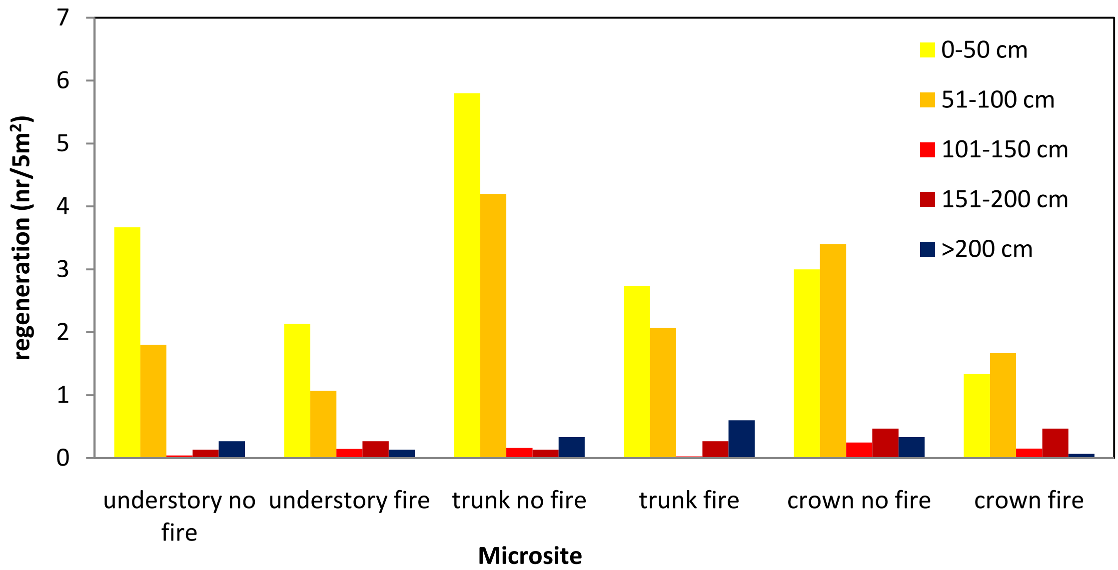


Figure 5
The effect of fire and different microsites (understory, trunk and crown) on population size structure of regeneration (nr/5m^2). The regeneration is divided in 5 size classes (0-50 cm, 51-100 cm, 101-150 cm, 151-200 cm and >200 cm height).

All treatment combinations showed a reverse J-shaped size structure of woody plant regeneration (Figure 5). The trunk - no fire treatment had the steepest decline in amount of regeneration with size class, and the crown - fire treatment had the shallowest decline.

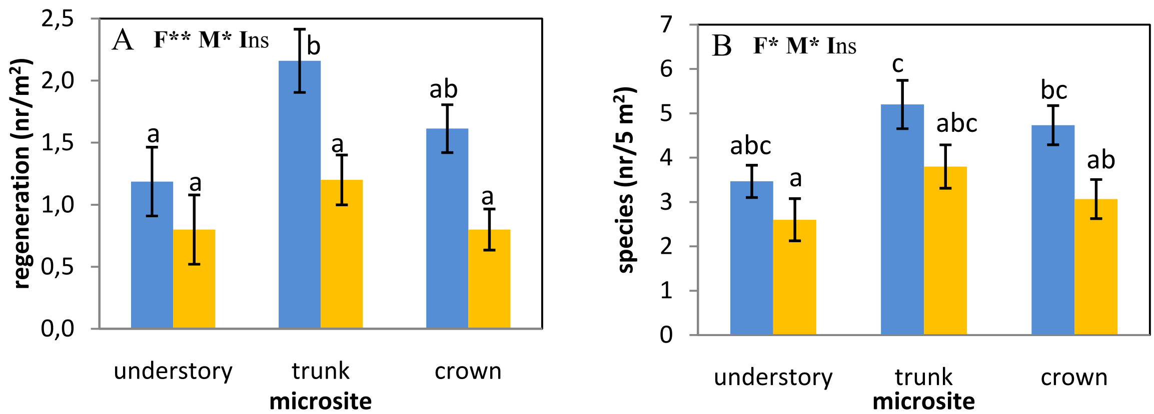


Figure 6
The effect of fire (blue bars no fire, orange bars fire) and microsite (understory, trunk and crown) on A) regeneration (seedlings and resprout remets) (nr/m^2) and B) number of species (nr/5m^2). Back transformed means and standard errors are shown. Bars accompanied by a different letter are significantly different at $p \leq 0.05$ (Tuckey PostHoc test). F=Fire M=Microsite I=Interaction $*p \leq 0.05 ** p \leq 0.001$ ns = not significant (ANOVA).

Fire decreased the density of woody regeneration ($p < 0.001$) (Table 1). Highest density of regeneration was found in the trunk-sites ($p = 0.013$) (Figure 6A).

In burned sites there was a lower number of species (p = 0.001) compared to unburned sites (Table 1). For the microsites, the highest number of species was found in the trunk sites (p = 0.008) (Figure 6B).

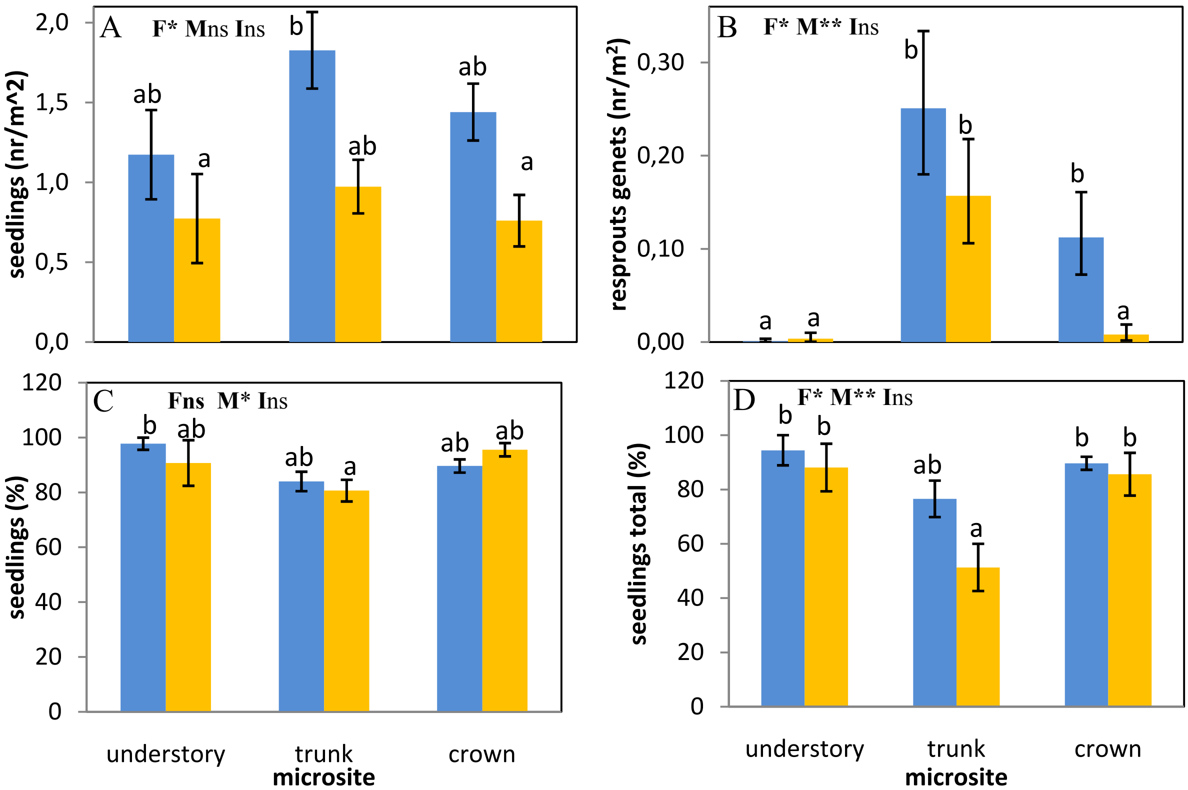


Figure 7
The effect of fire (blue bars no fire, orange bars fire) and microsite (understory, trunk and crown) on A) Seedlings (nr/m^2), B) Resprouts genets (all genetic individuals) (nr/m^2), C) Percentage of tree regeneration (Seedlings and sprouts genets [only genetic individuals]), that is made up by seedlings and D) Percentage of total tree regeneration (seedlings and resprout ramets [all resprouts]) that is made up by seedlings (%). Back transformed means and standard errors are shown. Bars accompanied by a different letter are significantly different at p≤0.05 (Tuckey PostHoc test). F=Fire M=Microsite I=Interaction *p≤0.05**p≤0.001 ns = not significant (ANOVA).

There was a lower number of seedlings in the burned sites (p = 0.001) (Table 1). Microsite had no significant effect on number of seedlings (p = 0.152) (Figure 7A).
Fire had a negative effect on the number of resprout genets (only genetic individuals) (p = 0.026) (Table 1). Highest number of resprout genets was found in the trunk-sites (p < 0.001) (Figure 7B). If the same analysis was repeated but now including the resprouts ramets (all resprouts) fire did not have a significant effect (p = 0.410) (Table 1), but microsites again did (p < 0.001) and again showed most resprout ramets in trunk sites (Appendix 4A).

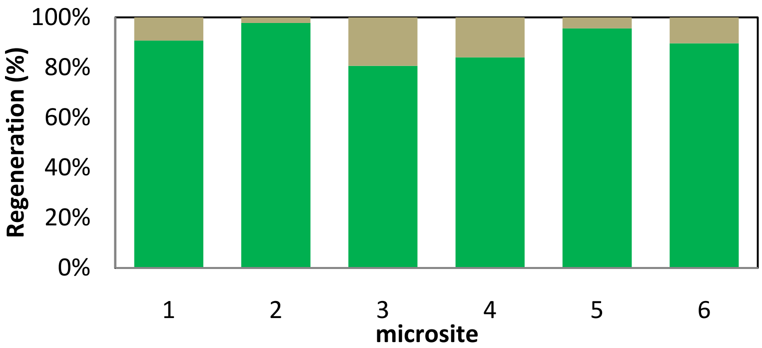


Figure 8
The effect of fire and microsite (1=understory sites burned 2=understory sites not burned 3=trunk-sites burned 4=trunk-sites not burned 5=crown sites burned 6=crown sites not burned) on mode of regeneration (green bars seedlings, brown bars resprouts genets)

In all sites there were more seedlings than resprouts (Figure 8). Fire did not show a significant effect on the percentage mode of regeneration (% seedlings and % resprouts genets) (p = 0.654 for both) (Table 1), whereas microsites did have a significant effect; the highest percentage of seedlings was found in understory sites (p = 0.008) (Figure 7C and fig 8) and highest percentage of resprout genets (only genetic individuals) in trunk-sites (p = 0.008) (Appendix 4B). The same analysis was repeated, but including this time the resprout ramets (all resprouts). Fire had a positive effect on the percentage resprout ramets (p = 0.035 for both). For microsites, understory- and crown sites are higher in percentage total seedlings than trunk-sites ($p < 0.001$) (Figure 7D). For resprouts ramets highest percentage is again found in trunk-sites ($p < 0.001$) (Appendix 4C).

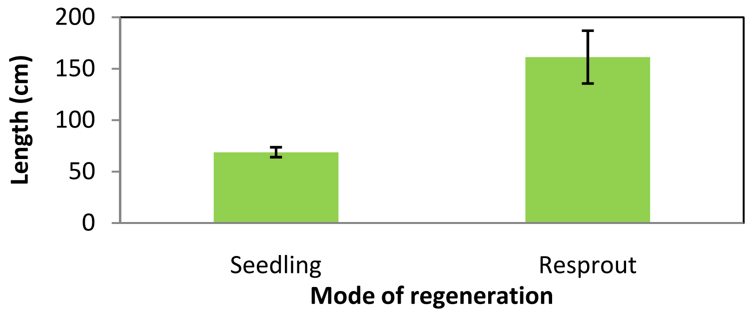


Figure 9
Mean length (cm) and error of seedlings and resprouts are shown for the burned gap-sites (trunk- and crown sites two years after being burned).

In burned trunk- and crown sites resprouts (mean=161,2 cm) are more than two times taller than seedlings (mean=68,8 cm) (t-test N=211 d.f.=209 t=-5.617 p<0.001) (fig 9).

After fire there was a significant higher abundance of pioneers (p = 0.009) (Table 1). Most pioneers were found in trunk- and crown sites (p = 0.036). The effect in microsites was only caused by fire (interaction p = 0.038) (Appendix 5B).

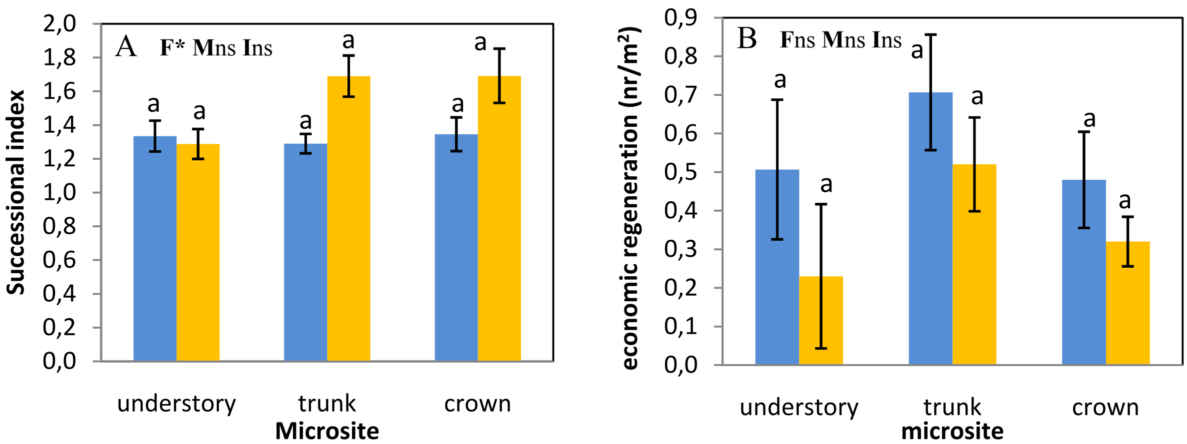


Figure 10
The effect of fire (blue bars no fire, orange bars fire) and microsite (understory, trunk and crown) on A) Successional index and B) Number of economic regeneration (seedlings and resprout genets) (nr/m^2). Back transformed means and standard errors are shown. Bars accompanied by a different letter are significantly different at $p \leq 0.05$ (Tuckey PostHoc test). F=Fire M=Microsite I=Interaction $*p \leq 0.05$ $**p \leq 0.001$ ns = not significant (ANOVA).

Successional index changed after fire (p = 0.010) (Table 1). In areas without fire mostly shade-tolerant regeneration was found. After fire this changed in the trunk- and crown sites to a mostly partial shade-tolerant regeneration. Microsites did not have a significant effect (p = 0.129) (Figure 10A).
Due to large variation among plots, I did not find a significant effects after fire (p = 0.134) or microsite (p = 0.256) on the abundance of commercial species (Figure 10B).

For the most common woody species regeneration it was tested whether their abundance varied with fire and microsite. To this end two separate X^2 tests were used (Table 2). *Anadenanthera columbrina* (Curupau) and *Tabebuia spp.* (Tajibo Amarillo and Tajibo Negro) showed a significant increase in abundance after fire, whereas *Machaerium acutifolium* (Moradillo*)*, *Phyllanthus sp. nov* (Maria Pretinha), *Myrcia guianensis* (Guapurucillo), *Neea cf. steimbachii* (Mapabi) and *Acosmium cardenasii* (Tasaa) showed a significant decrease of abundance after fire (Tabel 2). For microsites a significant higher abundance of *Tabebuia spp.* (Tajibo Amarillo and Tajibo Negro), *Myricia guianensis* (Guapurucillo) and *Acosmium cardenasii* (Tasaa) was found in the trunk-sites. Abundance of *Caesalpinia pluviosa* (Momoqui) *Allophylus edulis* (Pata de pollo) *and Guibourtia chodatiana* (Sirari) did not vary significantly with fire or between microsites.

Table 2
The X^2 test for abundance of species in different microsites and after fire or fire.
Species with in total more than 10 individuals in the different treatment combinations are used. Percentage of the specie for fire and no fire and in different microsites, degrees of freedom (df), significant difference (P), number of trees (N) and if the specie is a timber specie (T) Y=yes and N=no, are given.
* Significance levels: p 0.05 ** Significance levels: p 0.01 ns Significance levels: not significant.

species	Microsites						Fire					
	% underbrush	% trunk	% crown	X^2	df	p	% fire	X^2	df	p	N	T
Anadenanthera culubrina	50	24	26	4,29	2	ns	88	19,88	1	**	34	Y
Myrciaria guianensis	17	52	31	10,11	2	**	22	16,67	1	**	54	N
Neea cf. steimbachii	44	31	24	2,80	2	ns	29	10,77	1	**	45	N
Phyllanthus sp. nov	26	41	33	2,73	2	ns	21	26,45	1	**	80	N
Caesalpinia pluviosa	18	27	55	2,36	2	ns	27	2,27	1	ns	11	Y
Machaerium acutifolium	32	43	25	4,80	2	ns	15	51,74	1	**	103	Y
Allophylus edulis	8	42	50	3,50	2	ns	25	3,00	1	ns	12	N
Guibourtia chodatiana	19	44	38	1,63	2	ns	29	2,57	1	ns	14	Y
Tabebuia spp.	0	93	7	17,76	1	**	79	4,57	1	*	14	Y
Acosmium cardenasii	20	51	29	19,00	2	**	38	7,45	1	**	129	N

6. Discussion

6.1. Abiotic factors

It was hypothesized that canopy openness would be higher after fire or logging, because of removal of the aboveground vegetation by fire or logging increasing light and nutrient availability. Canopy openness was indeed highest after fire, in line with the prediction, but for microsite highest in understory- and crown sites, which is in contrast with the prediction. Fire has therefore a stronger effect on canopy openness than microsite. Canopy openness was measured with a densiometer at 1 meter height, but many climbers where already exceeding this height and thus could have influenced the measurements. A strong and fast regrowth of climbers and forbs was especially observed in the trunk-sites, which might explain the counterintuitive results. Fredericksen and Mostacedo (2000) found that after a period of 6 to 14 months after logging canopy openness was already reduced by nearly 20%, so after the period of two years canopy could have recovered even more. Gerwing (2002) did not even find a difference at all in canopy cover between logged, light burned and control sites. Another possibility here is that resprouts especially in trunk-sites, have already grown so much that they decreased canopy openness, because resprouts can form a dens canopy of four meters in height after only 20 months (Kauffman, 1991). This was also observed during the measurements in some trunk sites. And this can especially be the case for trunk-sites, because the trunk itself was base for a lot of resprouts, and they benefit from the large root system of the trunk.

After fire bulk density increased, because of ash accumulation in soil pores. For microsites bulk density was expected to be highest in the trunk sites, because of soil compaction by the logging machinery, but differences in bulk density where relatively small. Bulk density was highest in understory, which was not expected because of lack of logging machinery in this area. Apparently the influence of logging machinery is not big enough to increase bulk density in trunk - and crown sites. Or the effect is no longer observable, because the bulk density has decreased already after two years due to recovery of soil organic matter caused by decomposing fine roots and litter from incoming vegetation (Kennard and Gholz, 2001) and higher amount soil organic matter increases soil porosity, reducing bulk density (Franzluebbers, 2002).

It was hypothesized that water infiltration would be highest in burned sites, because of higher bulk density due to ash accumulation in soil pores, but in this study water infiltration was not affected by fire. The study of Kennard and Gholz (2001) found the same result after low intensity fires. They argued that this could be due to the effect of organic matter on soil physical characteristics, because soil organic matter sustains many key soil functions affecting for instance soil aggregation and increase in soil aggregation increases water infiltration rate (Franzluebbers, 2002). Furthermore bulk density was expected to be highest in trunk-sites because of higher bulk density caused by influence of logging machinery. Although water infiltration rate was highest in understory sites this was not caused by the lowest bulk density as thought in the hypotheses, because difference in bulk density where relatively small. The higher water infiltration rate in understory sites may be caused by other factors like soil organic matter (Franzluebbers, 2002).

Fire was expected to reduce percentage of litter cover, due to burning, but no effect was found. In this study only cover and not the thickness of the litter layer was evaluated. And because it was already two years after the fire, two dry periods have passed in which 95% of the trees lose their leaves (IBIF, 2006). This could easily have compensated for the loss of litter cover due to burning. Highest litter cover was found in understory - sites, because the litter producing trees were removed from trunk - and crown sites.

Highest bare mineral soil cover was found in the burned sites, because the existing vegetation was burned. Bare mineral soil cover was expected to be lowest in trunk- and crown sites, because of fast regrowth. But microsite did not have an effect on percentage of bare mineral soil cover. Apparently logging activities did not stimulate regrowth enough. Fredericksen and Mostacedo (2000) neither found a significant effect on mineral soil cover 6 months after logging.

6.2. Life forms

Fire was expected to increase cover of climbers, because of more available light and nutrients, but did not have a significant effect on the climber cover. In the study of Heuberger et al. (2002), a study also done in a dry forest in Bolivia, a lower density climber cover was found 1 month after fire, because it was burned. But after 8 months these differences were not visible anymore. The vines had regrown to the same abundance as in the unburned forest. There was no sign climber cover would grow into a higher abundance than it was before the fire and the lack of effect after two years in our study could have the same reason. Climbers have a competitive advantage in dry forest during the dry period (Schnitzer, 2005). This is because they have a deep root system reaching deep into the soil enabling them to reach deeper water and nutrient sources than other vegetation. Therefore climbers suffer less water stress and have a longer growing period during the year than other vegetation in dry forests. It is possible that the fire did not give the climbers an extra advantage in a forest were they already had a competitive advantage. Another possibility is that microsite was more important for climber cover than fire. Highest climber cover was found in trunk- and crown sites as was expected, because of higher light availability.

It was hypothesized that forb cover would increase after fire or logging because of more available light and nutrients. Forb cover indeed increased after fire, but did not vary with microsite. Maybe forbs need more disturbance than logging. Or the effect has already disappeared two years after fire. In Heuberger et al. (2002) no difference in forb cover was found in a similar forest after 1 and 8 months.

Tree cover decreased after fire, because of trees that burned. Tree cover was expected to be lowest in trunk- and crown sites, because of tree removal by logging but surprisingly a higher cover was found in trunk-sites. This could be due to the resprouts on the stump of the trunk-sites. Stump-resprouts were very dominant in trunk-sites. They were tall and had a lot of leaves. Most sprouts were found on the stumps. Mostacedo (2007) found in a dry tropical forest in Bolivia that 27 of 31 studied species resprouted on the stump of which 62% did so frequently. The number of sprouts found per stump varied between 1 and 25 in this study. Kauffman (1991) also found resprouts to form a dens canopy after 20 months and Miller and Kauffman (1998) also had resprouts with a significant crown area size after two years.

Fire decreased cover of ground bromeliads as was expected, because of their sensitivity to fire. It was also hypothesized that cover of ground bromeliads would be highest in understory plots, because they are intermediate shade-tolerant. But the bromeliads cover did not vary significantly between different microsites. Fredericksen and Mostacedo (2000) stated that bromeliads are dramatically reduced after large degree of soil disturbance. The logging activities in this forest apparently did not disturb the soil enough to affect the bromeliads, or there were too few plots (n=15) and bromeliads presence was too irregular to be able to detect such a pattern.

6.3. Woody regeneration

It was hypothesized that the density of woody regeneration would increase after fire or logging, because of more available nutrients and light. In contrast to the hypothesis, the regeneration density decreased after fire. Fire apparently killed the advanced regeneration which did not have the chance to regrow yet. This lack of effect after two years was also seen for saplings in a tropical forest in Malaysia (Woods, 1989) and in a seasonal deciduous forest in India (Saha and Howe, 2003). The same pattern was seen for seedlings and resprouts separately. Mostacedo (2007) also found a scarcity of natural regeneration in the forest of Inpa. In his study he mentions high seed predation, low seed viability and high seedling mortality during the dry season as reasons for this scarcity.

Number of resprout was expected to be higher in burned and logged areas, because they will resprout out of burned and damaged trees. Surprisingly I found less resprouts (genets) in the burned sites. In a study of Kauffman (1991) less resprouts were found after a high invasion of grasses. In our investigation there could be the same problem due to climbers, because there are a lot more climbers in the trunk-sites after fire than in the unburned sites, which can form a dense layer in logging gaps, smothering all other regeneration (Fredericksen and Mostacedo, 2000; Pinard et al., 1999). Only in the trunk-sites most resprouts were found, but these plots were measured with the stump left-over as the centre of the plot, and many trunks had abundant resprouts. This could have caused the higher abundance of *Tabebuia spp.* (Tajibo amarillo and Tajibo negro) in the trunk-sites, because almost most of the *Tabebuia spp.* I found were resprouts and could have resprouted out of the left tree stump and its roots. Close to the tree stump there are also more roots than further away increasing the change of finding a *Tabebuia spp.* that resprouted from a root close to the tree stump.

Seedling density was expected to be higher than resprout density after fire, because of more available nutrients and light. In microsites trunk and crown, seedling density was expected to be lower because damaged trees would resprout a lot. After analyzing our measurements seedling density turned out to be higher than resprout density in all microsites. It could be that number of resprouts abundance was too low to detect a higher abundance after logging. Also if we looked at seedling density itself the number decreased after fire, suggesting that the fire had burned seedlings and new seedlings did not have the change to establish yet. This could be due to seed limitation and therefore scarce regeneration. Also no difference was found in seedling density between microsites.

It was hypothesized that there would be more pioneers in the burned area, because of more available light and therefore the successional index in the burned area would be higher. In the trunk - and crown plots the successional index would also be higher than in understory plots because of the same reason. Although ANOVA found a difference between microsites for successional index, a less sensitive Tuckey post-hoc-test did not. The effect of microsites could be more effective if the logging gaps would be larger. Brokaw and Scheiner (1989) found that small gaps in the tropics, presented more opportunity for regeneration of shade-tolerant than shade-intolerant (pioneer) species. Only if the gaps where bigger (> 150 m^2), there would be more pioneers. Also the scarce number of regeneration in the small number of plots (15) could have caused the lack of strong statistical difference.

Economic regeneration was hypothesized to be higher in burned areas and in the trunk - and crown plots because of a higher availability of light and nutrients, and many economical valuable species are light demanding. But fire as well as microsite did not have a significant effect. It is possible that there were not enough economic trees per plot to distinguish the difference. The lack of statistical differences was also found by Heuberger et al. (2002) and could partly be the result of high variance in all the treatment combinations. Large variability may indicate that additional factors (like seed production and presence of seed trees as well as variation among gaps in microsite conditions [Fredericksen and Mostacedo, 2000]) have a bigger influence on commercial species than the treatment combinations. Furthermore the small number of plots (15) and the small density of regeneration could have caused the lack of statistical difference.

The whole research was done in a part of the forest where trees were harvested. Influence of logging gaps could therefore have affected the unlogged part of this forest and by this reduced the effect of different microsites; control-sites were not the same as a totally unlogged forest. Logging intensity in the forest is 5 trees per hectare. Logging gaps itself cover 2,3 % of the forest (Mostacedo et al., unpublished). Percentage area disturbed by primary - secondary - and third order skid trails is 4.3 %. This makes 6,6 % of the forest immediately affect by logging and of course there are also fourth order skid rails and more important the edge effect of all these features on the understory which should be taken into account (Guariguata and Dupuy, 1996). Therefore microsites could have been more different if the understory sites were measured in a forest in which there was no harvest of trees at all.

I can (almost) be sure the regeneration in the burned sites is not older than two years, because the fire has burned all regeneration en regrowth was only possible for the two years that have passed since then. But what about the regeneration in the unburned sites. It is possible that there are a lot small but old plants in the unburned plots and therefore the positive effect of trunk - and crown sites on seedlings can be masked. On the other hand maybe new vegetation like climbers and resprouts closes logging gaps rather soon giving new seedlings only a small amount of time to use the increased available light before it gets too dark to grow. Therefore the positive effect of logging can be a lot smaller than was expected.

When a forest fire burns in a forest the fire does not burn at one intensity and does not burn the whole area. Intensity and spread depends on different factors like fuel type, weather conditions and fuel continuity. Effect of fire as found in this study can change drastically in another type of forest or in the same forest under different fuel and weather conditions. For example in the burned understory sites fire did not actually burn all sites. In my study this could have effected comparisons between burned and unburned understory sites. And therefore the effect of fire in the understory could have been underestimated.

This study has been done in a nine hectare area that was experimentally burned two years ago and a nine hectare control plot. The initial idea of this fire experiment was to evaluate whether fire could enhance the otherwise poor regeneration of commercial tree species. Because of logistic constraints, this burned plot was not replicated. The 15 measurement plot per treatment combination are therefore, in fact pseudoreplicates. A significant fire effect could have been caused by differences in site characteristics between the burned and control plots. Because of logistic and time constraints it was not possible to replicate the current thesis study in other concessions or areas that had been burned, because these areas are far away. On the positive site, the burned and control areas were fairly large (9 ha), thus averaging out local microsite effects, and the individual measurement plots were reasonably far apart from each other. By carrying out the research in the same concession, with a same (logging/fire) history under similar environmental conditions, with presumably very similar environmental conditions, and a similar logging and fire treatment, the amount of natural variation is reduced, thus allowing to still detect treatment effect, with a fairly low number of replicates (given time constraints, it was not possible to substantially increase the number of replicates).

6.4 Implications for management

The influence of forest fire depends partly on characteristics of fuel (size, continuity, quality, and moisture content) (Hille, 2006). Apart from fuel characteristics, it depends on topography of the site and weather conditions the effect of fire is therefore not totally the same throughout the whole forest.

Fire is a very common phenomenon in the forests of Bolivia and in this study I could see positive effects of fire; after fire we can find ash on the soil that increases nutrient availability and soil pH (Figure 3C). Canopy cover was reduced, because of burned trees, thus increasing available light (Figure 3B). There is a higher cover of bare mineral soil in which seeds can establish more easily. We can find more pioneers (Appendix 5B) and forbs (Figure 4C) suggesting increase of light availability at the forest floor, and there is an increase in *Anadenanthera columbrina* (Curupau) and *Tabebuia spp.* (Tajibo Amarillo and Tajibo Negro) which are both commercial species (Table 2).

On the other hand, fire has a negative effect on density of woody regeneration (Figure 6A) and species richness (Figure 6B), which is also visible in density of seedlings and resprouts. It decreases tree cover (Figure), cover of ground bromeliads (Figure 4B) and has a negative effect on abundance of *Machaerium acutifolium* (Moradillo*)*, *Phyllanthus sp. nov* (Maria Pretinha), *Myrcia guianensis* (Guapurucillo), *Neea cf. steimbachii* (Mapabi) and *Acosmium cardenasii* (Tasaa) of which only *Machaerium acutifolium* (Moradillo*)* is a commercial species (Table 2).

Fire creates favourable abiotic conditions for regeneration but only two economical species show an increase in abundance after fire. Besides, this benefit in abiotic factors will decrease in following years (Kennard and Gholz, 2001). Furthermore fire reduces number of species and the density of woody regeneration. This is especially the case for high intensity or high frequency fires (Cochrane and Schulze, 1999). A following fire can for instance kill small seedlings and resprouts. (Otterstrom et al., 2006). Regeneration of a number of commercial species in dry Bolivian forests is lacking (Mostacedo and Frederickson, 1999). In other studies fire results in large increase of commercial tree regeneration especially if it was a high intensity fire (Kennard, 2004). It seems that they need fire as a big disturbance to regenerate. The two species that increased in abundance after fire (Curupau and Tajibo spp) are partial shade tolerant and long live pioneer respectively. All species decreasing after fire are (partial) shade tolerant and their advanced regeneration is most likely burned in the fire and did not have the change to regenerate in the past two years. Or at least not enough to see an effect.

Logging did not influence abiotic factors to favour regrowth, but did increase woody regrowth anyway (Figure 6A). Next to the increase of woody regeneration there was a increase in climber cover (Figure 4A) which can smother other vegetation if it gets too confounding (Fredericksen and Mostacedo, 2000; Pinard et al., 1999). In trunk sites there was highest species density (Figure 6B) and higher abundance of *Tabebuia spp.* (Tajibo Amarillo and Tajibo Negro), *Myricia guianensis* (Guapurucillo) and *Acosmium cardenasii* (Tasaa) of which *Tabebuia spp*. are commercial species (Table 2). The commercial species *Tabebuia spp*., has the capacity to resprout vigorously from stump and roots. Although there was an increase of these species in the trunk sites, we cannot be sure yet if (one of) these resprouts (or any other resprout) will ever reach maturity. This because there will be a high rate of sprout mortality in following years (Mostacedo 2007). If only one of the resprouts would reach maturity, this logging management will be a durable system.

Next to the long-term effects of logging on logging has direct impact during the logging process itself. 7,8% of the trees are damaged or killed by logging (Mostacedo et al., unpublished). Most damage is to the stem and most damage is severe. Damaged trees and branches will increase the woody debris. On the other hand can disturbance of logging machinery be seen as a sort of seedbed preparation increasing regeneration opportunities for incoming seeds (Mostacedo and Frederickson 2000).

In this research regeneration was scarce, number of plots limited (15) and the plot size relatively small. Number of commercial species found in the plots was scarce and therefore it was hard to get strong statistical effects in the statistical analysis. If there had been more regeneration or more plots it might have been more easy to find more statistical effects for fire or microsite. Regeneration of commercial species in tropical forests of Bolivia is not going well despite disturbances like fire and logging (Mostacedo and Fredericksen, 1999). Maybe because these species are very light depending and need larger disturbances.

In this research all treatment combinations showed a J-shaped size structure of woody plant regeneration (Figure 5), indicating that there is sufficient and continuous regeneration. But it should not be assumed that fire logging and their combination will always result in high abundance and successful regeneration. Vegetation like climbers may smother other more valuable vegetation like commercial trees on the long-term. Fire frequency should be limited to give regeneration the opportunity to outgrow any danger to die during the next fire. When logging the forest, care should be taken to leave enough seed - trees for seed production and shelter for seedlings. And gaps both after fire and logging should be large enough to stimulate commercial species, of which most are light demanding, to regenerate. Furthermore should they stimulate ecosystem functions and maintain biodiversity.

When using fire and logging the forester should look for a combination of both to ensure the forest not to be overexploited but on the same hand use their positive effects for regeneration in the best possible way. In the forest of Inpa managers should increase frequency of the now sporadic fire events, to ensure low intensity fires, (diminishing the change of devastating high intensity fires with high tree mortality) to generate stimulating abiotic factors, and continue current logging intensity. In this way biodiversity will maintain and conditions for regeneration of timber species will be guaranteed.

Regeneration after fire and logging in a sub-humid forest

Dry forests have a longer dry period than sub-humid forests (Mostacedo 2001). Ignition and spread of fire may therefore be more frequent in tropical dry forests, but its impact might be smaller because species are better adapted to fire. Trees in moist forest have thinner bark for example and are therefore more sensitive to fire (Mostacedo et al., 2001). It was found that in a Bolivian dry forest there was more regeneration after fire than a sub-humid forest, because more species are fire adapted (Gould et al., 2002). The regeneration after forest fire can be four times as high in a dry forest than in a sub-humid forest. And in burned areas of the humid forest no difference in regenerating stems was found compared to unburned areas (Gould et al., 2002).

In a moist forest fuel moisture is higher than in a dry forest, and this will prevent high intensity fires (Cochrane et al., 1999). But even at low intensity fire can be severe, because of mortality caused by long fire-contact times. A fire in a moist forest with large fuel parts, would smolder longer and is harder to extinguish (Cochrane, 2003) and consequently causes higher rates of tree mortality (Kauffman, 1991). Logging opens up the canopy and increases the amount of combustible fuel on the forest floor, therefore increasing fire susceptibility (Nepstad, 1998). After logging disturbances more regeneration is observed (Magnusson et al., 1999; Horne and Mackowski, 1987).

So fire does not increase opportunity for regeneration in sub-humid forests, and the change to destroy large parts of the forest during the fire is reasonable. Fire is therefore not considered to be a good management tool to stimulate regeneration in these kind of forests. But if a forest is being used for logging, this will stimulate regeneration. Logging is therefore considered to be a better tool for regeneration than fire in sub-humid forests. If a forest is being logged however, this makes the forest more susceptible to fire and prevention measures to reduce fire risks must be taken.

6.5 Limitations of this study and recommendations for further research

Percentage of cover of ash, litter, mineral soil, woody debris, canopy openness and life forms was estimated by eye and the question is whether this is sufficient precise. Because during the day a person can get more tired or bored and estimates just a bit different. This effect could have been reduced by estimating the same plots a second time another day. To compare the results between the two days an estimation of the error could be made.

Other studies have found that higher disturbance have bigger effects on for example abiotic factors like ash deposition and bulk density, regeneration of species in different shade tolerance classes and seedling establishment (Gerwing, 2002; Kennard and Gholz, 2001; Mostacedo and Fredericksen, 1999). There should be a following up research in this forest with larger logging gaps and some areas with higher intensities of fire.

Climbers can form a dens mat in which regeneration of trees is difficult because of the smothering effect (Gerwing, 2002; Fredericksen and Mostacedo, 2000; Woods, 1989). Further research should therefore also investigate the effect of removal of climbers on regeneration in this forest.

It is known that high frequency fires will kill small regeneration (Otterstrom et al., 2006), but larger trees survive. Further research should be done in this forest to determine the minimal length regeneration has to be to survive the next fire. Also more research in needed on resprouts. What percentage resprouts will grow into adult trees? When do changes for resprouts to grow into an adult tree become the same as for seedlings?

In this research regeneration was scarce, number of plots limited (15) and the plot size relatively small. Abundance commercial species was very small and therefore it was hard to find strong statistical differences. If this research would be repeated with a higher plot-number the changes to find more regeneration and more statistical effects would be larger. A following up study should be done with a higher number of plots per treatment combination.

7. Conclusions

The objective of this study was to compare consequences of fire and logging in the Bolivian dry forest of Inpa, two years after fire and logging. Therefore I measured abiotic factors, cover of life forms and regeneration (resprouts or seedlings, shade tolerance classes and commercial species) in three different microsites (understory, and the trunk - and crown zone in logging gaps)

Abiotic factors

Fire increased ash cover, pH. canopy openness and mineral soil, increasing light, nutrient and seedbed availability. In crown- sites there is highest ash cover after fire. Therefore fire increases resource availability and can stimulate regeneration and growth of the vegetation. Crown sites also increase resource availabilities a bit, but only in combination with fire. Microsites created by logging do not increase resource availability very much and do not have an important role for regeneration and growth in case of abiotic factors.

Life forms

Fire did not stimulate cover of life forms very much. Only forb cover increased after fire because they are more light-demanding and fast-growing, whereas tree - and ground bromeliads cover decreased after fire because they are more shade-tolerant and slow growing life forms. For microsites trunk - and crown sites showed a higher tree and climber cover. The climber cover in some plots was so abundant that it was overgrowing and therefore suffocating other vegetation.

Regeneration

All treatment combinations showed a J-shaped size structure of woody plant regeneration, indicating that there is sufficient and continuous regeneration. After fire there was a decrease in regeneration density of seedlings and resprouts, and a decreased number of species, suggesting that fire did not stimulate regrowth of woody regeneration. Five shade-tolerant and slow-growing species decrease in abundance after fire, which suggests that advanced regeneration was killed by fire and establishment from new regeneration from seed was slow. A light demanding pioneer and partial shade tolerant specie increase in abundance after fire (*Anadenanthera columbrina* (Curupau) and *Tabebuia spp.* (Tajibo amarillo and Tajibo negro)). Of these *Anadenanthera* mainly regenerated from seeds, and *Tabebuia* mainly from sprouts. As most commercial species in Inpa are light-demanding, and show poor regeneration, this might suggest that the fire burned in the forests of Inpa did not disturb the forest enough to enhance regeneration of all of these species. But because fire stimulates regeneration of two (timber) species it is more likely that the rest of the regeneration might not show an increase after fire, because there is a scarcity in seed trees. Microsites differed in several aspects of their regeneration. In trunk-sites was highest number of woody regeneration, species, resprouts, pioneers and a higher abundance of 3 species, of which only *tabebuia spp.* are commercial species. Resprouts were significantly higher in length than seedlings after fire in the gap-sites (trunk- and crown sites) which gives them a competitive advantage over seedlings for light. Logging could stimulate therefore the regeneration of commercial species, either by sprouts or by seeds.

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References;

Augspurger, C.K., 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. The journal of Ecology, 72(3), 777-795.

Blate, G.M., 2005. Modest trade-offs between timber management and fire susceptibility of a Bolivian semi-deciduous forest. Ecological Aplications, 15(5), 1649-1663.

Bradley, A.V., and Millington, A.C., 2006. Spatial and temporal scale issues in determining biomass burning regimes in Bolivia and Peru. International Journal of Remote Sensing, 27(11), 2221-2253.

Brokaw, N.V.L. and Scheiner S.M., 1989. Species composition in gaps and structure of a tropical forest, Ecology, 70(3), 538-541.

Brown, J.K. 1974. Handbook for inventorying downed woody material. United States Department of Agriculture Forest Service General Technical Report INT-6. Intermountain Research station, Ogden, Utah, U.S.A.

Cochrane, M.A., and Schulze, M.D., 1999. Fire as a recurrent event in tropical forests of Eastern Amazon: Effect on forest structure, biomass and species composition, Biotropic, 31(1), 2-16.

Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M., Nepstad, D.C., Lefebvre, P., and Davidson, E.A., 1999. Positive feedback in the fire dynamics of closed canopy tropical forests, Science, 248.

Cochrane, M.A., 2003. Fire science for rainforests, Nature, 421, 913-919.

Denslow, J.S., Ellison, A.M., Sanford, R.E., 1998, Treefall gap size effects on above- and below-ground processes in a tropical wet forest, Journal of Ecology, 86, 597-609.

Di Bella, C.M., Jobbagy, E.G., Paruelo, J.M., and Pinnock, S., 2006. Continental fire density patterns in South America, Global Ecology and Biogeography, 15, 192-199.

Edward, A., and Schuur, G., 2003. Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation, Ecology, 84(5), 1165-1170.

Francis, J.K., USDA Forest service, http://www.fs.fed.us/global/iitf/pdf/shrubs/Bromelia%20pinguin.pdf, Information derived on 6 march, 2008.

Franzluebbers, A.J., 2002. Water infiltration and soil structure related to organic matter and its stratification with depth. Soil & Tillage Research 66, 197-205

Fredericksen, T.S., and Mostacedo, B., 2000. Regeneration of timber species following selection logging in a Bolivian tropical dry forest. Forest Ecology and Management, 131, 47-55.

Fredericksen, T.S., and Pariona, W., 2002, Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical forest, Forest Ecology and Management, 171, 223-230.

Fredericksen, T.S., Putz, F.E., Pattie, P., Pariona, W., and Peña-Carlos, M., 2003. Sustainable forestry in Bolivia: Beyond planned logging. Journal of Forestry, 101(2), 37-40.
Gerwing, J.J., 2002. Degradation of forests through logging and fire in eastern Brazilian Amazon, Forest Ecology and Management, 157, 131-141.
Goldammer, J.G., 1999. Forests on fire, Science, New Series, 284(5421), 1782-1783.
Gould, K.A., Fredericksen, T.S., Morales, F., Kennard, D., Putz, F.E., Mostacedo, B., and Toledo, M., 2002. Post –fire tree regeneration in lowland Bolivia: implications for fire management. Forest Ecology and Management, 165, 225-234.
Grayson, D.K., 2001. The archaeological record of human impacts on animal populations, Journal of World Prehistory, 15(1).
Guariguata, M.R. And Dupuy J.M., 1997. Forest regeneration in abandoned logging roads in lowland Costa Rica, Biotropica, 29(1), 15-28.
Heuberger, K., Fredericksen, T., Toledo, M., Urquieta, W., Ramirez, F., 2002. Mechanical cleaning and prescribed burning for recruiting commercial tree regeneration in a Bolivian dry forest, New Forests, 24, 183-194.
Hille, M., 2006. Fire Ecology of Scots Pine in Northwest Europe. PhD thesis, Wageningen University, Wageningen.
Horne, R., Mackowski, C., 1987. Crown dieback, overstorey regrowth and regeneration response in warm temperate rainforest following logging, Forest Ecology and Management, 22, 283-289.
Hosking, J.S. 1938. The ignition at low temperatures of the organic matter in soils. J. Agric. Sci. 28, 393–400.
IBIF, 2006. www.ibifbolivia.org.bo, Information derived between July and August 2007
Kauffman, J.B., 1991. Survival by sprouting following fire in tropical forests of eastern Amazon, Biotropica, 23(3), 219-224.
Kennard, D.K., and Gholz, H.L., 2001. Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest, Plant and Soi, 234, 119 129.
Kennard, D.K., Could, K., Putz, F.E., Fredericksen, T.S., and Morales, F., 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest, Forest Ecology and Management, 162, 197-208.
Kennard, D., 2004. Commercial tree regenteation 6 years after high intensity burns in a seasonally dry forest in Bolivia, Can. J. For. Res., 34, 2199-2207.
Kennard, D.K., and Putz, F.E., 2005. Differential responses of Bolivian timber species to prescribed fire and other gap treatments, New Forests., 30, 1-20.
Killeen, T.J., Jardim, A. Mamani, F., and Rojas, N, 1998. Diversity, composition and structure of a tropical semideciduous forest in the Chiquitanía region of Santa Cruz, Bolivia, Journal of Tropical Ecology, 14, 803-827.
Kutt, A.S. And Woinarski, J.C.Z., 2007. The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia, Journal of Tropical Ecology, 23, 95-106.
Miller, P.M., and Kauffman, J.B., 1998. Seedling and sprout response to slash and burn agriculture in a tropical deciduous forest, Biotropica, 4, 538-546.
Magnusson, W.E., Lima de, O.P., Quintiliano Reis, F., Higuchi, N., Ferreira Ramos, J., 1999. Logging activity and tree regeneration in an Amazonian forest, Forest Ecology and Management, 113, 67-74.
Malmer, A. and Grip, H., 1990. Soil disturbance and loss of infiltrability caused by mechanized and manual extraction of tropical rainforest in Sabah, Malaysia, Forest Ecology and Management, 38, 1-12.
Markesteijn, L., Poorter, L., and Bongers, F., 2007. Light-dependent leaf trait variation in 43 tropical dry forest tree species, American Journal of Botany, 94(4), 515-525.
McDaniel, J., Kennard, D., and Fuentes, A., 2005. Smokey the Tapir: Traditional fire knowledge and fire prevention campaigns in lowland Bolivia, Society and Natural Resources, 18, 921-931.
Mostacedo C.B., and Fredericksen T.S., 1999. Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations, Forest Ecology and Management,124, 263-273.

Mostacedo, B., Fredericksen, T.S., Gould, K., and Toledo, M., 2001. Responses of community structure and composition to wildfire in dry and subhumid tropical forests in Bolivia, Journal of Tropical Forest Science, 13(3), 488-502.

Mostacedo, B., 2007. Natural regeneration of canopy trees in a tropical dry forest in Bolivia, PhD thesis, University of Florida.

Mostacedo, B., Pena-Claros, M., Alarcón, A., Licona J. C., Ohlson-Kiehn,C., Jackson, S., Fredericksen, T. S., Putz, F. E., Disturbance caused by different silvicultural systems in two Bolivian tropical. Unpublished.

Nepstad, D., Moreira, A., Veríssimo, A., Lefebvre, P., Schlesinger, P., Potter, C., Nobre, C., Setzer, A., Krug, T., Barros, A.C., Alencar, A., and Pereira, J.R., 1998. Forest fire prediction and prevention in the Brazilian Amazon, Conservation Biology, 12(5), 951-953.

Nepstad, D.C., VerõÂssimo, A., Alencar, A., Nobre, C., Lima, E. Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., and Brooks, V., 1999. Large-scale impoverishment of Amazonian forests by logging and fire, Nature, 398, 505-508.

Otterstrom, S.M., Schwartz, M.W., 2006. Responses to fire in selected tropical dry forest trees, Biotropica, 38(5), 592-598.

Pariona, W., Fredericksen, T.S., Licona, 2003. Natural regeneration and liberation of timber species in logging gaps in two bolivian tropical forests, Forest Ecology and Management, 181, 313-322.

Park, A., Justiniano, M.J., and Fredericksen, T.S., 2005. Natural regeneration and environmental relationships of tree species in logging gaps in a Bolivian tropical forest, Forest Ecology and Management, 217, 147-157.

Pinard, M., Howlett, B. And Davidson, D., 1996. Site conditions limit pioneer tree recruitment after logging of Diterocarp forests in Sahab, Malaysia, Biotropica, 28(1), 2-12.

Pinard, M.A., Puts, F.D., and Licona, J.C.,1999.Tree mortality and climber proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia, Forest Ecology and Management 116, 247-252.

Pinnard, M.A. Putz F.E., Rumíz, D., Guzmán, R., Jardim, A., 1999b. Ecological characterization of tree species for guiding forest management decisions in seasonally dry forest in Lomerío, Bolivia, Forest Ecology and Management, 113, 201-213.

Pinto, C., Respuesta de la vegetación de un bosque homedo tropical a incendios forestales en Bolivia, IBIF unpublished report.

Pyne, S., Andrews, P.L., and Laven, R.D., 1996. Introduction to wildland fire, second edition, John Wiley & Sons, Canada, ISBN 0-471-54913-4.

Reinhardt E.D., Keane R.E. and Brown J.K., 2001. Modeling fire effects, International journal of wildland fire, 10, 373-380.

Saha, S., Howe, H.F., 2003. Species composition and fire in a dry deciduous forest, Ecology, 84, 3118-3123.

Santiago, S.L., and Mulkey, S.S., 2005. Leaf productivity along a precipitation gradient in lowland Panama: patterns from leaf to ecosystem, Trees, 19, 349-356.

Sawadogo, L, Tiveau, D., Nygard, R., 2005. Influence of selective tree cutting, livestock and prescribed fire on herbaceous biomass in the savannah woodlands of Burkina Faso, West Africa, Agricuture, Ecosystems and Environment, 105, 335-345.

Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution, The American Naturalist, 166(2), 262-267.

Schuur, A.G.E, and Matson, 2001. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest, Oecologia, 128, 431-442.

Siegert, F., Ruecker, G., Hinrichs, A., and Hoffman, A.A., 2001. Increased damage from fires in logged forests during droughts caused by El Niño, Nature 414, 437-440.

Steininger, M.K., Tucker, C.J., Ersts, P., Killeen, T.J., Villegas, Z., and Hecht, S. B., 2001. Clearance and Fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Boliva, Conservation Biology, 15(4), 856-866.

Timmermann, A., Oberhuber, J. Bacher, A., Esch, M., Latif, M., and Roeckner, E., 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming, Nature, 392, 694-697.

Townsend, C.R., Harper, J.L. and Begon, M., 2000. Essentials of ecology. Blackwell Science, inc. Massachusetts.
Uhl, C., and Kauffman, J.B., 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon, Ecology, 71(2), 437-449.
Van Nieuwstadt, M.G.L., Sheil, D., and Kartawinata, K., 2001. The ecological consequences of logging in the burned forest of East Kalimantan, Indonesia, Conservation Biology, 15(4), 1183-1186.
Vitousek, P.M., and Sanford, Jr. R. L., 1986. Nutrient cycling in moist tropical forest, Annual Review of Ecology and Systematics, 17, 137-167.
Woods, P., 1989. Effects of logging, drought and fire on structure and composition in tropical forest in Sabah, Malaysia, Biotropica, 21(4), 290-298.
Whitmorte., C. 1985. Tropical rain forests of the Far East. Ed. 2. Clarendon Press, Oxford .