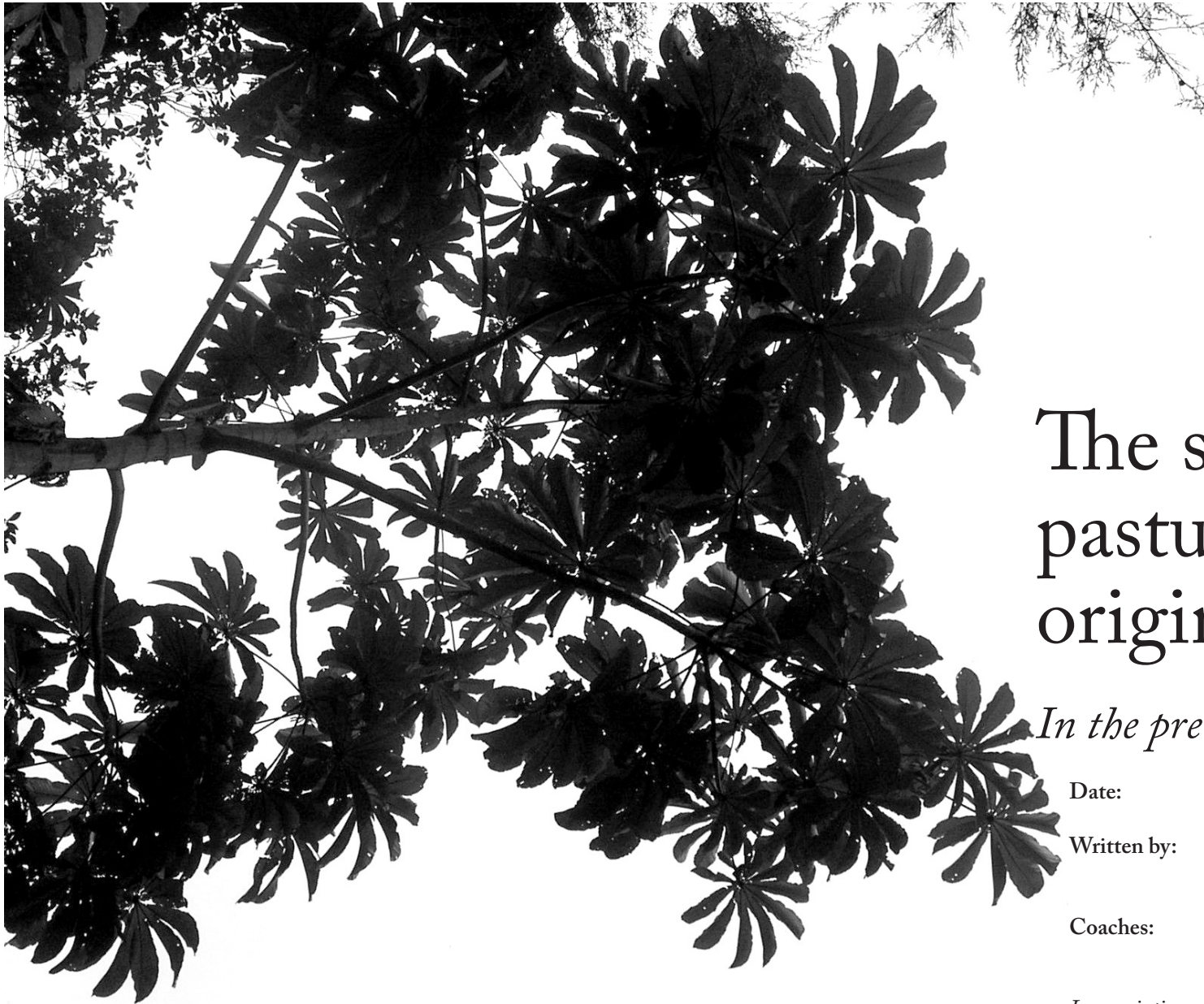


The succession of pasture land towards original cloud forest *In the pre-mountain area of Costa Rica*





The succession of pasture land towards original cloud forest

In the pre-mountain area of Costa Rica

Date: 28-08-2008

Written by: Matthijs Bol
Dennis Vroomen

Coaches: Ian Giddy
Jaap de Vletter

In association with Cloudbridge Nature reserve

*Conducted as bachelor thesis research for Tropical Forestry
at the Van Hall Larenstein Institute*

Foreword

For our study Tropical Forestry at the Van Hall Larenstein Institute we carried out a thesis research at the research station situated in the Cloudbridge Private Nature Reserve, Costa Rica. This reserve is situated in the South Central of Costa Rica along the Cordillera Talamanca mountain chain.

This study investigate if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting. With this information we hope to help the owner of the Cloudbridge Reserve with his reforestation efforts.

We want to thank the organization of the Cloudbridge reserve and especially Ian Giddy for giving us the opportunity to carry out our thesis research in their organization. We found our work very pleasing and rewarding.

Summary

In the last years nature conservationists are becoming more aware that conservation of species habitats in the tropics is only possible if fragmented ecological regions are linked, rather than conserving small specific areas. Efforts are made to link different ecological zones, to make it possible for animals and plants to migrate through bigger areas. For this reason a reforestation project is started in the Cloudbridge reserve to link the mountain regions of Chiripo with the pre-mountain regions of the central Valley. There is still a lack of knowledge on how to reforest former cloud forest areas and accelerate restoration of the original vegetation. From the start of the Cloudbridge tree planting program a selection of planted trees were monitored over the years for their survival rates, vitality and canopy closure. With these data collected over the years, this research investigate if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting.

To answer this overall question several steps were taken. First had to be clear how natural regeneration takes place in an undisturbed cloud forest. Further was examined why forest establishment, on small and large degraded sites, takes a considerable period of time and what the mayor barriers are preventing this recovery process. Human interference in the recovery process seemed to be a valuable option, to counter these barriers for natural regeneration. One of the most important human interventions that came forward was the establishment of remnant trees in the degraded pasture lands. To test the assumption that tree planting promotes the establishment of natural regeneration a regeneration monitoring was conducted. The most significant difference in regeneration found between the two research areas is the species composition of the regenerating trees and the frequency of regenerating species. Under the planted trees a mixture of pioneer and climax species was found, while in the subplot that was left to recover naturally only pioneer specialists were established. The finding of this difference in tree regeneration composition is a sign that tree planting on an abandoned pasture land can promote the range of tree species that can establish.

The return of climax species seems to accelerate the recovery process towards the original Cloud forest. After assessing the different planted tree species, *Cupressus lusitanica* and *Quercus copeyensis* came forward as the most promising species to promote natural regeneration at this stage. This because under these species established the most diverse regeneration, further were this the only planted trees species under which shade-tolerant regeneration established.

Table of contents

Introduction.....	8	5 The influence of the planted trees on the establishment of	
Problem statement.....	9	regeneration.....	28
Research questions.....	10	5.1 Initial criteria for planted tree species.....	28
Methods.....	11	5.2 Planted tree species.....	28
1 Natural regeneration in a virgin cloud forest.....	12	5.3 Growth characteristics of the planted trees.....	30
1.1 Gaps.....	12	5.4 Amount of regeneration per planted tree species.....	32
1.2 Gap closure.....	12	5.5 Circumstances desired by the different regenerating species...	36
1.3 Two main tree colonization strategies.....	13	5.6 Shade conditions provided by the planted tree species.....	38
1.4 Actual species composition in gaps.....	14	5.7 Overall findings and conclusions of the planted tree species..	40
1.5 Micro-site.....	14	6 Conclusions.....	46
1.6 Conclusion.....	15	7 Discussions.....	48
2 Major barriers to natural regeneration on abandoned and		References.....	49
degraded pasture lands.....	15		
2.1 Barriers to restoration.....	15		
2.2 Shortage of tree seeds.....	15		
2.3 Lack of micro-climate and water availability.....	16		
2.4 Importance of distance to forest edge.....	16		
2.5 Competition with established grasses and weeds.....	16		
2.6 Soil and nutrient properties.....	17		
2.7 Discussion and conclusions.....	17		
3 How to overcome these major barriers by human interventions.....	17		
3.1 Shortage of tree seeds.....	18		
3.2 Lack of micro-climate and water availability.....	18		
3.3 Importance of distance to forest edge.....	19		
3.4 Competition with established grasses/weeds.....	19		
3.5 Soil properties.....	19		
3.6 Conclusions and discussions.....	19		
4 The influence of tree planting on the establishment of natural			
regeneration in the Cloudbridge Reserve.....	20		
4.1 Regeneration count plantation.....	20		
4.2 Regeneration count subplot.....	25		
4.3 Differences in found regeneration.....	26		
4.4 Conclusions and discussion.....	26		

Introduction

The cloud forests of the southern region of Costa Rica are of exceptional conservation importance, owing to their high species diversity and endemism **1**. In the last decades these important cloud forest areas have been degraded and severely fragmented **2**. The most destructive form of development is the creation of pastureland which are abandoned after several years **3**. Fragmentation negatively influences most native biota and habitat, it is a major cause of biodiversity loss in tropical and temperate forests **4**. The recovery of forest, after these converted lands are abandoned will take many years **5**. To accelerate this slow recovery process conservationists try to come to good technical approaches to reforest abandoned pasturelands and try to counter the fragmentation of the original Cloud forest.

In recent years several studies have shown that, once pastureland is abandoned, native species seedling recruitment is poor **6**. Major factors for this are lack of soil seed bank and seed rain input **7**.

A wide variety of studies point out that several site factors are also slowing down forest recovery, including lack of soil nutrients, soil compaction, competition with aggressive non native pasture grasses, seasonal drought, low rates of seedling colonization and predation **8**. However, the relative importance of these factors limiting recovery has varied greatly among studies and sometimes results have been contradictory.

Remnant trees may increase seed dispersal, increase soil nutrients and reduce soil temperatures **9**. Another study recorded lower growth rates of some species of native tropical forest, between seedlings planted in open pasture compared with those planted under remnant trees **10**. The goal of this research will be to investigate if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting.

1. Challenger,1998
2. Amelung & Diehl, 1992;
Fearnside,1993;
Saldarriaga et al.,1988;
Brown & Lugo,1990
3. Buschbacher,1986
4. Saunders et al.,1991;
Taberelli et al.,1999
5. Uhl, Buschbacher
and Serrao,1988
6. Buschbacher,1986;
Aide et al.,2000;
Cubina & Aide,2001
7. Zimmerman,
Pascarella and Aide,
2000
8. Buschbacher et. al.,
1986;
Nepstad et al.,1996;
Aide and Cavellier,
1994
9. Belsky et al.,1989;
Campbell et al.,1990;
Samiento,1997;
Rhoades et al.,1998
10. Holl&Quiros-Nietzen,
1999

Problem statement

In the last years nature conservationists are becoming more aware that conservation of species habitats in the tropics is only possible if whole ecological regions are researched rather than small specific areas. Efforts are made to link different ecological zones, to make it possible for animals and plants to migrate through bigger areas. For this reason a reforestation effort is made in the Cloudbridge reserve to link the mountain regions of Chiripo with the pre-mountain regions of the central Valley. There is still a lack of knowledge on how to reforest former cloud forest areas and accelerate restoration of the original vegetation. In this research is tried to find out if planting of trees in abandoned pastures accelerates the restoration of the original cloud forest in the pre-mountain area.

At the start of the Cloudbridge tree planting programme a great diversity of tree species were planted and monitored over the years for their survival rates, vitality and canopy closure. With these data collected over the years, this study investigates if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting.

Research questions

Can planting of trees promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting?

- How does natural regeneration occur in a virgin cloud forest?
- What are the major barriers to natural regeneration on abandoned and degraded pasture lands?
- In which ways can these major barriers be overcome by human interventions?
- Did the planting of native trees promote the establishment of natural regeneration in the Cloudbridge reserve after six years?

Sub1: How much regeneration is establishing in the area that was not planted with trees?

Sub2: How much regeneration is establishing under the different planted tree species?

Sub3: What is the species composition of the established regeneration in those different research areas?

- Which of the planted tree species are the most promising species to promote natural regeneration after six years?

Sub1: Which planted tree species are suitable to plant on the plantation sites in the Cloudbridge reserve?

Sub2: Under which of the planted tree species established the highest diversity and amount of natural regeneration?

Sub3: Which light level conditions are desired by the different regenerating species?

Sub4: Which light level conditions are provided by the different planted tree species?

Sub5: Which of the planted species have additional characteristics that can accelerate forest recovery?

Methods

Study area

This study was conducted in the plantation sites of the Cloudbridge reserve. This reserve is situated in the South central of Costa Rica along the Cordillera Talamanca mountain chain on an elevation between 1.500 and 2.600 m. It covers roughly three hundred hectares and is part of an important bio-region, surrounded by cloud forest and high elevation shrub lands, with a high diversity of species. It borders the Chiripo national park, which has a status as an UNESCO World Heritage Site. The average rainfall is approximately 4300 mm yr⁻¹ and mean high and low temperatures are 23,1°C and 13,4°C. (temperatures and rain studies, 2004-2007, Gode, A.). In this research seven study sites were selected. These contained six plantation sites that were established in 2002 on recently abandoned pasture, that had been grazed for approximately twenty five years. Further a subplot was created in an area that was left to recover naturally.

Tree monitoring

The research area for the tree monitoring consists of the six plantation sites. For these plantation sites nineteen tree species were selected and planted in the year 2002. From 2003 on these trees were monitored annually by different Cloudbridge volunteers and worked out in an excel database. To make the data more complete the tree monitoring of 2008 (initiated in November 2007) is conducted within this research. After this, a database (use of Microsoft Access) was created for all the years to make it possible to analyze the growth, vitality, competition, ground coverage and crown diameter over the years. Later these data was used to determine, which planted tree species are suitable to plant on the plantation sites. More information on the methodology used for the tree monitoring can be found in appendix 1.

Regeneration monitoring

To determine if forest recovery is promoted by the planting of trees, there is looked at an area that was planted with trees and an area without any human intervention. For these areas is determined if a difference in the amount and species composition of established natural regeneration could be found. To analyse this, two inventories are conducted. First inventory is conducted in one of the plantation areas in the Cloudbridge reserve. This to determine the establishment of natural regeneration under the different planted tree species. The plantation chosen for this inventory is the River trail plantation. The reason for choosing this plantation is that it was established the most systematic of all the plantation sites (in a 4x4 spacing). Factors like easy access, most available data from the last six years, most diverse trees planted, situated in the centre of the Cloudbridge reserve justified the choice further.

The second inventory is conducted in a research plot that is created next to the river trail plantation. This to determine the establishment of natural regeneration in an area that was left to recover naturally. The location of this subplot was chosen for its similar site conditions (elevation, soil, aspect, distance to the river, distance to the forest edge, etc.) as the plantation. Also, the accessibility from the river trail, made this location suitable to conduct this inventory.

After these inventories were done a database (use of Microsoft Access) was created to compare the two research sites. This data was later used to determine if there is a difference in the amount and species composition of established natural regeneration, between the two research sites and which planted tree species is most effective to plant. More detailed information on the methodology used for the regeneration monitoring can be found in appendix 2.

1

Natural regeneration in a virgin cloud forest

Introduction

Before anything can be said about forest recovery on abandoned pastures, the natural regeneration in an undisturbed forest has to be examined. In this chapter the main colonization events and the different colonization systems used by different groups of tree species are explained. Further will be explained what the causes are for this difference in colonization systems.

1.1 Gaps

The most important event in the tree regeneration process within a virgin cloud forest is when an opening of the canopy occurs. “75% of the tree species at the La Selva Biological station, Costa Rica are dependent on canopy opening for seed germination or growth beyond sapling stage” **1**. The term gap or canopy gap is generally used to refer to such empty areas within forest canopies. Gaps are the sites of the greatest understory regeneration and recruitment **2**. Many tree species depend on gaps for seed germination and seedling growth, gap dynamics are therefore closely linked to the “next generation” of trees. This creates a potentially complex interdependence between two major ecological features of forests: Canopy composition and structure affects like gap size, shape, and frequency, while gap characteristics affect seedling establishment and thus the future canopy composition.

Gaps can range from sub canopy spaces between individual trees or branches **3** to the more classical complete gaps, consisting of holes in the canopy that extend all the way to ground level **4**. In forests protected from large-scale disturbances of wind or fire, openings created by the death of a single canopy tree, part of a canopy tree, or a few individuals play a key role in regulating stand development **5**. Gaps in the over story are usually caused by wind throw of one or more canopy dominants and become areas of the forest that have greater levels of light and available moisture and nutrients **6**. Small canopy gaps can also be caused by other agents of disturbance such as lightning, insects or pathogenic fungi.

Since the size of a tree fall gap is proportional to the height of the individual that caused it, stands with larger trees would be expected to have larger average gap sizes. Heterogeneity in tree height increases the variability in gap size. Emergent trees may create disproportionately large gaps by knocking over trees beneath them as they fall, and the presence of lianas in the canopy (as in many tropical forests) increases average gap size because a single falling tree may pull down a very large tangle of lianas. This spatial heterogeneity of canopy structure means that gaps of widely varying shape and size exist throughout a forest stand. The distribution of gap types appears to be similar in temperate and tropical forests **7**.

The most important factor affecting the regeneration within these canopy gaps is the micro-climate. Gaps were at first regarded as having a micro-climate varying with their size in contrast with the overall closed forest climate, however, this is a simplification **8**. In micro-climatic terms forests are not just Swiss cheese: gaps are neither homogeneous nor are they sharply bounded **9**. Within a canopy gap the micro-climate is most extreme in the centre and changes outwards to the physical gap edge and beyond. The larger the gap, the more extreme the micro-climate of its centre. It is more likely that there is a larger area of small gap micro-climate around the centre of large gaps than there is in the centres of small gaps. Also there is a lot of variation in micro-climate between small gaps. The position of the gaps and the amount of direct sunlight heavily affect the micro-climate.

1.2 Gap closure

Canopy closure can occur in two ways. Individuals below the top of the canopy can grow taller, expanding their canopies in all dimensions while gaining height. Neighbouring individuals can also increase horizontal branch growth, thereby growing into the gap. This might be thought of as ‘side-closure’. Research has shown that most gaps close from below, i.e. individuals grow up into the gap and fill the growing space. Such vertical recruitment is a dominant succession process in many forest ecosystems **10**. It is important to remember that it may take several episodes of gap opening and closure for an individual tree to reach a dominant canopy position. Because of the competitive environment in the forest understory, individual trees

1. Hartshorn, 1978

2. Gray and Spies, 1996

3. Connell et al., 1997

4. Brokaw, 1982

5. Runkle, 1982

6. Van Pelt, 1995

7. Bongers, 2001

8. Brown, 1993

9. Lieberman et al., 1989

10. Whitmore, 1998

have a high probability of dying when they are small; the probability of mortality then decreases for a time when the individuals reach a dominant canopy position. Finally, as trees age, the chances of dying increase again, and the recruitment process can start all over again

1.3 Two main tree colonization strategies

Availability of light

Most studies on tree regeneration and gap structure have focused on the relationship among gap size, associated light levels, and regeneration success. The effects of gap size and gap position on the flux of solar radiation and its effect on the germination, survival, and growth of tree species have been of particular interest. The spatial and daily flux of photo-synthetically active radiation in forest gaps has been shown to be a pre-eminent factor in seedling survival and growth, particularly in tropical forests **11**. At any particular location, the amount of light entering the gap depends on the size and topographic position of the gap, the position within the gap, the height of the surrounding canopy, the sun angle, and sky conditions **12**. Differential response of tree species to light flux under closed forest canopies and in gaps has long been known to foresters who have provisionally segregated tree species in terms of their ability to germinate, survive, and grow under varying degrees of shade **13**.

Forests respond to canopy openings from disturbance in two major ways: by responding through reorganization of vegetation established prior to disturbance or by responding as vegetation that becomes established following disturbance **14**. The coupling of the long-held notions of shade tolerance with the recent interest in gap dynamics has emerged as workers attempt to relate gap physiognomy with difference in recruitment of tree species. The size of gaps in closed forests has been shown to determine the type of trees recruited in the gaps. Small gaps coupled with advance regeneration of shade-tolerant species would favour the “reorganization” response while seed colonization of large gaps by shade-intolerant species would define the other extreme **15**. From this observation researchers have tried to divide gap colonization by trees into two contrasting ecologic groups: those termed climax or primary species (non-pioneer) and pioneer species **16**. Despite the recognition that a continuum of regeneration

strategies exist, the classification of trees into two regeneration types has proven quite useful.

Pioneer species

Pioneer species germinate and establish in big gaps after their creation. Their basic strategy is to become a dominant canopy tree as fast as possible. To do this, pioneer species have evolved similar characteristics to quickly and efficiently attain a dominant canopy position in the forest. Typically they produce a large volume of low density wood by fast growth and are characterized by open-branched crowns that fill as much space as possible to reduce competition. They start to reproduce early in life and produce large quantities of small seeds that disperse easily and that stay viable for a long period of time in seed banks. This way they can colonize new gaps efficiently as they occur shattered through the forest. Their leaves are short-lived and their nutrients are rapidly recycled for new flushes. This strategy makes it inefficient to invest in mechanical or chemical protection against herbivores. Because of the continuum of regeneration strategies amongst trees and the ongoing debate if two distinct groups can be identified, the true pioneer species are defined as those tree species that can only germinate and establish in full light conditions. All other species that have the ability to germinate and/or establish in shade conditions are considered climax species.

Climax species

Climax or shade-tolerant species are able to establish themselves under a canopy cover as advance regeneration and will respond to small gaps. It is a very diverse group of tree species. Some of these species are able to germinate in full shade, but need full light within a year to survive, while other tree species can wait several years in the canopy's under story and use several canopy openings and closures to grow before reaching a dominant canopy position. In contrast with the pioneer species, climax species are slower growing species that produce denser timber and crowns. Because of the low energy availability under the canopy, shade tolerant species have developed numerous adaptations to become as efficient as possible. They have adaptations to lower grazing pressure by herbivores, multiple layers of leaves to collect as much as possible of the available light and specialized seeds in order to establish successfully under the canopy. These

Whitmore,1989;
Brokaw,1985

11. Denslow,1987;
Denslow and
Hartshorn,1994;
Nicotra et al.,1999
12. Messier,1996

13. Baker,1949

14. Marks,1974

15. Marks,1974

16. Whitmore,1978;

seeds have to contain sufficient reserves to grow a root system and the first photosynthetic organs to survive. The negative effect of this is that they are more susceptible to seed predation, which makes it necessary for them to germinate within a few days. For these reasons climax species need to put a lot of energy in their seeds, thus limiting their seed quantities and extending the maturity time of the tree.

1.4 Actual species composition in gaps

The preceding paragraph emphasized the relationship between gap size, geometry and light resources in the determination of the species composition of forest gaps. Many other factors, however, determine which individuals or species are able to successfully establish themselves in forest gaps. Hartshorn recognized the importance of variables other than gap size that influence the successful regeneration of tree species in gaps **17**. These included (1) time of gap occurrence, (2) proximity of seed source to gaps and mechanism of seed dispersal, (3) substrate conditions, and (4) plant-herbivore relations. Furthermore, **18** described a number of plant traits that even further complicate gap dynamic processes: (1) many shade-tolerant species require gaps in the canopy to reach maturity, (2) understory seedlings may experience damage or mortality in response to sudden increases in light flux, (3) some pioneer species may be able to take advantage of diffuse radiation, whereas many shade tolerant species are dependent on some brief period of direct radiation, and (4) even when resources such as light and nutrients are limiting, tree seedlings may not always respond to increased resource levels. Another research stressed the complicated nature of resource heterogeneity across the gap/non-gap continuum **19**. Because spatial-temporal heterogeneity is scale dependent, it may not be obvious which scale is appropriate to detect meaningful variation that is causing differences in species composition and density. Furthermore, **20** distinguished between what they termed “measured” and “functional” heterogeneity. Measured heterogeneity is what ecologists record with their instruments in the field. Functional heterogeneity, on the other hand, is what plants actually respond to. The gradients, therefore, of one or several variables measured across the gap – closed canopy continuum may not correspond to the actual gradients experienced by different species, genotypes, or phenotypes. For example, changes in gap size may not result in changes in gap microclimate **21** or resource al-

location **22**. It is with caution, therefore, that one accepts the simple gap-non-gap or “Swiss cheese” description of forest ecosystems **23**.

While cognizant of this fact, however, the vast majority of gap researchers have focused on the resource gradient and species response across the gap-under story continuum. Bazzaz and Wayne described it succinctly: “The primary questions we focus on (in gap dynamic research) are: What are the ecologically relevant quantitative and (or) qualitative differences in the micro-environmental conditions at different points across the gap-under story continuum, and what are the physiological and demographic characteristics of species’ seedlings that occupy different portions of the continuum **24**?” It is evident, however, that an understanding of the gap-non-gap interface as a continuum is somewhat limited. Resources do not necessarily display a gradual continuum in flux and concentration but are inherently heterogeneous from the gap centre into the closed forest. A prime determinant of such heterogeneity is the micro-site.

1.5 Micro-site

Of particular importance in determining seed germination and early tree establishment in gaps is the nature and abundance of forest floor substrates or micro-sites found in sub-canopy and open gap positions **25**. Tree recruitment is often more dependent on micro-site quality, which may override the effect of standing tree basal area, gap size, and resource gradients in gaps **26**. Micro-site variability may be a factor of forest floor disturbance and the presence of exposed mineral soil, amount and type of coarse woody debris, and degree of competing vegetation. The amount, type, and degree of decomposition of coarse woody debris on the forest floor significantly determine seed germination and survival and growth of tree seedlings in many forest ecosystems **27**. Fallen logs, upon suitable decay, act as nurse logs or preferred sites of germination. Fallen wood, although making up only a small percentage of the micro-sites, accounts for a disproportionate percentage of established seedlings. This differentiation in density and species composition on rotten wood has been attributed to the reduced competition from herbs and mosses on the raised surfaces of the coarse woody debris **28** and retention of favourable moisture supplies **29**. Tree falls that expose mineral soil and produce pit and mound topography create a diversity of micro-sites conducive to the

22. Kuuluvainen et al.,1993

23. Lieberman et al.,1989

24. Bazzaz and Wayne,1994

25. Zasada et al.,1992;
Duchesneau and Morin,
1999;

Greene et al.,1999

26. Houle,1992;
Lundqvist and Fridman,
1996;

Gray and Spies,1997

27. Harmon et al.,1986

28. Harmon and Franklin,
1989

29. Place,1955

17. Hartshorn,1978

18. Bazzaz,1996

19. Bazzaz and
Wayne,1994

20. Bazzaz and
Wayne,1994

21. Brown,1993

30. Beatty and Stone,1986; Schaetzl et al., 1989a,1989b; Jonsson and Esseen,1990; Jonsson and Dynesius, 1993; den Ouden and Alaback,1996; Rydgren et al.,1998; Ulanova,2000
31. Peterson and Pickett,1990; Peterson et al.,1990
32. Henry and Swan,1974; Putz,1983; Nakashizuka,1989
33. Huenneke,1983
- establishment and growth of particular tree, moss, and herbaceous species **30**. Whether a tree dies and remains standing for a significant period of time, breaks off above the ground, or uproots to create forest floor and soil disturbance will determine the type of micro-site available for subsequent colonization. The pit and the mound act as unique micro-sites that can determine tree species composition, growth, and density **31**.
- Trees classified as pioneers are often found regenerating preferentially on disturbed soil in tree fall gaps **32**. Hence, so-called “early successional species” are able to persist in the canopy dominated by late successional species because of periodic tree uprooting. Non-tree vegetation may often respond to the increased resource fluxes in gaps and act as an important factor militating against the successful response of tree species. Trees may not respond, therefore, in a predictable fashion to gap openings because of above- and below-ground competition effected by flourishing ground vegetation. Response of competing vegetation may depend on gap size. Single elm (*Ulmus americana* L.) tree gaps resulted in the regeneration of canopy dominants whereas multiple-tree gaps enhanced successful shrub regeneration, effectively suppressing regeneration of the tree dominants **33**.

1.6 Conclusion

Literature studies on natural regeneration in a virgin cloud forest showed that the most important event in the tree regeneration process within a virgin cloud forest is when an opening of the canopy occurs. Further came forward that the size of gaps in closed forests determines the type of trees recruited in the gaps. Small gaps coupled with advance regeneration of shade-tolerant species (climax species) would favour the “reorganization” response while seed colonization of large gaps by shade-intolerant species (Pioneer species) would define the other extreme **34**. From this observation researchers have tried to divide gap colonization by trees into two contrasting ecologic groups: those termed climax or primary species (non-pioneer) and pioneer species **35**. Tree recruitment is often more dependent on micro-site quality, which may override the effect of standing tree basal area, gap size, and resource gradients in gaps **36**.

34. Marks,1974
35. Whitmore,1978,1989; Brokaw,1985b
36. Houle,1992; Lundqvist and Fridman,1996; Gray and Spies,1997

2

Major barriers to natural regeneration on abandoned and degraded pasture lands

Introduction

To give a good impression about how to reforest an abandoned pasture land it is very important to know what the major barriers are to the natural regeneration, and how they are caused. This because without knowing anything about the behaviour of the natural regeneration on those pastures, there will be never a successful reforestation project. With this information available a structured overview can be made, on which problems have to be taken into account when reforestation efforts are made to stimulate the natural regeneration. In the following paragraphs all the major barriers to natural regeneration on abandoned and degraded pasture lands are summarized.

2.1 Barriers to restoration

Several studies have shown that, once pasturelands have been abandoned, native species seedling recruitment is poor **37**. A study by **38** examining barriers to forest regeneration in an abandoned pasture in Puerto Rico, showed that the major factors were lack of soil seed bank, and seed rain input. Similarly, studies **39** pointed out that factors which could delay or slow forest recovery were: shortage of tree seeds, seed and seedling predation, drought, competition with established grasses/weeds, exhaustion of soil nutrients and changes in soil physical properties.

2.2 Shortage of tree seeds

The study of seed availability as a limiting factor in forest recovery processes **40** clearly indicates that seed availability is a major limiting factor in forest recovery in three important ways: (1) tree seed density in pasture seed banks is low, (2) the immigration of new recruits is hampered, and (3) seed predation seriously limits the available pool of species. Not only is seed availability limited, but several studies indicate or suggest that the potential available assemblage of species may also be restricted.

37. Buschbacher,1986; Aide, Zimmerman, Herrera & Rosario,1995; Aide et al.,2000; Cubina & Aide,2001
38. Zimmerman, Pascarella and Aide,2000
39. Richards,1996; Cubina andAide,2001; Florentine, Craig, and Westbrooke,2003
40. Holl, Loik, Lin & Samuels,2000

41. Garwood,1989

42. Whitmore,1983;
Vazquez-Yanes &
Orozco Segovia,1984

43. Charles-Dominique,
1986;
Nepstad et al.,1990,
1996

44. de Steven,1991;
Hammond,1995

45. Charles-Dominique,
1986;
Nepstad et al.,1990,
1996;
Aide & Cavelier,1994

46. Grubb 1996,1988;
Metcalf & Turner,
1998

47. Charles-Dominique,
1986

48. Nepstad et al.,1996

49. Fox,1976

50. Nepstad et al.,1991,
1996

51. Uhl,1987

52. Nepstad et al.,1991

53. Nepstad et al.,1996

54. Aide & Cavelier,1994

First, the tree seed composition in seed banks is virtually limited to pioneer species **41**, such as *Cecropia obtusifolia* and *Helioscarpus americanus*. Most of the pioneer species have the capacity of long viability and/or dormancy, in contrast to most mature forest tree species **42**. Second, the main seed vectors for open areas, birds and bats, disperse generally only small, light weight seeds of pioneer species, opposed to the larger, heavier seeds of climax species **43**. Finally, larger seeds with higher energy content (often climax species) are more attractive to seed predators than small seeds, which may be difficult to find in grasslands **44**. These factors may thus result in al limited and skewed assemblage of species available for forest recovery processes **45**.

Various aspects of these general trends may be questionable, however. Climax species and pioneer species have a wide and overlapping range of seed sizes, both including species capable of persisting in the soil seed bank (irrespective of seed size) for a substantial period of time **46**. Species with small seeds can be dispersed by birds and bats **47** but also risk predation by small rodents and ants **48**.

2.3 Lack of micro-climate and water availability

For tropical rainforest species, soil surface microclimate is very important for successful germination. Germination rate and subsequent survival rate are very high if the soil moisture and temperature are conducive **49**.

The research **50** suggests that high temperatures and lower moisture availability in pastures compared to forests may result in water stress for plants and may limit seedling establishment and survival **51**. Nepstad reported that soil water potential in the top 15 cm of soil of an abandoned pasture in the Brazilian Amazon was low for a number of weeks during the dry season **52**. In related research, xylem pressure potential was two to five times lower for seedlings planted in a pasture compared to those planted in tree fall gaps **53**. Dense grasses can also influence the forest recovery on highly degraded pastures by reducing evaporation from the soil **54**. Available moisture may not be limiting at all abandoned pastures but it depends on the duration of the dry season. For example when the dry season has a duration of three months the influence of water stress is much lower than when the dry season takes six months.

2.4 Importance of distance to forest edge

However, even if the microclimate is suitable and enough water is available, without enough seed supply into abandoned lands recruitment will be nil. Therefore seeds dispersing into a reforested site are important in enhancing the reforestation and will accelerate the recovery process. Seed supply from natural forest to abandoned lands, however, is very poor. Another research showed that few seeds were found that disperse more than 10m from the forest edge and seedling numbers declined to nearly zero, 20m from the forest edge **55**. In a study conducted in Puerto Rico, out of 35 species producing fruit in the surrounding forest, only five species were detected in the seed rain or seed bank 44m from the forest edge **56**. Lack of seed movement from the primary rainforest to abandoned pasturelands or reforested lands is dependent on several factors. Most tropical rainforest trees and shrubs depend on animals, however, considerable numbers of animals such as frugivorous and bats avoid large open areas where they could be easily targeted by predators **57**. Several studies have shown that frugivorous birds visiting degraded pasture from forest remained within 80m of the forest **58**.

2.5 Competition with established grasses and weeds

Invasion of exotic species into abandoned lands or fragmented forest landscapes is inevitable. Once they have invaded, they alter the structure and function of the area **59**. These invaders prevent native species colonisation in several ways. Thick weed cover may prevent the native species seed from reaching the soil **60**. Even if native species reach the ground, invaders compete for nutrients and moisture with newly recruited seedlings **61**. Dense grasses can also influence the forest recovery on highly degraded pastures by reducing evaporation from the soil **62**. Above and belowground competition with pasture grasses has been suggested as a major factor that limits growth of certain plant species in tropical pastures **63**.

55. Charles-Dominique,
1986;
Gorchov, Cornejo,
Ascorra, & Jaramillo,
1993;

Aide & Cavelier,1994
56. Cubina & Aide,2001

57. Howe & Smallwood,
1982

58. da Silva, Uhl & Murray,
1996

59. Vitousek, Antonio,
Loope & Rejmanek,1997;
Horvitz, Pascarella,
McMann, Freeman &
Hofstetter,1998

60. Aide et al.,1995

61. Vieira, Uhl & Nepstad,
1994;
Nepstad, Uhl, Pereira &
da Silva,1996

62. Aide & Cavelier,1994

63. Nepstad et al.,1991;
Guariguata et al.,1995;
González Montagut,1996;
Sun & Dickinson,1996

2.6 Soil and nutrient properties

Information on the changes in soil properties before and after deforestation and under grazed pasture and/or under anthropogenic pasture or secondary forests is scarce **64**. The research **65** reported significant changes in selected soil properties subsequent to recreational use of a forested reserve in Malaysia. The major changes were; increases in bulk density, compaction, soil erosion, and runoff, decreases in infiltration porosity, and water-holding capacity. Similar information for deforested pastureland turned to anthropogenic grassland and/or secondary forests is scarce for the tropical rainforest listed as a Natural Heritage Reserve by the UN, in north Queensland, Australia. Most previous research in the tropics has indicated that plants are commonly limited by phosphorus **66**, although there are exceptions **67**. Low levels of available P are common in volcanic soils because binding of this element with clay results in high P retention rates **68**. Most studies comparing nutrient levels in pasture and forest have reported lower levels of cations in the pastures than in primary and secondary forests **69**. Previous bioassay studies have suggested that seedlings grown in pasture soils are more nutrient limited than those grown in forest soils **70**. Tropical forest soils are extremely variable with respect to their mineralogy and management history **71**, which largely accounts for site-specific differences in the extent to which nutrient availability limits forest recovery.

2.7 Discussion and conclusion

It is clear that regeneration of tropical forest vegetation in abandoned pasture is limited at all early-successional stages: colonization, establishment, growth, and survival. Lack of seed availability appears to be the overriding factor limiting forest recovery in tropical pastures. Not only is dispersal of forest seeds into open areas minimal, the few seeds that do arrive are commonly subjected to high rates of predation **72**. Questions of drought stress and nutrient limitations become moot if seeds of forest species are not dispersed into pasture. Therefore, efforts to facilitate recovery must focus on strategies to evaluate seed dispersal, such as planting native tree seedlings to increase canopy architecture, installing bird perching structures, or artificially establishing shrubs that rapidly mature and fruit, thereby attracting

seed dispersers.

If barriers to seed dispersal are overcome, a number of interrelated factors may influence seed germination, as well as seedling growth and survival. These factors include lack of micro-climates, water availability, soil and nutrient properties and competition with established grasses/weeds. The degree to which drought stress affects recovery is highly variable over spatial and temporal scales, depending on the length and severity of the dry season. Nutrient limitation is strongly influenced by soil type, climate, and past land use, further complicating the interaction among these variables. Given the variability in the relative importance of these factors, it is essential to identify rate-limiting factors at individual sites in order to be able to design site-specific management plans to accelerate forest recovery.

3

How to overcome these major barriers by human interventions

Introduction

Forest establishment on small and large degraded sites, takes a considerable period of time because of the major barriers discussed in the chapter 2. Human interference in the recovery process may be regarded as a valuable option, considering the possible functions and values of the restored forest area.

Major barriers discussed in chapter 2:

- Shortage of tree seeds;
- Lack of micro-climate and water availability;
- Importance of distance to forest edge;
- Competition with established grasses and weeds;
- Soil properties.

The following paragraphs will describe which methods can be used to overcome these major barriers for natural regeneration of trees in abandoned and/or degraded pasture lands.

64. Johnston,1992;
Reiners, Bouwman,
Parson & Keller,1994
65. Jusoff,1989

66. Golley et al.,1975;
Vitousek,1984;
Ewel,1986

67. Vitousek et al.,1987;
Tanner et al.,1992

68. Uehara & Gillman,
1981

69. Krebs,1974;
Montagnini & Sancho,
1990;
Aide & Cavelier,1994;
Reiners et al.,1994

70. Aide & Cavelier,1994;

71. Sanchez,1976;
Landon,1984

72. Janzen,1971;
Uhl,1987;
Nepstad et al.,1990;
Aide & Cavelier,1994;
Holl & Lulow,1997

3.1 Shortage of tree seeds

Direct seedling or transplanting of seedlings

In highly degraded or abandoned pasturelands, soil stored seed bank of native species composition is very poor, mainly because tropical rainforest seeds cannot stay in the soil for a long period **73**. In addition, tropical rainforest seed dispersal agents such as birds and mammals may not utilize the open pasturelands very often. Under these circumstances direct seeding or transplanting of seedlings is essential **74**. Studies have shown that human intervention in pasturelands may facilitate and accelerate the re-colonization of tropical rainforest species.

73. Whitmore,1997

74. Wunderle,1997

Addition of seeds from the forest soil

Potential approaches to restoration include assisting natural regeneration by protecting the site from further disturbances and by allowing natural succession processes, and accelerating natural colonization through artificial establishment of seedlings **75**. In another study **76** they added soil from the forest (seed bank) to various treatments of the pasture vegetation. The experiments indicated that the addition of seeds from the forest soil, irrespective of treatment, greatly increased the density of germinated tree seedlings. Thus, an artificial increase in seed availability may be one of the crucial components.

75. Lamb et al.,1997;

Holl et al.,2000

76. Kuzee & Wijdeven,
unpublished study

Attract the main dispersers

Another method to counter against the shortage of tree seeds, is by trying to attract the main dispersers back on the pasture lands. To achieve this it is necessary to plant pioneer species in the abandoned pasture lands which are attractive to birds and mammals, the major seed dispersal agents **77**. It is for this reason that species selection is very important for most restoration programs. Significant numbers of fast growing fruit and flower producing trees may help to bring seed dispersal agents into the restored sites.

77. Whitmore,1997;
Goosem & Tucker,
1995;
Wunderle,1997

3.2 Lack of micro-climate and water availability

Differences in moisture availability may also account for the differences in seedling survival and growth outside and inside the forest fragments, at least in part. Water deficit has been reported as a major cause of seedling death of tropical trees in gaps **78**. Outside the forest, the lower air humidity's recorded may have increased the rate of water loss from the seedlings and caused soil desiccation.

Studies have shown that human intervention in pasturelands may facilitate and accelerate the re-colonization of tropical rainforest species. But restoration ecologists are struggling to determine which techniques are most appropriate to restore degraded and abandoned pasturelands in tropics.

A study suggested that plantations are one alternative way to accelerate natural regeneration of native species on abandoned pasturelands **79**. Further techniques, such as broadcasting of seed, and cutting of native tree species must also be examined. It is widely accepted that one cannot simply introduce primary forest species (either seed or seedling) into abandoned pasturelands, mainly because primary forest species may not survive under full sunlight, or high soil temperature **80**.

78. Turner,2001

79. Chapman and Chapman,
1996

80. Whitmore,1991

Further a research proposed that artificial tree planting should be exercised on the abandoned lands to accelerate the recovery process **81**. In rainforest succession, colonization of pioneer species creates a suitable condition for climax species to germinate and grow. Pioneer species grow fast and must produce canopy as quickly as possible. This will reduce the weed cover and create a favourable microhabitat and microclimate for climax species to germinate and often increase soil nutrients.

81. Lugo,1992

Another research highlight the role of remnant tree shade in providing a favourable environment for seedling growth of certain species **82**. Previous studies have suggested that trees may ameliorate micro-climatic conditions, but have focused on the role of trees in reducing soil water loss **83** and soil temperature **84**, without considering the direct effect of light intensity for planted seedlings.

It is important to recognize that photosynthetic rates can be influenced by combinations of light and other stresses, such as high temperature **85**, drought **86**, and lack of nutrients **87**.

82. Harvey and Haber,1999

83. Belsky,1994;
Verdú&GarcíaFayos,1996

84. Belsky et al.,1989

85. Mulkey & Pearcy,1992

86. Maxwell et al.,1994

87. Castro et al.,1995

3.3 Importance of distance to forest edge

Chapter 2.4 mentioned that the distance from the degraded area to the forest edge has a significant influence. Human intervention can play an important role in restoring a degraded forest but it does not have any influence on how far the degraded pasture land is situated from the original forest edge. But still the distance between the degraded area and the forest edge has to be known, because this way all the influences of the original forest can be taken in consideration. For example, if the degraded area is close to the forest edge (within 20m) there will be seed rain from the original forest in the degraded area, but if the distance is larger than forty meters, human interventions may be necessary to achieve the demanded seed rain in the degraded area. One of these interventions could be the planting of pioneer species with suitable characteristics to attract birds from the forest edge into the degraded area. The same intervention could be used to attract other animals like squirrels and other rodents.

3.4 Competition with established grasses/weeds

As mentioned in chapter 2.5 invasion of exotic species into abandoned lands or fragmented forest landscapes, prevent native species colonization in several ways. There are different ways to overcome these problems. There can be tried to remove all the exotic grasses by cutting, removing by hand\machine or poisoning, but this will be very labour intensive and time consuming. However it is easier to create a situation that will lead to unsuitable circumstances for the exotic grasses to grow. To create such a situation planting pioneer species is one of the best solutions, this because pioneer species have the characteristics of fast growth and the quick creation of a canopy. This will lead to reduction of available sunlight for the grasses and weeds. Which will lead to reduction of the weed cover and able the climax species to establish.

3.5 Soil properties

As can be read in paragraph six of chapter two, the availability of essential nutrients for plants and trees is poor on an abandoned pasture land. There are several ways to re-establish the soil fertility but it is very time consuming and there is no ideal solution for this problem. One of the best options is to plant trees with a nitrogen fixing root systems. This will lead to more nitrogen available in the soil for other plants. Another reason trees should be planted is that trees drop their leaves once or sometimes more often in a year. This leads to more organic matter in the soil. Higher nutrient inputs through litter fall are likely to interact with the effects of light result in more abundant growth of seedlings below trees. Another method to fertile the soil are for example adding fertilizers, but this is inefficient and costly.

3.6 Conclusions and discussions

This chapter described how to deal with the major barriers of restoring rainforest in abandoned pastures. One of the most important human interventions will be the establishment of remnant trees in the degraded pasture lands. These trees not only serve as a source of seeds and not only enhance animal dispersal of seeds, they also ameliorate high light levels, modify the energy budget of other species under the canopy, and often increase soil nutrients. Species-specific differences in the ability to tolerate the high light environment of open pastures may be an important consideration in choosing pioneer species for reforestation. However the kind of fruits the trees are bearing is almost as important, because they promote the attraction of seed dispersers.

4

The influence of tree planting on the establishment of natural regeneration in the Cloudbridge Reserve.

Introduction

In recent years restoration attempts by converting abandoned pasturelands have increased significantly. But natural recovery will take many years to occur. Several factors were found that impeded forest recovery, like lack of soil nutrients, soil compaction, competition, seasonal droughts, seed colonization and seed/seedling predation. Native seedling availability is poor ⁸⁸. Loss of viable seeds can be caused by a variety of factors such as germination, unfavourable environments, pathogens, or predation ⁸⁹. Other studies concluded that lack of forest recovery was due to lack of soil seed bank and seed rain input ⁹⁰. The objective of this monitoring is to investigate if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting.

Before anything can be said about the acceleration of forest recovery by planting trees, first it has to be made clear how recovery takes place when pastureland is left to regenerate naturally. Only if a difference in the amount and species composition of established natural regeneration can be found, between the treated pasture land and the areas without treatment, it can be concluded that forest recovery was accelerated. To get a complete answer to this question two inventories are conducted. For the first inventory a research plot within the Cloudbridge reserve will be created in an area that was left to recover without any human interventions. In this research plot an inventory is done on the amount and species composition of the established natural regeneration. Secondly, an inventory on forest recovery will be conducted on one of the plantations within the Cloudbridge nature reserve. This inventory will be made on regeneration of cloud forest trees under different planted tree species. After this, they can be compared to see if planting of trees has promoted the establishment of natural tree regeneration.

- 88. Buschbacher,1986;
Aide et al,2000
- 89. Louda,1989;
Parker et al.,1989;
Hammond et al.,1995;
Hau,1997
- 90. Cubina and Aide,
2001;
Florentine, Craig and
Westbrooke,2003

4.1 Regeneration count plantation

As said in the previous paragraph the research will zoom in on one of the plantations to investigate, if planting of trees can accelerate the forest recovery on abandoned pastures. The inventory on regeneration is conducted at the river trail plantation. The plantation chosen for this inventory is the River trail plantation. The reason for choosing this plantation is that it was established the most systematic of all the plantation sites (in a 4x4 spacing). Factors like easy access, most available data from the last six years, most diverse trees planted, situated in the centre of the Cloudbridge reserve justified the choice further.

The river trail area is almost square shaped and is situated on an elevation of 1590 m north to 1620 m on the southern part. The slopes vary from 5 to 45% but there are still enough flat parts to grow trees. It contains 540 planted trees on a spacing of 4 x 4. Those trees were planted in the year 2002 and some dead trees were replanted in the following years. Their height ranges from 25 cm to 10 meters, which creates an enormous variety in structure throughout the plantation. There was little maintenance in the past; the only activity that was carried out was clearing the small trails once, sometimes twice a year, to monitor the planted trees. The exact location of the plantation can be found in *Fig 1*.

The purpose of the data is to see how much natural regeneration is establishing in an area that was planted with diverse tree species. The research area covers one of the reforested areas in the Cloudbridge reserve. Under each tree the natural regenerating trees and most abundant shrubs are counted within a radius of two meters and their species determined. This is to see which tree species have the highest regeneration and to find out about the species compositions that are established under different tree species. More information about the methodology can be found in appendix 2.

The data collected during this inventory were stored in Microsoft Excel sheets and later imported into a Microsoft Access database for analysis. This way the data collected in the regeneration monitoring can be used to compare tree regeneration among planted trees with an area left to recover naturally. More information about the creation of the database and the analyses of the data can be found in appendix 4.

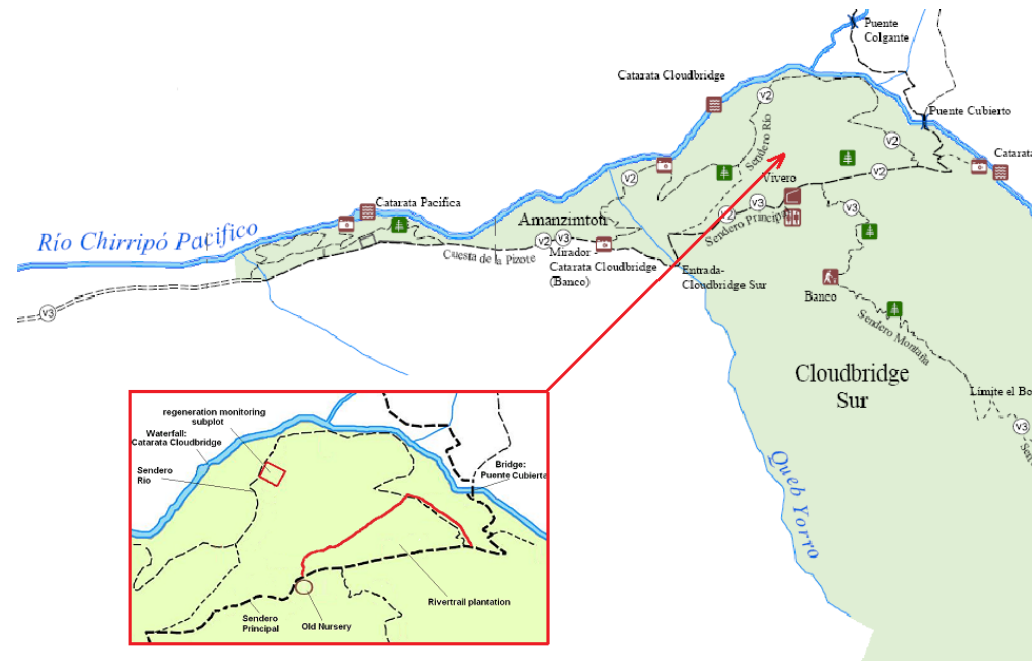


Fig 1: Overall map of Cloudbridge Reserve and location of research areas.

In *Table 1* the results of the regeneration count in the plantation can be found. From all the known regenerated species found in the plantation the amount, common name, type of tree and the scientific name are given. The average count per 36 measuring points is also given, so as to compare the regeneration of the plantation with the regeneration in the subplot without any human interventions.

As can be seen in the table the first twelve species are the dominant regenerated species in the plantation. Those species will be described in the following paragraphs.

Sorillo, Poro, Guacamalla, and Guarumo are shade-intolerant species. These species were found in relatively light areas on canopy edges of the mature trees where the number of weeds and grasses were reduced. Circumstances like enough available sunlight and low competition with weeds and grasses are ideal for those shade-intolerant species to germinate and establish themselves.

- The species Sorillo was the most abundant of these species and found throughout the whole plantation. This shade-intolerant tree is one of the fastest growing species in the surrounding area and can be found in abandoned pasture lands as well in secondary forests. From observations in the field it can be determined that this species is very resistant against competition of weeds and grasses. It can be concluded that this tree is the first species that establishes itself in the initial stage of natural succession on an abandoned pasture.

- *Erythrina poeppigiana* is a nitrogen fixing tree which is common in all of Costa Rica. It is used for agro-forestry purposes like fences and as a shadow tree in coffee plantations. Because the plantation area was used as pasture land before it was reforested, mature trees can still be found throughout the plantation area. The regeneration of *Erythrina poeppigiana* can be explained in two different ways. The mature trees already present are a good source of new seed input dispersed by wind. Also the seeds of this species stay viable for a long period in the soil seed bank. When the micro-climate becomes suitable for the seeds to germinate, abundant seedling establishment will take place here.

- *Cecropia polyphelbia* is a very important tree species in the ecology of Tropical forest. It is one of the main food sources of Howler

monkeys and the tree is a home base for sloths. It is found often on the edges of secondary forest and forest gaps. Mature trees are found on the edges of the plantation where small patches of forest were left unused because of steep slopes or closeness to the river. These mature trees are a good source of new seed input dispersed by frugivorous birds. The seeds of this species also stay viable for a long period in the soil seed bank.

- There is not much information available on the Guacamalla trees. This is due to the fact that the scientific name is not known yet. From observations during the regeneration monitoring it can be concluded that the tree has similar characteristics as the other two species.

Ortiga, *Quercus* sp. and *Quercus gulielmi-treleasei* are shade-tolerant species. They were found in groups of regeneration mainly under dense canopy closure under circumstances of minimum sunlight and few grasses and weeds present. This micro-climate was mainly found in the southern part of the plantation where a mix of Cypress and Oaks were planted.

- *Quercus* sp. and *Quercus gulielmi-treleasei* are found in the natural vegetation of primary Cloud forest within the region. Because of their position as climax Cloud forest species they are very important for the assessment of the effectiveness of tree plants on the stimulation of natural regeneration. Squirrels were observed in this part of the plantation and are the main dispersers of the oak seeds.

- There is no information available on the Ortiga trees. This is due to the fact that the scientific name is not known yet. From observations during the regeneration monitoring it can be concluded that the tree has similar characteristics as the other two species.

The mature Lengua de vaca trees are generally found in secondary forest and along forest edges but from observation it could also be concluded that regeneration can take place under close canopy. The regeneration was found on spaces with minimum sunlight as well as in open areas. For this reason it was classified neither a shade-intolerant nor a shade-tolerant species. More detailed information on growing requirements on the tree species could not be found.

Inga species is a fruit tree. It is an important tree for the attraction of dispersers like most fruit trees. Seedlings were mainly found in large groups on the north side of the plantation, and sporadically found

Common name	Family	Genus	Species	Species code	Total count regeneration	Average count per 36 measuring points
Sorillo				Sor	211	22,95
Poro		Erythrina	poepigiana	Por	36	3,92
Guacamalla				Gua	22	2,39
Mirto	Fabaceae	Inga	species	Ing	21	2,28
Quercus gt.	Fagaceae	Quercus	gulielmi-treleasei	Qgt	20	2,18
Ceresilla				Cer	19	2,07
Ortiga				Ort	17	1,85
Lengua de vaca	Melastomaceae	Conostegia	oerstediana	Ldv	16	1,74
Unidentified 6				Un6	15	1,63
Unidentified 5				Un5	15	1,63
Quercus c.	Fagaceae	Quercus	copeyensis	Qsp	15	1,63
Guarumo	Cecropiaceae	Cecropia	polyphlebia	Cec	13	1,41
Mosote		Triumfetta	semitriloba	Mos	7	0,76
Behuco,chajotlillo				Cha	5	0,54
Unidentified 3				Un3	3	0,33
Cedro dulce	Meliaceae	Cedrela	tonduzii	Ced	3	0,33
Unidentified 2				Un2	2	0,22
Amarillo				Ama	2	0,22
Raho ermao				Rer	2	0,22
Wild Avocado		Persea	caerulea	Avc	1	0,11
Behuco				Beh	1	0,11
Chajotillo				Chj	1	0,11
Lengua de vaca	Melastomaceae			Len	1	0,11
Moqillo,moco		Saurauia	montana	Moc	1	0,11
Yas		Persea	schiedeana	Yas	1	0,11
Unidentified 1				Un1	1	0,11
Unidentified 4				Un4	1	0,11
Limon		Citrus	aurantifolia	Lim	1	0,11

Table 1: Regeneration count plantation.

Common name	Family	Genus	Species	Species code	Total count regeneration
Mirto	Fabaceae	Inga	species	Ing	22
Guarumo	Cecropiaceae	Cecropia	polyphlebia	Cec	1
Poro		Erythrina	poeppigiana	Por	17
Sorillo				Sor	35
Unidentified 5				Un5	4

Table 2: Regeneration count subplot.

throughout the rest of the plantation. The large groups found on the north side are probably dispersed from the mature trees on the edges of the plantation where small patches of forest were left unused, due to steep slopes or closeness to the river. The seedlings that were sporadically found, are probably dispersed by animals. *Ceressila*, Unidentified 5 and 6 are regeneration of tree species that could not be identified yet. Therefore nothing can be said about their regeneration requirements. But these observations are not useless; they can still be used as indicators for the effectiveness of tree plant as a method for succession of natural regeneration on abandoned pasture land.

4.2 Regeneration count subplot

The purpose of the data collected is to determine the amount and species composition of established natural regeneration in the areas that did not get any special treatment and were left to regenerate naturally. A research area was created next to the river trail plantation as can be seen in fig... The location of this subplot was chosen for its similar site conditions (elevation, soil, aspect, distance to the river, distance to the forest edge, etc.) as the plantation. Also, the accessibility from the river trail, made this location suitable to conduct this inventory. Around this open area a couple of remnant *Inga* species and *Erythrina poeppigiana* trees remained during its former land use as pasture but there is still a lot of sunlight that reaches the ground. In the subplot itself the regeneration of these trees was assumed to have continued from the time after the pasture was abandoned and counted as natural regeneration of that species.

In the research site 36 Stakes will be planted in a square, in a 4x4 spacing (the same as the planted trees spacing). From the corner stakes locations are determined by a GPS system. Around each individual stake all the naturally regenerated trees and most abundant shrubs within a radius of 2 meters are counted and their species determined. These stakes are numbered so that data can be collected in the future. More information about the used methodology can be found in appendix 2. The data collected is stored in a Microsoft Excel data sheet and afterwards imported into a Microsoft Access database to compare the collected data individually and to compare them with the data found for the regeneration in the river trail plantation. More

information about the creation of the database and the analyses of the data can be found in appendix 4.

In *Table 2* the results of the regeneration count in the subplot can be found. From all the known regenerated species found in the plantation the amount, common name, type of tree and the scientific name are given.

As can be seen in *Table 2* there were only five different species found in the subplot. This can be explained by the size of the research area and by the fact that only a micro-climate with high light level conditions was found throughout the subplot. This makes it only possible for shade-intolerant species to establish in this area. This could further explain, why the species composition of the regeneration in the subplot consisted of only shade-intolerant species.

- The regeneration of the species *Sorillo* was found most abundantly, similar to the composition of the regeneration found in the plantation. This is another proof that this tree is the first species that establishes itself in the initial stage of natural succession on an abandoned pasture.
- Around the subplot there are several mature trees of *Inga* species and *Erythrina poeppigiana*, which provide a substantial seed rain of those species in the subplot. This can explain the high amount of regeneration of *Inga* species and *Erythrina poeppigiana* observed in the subplot.
- A significant amount of regeneration from unidentified 5 is found in the subplot. This is a tree species that could not be identified and therefore nothing can be said about their regeneration requirements. From the regeneration of this species in the subplot can be assumed that it is most certainly a shade-intolerant species.
- The regeneration of *Cecropia polyphelbia* can be explained by the influence of mature trees of this species found in secondary forest patches throughout the Cloudbridge reserve. These mature trees are a good source of new seed input dispersed by frugivorous birds. Also do the seeds of this species stay viable for a long period in the soil seed bank.

More information about these species can be found in paragraph 2.4.

4.3 Differences in found regeneration

In order to determine if planting of trees promote the establishment of natural regeneration in the Cloudbridge reserve after six years, the results of the regeneration monitoring are compared. To get a complete overview of differences between the regeneration found under the planted trees and the subplot, a graph is created. Because the subplot contained only 36 and the plantation 331 measuring points, the data of the regeneration of the plantation had to be averaged before they could be compared. The results of this comparison can be seen in the *Graph 1*.

As can be seen in the *Graph 1* there is a significant difference in the diversity of regenerated tree species. The average regeneration counted in the plantation shows a much higher diversity of species than in the subplot. On the plantation 28 different tree species were regenerating, while the regeneration in the subplot counted only 5. This difference in tree species regeneration can be explained in several ways:

The area of the planted trees creates a diversity of micro-climatic conditions. This is caused by the difference in growth characteristics between the 19 different planted tree species. For example, some trees provide a low light level micro-climate, caused by dense canopy closure, while other tree species provide micro-climates with a relatively high light level micro-climate. In this diversity of micro-climates a wider range of tree species can establish. This happens because some tree species require relative light conditions while others prefer the shade of canopy trees for their regeneration. This difference in micro-climates can also explain that both shade-intolerant and shade-tolerant species can be found in the plantation. In contrast with the planted areas the difference in micro-climates in the subplot is low. This could be a reason why diversity of regenerating species in the subplot is less than in the plantation. Another reason why a wider range of tree species establishes themselves under the planted trees is that the trees lower the competition for the regeneration with grasses and weeds. Thick weed cover may prevent the tree species seeds from reaching the soil ⁹¹. Even if the seeds reach the ground, invaders compete for nutrients and moisture with newly recruited seedlings ⁹². More information on the influence of micro-climate and the

influence of grasses and weeds on the species composition of regeneration can be found in chapter 2.

The difference in species composition can be further explained by the ability of some planted tree species to attract dispersers into the planted area. In total 19 different tree species are planted from which some have the ability to attract different kind of dispersers. This attraction of dispersers leads to a higher amount of seed input. Tree planting in general enhances the attraction of dispersers further. The reason is that most seed dispersers avoid large open areas because this makes them vulnerable for predators. More information on the effect of tree planting on seed dispersers can be found in chapter 2 and 3.

The amount of regeneration found per species was much higher in the subplot. This is probably due to the homogenous micro-climate in the area that favours shade-intolerant species. This micro-climate with high light levels is only suitable for colonization specialists which can withstand high light levels and are resistant to water stress. This select group of tree species finds suitable circumstances in these open areas and are capable of producing large numbers of regeneration. The competition with other tree species is reduced as well, because they cannot survive in these harsh conditions. Another reason for the high amounts of few tree species can be that seeds can only be dispersed in this area by wind. The reason for this is that most animal dispersers avoid open areas.

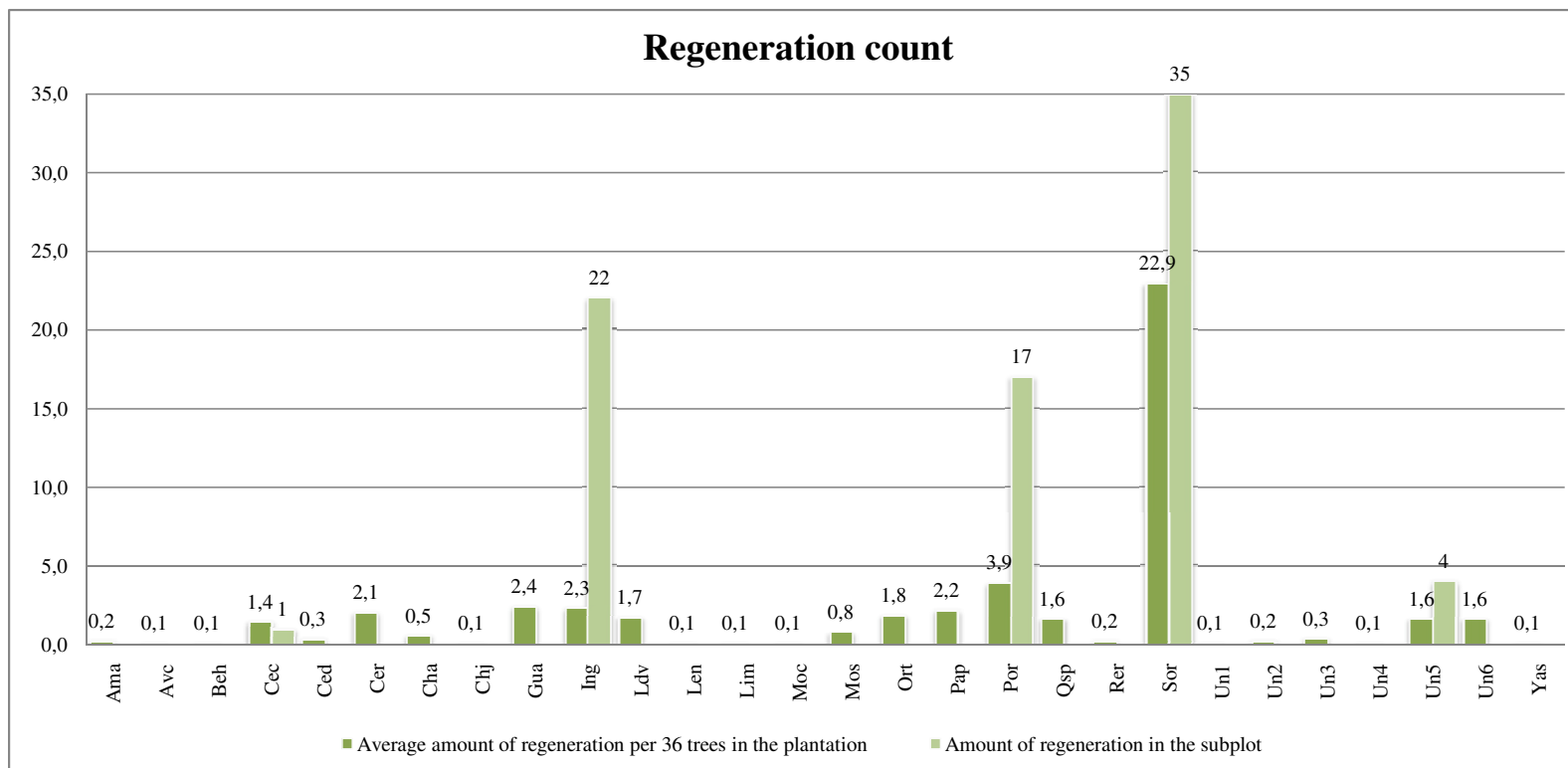
4.4 Conclusions and discussion

After comparing the results from the different research areas, the question if planting of trees promotes the establishment of natural regeneration in the Cloudbridge reserve after six years can be answered. From the data collected in the research area already a significant difference in regeneration can be found after only six years. The most significant difference in regeneration between the two research areas is the species composition of the regenerating trees and the frequency of regenerating species.

1994;
Nepstad, Uhl, Pereira
& da Silva, 1996

91. Aide et al., 1995

92. Vieira, Uhl & Nepstad,



Graph 1: Regeneration count on plantation compared with the subplot.

Under the planted trees a mixture of shade-intolerant and shade-tolerant species was found, while in the subplot that was left to recover naturally only pioneer specialists were found. The finding of this difference in tree regeneration composition can be a sign that tree planting on an abandoned pasture land promotes the range of tree species that can establish. The return of shade-tolerant species seems to accelerate the recovery process towards the original Cloud forest. The observation of several dispersing animals in the plantation is also a sign that planting of trees favours the recovery process. But it is still unclear if the method of planting trees actually accelerates the recovery process towards the original cloud forest in the long term. Before anything can be said on this matter additional research on the regeneration has to be conducted within several years. This new research has to find out if the established shade-tolerant species can survive in the long term and continue to colonize the area. This research also has to make clear if these shade-tolerant tree species are able to grow slowly into the dominant canopy and replace the planted trees. After this research more conclusions can be made about the effectiveness of tree planting on the recovery process. It will give a better overview if additional human intervention methods are used to reach the goal of restoring the original cloud forest vegetation.

5 The influence of the planted trees on the establishment of regeneration

Introduction

The previous chapter concluded that the planting of trees seems to favour the range of the establishment of natural regeneration. Especially the observation of several shade-tolerant species under the planted trees is promising. This indicates that human intervention by planting trees on an abandoned pasture has a positive effect on the forest recovery towards an original cloud forest.

By the assumption that human intervention by planting trees can have a positive effect on forest recovery towards an original cloud forest, this chapter will discuss the effect of the individual planted trees species on the establishment of natural regeneration. A research is conducted on the influence of the different planted tree species on the establishment of the natural regeneration. Further is looked at the potential influence of these planted tree species in the future.

To get a complete overview the following steps are taken: The first step will try to determine which planted tree species are suitable to plant on the plantation sites in the Cloudbridge reserve. The second step will determine under which of the planted tree species established the highest diversity and amount of natural regeneration. The third step will analyse the light level conditions desired by the different regenerating species and the light level conditions provided by the different planted tree species.

After all these steps are taken, overall conclusions on the influence of the different planted tree species on the establishment of the natural regeneration will be summed.

5.1 Initial criteria for planted tree species

For the initial selection procedure of the Cloudbridge Nature reserve three criteria were used to determine which tree species to plant on the planting areas. Each of the selected trees has to meet at least one or more of these criteria. The first criteria was that the planted trees have to represent a diversity of native pioneer and climax species. The second criteria was that some of the selected trees should attract animal dispersers back into the area. The trees selected on this criteria were mainly the fruit trees. The third criteria was that some of the trees should have potential for commercial harvest. This to use them as a demonstration project on sustainable harvesting methods and low impact logging. The trees that are able to fulfil this criteria are fast growing trees with reasonable timber value.

5.2 Planted tree species

From the criteria mentioned in the previous paragraph 19 tree species were selected and planted in the year 2002 on 6 plantation sites in the Cloudbridge reserve. From 2003 on these trees were monitored annually by different Cloudbridge volunteers and worked out in an Excel database. *Table 3* shows which tree species were planted. From all planted species in the plantation the total number of trees, common name, type of tree and the scientific name are given. More detailed information on the individual species can be found in appendix 5.

Genus	Species	Common name (english)	Family	Species Code	Total number of trees
Quercus	copeyensis	oak	Fagaceae	QC	229
Cupressus	lusitanica	Cypress		CY	134
Cedrela	tonduzii	Sweet Cedar	Meliaceae	CD	93
Ulmus	mexicana	Elm	Ulmaceae	UL	70
Cytharexylum	donnell-smithii	Dama		DA	67
Persea	caerulea	Wild Avacado		AG	55
Alnus	acuminata	Alder	Betulaceae	AL	38
Manikara	zapota	chicle		MZ	35
Inga	species	wild guava	Fabaceae	IG	34
Tecoma	stans	Yellow Elder		TS	33
Sapium	pachystachys	Yos		SP	30
Pouteria	fossicola	Nispero		PF	26
Eugenia	jambos	Rose Apple		MR	22
Guarea	kunthiana		Meliaceae	GK	8
Quercus	seemannii	oak	Fagaceae	QS	5
Lauraceae		Laurel	Lauraceae	LS	5
		small avocado		AV	3
Spathodea	campanulata	Flame of the forest	Bignoniaceae	SC	3
Diphysa	americana	Guachipelin		DP	2

Table 3: Planted tree species.

5.3 Growth characteristics of the planted trees

As mentioned in the introduction of this chapter, the first step will try to determine which planted tree species are suitable to plant on the plantation sites in the Cloudbridge reserve. *Table 4* gives the average numbers of the measured growth indicators of the planted trees in the plantations. These average numbers are calculated from the results of the tree monitoring by using Microsoft Access. More information on the used queries can be found in appendix 3 on the creation of the tree monitoring database. The methodology used for the tree monitoring can be found in appendix 1.

The figures of average DBH, height and crown diameter are visualized in *Graph 2* and is used to determine which planted tree species have rapid growth in the first six years. This will indicate which planted tree species are the first ones to become dominant canopy trees.

As can be seen in *Graph 2* are there three planted tree species that show much faster growth than the other ones. These species are the *Alnus acuminata*, *Cupressus lusitanica* and *Ulmus mexicana*. They have become much taller, thicker and have a larger crown diameter than the other planted tree species during the past 6 years of growth. When looked at *Table 4* on vitality and mortality can be seen that *Cupressus lusitanica* and *Ulmus mexicana* also have very low mortality rates and are relatively healthy. The *Alnus acuminata* has an average mortality rate, but when the planted tree survives the first years, these trees become the most vital fast growing trees within the plantation. For this reason are these three planted tree species dominant in the plantation canopy and can have an important influence on the micro-climates found in the plantations. More information on the influence of the planted tree species on the establishment of natural regeneration will be discussed in the next paragraph.

The trees planted of the species Small avocado and *Diphysa americana* all died in the first years after planting. This indicates that these species are not suitable to plant in the initial stage of the plantation. They might still have an influence on the establishment of natural regeneration. More information on the influence of the planted species on the establishment of natural regeneration will later be discussed.

The trees planted of the species *Eugenia jambos*, *Manikara zapota* and *Quercus seemannii* stayed relatively small. *Eugenia jambos* and *Quercus seemannii* are naturally slow growing species. They are vital trees with low mortality rates which indicates that they are suitable to plant. The *Quercus seemannii* is native to the area and therefore a wanted species for the future cloud forest. The planted *Manikara zapota* trees have the lowest vitality of all species measured in the plantation and a high mortality rate. Together with the fact that it has a slow growth rate it might indicate that this species is not suitable for planting in the initial stage of reforestation. Similar to the *Quercus seemannii* this species is able to attract seed dispersers when the tree is matured and further a wanted species for the future cloud forest. More information on the influence of the planted species on the regeneration of the cloud forest species will be discussed in the next paragraph.

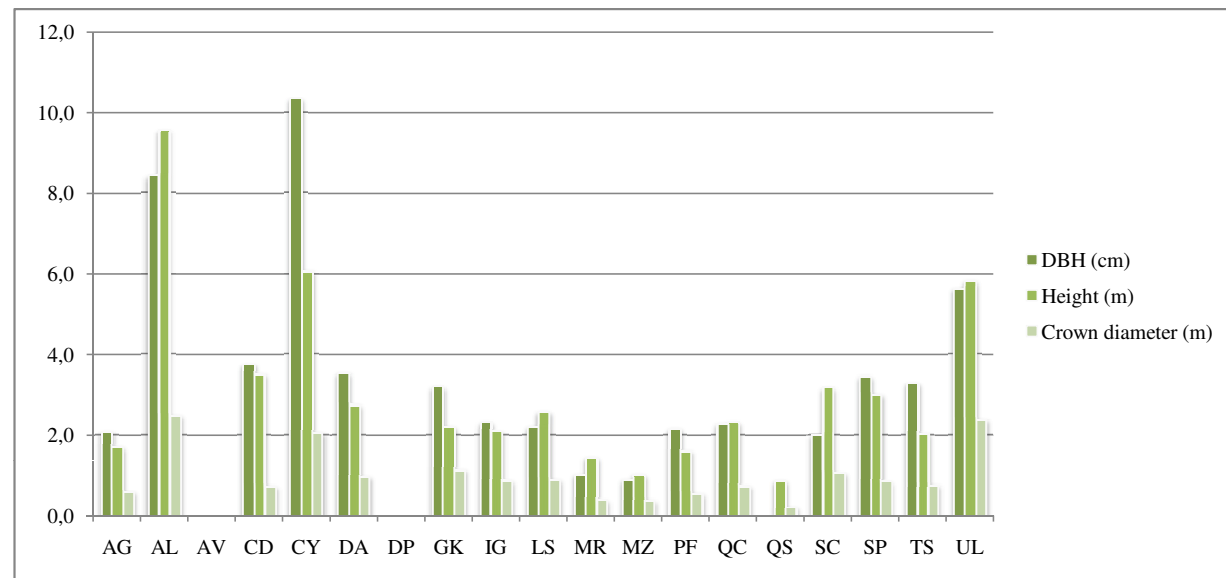
All other planted tree species have an average growth rate and are the second category of species to become canopy dominants. In the future these tree species will compete for canopy dominance with the fast growing tree species of growth category one. The difference between the planted species in this growth category is made up by the difference in vitality and mortality rate. First group represents the species that show a very high vitality and low mortality rate. This group consists of the species *Inga* species, Laurel, *Spathodea campanulata* and *Sapium pachystachys*. The results of this data indicate that this are very resistant tree species that are suitable to plant in the initial stage of reforestation.

The second group consists of *Persea caerulea*, *Pouteria fossicola* and *Quercus copeyensis*. They all have a high vitality and mortality rate. This high mortality rate is caused by the fact that the trees died frequently in the first years after planting. When the tree survived this initial period, the chance of mortality decreased drastically. *Persea caerulea* and *Pouteria fossicola* are fruit bearing trees that were planted to attract dispersers into the plantation. *Quercus copeyensis* was planted because it is one of the dominant species that occurs in the natural cloud forest. Also *Persea caerulea* and *Pouteria fossicola* are native species and therefore all three species are wanted in the future cloud forest.

The third group contains only one tree species *Cytharexylum donnell-smithii*. It has a low vitality and mortality rate. It is a climax species which prefers shade conditions to grow, which means that this

Common name	Genus	Species	Species Code	DBH (cm)	Height (m)	Crown diameter (m)	Vitality (0-5)	Mortality (%)
Wild Avacado	Persea	caerulea	AG	2,1	1,7	0,6	3,3	36
Alder	Alnus	acuminata	AL	8,4	9,6	2,5	3,3	39
Small avocado			AV					100
Sweet Cedar	Cedrela	tonduzii	CD	3,8	3,5	0,7	2,7	39
Cypress	Cupressus	lusitanica	CY	10,3	6,1	2,0	2,9	15
Dama	Cytharexylum	donnell-smithii	DA	3,5	2,7	0,9	2,6	22
Guachipelin	Diphysa	americana	DP					100
	Guarea	kunthiana	GK	3,2	2,2	1,1	2,5	67
Wild guava	Inga	species	IG	2,3	2,1	0,9	3,2	22
Laurel			LS	2,2	2,6	0,9	3,5	0
Rose Apple	Eugenia	jambos	MR	1,0	1,4	0,4	3,3	14
Chicle	Manikara	zapota	MZ	0,9	1,0	0,4	2,3	55
Nispero	Pouteria	fossicola	PF	2,2	1,6	0,5	3,0	60
Oak	Quercus	copeyensis	QC	2,3	2,3	0,7	3,0	39
Oak	Quercus	seemannii	QS		0,9	0,2	3,0	20
Flame of the forest	Spathodea	campanulata	SC	2,0	3,2	1,0	3,5	0
Yos	Sapium	pachystachys	SP	3,5	3,0	0,8	3,2	11
Yellow Elder	Tecoma	stans	TS	3,3	2,0	0,7	2,2	48
Elm	Ulmus	mexicana	UL	5,6	5,8	2,4	3,1	6

Table 4: Average growth indicators of the planted trees.



Graph 2: Average DBH, height and crown diameter of the planted trees.

species has a slow but steady growth rate over the first years as can be seen in the monitoring data from the past six years. It is common in cloud forest and mountain rainforest of Central America and for this reason this species is wanted in the future forest.

The last group consists of *Cedrela tonduzii*, *Guarea kunthiana* and *Tecoma stans*. Although these species show an average growth rate, the vitality and mortality rates do not look promising. Especially the *Guarea kunthiana* and *Tecoma stans* seem to have a lot of problems to cope with the harsh conditions of the open areas. For this reason it is probably more efficient to plant these species in a later stadium of the reforestation effort. *Cedrela tonduzii* is a wanted species for the future cloud forest. It also shows a slightly better vitality and mortality rate, than the other two species. This species is a half-shade tolerant species, therefore its planting effort is more effective when an initial canopy is already formed on the plantation sites. More information on the influence of the planted species on the natural regeneration will be discussed in the next paragraph.

More detailed information about the characteristics of all the planted tree species can be found in appendix 5.

5.4 Amount of regeneration per planted tree species

Last paragraph showed which species are suitable to plant on the plantation sites. This paragraph tries to determine under which of the planted tree species established the highest diversity and amount of natural regeneration.

The data collected in the regeneration monitoring (appendix 2) is used to determine under which of the planted tree species established the highest diversity and amount of natural regeneration. Before this raw data could be analyzed and give useful information on the established natural regeneration, first the raw data had to be imported into a Microsoft Access database. After this averages of regeneration for each planted tree species are calculated. More information about the creation of the database and the analyses of the data can be found in appendix 4. The averages of regeneration for each planted tree species can be seen in *Table 5*.

As can be seen in *Table 5* most established natural regeneration was found under *Cupressus lusitanica*, *Quercus copeyensis*, *Ulmus mexicana* and *Persea caerulea*. This is partially caused by the amount of planted trees from these species that were measured during the inventory. To make the results more comparable, average number of regeneration per measured tree is calculated. From this average number of regeneration per measured tree, can be concluded that there is a considerable difference in the amount of regeneration under the different planted tree species. Especially *Tecoma stans* and *Cupressus lusitanica* show high figures in regeneration amounts. This average number only gives information on the amount of regeneration and does not include the composition of the regenerated species. Now the amount of natural regeneration found under each different planted tree species is known, will be looked at the species composition of the established natural regeneration.

Table 6 contains the field data found during the regeneration monitoring (appendix 2). The amount of the twelve most dominant tree species is given for each planted tree species. The observations of other species are excluded for several reasons. The *Mosote* and *Rahoe* were excluded because after research they were identified as plants instead of trees. Other species which are not in this table were excluded because there was not enough information available on this species and their amount of regeneration negligible.

As can be seen in the table most species diversity is observed under the *Cupressus lusitanica* and *Quercus copeyensis*. This number can give a wrong impression about the high species diversity under these planted tree species. The reason for the high species diversity number can also be explained by the fact that these planted trees species were most abundant on the plantation. To make the results more comparable, average amount of regenerated species is calculated for each planted tree species. This is done by dividing the amount of regenerated species under a planted tree species (for example *Sorillo*) by the total amount of trees measured from this planted tree species (for example *Cupressus lusitanica*). In *Table 7* and *Graph 3* can the results of this calculation be seen.

Genus	Species	Total number of regeneration measured	Total number of measured trees	Average number of regeneration per per tree
Cupressus	lusitanica	229	100	2,3
Quercus	copeyensis	72	61	1,2
Ulmus	mexicana	43	39	1,1
Persea	caerulea	27	19	1,4
Cedrela	tonduzii	19	23	0,8
Tecoma	stans	16	6	2,7
Cytharexylum	donnell-smithii	15	25	0,6
Inga	species	4	5	0,8
Sapium	pachystachys	1	2	0,5
Quercus	seemannii	0	1	0
Eugenia	jambos	0	2	0
Alnus	acuminata	0	3	0

Table 5: The average number of regeneration per measured tree.

planted tree species												
Regenerated species	Scientific name	CY	QC	UL	DA	CD	AG	U	TS	IG	SP	Total regenerated species
Sorillo		124	29	23	9	12	6	8				211
Poro	Erythrina poeppigiana	6	6	8	1	5	6	1	1	1	1	36
Guacamalla		10	1	1	2		6			2		22
Mirto	Inga species	4		5				9	3			21
Quercus g	Quercus gulielmi-treleasei	18	1					1				20
Ceresilla		8	1				1	2	7			19
Ortiga		8	9									17
Lengua de vaca	Conostegia oerstediana	11						5				16
Unidentified 6		2	1	3		1	6		2			15
Unidentified 5		3	5	3	1		1		1	1		15
Quercus s.	Quercus copeyensis		15									15
Guarumo	Cecropia polyphlebia	7	3		2		1					13
species diversity		11	10	6	5	3	7	6	5	3	1	

Table 6: Regeneration found per planted tree species.

The figures of *Table 7* are visualized in *Graph 3* to get a better overview. For each planted tree species average amount and species composition of the regeneration is shown. This can be used to estimate which regeneration can be expected under different planted tree species.

When looked at *Graph 3* differences in amount and species composition of regeneration can be observed between the planted tree species. The following paragraph will discuss the established natural regeneration per planted tree species.

Cupressus lusitanica shows a high average of regenerated tree species per tree and a high variety in species composition. Species that were mostly found under the *Cupressus lusitanica* trees are: Sorillo, *Quercus gulielmi-treleasei*, *Conostegia oerstediana* and *Ortiga*. The most remarkable observations are:

- Sorillo was found twice as much under the *Cupressus lusitanica* as under the other planted tree species.
- *Conostegia oerstediana*, because this species did not regenerate in large quantities under the other planted tree species.
- *Quercus gulielmi-treleasei*, because it was only found under *Cupressus lusitanica* and *Quercus copeyensis*.
- *Ortiga*, because it was only found under *Cupressus lusitanica* and *Quercus copeyensis*.
- The species *Erythrina poeppigiana*, because it regenerated under almost every tree but very few were found under the *Cupressus lusitanica*.

Quercus copeyensis shows a high diversity in tree species regeneration, but average amount of regeneration quantities. Species that were mostly found under the *Quercus copeyensis* are: Sorillo, *Ortiga* and *Quercus copeyensis*. The most remarkable observations are:

- *Ortiga*, because it was only found under *Cupressus lusitanica* and *Quercus copeyensis*.
- *Quercus gulielmi-treleasei*, because it was only found under *Cupressus lusitanica* and *Quercus copeyensis*.
- *Quercus copeyensis*, because this species was only found under *Quercus copeyensis*.

Ulmus mexicana shows an average diversity in tree species regeneration and average quantities of regeneration. Species that were mostly

found under the *Ulmus mexicana* are: Sorillo, *Erythrina poeppigiana* and *Inga* species. The most remarkable observations are:

- *Inga* species, because it was only found in larger numbers under *Ulmus mexicana* and *Tecoma stans*.

Cytharexylum donnell-smithii shows an average diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Cytharexylum donnell-smithii* are: Sorillo, Guacamalla and *Cecropia polyphlebia*. The most remarkable observations are:

- *Cecropia polyphlebia*, because it regenerates most abundant under the *Cytharexylum donnell-smithii*.

Cedrela tonduzii shows low diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Cedrela tonduzii* are: Sorillo and *Erythrina poeppigiana*. The most remarkable observations are:

- There are no remarkable observations for this planted tree species.

Persea caerulea shows an average diversity in tree species regeneration and high quantities of regeneration. Species that were mostly found under the *Persea caerulea* are: Sorillo, *Erythrina poeppigiana*, Guacamalla and Unidentified 6. The most remarkable observations are:

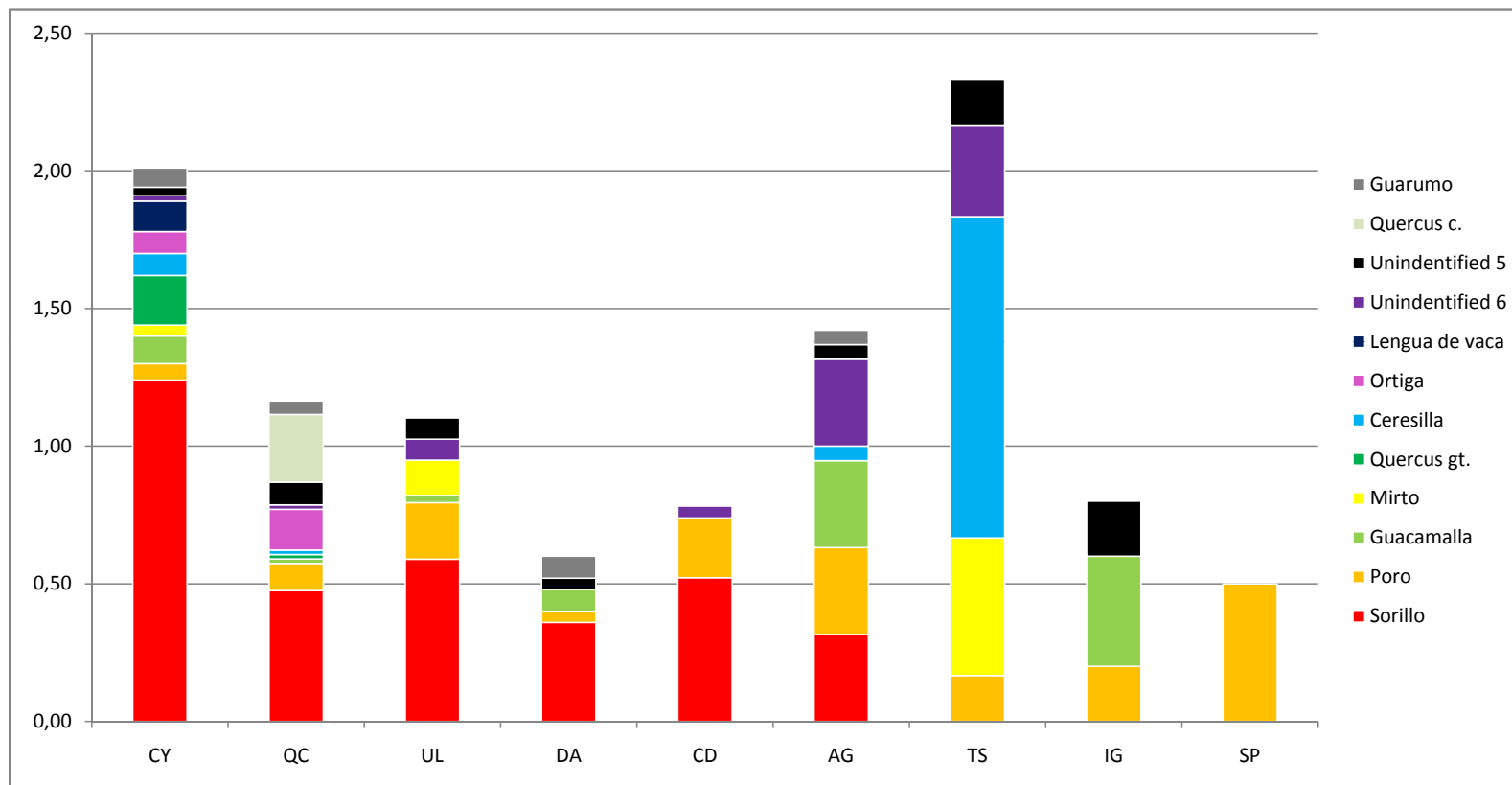
- Species composition is divided equally over this most abundant regenerating species.
- *Erythrina poeppigiana*, because it was found in larger numbers under *Persea caerulea* then under most other planted tree species.
- Guacamalla, because it was found in larger numbers under *Persea caerulea* then under most other planted tree species.
- Unidentified 6, because it was found in larger numbers under *Persea caerulea* then under most other planted tree species.

Tecoma stans shows an average diversity in tree species regeneration and high quantities of regeneration. Species that were mostly found under the *Tecoma stans* are: *Inga* species, Ceresilla, Unidentified 5 and Unidentified 6. The most remarkable observations are:

- The average number of regeneration measured per tree is highest of all planted tree species.
- *Inga* species, because it was found in larger numbers under *Tecoma stans* then under any other planted tree species.
- Ceresilla, because it was found in larger numbers under *Tecoma stans* then under any other planted tree species.

Regenerated species	Scientific name	CY	QC	UL	DA	CD	AG	TS	IG	SP
Sorillo		1,24	0,48	0,59	0,36	0,52	0,32	0,00	0,00	0,00
Poro	Erythrina poeppigiana	0,06	0,10	0,21	0,04	0,22	0,32	0,17	0,20	0,50
Guacamalla		0,10	0,02	0,03	0,08	0,00	0,32	0,00	0,40	0,00
Mirto	Inga species	0,04	0,00	0,13	0,00	0,00	0,00	0,50	0,00	0,00
Quercus	Quercus gulielmi-treleasei	0,18	0,02	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ceresilla		0,08	0,02	0,00	0,00	0,00	0,05	1,17	0,00	0,00
Ortiga		0,08	0,15	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Lengua de vaca	Conostegia oerstediana	0,11	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Unidentified 6		0,02	0,02	0,08	0,00	0,04	0,32	0,33	0,00	0,00
Unidentified 5		0,03	0,08	0,08	0,04	0,00	0,05	0,17	0,20	0,00
Quercus c.	Quercus copeyensis	0,00	0,25	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Guarumo	Cecropia polyphlebia	0,07	0,05	0,00	0,08	0,00	0,05	0,00	0,00	0,00
Total regeneration amount per tree species		2,01	1,16	1,10	0,60	0,78	1,42	2,33	0,80	0,50

Table 7: Average amount and species composition of the regeneration per planted tree species..



Graph 3: Average amount and species composition of the regeneration per planted tree species..

- Unidentified 5, because it was found in larger numbers under *Tecoma stans* than under most other planted tree species.
- Unidentified 6, because it was only found in larger numbers under *Tecoma stans* and *Persea caerulea*.

Inga species shows low diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Inga* species are: *Erythrina poeppigiana*, *Guacamalla* and Unidentified 5. The most remarkable observations are:

- The species diversity of the regeneration is very low.
- The regenerated species that occur do this in high amounts when compared with regeneration amounts under other planted tree species.
- *Guacamalla*, because it was found in larger numbers under *Inga* species than under any other planted tree species.
- Unidentified 5, because it was found in larger numbers under *Inga* species than under any other planted tree species.

Sapium pachystachys shows low diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Sapium pachystachys* are: *Erythrina poeppigiana*. The most remarkable observations are:

- The species diversity and quantity of the regeneration is lowest of all planted tree species.
- *Erythrina poeppigiana*, because it was found in larger numbers under *Sapium pachystachys* than under any other planted tree species.

5.5 Circumstances desired by the different regenerating species

In the previous paragraphs is discussed which planted tree species are suitable to plant on the plantation sites in the Cloudbridge reserve. Further is determined under which of the planted tree species established the highest diversity and amount of natural regeneration. In this paragraph is determined under which light level conditions the different natural regenerated tree species established. When this is clear the conditions provided by the different planted tree species are analysed to find out if these provided light level conditions are related with the establishment of the different natural regenerated tree species.

Table 8 shows the average shade conditions under which each regenerated tree species was found. With this information can be indicated which shading the different regenerated tree species prefer. The shade conditions are measured in the field during the tree monitoring at the individual tree planting sites (appendix 1). The influence of the shade conditions on the regenerated species is obtained, through a query in Microsoft Access, by linking tree monitoring data with the regeneration monitoring data. This average shade conditions under which the regenerated tree species occur is afterwards converted into average shade conditions in percentages. More information about the database tables can be found in appendix 3 and 4.

When looked at the table some indications can be found on which regenerated tree species prefer which kind of shading percentage to establish. The indications found for the individual regenerated species will be discussed in the following paragraph.

- *Ortiga* is found under the highest average shade conditions and was never observed in high light level conditions. This is a strong indication that *Ortiga* is a shade tolerant species that needs a lot of shading to regenerate.

- *Quercus gulielmi-treleasei* is found under high average shade conditions and never observed under high light level conditions. This observation is in line with the information found in literature studies that this is a species that needs low light levels to regenerate.

- *Conostegia oerstediana* is found under high average shade conditions. From the literature study on this species came forward that the species is generally found in secondary forest, on forest edges and old pasture lands. When all of this is taken into account this species seems to be a half-shade species that needs low light levels to regenerate, but needs higher light levels in their further development towards a dominant canopy tree.

- *Cecropia polyphlebia* is found under average light level conditions. From the literature study on the tree species came forward, that this species is a pioneer tree that dominates the first succession stage. From the observation that the regeneration was mainly found near mature trees of this species can be concluded that the mature trees have a significant effect on the regeneration of this tree species.

Common name	Genus	Species	Average shade (%)
Ortiga			71
Quercus gt.	Quercus	guelmi-trelesei	58
Lengua de vaca	Conostegia	oerstediana	53
Guarumo	Cecropia	polyphlebia	45
Sorillo			38
Mirto	Inga	species	37
Poro	Erythrina	poepigiana	33
Unidentified 5			30
Ceresilla			28
Unidentified 6			26
Guacamalla			22
Quercus c.	Quercus	copeyensis	15

Table 8: Average shade conditions found under each regenerated tree species.

Common name	Genus	Species	Average crown diameter (m)
Alder	Alnus	acuminata	2,58
Elm	Ulmus	mexicana	2,41
Cypress	Cupressus	lusitanica	2,07
Dama	Cytharexylum	donnell-smithii	1,06
Yellow Elder	Tecoma	stans	1,03
wild guava	Inga	species	1,01
Quercus c.	Quercus	copeyensis	0,85
Unidentified	Unidentified	taxon	0,82
Sweet Cedar	Cedrela	tonduzii	0,74
Wild Avacado	Persea	caerulea	0,55
Rose Apple	Eugenia	jambos	0,50
Yos	Sapium	pachystachys	0,28
Quercus s.	Quercus	seemannii	0,20

Table 9: Average crown diameter of the planted tree species.

This was also verified by similar observations on the regeneration in the subplot. The reason for the average light level conditions under which the regeneration of this species established can be explained by the advance in growth of the regeneration of this species. This can be explained by the reason that this species establishes in early succession of an abandoned pasture land. For this reason this species established in the first years of the plantation and therefore had a significant advance in becoming dominant in the canopy. This is why the regeneration of the *Cecropia polyphlebia* is not affected by the shading produced by the planted tree species in a later stage. The youngest regeneration of the *Cecropia polyphlebia* did not have this advance and therefore is it only found in high light level conditions.

- Sorillo is found under average to low light level conditions. The observation that this species was found throughout the whole plantation and the subplot is an indication that this species is not directly bound to a certain light level condition.

- Inga species is found under average to low light level conditions. The observation that this species was found almost exclusively in one part of the plantation, indicates that the regeneration is highly dependent on mature trees in its direct surroundings rather than the light level conditions.

- *Erythrina poeppigiana* is found under high light conditions, throughout the whole plantation. From the literature study on the tree species came forward, that this species is a true pioneer species. This explains why this species regenerates throughout the whole plantation in high light level conditions.

- Unidentified 5 and Unidentified 6 are found under high light conditions, throughout the whole plantation. There is no information on these tree species due to the fact that they are not identified yet. Difference between the two species is that Unidentified 5 seems to be a bit more shade-tolerant than Unidentified 6, which was only found in very high light level conditions.

- Ceresilla was found under high light level conditions. There is no information on this tree species due to the fact that it is not identified yet. Observations in the field indicate that this species regenerates in high light level conditions.

- Guacamalla was found under high light level conditions. There is no information on this tree species due to the fact that it is not identified yet. Observations in the field indicate that this species regenerates in high light level conditions.

- *Quercus copeyensis* was found under extreme high light level conditions. This data is misleading, because this species was found regenerating directly under a planted tree from its own species. This planted tree provides almost maximum shade under its canopy, which is suitable for its own regeneration to establish. From this observation and from the literature study can be concluded that it is a climax species.

5.6 Shade conditions provided by the planted tree species

Last paragraph tried to determine under which light level conditions the different regenerated tree species established. In this paragraph the light level conditions provided by the different planted tree species are analysed to find out if these provided conditions are related with the establishment of the different natural regenerated species. These conditions provided by the planted tree species are determined through analyses of the average crown diameter created by the individual planted tree species after six year. This information will be combined with the crown characteristics of the different planted tree species that were determined through observations in the field and literature studies. This will give a good impression on the actual light level conditions provided by the individual planted tree species.

Table 9 shows the average crown diameter for the different planted tree species. The crown diameters were measured in the tree monitoring (appendix 1). After this, the average crown diameter for the individual planted tree species is calculated through a query in Microsoft Access database of the tree monitoring (appendix 4).

Alnus acuminata shows as can be seen in *Table 9* the largest average crown diameter. This species is a true pioneer in the cloud forest. From literature studies and the observations in the field can be concluded, that this species creates a deep, wide crown with an open foliage. These crown characteristics lead to large areas of high light level conditions under the tree crowns.

Ulmus mexicana shows a large average crown diameter. This species is a shade-tolerant species and one of the largest trees in the cloud forest. Literature studies indicate that this species creates a deep, wide crown with a very dense foliage. In the field different crown characteristics were observed. Here the tree shows a wide open crown with an open foliage. The reason for this is that crown foliage becomes denser after maturing. The crown characteristics in juvenile stage observed in the field, lead to large areas of high light level conditions under the tree crowns. After maturing almost no light passes through the dense foliage and creates large areas of low light level conditions under the tree crowns.

Cupressus lusitanica shows a large average crown diameter. The tree is native to the Northern regions of Central America. From literature studies and the observations in the field can be concluded, that this species creates a deep wide crown with a dense foliage. This crown characteristics lead to large areas of low light level conditions under the tree crowns.

Cyatharexylum donnell-smithii shows an average crown diameter. This species is a shade-tolerant species native in the cloud forest. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth the tree shows a narrow crown with a dense foliage. The crown characteristics in the juvenile stage lead to small areas of low light level conditions under the planted trees. In coming years the average crown diameter will increase which will lead to larger areas of low light level conditions under the planted trees.

Tecoma stans shows an average crown diameter. This species needs full sunlight to grow. Literature studies indicate, that this species creates an irregular oval crown with moderate to dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows a narrow crown with a moderately dense foliage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees. In the coming years the average crown diameter will increase which will lead to larger areas of moderate light level conditions under the planted trees.

Inga species shows an average crown diameter. This species needs full sunlight to grow. Literature studies indicate, that this species creates a wide, flat crown with moderate to dense foliage. In the field different crown characteristics were observed. Due to slow growth the tree shows a narrow crown with a moderately dense foliage. The crown characteristics in the juvenile stage observed in the field, lead to small areas of moderate light level conditions under the planted trees. In coming years the average crown diameter will increase which will lead to larger areas of moderate light level conditions under the planted trees.

Quercus copeyensis shows an average crown diameter. This species is a shade-tolerant species that is an abundant tree species in the cloud forest. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows a narrow crown with a dense foliage. The crown characteristics in the juvenile stage lead to small areas of low light level conditions under the planted trees. In coming years the average crown diameter will increase which will lead to larger areas of low light level conditions under the planted trees.

Cedrela tonduzii shows an average crown diameter. This species is a half shade-tolerant species and native in the cloud forest. From literature studies and the observations in the field can be concluded, that this species creates an wide crown with an open foliage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees. In coming years the average crown diameter will increase which will lead to large areas of high light level conditions under the planted trees. Another reason for the low impact of this tree species on light level conditions can be explained by the fact that the tree loses its leaves in the dry period.

Persea caerulea shows a low to moderate, average crown diameter. This species is a shade-tolerant species and native in the cloud forest. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. The trees only showed height growth and did not create a distinct crown in this juvenile stage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the

light level conditions under the planted trees. In the coming years the trees will create a more distinct crown, which will lead to large areas with low light level conditions under the planted trees.

Eugenia jambos shows a low to moderate average crown diameter. This species is endemic to South east Asia. The tree species favours sunny conditions. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows a narrow crown with a dense foliage. The crown characteristics in the juvenile stage lead to small areas of low light level conditions under the planted trees. In coming years the average crown diameter will increase which will lead to larger areas of low light level conditions under the planted trees.

Sapium pachystachys shows a low average crown diameter. This species is a true pioneer in the cloud forest. Information on the crown growth of this species could not be found. During observation in the field, the trees only showed height growth and did not create a distinct crown in this juvenile stage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees.

Quercus Seemannii shows a low average crown diameter. This species is a shade-tolerant species that is an abundant tree species in the cloud forest. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows almost no crown. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees. In coming years the average crown diameter will increase which will lead to larger areas of low light level conditions under the planted trees.

5.7 Overall findings and conclusions of the planted tree species

In the previous paragraphs is discussed which planted tree species are suitable to plant on the plantation sites in the Cloudbridge reserve. Further is determined under which of the planted tree species established the highest diversity and amount of natural regeneration. Third

paragraph tried to determine under which light level conditions each regenerated tree species established. Last paragraph the light level conditions provided by the different planted tree species are analysed.

This paragraph tries to answer, if these provided conditions by the different planted tree species are related with the establishment of the different found regeneration under the planted trees. This is done to determine which planted tree species have already a significant influence on the establishment of the natural regeneration. Further the potential influence in the future of these planted tree species on the establishment of natural regeneration is assessed. The overall findings on these planted tree species are summarized in a final overview.

Cupressus lusitanica

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows a large average crown diameter and creates a deep wide crown with a dense foliage. This crown characteristics lead to large areas of low light level conditions under the tree crowns. When looked at the light level conditions provided by the *Cupressus lusitanica*, it is expected to find only regeneration of shade-tolerant tree species under these planted trees.

The actual regeneration monitoring on the *Cupressus lusitanica* shows a high average of regenerated tree species per tree and a high variety in species composition. Species that were mostly found under the *Cupressus lusitanica* trees are: *Sorillo*, *Quercus gulelmi-trelesei*, *Conostegia oerstediana* and *Ortiga*. All these regenerated tree species seem to be shade-tolerant species as mentioned in paragraph 5.5. These findings are in line with the expectations from the light level conditions provided by the planted trees. This is an indication that *Cupressus lusitanica* has a positive influence on the regeneration of shade-tolerant tree species. The only tree species which does not fit this description is *Sorillo*. The observation that this species was found throughout the whole plantation and the subplot is an indication that the regeneration of this species is not directly bound to a certain light level condition. For this reason the regeneration of this species will not be discussed in the description of the other planted tree species.

Overall findings

- The tree species is suitable to grow on the plantation site.
- The tree species is not native for the area and is therefore not wanted in the future forest. Reason for planting this tree species is that it is a fast growing commercial tree for wood production.
- From observations in the field can be concluded that the tree attracts squirrels to the area and that it provides a good hiding place for birds.
- The tree seems to have a positive effect on the establishment of shade-tolerant species in the plantation area.
- The main concerns for the future, when planting this species are the influence on soil acidity and establishment of seedlings of this species in the surrounding area. At this moment there are no indications observed in the field which show these negative influences. Further research is needed to assess if this can cause problems in the future.

Quercus copeyensis

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows an average crown diameter. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows a narrow crown with a dense foliage. The crown characteristics in the juvenile stage lead to small areas of low light level conditions under the planted trees.

The actual regeneration monitoring on the *Quercus copeyensis* shows a high diversity in tree species regeneration, but average amount of regeneration quantities. Species that were mostly found under the *Quercus copeyensis* are: Sorillo, Ortiga and *Quercus copeyensis*. All these regenerated tree species seem to be shade-tolerant species as mentioned in paragraph 5.5. These findings are in line with the expectations from the light level conditions provided by the planted trees. This is an indication that *Quercus copeyensis* has a positive influence on the regeneration of shade-tolerant tree species.

Overall findings

- The species shows high mortality rate in the first years after planting. When the tree survived this initial period, the chance of mortality decreased drastically.
- *Quercus copeyensis* was planted because it is one of the dominant climax species that occurs in the natural cloud forest.
- The tree attracts several seed dispersers into the field. Observation in the field showed that the trees are used as nesting place of certain bird species.
- The tree seems to have a positive effect on the establishment of shade-tolerant species in the plantation area. Also the observation of established regeneration from its own species under the planted trees looks promising.
- Most of the trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a dominant canopy tree, it will lower light levels under the dominant canopy drastically. This way it has a positive effect on the establishment of shade-tolerant cloud forest species on the plantation site.

Ulmus mexicana

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows a large average crown diameter. Literature studies indicate that this species creates a deep, wide crown with a very dense foliage. In the field different crown characteristics were observed. Here the tree shows a wide open crown with an open foliage. The reason for this is that crown foliage becomes denser after maturing. The crown characteristics in juvenile stage observed in the field, lead to large areas of high light level conditions under the tree crowns.

The actual regeneration monitoring on the *Ulmus mexicana* shows an average diversity in tree species regeneration and average quantities of regeneration. Species that were mostly found under the *Ulmus mexicana* are: Sorillo, *Erythrina poeppigiana* and Inga species. *Erythrina poeppigiana* is a pioneer species and needs full sunlight to grow as mentioned in paragraph 5.5. This finding is in line with the expectations from the light level conditions provided by the

planted trees. Inga species was found in large groups under the biggest planted trees of this species. These findings are in line with the expectations from the light level conditions provided by the biggest planted trees of this species.

Overall findings

- The tree species is suitable to grow on the plantation site.
- *Ulmus mexicana* is a shade-tolerant species and one of the largest trees in the natural cloud forest.
- The species does not seem to influence the regeneration of shade-tolerant species after six years. In the future this tree will create a dense foliage, which will promote the establishment of shade-tolerant species regeneration.

Cytharexylum donnell-smithii

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows an average crown diameter. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth the tree shows a narrow crown with a dense foliage. The crown characteristics in the juvenile stage lead to small areas of low light level conditions under the planted trees.

Cytharexylum donnell-smithii shows an average diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Cytharexylum donnell-smithii* are: Sorillo, Guacamalla and *Cecropia polyphlebia*. Guacamalla and *Cecropia polyphlebia* are pioneer species and needs full sunlight to grow as mentioned in paragraph 5.5. This finding is in line with the expectations from the light level conditions provided by the planted trees.

Overall findings

- It has a low vitality and mortality rate. Which indicate that the species is suitable to grow on the plantation site.
- *Cytharexylum donnell-smithii* is common in cloud forest and

mountain rainforest of central America and for this reason planted.

- The tree attracts several seed dispersers into the field. Observation in the field showed that the trees are used as nesting place of certain bird species.
- Most of the trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a dominant canopy tree, it will lower light levels under the dominant canopy drastically. This way it has a positive effect on the establishment of shade-tolerant cloud forest species on the plantation site.

Cedrela tonduzii

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites. The high mortality rate in the initial stage of the plantation indicates that it is more effective to plant this tree species in a later stage of reforestation.

The species shows an average crown diameter. From literature studies and the observations in the field can be concluded, that this species creates an wide crown with an open foliage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees.

Cedrela tonduzii shows low diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Cedrela tonduzii* are: Sorillo and *Erythrina poeppigiana*. *Erythrina poeppigiana* is a pioneer species and needs full sunlight to grow as mentioned in paragraph 5.5. This finding is in line with the expectations of minimum influence by the planted trees.

Overall findings:

- The species shows high mortality rate in the first years after planting. When the tree survived this initial period, the chance of mortality decreased drastically. The tree species is a half shade species and therefore is its planting effort more effective when an initial canopy is already formed on the plantation sites.
- *Cedrela tonduzii* is common in cloud forest and mountain rainforest of Central America and for this reason planted. Another reason for planting is that this tree species is a fast growing commercial tree

for wood production. Locally also used as fuel wood tree.

- Most of the trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a dominant canopy tree and has a crown with a open foliage. It will lower light levels under the dominant canopy. This way it has a positive effect on the establishment of half shade-tolerant cloud forest species on the plantation site.

Persea caerulea

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

This species shows an low to moderate, average crown diameter. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. The trees only showed height growth and did not create a distinct crown in this juvenile stage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees.

Persea caerulea shows an average diversity in tree species regeneration and high quantities of regeneration. Species that were mostly found under the *Persea caerulea* are: Sorillo, *Erythrina poeppigiana*, Guacamalla and Unidentified 6. These species are all light demanding species that needs full sunlight to establish as mentioned in paragraph 5.5. This finding is in line with the expectations of minimum influence by the planted trees.

Overall findings

- The species shows high mortality rate in the first years after planting. When the tree survived this initial period, the chance of mortality decreased drastically.
- *Persea caerulea* is common in cloud forest and mountain rainforest of central America and for this reason planted.
- The tree attracts several seed dispersers into the field. It is a common food source for monkey's and several birds.
- Most of the trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a domi-

nant canopy tree, it will lower light levels under the dominant canopy drastically. This way it has a positive effect on the establishment of shade-tolerant cloud forest species on the plantation site.

Tecoma stans

Although these species show an average growth rate, the vitality and mortality rates do not look promising. Therefore it is not effective to plant this tree species for the reforestation efforts in the Cloudbridge reserve.

The species shows an average crown diameter. Literature studies indicate, that this species creates an irregular oval crown with moderate to dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows a narrow crown with a moderately dense foliage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees.

Tecoma stans shows an average diversity in tree species regeneration and high quantities of regeneration. Species that were mostly found under the *Tecoma stans* are: Inga species, Ceresilla, Unidentified 5 and Unidentified 6. These are all light demanding species and needs full sunlight to grow as mentioned in paragraph 5.5. This finding is in line with the expectations from the light level conditions provided by the planted trees.

Overall findings

- The tree species is unsuitable to plant in the Cloudbridge reserve. Therefore it is not recommended for the reforestation effort.
- The tree is native to the mountain and cloud forests in Central and South America. For this reason more research has to be done on the reasons why this species does not grow well in the plantation site.

Inga species

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows an average crown diameter. Literature studies indicate, that this species creates a wide, flat crown with moderate to dense foliage. In the field different crown characteristics were observed. Due to slow growth the tree shows a narrow crown with a moderately dense foliage. The crown characteristics in the juvenile stage observed in the field, lead to small areas of moderate light level conditions under the planted trees.

Inga species shows low diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the Inga species are: *Erythrina poeppigiana*, *Guacamalla* and *Unidentified 5*. These are all light demanding species and need full sunlight to grow as mentioned in paragraph 5.5. This finding is in line with the expectations from the light level conditions provided by the planted trees.

Overall findings

- The tree species is suitable to grow on the plantation site.
- Inga species is common in cloud forest and mountain rainforest of central America, together with the fact that this species has nitrogen fixing properties was the reason for planting.
- The tree attracts several seed dispersers into the field. It is a common food source for monkey's and several birds.
- Most of the trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a dominant canopy tree, it will lower light levels under the dominant canopy drastically. This way it has a positive effect on the establishment of shade-tolerant cloud forest species on the plantation site.

Sapium pachystachys

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows a low average crown diameter. Information on the crown growth of this species could not be found. During observation in the field, the trees only showed height growth and did not create a distinct crown in this juvenile stage. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees.

Sapium pachystachys shows low diversity in tree species regeneration and low quantities of regeneration. Species that were mostly found under the *Sapium pachystachys* are: *Erythrina poeppigiana*. This is a light demanding species and needs full sunlight to grow as mentioned in paragraph 5.5. This finding is in line with the expectations from the light level conditions provided by the planted trees.

Overall findings

- The tree species is suitable to grow on the plantation site.
- *Sapium pachystachys* is a common pioneer in cloud forest and mountain rainforest of central America and for this reason planted.
- Information on the crown growth of this species could not be found. Therefore cannot be assessed what the influence on regeneration will be in a later stage.

Alnus acuminata

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows the largest average crown diameter. From literature studies and the observations in the field can be concluded, that this species creates a deep, wide crown with an open foliage. These crown characteristics lead to large areas of high light level conditions under the tree crowns.

Under the trees of this species no regeneration was measured during the regeneration monitoring. Therefore no information is available on the effect of this species on establishment of regenerating tree species.

Overall findings

- The tree species is suitable to grow on the plantation site.
- *Alnus acuminata* is a common pioneer in cloud forest and for this reason planted. Another reason for planting is that this tree species is a fast growing commercial tree for wood production and has nitrogen fixing properties.
- In the regeneration inventory no regeneration was found under the trees of this species. This might be caused by the low number of measurements under this tree species. Therefore additional research has to be conducted in the future to determine if the species can have a positive influence on the establishment of natural regeneration.

Eugenia jambos

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows a low to moderate average crown diameter. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows a narrow crown with a dense foliage. The crown characteristics in the juvenile stage lead to small areas of low light level conditions under the planted trees.

Under the trees of this species no regeneration was measured during the regeneration monitoring. Therefore no information is available on the effect of this species on establishment of regenerating tree species.

Overall findings

- The tree species is suitable to grow on the plantation site.
- *Eugenia jambos* favours sunny conditions and is native to South east Asia.
- The tree attracts several seed dispersers into the field after maturing.
- The trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a dominant canopy tree, it will lower light levels under the dominant canopy drastically. This way it has a positive effect on the establishment of shade-tolerant cloud forest species on the plantation site.

Quercus Seemannii

As can be concluded from the paragraph on the growth characteristics of the planted trees is this tree species suitable to plant on the plantation sites.

The species shows a low average crown diameter. Literature studies indicate, that this species creates a wide crown with a dense foliage. In the field different crown characteristics were observed. Due to slow growth, the tree shows almost no crown. The crown characteristics in the juvenile stage observed in the field, lead to minimal influence on the light level conditions under the planted trees.

Under the trees of this species no regeneration was measured during the regeneration monitoring. Therefore no information is available on the effect of this species on establishment of regenerating tree species.

Overall findings

- The tree species is suitable to grow on the plantation site.
- *Quercus Seemannii* was planted because it is one of the dominant climax species that occurs in the natural cloud forest.
- The tree attracts several seed dispersers into the field. Observation in the field showed that the trees are used as nesting place of certain bird species.
- Most of the trees of this species are still too small to have a significant effect on the regeneration. When this species becomes a dominant canopy tree, it will lower light levels under the dominant canopy drastically. This way it has a positive effect on the establishment of shade-tolerant cloud forest species on the plantation site.

Diphyssa americana

The trees planted of the species *Diphyssa americana* all died in the first years of the plantation. This indicates that this species is not suitable to plant in the initial stage of tree planting.

Literature studies indicate, that this species creates a irregular wide crown with an open foliage. Observations in the field cannot verify this, caused by the reason that this tree species does not grow on the plantation site. Literature studies showed that this species is common

on flatlands or moderate slopes in tropical dry forests at elevations of 0 to 800 m (Salas 1993). For this reason the *Diphysa americana* seems to be unsuitable to plant in the Cloudbridge reserve.

Under the trees of this species no regeneration was measured during the regeneration monitoring. Therefore no information is available on the effect of this species on establishment of regenerating tree species.

Overall findings

- The species is unsuitable to plant in the Cloudbridge reserve.
- The species is native to the whole of Central America.
- The tree is used as a timber tree and in several countries, the timber is used as fuel (Mabberley 1997).

Small avocado

The trees planted of the species Small avocado all died in the first years of the plantation. This indicates that this species is not suitable to plant in the initial stage of tree planting.

No information about this tree species could be found, this is due to the fact that this species is not identified yet. Further research on this species is needed, before anything can be concluded about its suitability and its influence on natural regeneration.

6 Conclusions

This study investigated if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting. Literature studies on natural regeneration in a virgin cloud forest showed that the most important event in the tree regeneration process within a virgin cloud forest is when an opening of the canopy occurs. Further came forward that the size of gaps in closed forests determines the type of trees recruited in the gaps. Small gaps coupled with advance regeneration of shade-tolerant species would favour the “reorganization” response while seed colonization of large gaps by

shade-intolerant species would define the other extreme ⁹³. From this observation researchers have tried to divide gap colonization by trees into two contrasting ecologic groups: those termed climax or primary species (non-pioneer) and pioneer species ⁹⁴. Tree recruitment is often more dependent on micro-site quality, which may override the effect of standing tree basal area, gap size, and resource gradients in gaps ⁹⁵.

Several studies on regeneration have shown that, once pastureland is abandoned, native species seedling recruitment is poor ⁹⁶. Natural regeneration of tropical forest vegetation in abandoned pasture is limited at all early-successional stages: colonization, establishment, growth, and survival. Lack of seed availability appears to be the overriding factor limiting forest recovery in tropical pastures. Not only is dispersal of forest seeds into open areas minimal, the few seeds that do arrive are commonly subjected to high rates of predation ⁹⁷. If barriers to seed dispersal are overcome, a number of interrelated factors may influence seed germination, as well as seedling growth and survival. These factors include lack of micro-climates, water availability, soil and nutrient properties and competition with established grasses/weeds.

After these mayor barriers were identified, a literature study indicated on how to overcome these major barriers for restoring rainforest in abandoned pastures. One of the most important human interventions that came forward is the establishment of remnant trees in the degraded pasture lands. These trees are able to serve as a source for seeds and enhance animal dispersal of seeds. Further they ameliorate high light levels, modify the energy budget of other species under the canopy, and often increase soil nutrients. Species-specific differences in the ability to tolerate the high light environment of open pastures may be an important consideration in choosing pioneer species for reforestation. However the kind of fruits the trees are bearing is almost as important, because they promote the attraction of seed dispersers.

To test the assumption that tree planting promotes the establishment of natural regeneration a regeneration monitoring was conducted. The most significant difference in regeneration found between the two research areas is the species composition of the regenerating trees and the frequency of regenerating species. Under the planted trees a mixture of pioneer and climax species was found, while in the subplot that was left to recover naturally only pioneer specialists were established. The finding of this difference in tree regeneration composition

93. Marks,1974
94. Whitmore,1978,1989;
Brokaw,1985b
95. Houle,1992;
Lundqvist and Fridman,
1996;
Gray and Spies,1997
96. Buschbacher,1986;
Aide et al,2000;
Cubina & Aide, 2001
97. Janzen,1971;
Uhl,1987;
Nepstad et al.,1990;
Aide & Cavelier,1994;
Holl & Lulow,1997

is a sign that tree planting on an abandoned pasture land can promote the range of tree species that can establish. The return of climax species seems to accelerate the recovery process towards the original Cloud forest. The observation of several dispersing animals in the plantation is also a sign that planting of trees favours the recovery process. But it is still unclear if the method of planting trees actually accelerates the recovery process towards the original cloud forest in the long term.

After assessing the different planted tree species, *Cupressus lusitanica* and *Quercus copeyensis* came forward as the most promising species to promote natural regeneration at this stage. This because under these species established the most diverse regeneration, further were this the only planted trees species under which shade-tolerant regeneration established. *Ulmus mexicana* looks promising for the future because it showed considerable growth, and has already a large wide crown with an open foliage. In the near future the trees will create a more dense foliage, leading to a change in light level conditions found under the tree. The high light level conditions under the trees will change in low light level conditions in which shade-tolerant species can establish. Most other planted species were still too small to have a significant effect on the regeneration and their effectiveness has to be determined in a later stage. The research showed further that *Diphysa americana* and Small avocado are unsuitable to plant in the research area. This because all of these planted trees died in the first years.

From literature study and observations in the field several additional characteristics of the planted tree species came forward. The species *Alnus acuminata* and *Inga* sp. have the ability to increase nitrogen levels in the soil. These trees show significant growth in the plantation area and are therefore able to increase nitrogen availability in the soil of the plantation area. Other planted tree species seem to have a significant influence on the attraction of seed dispersers. Literature study indicates that *Eugenia jambos*, *Inga* sp., *Persea caerulea*, *Quercus copeyensis*, *Quercus seemannii* and *Cytharexylum donnell-smithii* have the ability to attract seed dispersers into the area. Observations in the field showed that *Quercus copeyensis*, *Quercus seemannii* and *Cytharexylum donnell-smithii* already attract small birds that nest in the plantation site and that *Cupressus lusitanica* attracts squirrels, which are vital for the dispersal of acorns.

The goal of this research was to investigate if planting of trees can promote the seed rain and the establishment of natural regeneration on abandoned pastures in the Cloudbridge Reserve and when this is the case, which tree species are most effective in this respect and thus recommended for planting. There seems to be a positive impact of planting trees to promote the establishment of natural regeneration on abandoned pastures in the Cloudbridge reserve. Especially the provided light level conditions by the planted trees seemed to have a significant influence on the diversity of the establishing natural regeneration. However this research did not determine how the individual barriers to natural regeneration were promoted individually by the trees, but only determined the actual influence on the establishment of natural regeneration by the human intervention of tree planting as a whole. For this reason additional research is needed to determine, the influence of the intervention on the individual barriers. Possible research questions for this additional research are: Is it the ability of the trees to attract seed dispersers into the area, which promoted the establishment of natural regeneration, or are it the light level conditions created by the trees which led to more establishment? And does planting of nitrogen fixing trees has a significant influence on the forest recovery? These are all interesting questions for a further research.

From this research came forward that the *Cupressus lusitanica* and *Quercus copeyensis* are the most promising species to promote natural regeneration at this stage. This because under these species established the most diverse regeneration, further were this the only planted tree species under which shade-tolerant regeneration established. The fact that the *Cupressus lusitanica* is not native for the area is the reason that this species is not wanted in the future forest. Therefore main concerns for the future when planting this species are; the influence on soil acidity and establishment of seedlings of this species in the surrounding area. At this moment there are no indications observed in the field which show these negative influences. Further research is needed to assess if this can cause problems in the future.

From literature study and observations in the field several additional characteristics of the planted tree species came forward. Like the influence of several tree species that seem to have the ability to attract seed dispersers and species that have the ability to increase nitrogen levels in the soil. What the effect on forest recovery is of these abilities in the future is not sure, further research on these additional characteristics should be investigated. Or a research on the influence of these additional characteristics should be conducted when the planted trees are grown bigger.

Also tried this research to determine under which light level conditions the different regenerated tree species established and which light level conditions were provided by the different planted tree species. This to analyse if these provided conditions are related with the establishment of the different natural regenerated species. The conditions provided by the planted tree species are determined through analyses of the average crown diameter created by the individual planted tree species after six years. This information is combined with the crown characteristics of the different planted tree species that were determined through observations in the field and literature studies. This gave a good impression on the actual light level conditions provided by the individual planted tree species. But it would be much better if there was a fish eye lens for a photo camera available to measure the exact light passing through the canopy of the different planted trees. The reason why this lens is not used for this study was because there was not enough money available.

References

- Aguilar, A. No year available. Patterns of forest regeneration in cel-
aque national park, Honduras. [http://satjournal.tcom.
ohiou.edu/pdf/aguilard.pdf](http://satjournal.tcom.ohiou.edu/pdf/aguilard.pdf).
- Aide, M., and Cavellier, J. 1994. Barriers to lowland tropical forest
restoration in the Sierra Nevada de Santa Marta, Colombia.
Restoration Ecology 2(4): 219–29.
- Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., and
Marcano-Vega, H. 2000. Forest regeneration in a chronose-
quence of tropical abandoned pastures: Implications for restora-
tion ecology. *Restoration Ecology* 8: 328–338.
- Aide, T.M., Zimmerman, J.K., Herrera, L., Rosario, M., and Serrano,
M. 1995. Forest recovery in abandoned tropical pasture in Puerto
Rico. *Forest Ecology and Management* 77: 77–86.
- Alvarez-Aquino, C., Williams-Linera, G., and Newton, A. C. 2004.
Experimental native tree seedling establishment for the restora-
tion of a Mexican cloud forest. *Restoration Ecology* vol. 12 (3):
412–418.
- Cubina, A., and Aide, T. M. 2001. The effect of distance from forest
edge on seed rain and soil seed bank in a tropical pasture. *Biotro-
pica* 33: 260–267.
- Amelung, T., and Diehl, M. 1992. Deforestation of tropical rain-
forests: economic causes and impact on development. Mohr,
Tübingen, Germany.
- Baker, F.S. 1949. A revised tolerance table. *J. For.* 47: 179–181.
- Bazzaz, F.A., and Wayne, P.M. 1994. Coping with environmental
heterogeneity: the physiological ecology of tree seedling regen-
eration across the gap-understory continuum. In *Exploitation of
environmental heterogeneity by plants: ecophysiological process-
es above- and belowground*. Edited by M.M. Caldwell and R.W.
Pearcy. Academic Press, San Diego, Calif. pp. 349–390.
- Bazzaz, F.A. 1996. *Plants in changing environments: linking physi-
ological, population, and community ecology*. Cambridge Univer-
sity Press, Cambridge, U.K.
- Beatty, S.W., and Stone, E.L. 1986. The variety of soil microsites cre-
ated by tree falls. *Can. J. For. Res.* 16: 539–548.
- Belsky, J. M. 1994. *Soil Conservation and Poverty: Lessons from
Upland Indonesia*. Society and Natural Resources Volume 7:
429–443.
- Belsky, J. M., Buttel, and Frederick, H. 1989. *Biotechnology, Plant
Breeding and Intellectual Property: Social and Ethical Dimen-
sions*. In *Owning Scientific and Technical Information: Values
and Ethical Issues*, Weil, Vivian and John W. Snapper (eds.).
Rutgers University Press, 110–131 and in *Science, Technology
and Human Values*, Volume 12 (January 1987).
- Bongers, F. 2001. Methods to assess tropical rain forest canopy struc-
ture: an overview. *Plant Ecology* 153: 263–277.
- Brokaw, N. V. L. 1982. The definition of a treefall gap and its effect
on measures of forest dynamics. *Biotropica* 14: 158–160.
- Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure
in tropical forests. Pp. 53–61.
- Brown, S., and Lugo, A. E. 1990. Tropical secondary forests. *Journal
of Tropical Ecology* 6: 1–32.
- Brown, N. 1993. The implications of climate and gap microclimate
for seedling growth conditions in a Bornean lowland rain forest.
J. Trop. Ecol. 9: 153–168.
- Buschbacher, R. 1986. Tropical deforestation and pasture develop-
ment. *Bioscience* 36: 23–27.
- Campbell, G. S. and Norman, J. M. in *Plant Canopies: Their Growth,
Form, and Function* (eds. Russell, G., Marshall, B. and Jarvis, P.)
pp. 1–19. Cambridge University Press, Cambridge, UK, 1990.
- Cavellier J. 1994. Reforestation with the native tree *Alnus acuminata*:
effects of phytodiversity and species richness in an upper mon-
tane rain forest area of Colombia. In: Hamilton L.S., Juvik J.O.
and Scatena F.N. (eds), *Tropical Montane Cloud Forest*. Spring-
er-Verlag, New York, pp. 125–137.
- Challenger A. 1998. *Utilizaci3n y Conservaci3n de los Ecosistemas
Terrestres de Me´xico. Pasado, Presente y Futuro. Comisi3n Na-
cional para el Conocimiento y Uso de la Biodiversidad. UNAM,
Agrupaci3n Sierra Madre, S.C., Mexico, DF.*
- Chapman, C. A., and Chapman, L. J. 1996. Exotic tree plantations
and the regeneration of natural forest in Kibale National Park,
Uganda. *Biological Conservation* 76: 253–257.
- Charles-Dominique, P. 1986. Inter-relations between frugivorous
vertebrates and pioneer plants: Cecropia, birds and bats in French
Guyana. Pp. 119–136 in Estrada, A. & Fleming, T. H. (eds). *Fru-
givory and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.
- Connell, J. H., Lowman, M. D. and Noble, I. R. 1997. Subcanopy
gaps in temperate and tropical forests. *Australian Journal of
Ecology* 22: 163–168.

- Cardosa da Silca, J. M., Uhl, C., and Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Cons. Biol.* 10: 491-503.
- Cayuela, L., and Benayas, J. M. R., 2006. The Extent, distribution and fragmentation of vanishing montane cloud forest in the highlands of Chiapas, Mexico. *Biotropica* 38(4): 544-554.
- Den Ouden, J., and Alaback, P.B. 1996. Successional trends and biomass of mosses on wind throw mounds in the temperate rainforests of southeast Alaska. *Vegetatio* 124: 115-128.
- Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 431-451.
- Denslow, J. S., and Hartshorn, G. S. 1994. Treefall gap environments and forest dynamic processes. Pp. 120-127 I McDade, L. A., Bawa, K. S., Hespeneide, H. A., and Hartshorn, G. S. (eds.). *La Selva: ecology and natural history of a tropical rainforest*. University of Chicago Press, Chicago, IL, USA.
- Doumenge, C., Gilmour, D., Perez, M. R., and Blockhus, J. No year available. Tropical Montane Cloud Forests: Conservation status and management issues. http://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_6/b_fdi_35-36/41295.pdf.
- Duchesneau, R., and Morin, H. 1999. Early seedling demography in balsam fir seedling banks. *Can. J. For. Res.* 29: 1502-1509.
- Dunn, W.W., Morgan, P., and Lynch, A.M. 1990. Production of alder to meet fuelwood demand in the sierra of Ecuador. *Agroforestry Systems* 10: 199-211.
- Ewel, J. J. 1986. Designing agricultural ecosystems for the humid tropics. *Annu. Rev. Ecol. Syst.* 17: 245-271.
- Fearnside, P. M. 1993. Deforestation in Brazilian Amazonia: the effect of population and land tenure. *Ambio* 2: 537-545.
- Florentine, S. K., and Westbrooke, M. E. 2004. Restoration on abandoned tropical pasturelands- do we know enough? *Journal for Nature Conservation*, Vol. 12(2): 85-94.
- Florentine, S. K., Craig, M., & Westbrooke, M. E. 2003. Flowering, fruiting, germination and seed dispersal of the newly emerging weed *Solanum mauritianum* Scop. (Solanaceae) in the wet tropics of north Queensland. *Plant Protection Quarterly* 18: 116-120.
- Fox, J. E. D. 1976. Constraints on the natural regeneration of tropical moist forest. *Forest Ecology and Management* 1: 37-65.
- Garwood, N. C. 1989. Tropical soil seed banks: a review. In M. A. Leck, V. T. Parker, and R. L. Simpson (Eds.). *Ecology of soil seed banks*, pp. 149-208. Academic Press, Inc., San Diego, California.
- Golley, F. B., McGinnis, J. T., Clements, R. G., Child, G. I., and Duever, M. J. 1975. *Mineral cycling in a tropical moist forest*. University of Georgia Press, Athens, Georgia.
- Gonzalez Montagut, R. 1996. Establishment of three rain forest species along the riparian corridor-pasture gradient in Los Tuxtlas, Mexico. Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts.
- Goosem, S. P., & Tucker, N. I. J. (1995). *Repairing the rainforest—Theory and practices of rainforest reestablishment in North Queensland's Wet Tropics Management Authority*. Cairns Australia.
- Gorchov, D. L., Cornejo, F., Ascorra, C., & Jaramillo, M. (1993). The role of seed dispersal in the natural regeneration of rain forest after strip cutting in the Peruvian Amazon. *Vegetation* 107/108: 339-349.
- Gray, A.N., and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78: 2458-2473.
- Gray, A.N., and Spies, T.A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84: 635-645.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.-J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* 29: 824-839.
- Grubb, P.J., 1996. Rain forest dynamics: the need for new paradigms. In: Edwards, D., Booth, W., Choy, S. (Eds.), *Tropical rainforest research current issues*. Kluwer Dordrecht, pp. 215±233.
- Guariguata, M. R., Rheingans, R., and Montagnini, F. 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. *Rest. Ecol.* 3: 252-260.
- Gunter, S., Weber, M., Erreis, R., and Aguirre, N. 2006. Influence of distance to forest edges on natural regeneration of abandoned pastures: a case study in the tropical mountain rain forest of southern Ecuador. *European Journal of Forest Research* Vol. 126(1): 67-75.
- Hammond, D.S., 1995. Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. *J. Trop. Ecol.* 11: 295-313.

- Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. *Ecology* 70: 48–59.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133–302.
- Hartshorn, G.S. 1978. Tree falls and tropical forest dynamics. In *Tropical trees as living systems*. Proc. Fourth Cabot Symposium, Harvard Forest, Petersham, Massachusetts. Edited by P.B. Tomlinson and M.H. Zimmermann. Cambridge University Press, Cambridge, U.K., pp. 617–637.
- Harvey, C.A., and Haber, W.A., 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. *Agroforestry systems* Vol. 44(1): 37–68.
- Hau, C. H. 1997. Tree seed predation on degraded hillsides in Hong Kong. *Forest Ecology and Management* 99: 215– 221
- Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material — an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772–783.
- Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture. *Biotropica* Vol. 31(2): 229–242.
- Holl, K. D., and Lulow, M. E. 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. *Biotropica* 29: 359–468.
- Holl K.D. and Quiros-Nietzen E. 1999. The effect of rabbit herbivory on reforestation of abandoned pasture in southern Costa Rica. *Biol. Cons.* 87: 391–395.
- Holl, K. D., Loik, M. E., Lin, E. H. V., & Samuels, I. A. (2000). Tropical montane forest restoration Costa Rica: Overcoming barriers to dispersal and establishment. *Restoration Ecology* 8: 339–349.
- Horvitz, C. C., Pascarella, J. B., McMann, S., Freeman, A., & Hofstetter, R. H. (1998). Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Application* 8: 947–974.
- Houle, G. 1992. The reproductive ecology of *Abies balsamea*, *Acer saccharum*, and *Betula alleghaniensis* in the Tantaré Ecological Reserve, Québec. *J. Ecol.* 80: 611–623.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecological Systematics* 13: 201–228.
- Hueneke, L.F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bull. Torrey Bot. Club* 110: 170–175.
- Janzen, D. H. 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2: 465–492.
- Johnston, M. H. (1992). Soil-vegetation relationships in a Tabonuco forest community in the Luquillo Mountains of Puerto Rico. *Journal of Tropical Ecology* 8: 252–263.
- Jonsson, B.G., and Dynesius, M. 1993. Uprooting in boreal spruce forests: long-term variation in disturbance rate. *Can. J. For. Res.* 23: 2383–2388.
- Jonsson, B.G., and Essen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J. Ecol.* 78: 924–936.
- Jusoff, K. (1989). Physical soil-properties associated with recreational use of forested reserve area in Malaysia. *Environmental Conservation*, 16, 339–342.
- Kartzinel, T. R. 2007. Understanding tropical montane reforestation. <http://www.rollins.edu/olin/rurj/tyler.pdf>.
- Krebs, J. E. 1974. A comparison of soils under agriculture and forests in San Carlos, Costa Rica. In F. B. Golley and E. Medina (Eds.), *Tropical ecological systems: trends in terrestrial and aquatic research*, pp. 381–390. Springer-Verlag, New York, New York.
- Kuuluvainen, T., Hokkanen, T.J., Järvinen, E., and Pukkala, T. 1993. Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation-soil system. *Can. J. For. Res.* 23: 2101–2109.
- Kuzee & Wijdeven unpublished study.
- Lamb, D., Parrotta, J., Keenan, R., and Tucker, N. 1997. Rejoining habitat remnants: Restoring degraded rainforest lands. In “Tropical Forest Remnants: Ecology, management, and conservation of fragmented communities.” (W. F. Laurance, and R. O. Bierregaard, Eds.), pp. 366–385. The University of Chicago Press, Chicago.
- Landon, J. R. 1984. *Booker tropical soil manual*. Booker Agriculture International Limited, London, England.
- Lieberman, M., Lieberman, D., and Peralta, R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70: 550–552.

- Loik, M. E., and Holl, K. D. 2000. Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. *Restoration ecology* vol. 7(4): 382-391.
- Louda, S. M. 1989 Predation in the dynamics of seed regeneration. *Ecology of Soil Seed Banks* (eds M. Allesio-Leck, V. T. Parker & R. L. Simpson), pp. 25-51. Academic Press, San Diego, CA.
- Lugo, A. E. (1992). Tree plantations for rehabilitating damaged forestlands in the tropics. In M. K. Wali (Ed.). *Ecosystem rehabilitation* (pp. 247-255). The Hague: Academic Press.
- Lundqvist, L., and Fridman, E. 1996. Influence of local stand basal area on density and growth of regeneration in uneven-aged *Picea abies* stands. *Scand. J. For. Res.* 11: 364-369.
- Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* 44: 73-88.
- Maxwell C, Griffiths H, Young A. J. 1994. Photosynthetic acclimation to light regime and water stress by the C3-CAM epiphyte *Guzmania monostachia*: gas-exchange characteristics, photochemical efficiency and the xanthophyll cycle. *Functional Ecology* 8: 746-754.
- Messier, C. 1996. Managing light and understory vegetation in boreal and temperate broadleaf-conifer forests. In *Silviculture of temperate and boreal broadleaf-conifer mixtures*. Edited by P.G. Comeau and K.D. Thomas. Province of British Columbia, Ministry of Forests Research Program, pp. 59-81.
- Metcalf and Turner. 1998. Soil seed bank from lowland rain forest in Singapore, canopy-gap and litter-gap demanders. *J. Trop. Ecol.* 14: 103-108.
- Montagnini, F., and Sancho, F. 1990. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio* 19: 386-390.
- Mulkey, S.S. & Pearcy, R.W. 1992. Interactions between acclimation and photoinhibition of photosynthesis of a tropical forest understorey herb, *Alocasia macrorrhiza*, during simulated canopy gap formation. *Functional Ecology* 6: 719-729.
- Muniz-Castro, M. A., and Benayas, J. M. R. 2006. Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. *Journal of tropical ecology*, Vol. 22 (4): 431-440.
- Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology* 70: 1273-1278.
- Nepstad, D. C., Uhl, C., and Serrao, E. A. S. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Pará, Brazil. In A. B. Anderson (Ed.). *Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest*, pp. 215-229. Columbia University Press, New York, New York.
- Nepstad, D. C., Uhl, C., and Serrao, E. A. S. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* 20: 248-255.
- Nepstad, D. C., Uhl, C., Pereira, C. A., and Cardoso da Silva, J. M. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76: 25-39.
- Nicotra, A.B., Chazdon, R.L., and Iriarte, S.V.B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80: 1908-1926.
- Parker, G.R., and Ward, J.S. 1989. Spatial dispersion of woody regeneration in an old-growth forest. *Ecology* 70: 1279-1285.
- Pedraza, R.A., and Williams-Linera, G. 2003. Evaluation of native tree species for the rehabilitation of deforested areas in a Mexican cloud forest. *New forests* Vol. 26(1): 83-99.
- Perz, S. G. 2007. Grand theory and context-specificity in the study of forest dynamics: Forest transition theory and other directions. *The professional geographer* 59(1): 105-114.
- Peterson, C.J., and Pickett, S.T.A. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *J. Veg. Sci.* 1: 657-662.
- Peterson, C.J., Carson, W.P., McCarthy, B.C., and Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58: 39-46.
- Place, I.C.M. 1955. The influence of seed-bed conditions on the regeneration of spruce and balsam fir. *Can. Dept. Northern Affairs Natl. Resources, For. Br., For. Res. Div., Bull.* 117.
- Powers, J. S., Haggard, J. P., and Fisher, R. F. 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. *Forest Ecology and Management* Vol. 99(1): 43-54.
- Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64: 1069-74.
- Ramirez-Bamonde, E.S., Sanchez-Vasquez, L.R., and Andrade-Torres, A. 2004. Seedling survival and growth of three species of

- mountain cloud forest in Mexico, under different canopy treatments. *New Forests* Vol. 30(1): 95-101.
- Rasiah, V., Florentine, S. K., Williams, B. L., & Westbrooke, M. E. 2004. Soil properties dynamics under abandoned pasture in deforested tropical rainforest in Australia. *Geoderma* 120: 35-45.
- Reiners, W. A., Bouwman, A. F., Parsons, W. F. J., and Keller, M. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecol. Appl.* 4: 363-377.
- Richards, P. W. (1996). *The tropical rainforest: An ecological study*. New York: Cambridge University Press.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-46
- Rydgren, K., Hestmark, G., and Økland, R.H. 1998. Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. *J. Veg. Sci.* 9: 763-776.
- Saldarriaga, J.G., West, D.C., Tharp, M.L. and Uhl, C. 1988. Long-term chronosequence of forest succession in the upper Río Negro of Colombia and Venezuela. *Journal of Ecology* 76: 938-958.
- Sanchez, P. A. 1976. *Properties and management of soils in the tropics*. John Wiley & Sons, New York, New York.
- Sarmiento, F. O. 1997. Arrested succession in pastures hinders regeneration of Tropicandean forests and shreds mountain landscapes. *Environmental Conservation* 24: 14-23.
- Saunders, D. A., Hobbs, R. J., and Margules, C. R. 1991. Biological consequences of ecosystem fragmentation, a review. *Conservation Biology* 5: 18-32.
- Schaetzl, R.J., Burns, S.F., Johnson, D.L., and Small, T.W. 1989a. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79: 165-176.
- Schaetzl, R.J., Johnson, D.L., Burns, S.F., and Small, T.W. 1989b. Tree uprooting: review of terminology, process and environmental implications. *Can. J. For. Res.* 19: 1-11.
- Steven, D. D. (1991). Experiments on mechanisms of tree establishment in old-field succession; seedling emergence. *Ecology* 72: 1066-1075.
- Tabarelli M., Mantovani W. and Peres C.A. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 91: 119-127.
- Tanner, E. V. J., Kapos, V., and Franco, W. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73: 78-86.
- Turner, I.M. 2001. *The ecology of trees in the tropical rain forest*. Cambridge University Press, New York.
- Uehara, G., and Gillman, G. 1981. *The mineralogy, chemistry, and physics of tropical soils with variable charge clays*. Westview Press, Boulder, Colorado.
- Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture. *J. Ecol.* 75: 377-407.
- Uhl, C., Buschbacher, R., and Serrao, E. A. S. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *J. Ecol.* 76: 663-681.
- Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. *For. Ecol. Manage.* 135: 155-167.
- Van Pelt, R. 1995. *Understory Tree Response to Canopy Gaps in Old-growth Douglas-fir Forests of the Pacific Northwest*. Dissertation. University of Washington, Seattle, WA.
- Vazquez-Yanes, C., and Orozco-Segovia, A. 1985. Posibles efectos del microclima de los claros de la selva, sobre la germinación de tres especies de árboles pioneros: *Cecropia obtusifolia*, *Heliocarpus donnell-smithii* y *Piper auritum*. Pp. 241-253.
- Verdú, M. & García-Fayos, P. 1996. Postdispersal seed predation in a Mediterranean patchy landscape. *Acta Oecologica* 17: 379-391.
- Vieira, I. C. G., Uhl, C., and Nepstad, D. 1994. The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* 115: 91-99.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, F. (Wash. DC) 238: 802-804.
- Vitousek, P. M., Antonio, C. M. D., Loope, L. L., & Rejmanek, M. 1997. Introduced species: A significant component of human caused global change. *New Zealand Journal of Ecology* 21: 1-16.
- Whelan, C. J., Wilson, M. F., Tuma, C. A., & Soulaz-Pinta, I. (1991). Spatial and temporal patterns of post dispersal seed predation. *Canadian Journal of Botany* 69: 428-436.
- Whitmore, T. C. 1991. *An introduction to tropical rain forests*. Oxford: Clarendon Press.
- Whitmore, T. C. 1997. Tropical rainforest disturbance disappearance and species loss. In W. F. Laurance, & R. O. Bierregaard Jr. (Eds.). *Tropical forest remnants: Ecology management and conservation of fragmented communities* (pp. 3-12). Chicago,

- IL: University of Chicago Press.
- Whitmore, T. C. 1978. Gaps in the forest canopy. Pp. 639-55.
- Whitmore, T. C. 1983. Secondary succession from seed in tropical rain forests. *For. Abstr.* 44: 767-779.
- Whitmore, T. C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70: 536-538
- Whitmore, T. C. 1998. *An Introduction to Tropical Rain Forests*. Oxford University Press.
- Wijdeven, S. M. J., and Kuzee, M. E. 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration ecology* vol. 8(4): 414-424.
- Williams-Linera, G. 2002. Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation* 11: 1825-1843.
- Wunderle, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 223-235.
- Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproductive process in boreal forest trees. In *A systems analysis of the global boreal forest*. Edited by H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, Cambridge, U.K., pp. 85-125.
- Zimmerman, A. E., Pascarella, J. B., and Aide, T. M. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8: 350-360.



Date: 28-08-2008

Written by: Matthijs Bol
Dennis Vroomen

Coaches: Ian Giddy
Jaap de Vletter

In association with Cloudbridge Nature reserve

*Conducted as bachelor thesis research for Tropical
Forestry at the Van Hall Larenstein Institute*