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Natural succession and tree plantation as alternatives for restoring abandoned lands in the Andes of Southern Ecuador: Aspects of facilitation and competition

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Summary

Ecuador holds one of the highest levels of biological diversity in the world, but it is threatened by deforestation and unsustainable land-use, like many other tropical regions. One of the consequences is that abandoned areas are emerging where either "passive" or "active" restoration alternatives are needed to reestablish ecosystem functions and biodiversity. One aim of this study is to evaluate two restoration alternatives and their ecological aspects of facilitation and competition on the three dominant types of successional sites (freshly abandoned Pasture, Bracken and Shrub) in the San Francisco valley in Southern Ecuador, which has been subject to large scale conversion of forest to pasture, mainly for cattle ranching. Another aim is to establish whether human intervention can accelerate the processes of forest recovery on the three sites.

The pastures are mostly cultivated with *Setaria sphacelata*, an exotic grass which is preferred by the landowners in the region. Due to the slash and burn technique usually employed for the conversion of forest, the burnt land is invaded by bracken fern *Pteridium arachnoideum,* creating lands denoted in this study as 'Bracken site'. Secondary vegetation (Shrub site) is also well represented in the study area, which has had progressive natural succession since abandonment.

In total three experiments were carried out in this study:

1) Reforestation experiment using native species which includes the monitoring of natural succession over time and their response to the removal of competitive vegetation.
2) Seedling pretreatment experiment comprising of fertilization, inoculation with arbuscular mycorrhiza fungi (AMF) and shading.
3) Rhizotron experiment which evaluated the effects of fertilization and grass competition (*S. sphacelata*) on root development and biomass allocation of three native tree species.

The **dynamic of natural succession** was compared in terms of species richness and abundance of woody species on three sites and the effectiveness of manual competitive vegetation removal was also assessed. The monitoring was done in 2003, 2005 and 2007 on 16 plots (116 m^2 each) per site and the successional trajectory was also analyzed. The results showed that the Bracken and Shrub sites became floristically similar with an effect of facilitation; this similarity could be due to comparable land-use history and better light availability. These two sites appeared to be following a parallel successional trajectory with the Shrub site having a higher species richness and abundance of woody species followed by Bracken site. The Pasture site, however, demonstrated a competitive effect from exotic grasses on woody species recruitment with much lower diversity recruitment; the successional trajectory is as yet unclear.

In the **reforestation experiment** with six natives species corresponding to mid-successional species (*Cedrela montana*, *Tabebuia chrysantha* and *Juglans neotropica*), and early- successional species (*Alnus acuminata*, *Heliocarpus americanus, Morella pubescens)* were planted during 2003 and 2004 on all sites with a total of 288 plots (10.8 x 10.8 each). Survival, height and root collar diameter were monitored annually until 2008 for each species with the aim of evaluating plant performance over time and to determine if the current vegetation on the three sites facilitates or suppresses tree establishment. A weeding treatment was added to reduce the weed herbaceous competition with machete during the first two years (manual treatment) and a chemical treatment was applied (Glyphosate, Ranger 480 g/l at 2% concentration) at 48 months. Half of plots were exposed to manual and chemical treatment and consequently the plant performance was evaluated. The results of this experiment showed that certain species were well adapted to certain sites; *A. acuminata* on the Pasture site, *M. pubescens* on the Bracken site and *T. chrysantha* on the Shrub site. Furthermore a micro-site effect was observed, which is an important aspect for addressing further recommendations. The weeding treatment within the reforestation experiment revealed that the majority of species had a positive effect under treated plots although no statistical significance was found, except for *T. chrysantha* which reacted well to the treatment on all sites but particularly on the Shrub site, where shade or shelter vegetation facilitated plant growth and the direct competition for nutrients and water could be reduced.

Based on the poor natural successional development and performance of native tree species, in particular mid-successional species, on the Pasture site, a further experiment was established in 2009 using **seedlings pretreated** with five different treatments. The aims of this experiment were primarily to quantify the effect of fertilizer and AMF on survival, height and root collar diameter increment (RCD) of the three native species and secondarily to evaluate the effect of shade and treatment on the same plant parameters for *T. chrysantha*. The treatments used in the experiment were 1) Full fertilizer, 2) low fertilizer with devitalized AMF inoculum, 3) low fertilizer with living AMF inoculums, 4) living AMF and 5) control. The effects of the treatments were assessed two years after planting with regard to survival, growth performance and plant quality. The native species used in the experiment were *C. montana, T. chrysantha* and *H. americanus*. The tendency of results indicated a species-specific trait response to the treatments although no statistical significance has been found so far, other than the survival of *T. chrysantha*. This species and *C. montana* reacted positively beneath Low Fertilizer with devitalized AMF treatment for plant growth whereas only *H. americanus* was favored by full fertilizer. Interestingly, the effectiveness of living AMF is clear in terms of survival, although this is not accompanied by improved growth performance. Furthermore, *T. chrysantha* responded positively to shading in all the treatments.

The **rhizotron experiment** was carried out in the nursery to understand better the effects of grass competition (*S. sphacelata*) and fertilization on the root length density (RLD) and biomass allocation of *C. montana, T. chrysantha* and *A. acuminata* seedlings. In total 60 rhizotrons were used for monitoring root development. At the end of monitoring all the plants were harvested and oven dried to calculate above- and belowground biomass allocation. The results confirmed the aggressiveness of *S. sphacelata.* It had a notable capacity to allocate above-and belowground biomass and had a much greater root length density in comparison to the tree species. *C. montana* and *T. chrysantha* were negatively affected by the presence of the grass competitor, while *A. acuminata* was more successful in producing a greater root length density and higher amount of above- and belowground biomass.

Overall, the results may strongly influence silvicultural and restoration efforts in the tropical mountain forest region of South Ecuador. Specific recommendations are addressed according to the successional site conditions.

On the Pasture site, human intervention is preferable; *A. acuminata* would be a good candidate for plantation as it is well adapted to the conditions and has the capacity to bear the high competition of the grass. On the Bracken site, where natural succession is occurring, natural or artificial perches should be established to attract seed dispersal agents or an enrichment plantation or direct seeding of *Morella pubescens* should be done in order to enhance restoration. On the Shrub site, similar efforts should be put into the recruitment of animal-dispersed woody species, along with enrichment planting with native species such as *T. chrysantha*, which demonstrated to be well adapted to the secondary vegetation.

Further studies have to be conducted using other native shrubs or tree species with N-fixing capabilities and it is recommended that micro-site soil characteristics on all sites are comprehensively investigated in order to selectively plant groups of trees which perform well on the micro-sites.

Mid- and long–term monitoring should be done to provide knowledge of site specific vegetation community dynamics and consider local- scale smallholder needs to achieve restoration of abandoned lands and conservation of biodiversity in the San Francisco valley.

Zusammenfassung

Ecuador verfügt über eine der höchste Biodiversitätsraten weltweit, aber das Land ist ebenso wie viele andere tropische Bereiche von Entwaldung und nicht nachhaltiger Landnutzung betroffen. Dadurch entstehen Brachflächen, welche entweder im Rahmen der natürlichen Sukzession (passiv) oder durch Wiederaufforstungsmaßnahmen (aktiv) restauriert werden können, um die Produktivität oder Biodiversität wiederherzustellen. Die vorliegende Arbeit untersucht diese beiden Sanierungsalternativen sowie Verbesserungsmöglichkeiten zur Beschleunigung des Entwicklungsprozesses anhand von unterschiedlichen Experimenten im San Francisco Tal im südlichen Ecuador auf den drei dort dominierenden Sukzessionstypen (kürzlich aufgelassene Weiden; Stadium mit Farnbewuchs; Stadium mit Strauch- und Gebüschvegetation). In diesem Tal wurde im großen Umfang Wald in Weideflächen für Rinder umgewandelt. Die Weiden werden zumeist mit *Setaria sphacelata* begründet, eine exotische Gräserart, welche von den lokalen Landeigentümern bevorzugt wird. Durch Brandrodung (das gebräuchliche Verfahren vor Ort zur Weidelandgewinnung) wandert der Adlerfarn *Pteridium arachnoideum* auf die Flächen ein. Sekundäre Vegetation (Strauch- und Gebüschvegetation), die sich nach der Aufgabe der Weideflächen entwickelte, ist im Untersuchungsgebiet ebenso wie die Adlerfarnstandorte in großem Umfang vorhanden.

Um die Möglichkeiten zur Restauration dieser Flächen zu untersuchen, wurden in dieser Studie drei Experimente durchgeführt:

1) Ein Aufforstungsexperiment mit standortheimischen Baumarten. Analog dazu wurde die natürliche Sukzession über die Zeit beobachtet und die Reaktion auf das Entfernen von Konkurrenzvegetation festgehalten.
2) Ein Versuch zur Vorbehandlung von Sämlingen durch Düngung, Inokulation mit arbuskulären Mykorrhizen (AMF) und Beschattung.
3) Ein Rhizotron-Experiment zur Untersuchung der Effekte von Düngung und Graskonkurrenz (*S. sphacelata*)auf die Wurzelentwicklung und die Biomasseallokation von drei ausgewählten einheimischen Baumarten.

Die **Dynamik der natürlichen Sukzession** auf den drei ausgewiesenen Sukzessionstypen wurde hinsichtlich Artenreichtum und Häufigkeit von verholzenden Pflanzen beurteilt. Die Effektivität der Begleitwuchsregulierung wurde ebenfalls untersucht. Die Aufnahmen wurden in den Jahren 2003, 2005 und 2007 auf 16 Plots (je 116m^2) pro Sukzessionstyp durchgeführt und die Sukzessionpfade wurden analysiert. Die Ergebnisse zeigten, dass die Sukzessionstypen „Farn" und „Gebüsch" sich in floristischer Hinsicht ähnlich entwickeln und über förderliche Effekte für die Restaurierung verfügen. Diese Ähnlichkeit könnte auf vergleichbarer Nutzung in der Vergangenheit und besserer Lichtverfügbarkeit beruhen. Beiden Standorte zeigten einen parallelen Sukzessionsverlauf, wobei der Standort „Gebüsch" über eine höhere Artenzahl als auch Abundanz an verholzenden Pflanzen verfügte. Auf dem Weideland zeigte sich ein Konkurrenz- Effekt des exotischen Grases auf die Verjüngung von verholzenden Pflanzen mit der Folge einer deutlich geringeren Artenvielfalt. Der anfängliche Verlauf der Sukzessionspfade konnte auf den drei Standorten identifiziert werden, die zukünftige Entwicklung kann aber noch nicht abgeschätzt werden.

Im **Aufforstungsexperiment** mit 6 heimischen Baumarten wurden in den Jahren 2003 und 2004 auf den drei Sukzessionstypen insgesamt 288 Plots zu je 10,8m x 10,8m bepflanzt. Dabei wurden 3 mittel-sukzessionale Baumarten *(Cedrela montana*, *Tabebuia chrysantha* und *Juglans neotropica*) sowie 3 früh-sukzessionale Arten (*Alnus acuminata*, *Heliocarpus americanus* und *Morella pubescens*) verwendet. Das Überlebensprozent, die Höhe sowie der Wurzelhalsdurchmesser wurden bis zum Jahr 2008 jährlich erhoben. Ziel dabei war die Wuchsleistung der Pflanzen über die Zeit zu beobachten und bereits vorhandene Vegetation als Förderer oder Unterdrücker von Etablierung zu identifizieren. Um die Effekte einer Beseitigung der Konkurrenz durch krautige Pflanzen zu untersuchen, wurden auf der Hälfte der Untersuchungsplots in den ersten 2 Jahren die jungen Bäume per Machete ausgekesselt und nach 48 Monaten außerdem eine chemische Behandlung (Glyphosphate, Ranger 480g/l mit 2% Konzentration) durchgeführt. Die Ergebnisse dieses Versuchs zeigten, dass gewisse Arten an bestimmte Standorte gut angepasst sind: *A. acuminata* für das Weideland, *M. pubescens* für die Farnstandorte und *T. chrysantha* auf den Strauch- und Gebüschstandorten. Weiterhin wurde ein Mikro-Standortseffekt beobachtet, der für weitere Empfehlungen einen wichtigen Gesichtspunkt darstellt. Das Entfernen von krautiger Vegetation innerhalb des Aufforstungsexperiments zeigte, dass die Mehrheit der Baumarten in Überleben und Wachstum profitierte, auch wenn sich dies statistisch nicht nachweisen ließ, mit Ausnahme von *T. chrysantha,* welche auf allen sukzessionalen Standorten signifikant positiv auf die Behandlung reagierte. Besonders zeigte sich dies auf den Strauch- und

Gebüschstandorten, wo Schatten und Schutz durch vorhandene Vegetation sich positiv auf das Wachstum auswirkten und die direkte Konkurrenz um Wasser und Nährstoffe reduziert war.

Bedingt durch die schwache natürliche Sukzession und die schwache Wuchsleistung der heimischen Baumarten, insbesondere der mittel-sukzessionalen auf dem Weidestandort, wurde im Jahr 2009 ein weiteres Experiment etabliert. Vorrangiges Ziel dieses Versuches war, den Einfluss von Düngung und AMF auf das Überleben, die Höhe und den Wurzelhalsdurchmesser-Zuwachs zu untersuchen. Zusätzlich sollten für *T. chrysantha* die Effekte einer Beschattung in Kombination mit den verschiedenen Behandlungen auf die drei genannten Parameter untersucht werden. Hierzu wurden eine **Vorbehandlung der Sämlinge** mit fünf verschiedenen Varianten durchgeführt: 1) Volldüngung, 2) geringe Düngung mit entkräfteten AMF-Inokuli, 3) geringe Düngung mit lebenden AMF-Inokuli, 4) lebende AMF-Inokuli und 5) Kontrolle ohne Vorbehandlung. Die Effekte der Behandlung wurden zwei Jahre nach der Pflanzung hinsichtlich Überlebensprozent und Wachstum beurteilt. Die heimischen Baumarten in diesem Experiment waren *C. montana*, *T. chrysantha* und *H. americanus.* Die Ergebnisse zeigen Tendenzen der Baumarten, spezifisch auf die Behandlungen zu reagieren obwohl mit Ausnahme von *T. chrysantha* keine statistische Signifikanz festgestellt werden konnte. Letztgenannte und *C. montana* reagierten bezüglich ihres Wachstums positiv auf eine Vorbehandlung mit geringer Düngung und entkräfteten AMF-Inokuli, wohingegen nur im Falle der Baumart *H. americanus* eine Vorbehandlung mit Volldüngung positive Effekte zeigte. Interessanterweise führte eine Vorbehandlung mit lebenden AMF-Inokuli zu einem höheren Überlebensprozent, jedoch nicht gleichzeitig zu einem verbesserten Wachstum. *T. chrysantha* reagierte positiv auf Beschattung in allen Behandlungsvarianten.

Das **Rhizotron-Experiment** wurde in der Baumschule durchgeführt. Ziel war es besser zu verstehen, welchen Einfluss Graskonkurrenz (*S. sphacelata*) und Düngung auf die Entwicklung der Wurzellänge und -dichte sowie den Biomassezuwachs von *C. montana*, *T. chrysantha* und *A. acuminata* haben. In Summe wurden 60 Rhizotrone zur Beobachtung in der Baumschule etabliert. Zum Abschluss der Aufnahmen wurden alle Pflanzen geerntet und für die Berechnung der ober- und unterirdischen Biomasseallokation getrocknet. Die Beobachtungen untermauerten, dass *S. sphacelata*

sehr aggressiv wächst. Dieses Gras zeigt eine bemerkenswerte Fähigkeit, ober- und unterirdische Biomasse sowie Wurzeldichte zu bilden und ist dabei den einbezogenen Baumarten überlegen. *C. montana* und *T. chrysantha* wurden negativ durch die Graskonkurrenz beeinflusst, wohingegen *A. acuminata* bei Graskonkurrenz erfolgreicher in der Entwicklung von Wurzellänge und -dichte sowie in der Produktion von ober- und unterirdischer Biomasse war.

Insgesamt könnten diese Ergebnisse die forstlichen und restaurativen Maßnahmen in der tropischen Bergregenwaldzone Ecuadors stark beeinflussen. Gezielte Empfehlungen werden gemäß dem jeweiligen Sukzessionsstadium ausgesprochen:

Auf dem Weideland sollten menschliche Eingriffe erfolgen. *A. acuminata* könnte eine geeignete Baumart für die Pflanzung darstellen, da sie gut an die Bedingungen auf diesem Sukzessionstyp angepasst ist und sich gegen die Graskonkurrenz durchsetzen kann. Die vom Adlerfarn besiedelten Flächen zeigen eine natürliche Sukzession. Natürliche oder künstliche Sitzwarte sollten etabliert werden, um Tiere für die Verbreitung von Saatgut anzulocken. Außerdem wären Anreicherungspflanzungen oder eine Direktsaat mit *M. pubescens* für die Restauration dieser Standorte förderlich. Auf den Strauch- und Gebüschstandorten sollten ähnliche Anstrengungen unternommen werden, um die Verjüngung von Baumarten zu fördern, deren Saatgut über Tiere verbreitet wird. Außerdem können einheimische Baumarten wie zum Beispiel *T. chrysantha* im Zuge einer Anreicherungspflanzung eingebracht werden, da sie eine gute Anpassung an die Sekundärvegetation gezeigt hat.

Weitere Untersuchungen mit anderen einheimischen Stickstoff-bindenden Baum- und Straucharten sollten unternommen werden. Darüber hinaus sollten die Bodeneigenschaften der Mikrostandorte auf allen drei Sukzessionstypen umfassend untersucht werden, um baumartenspezifisch gezielte Gruppenpflanzungen an erfolgversprechenden Stellen durchzuführen.

Ein mittel- und langfristiges Monitoring sollte für weitere Erkenntnisse über die standortspezifische Vegetationsdynamik durchgeführt werden und für die Restaurierung der brachliegenden Flächen im San Francisco Tal durch die Berücksichtigung der Bedürfnisse der lokalen Kleinbauern ergänzt werden.

Resumen

Ecuador posee uno de los más altos niveles de diversidad biológica en el mundo, pero está amenazada al igual que en otras regiones tropicales por la deforestación y el uso no sostenible de suelo. Una de las consecuencias es el abandono de tierras, por tanto cualquier alternativa de restauración "pasiva" o "activa" es necesaria para restablecer las funciones del ecosistema y la biodiversidad. Un objetivo de este estudio es evaluar dos alternativas de restauración y sus aspectos de facilitación y competencia en tres sitios sucesionales (Pastos recientemente abandonados, Llashipa y Arbustivo) en el valle de San Francisco en el Sur del Ecuador, el mismo que ha sido sujeto a la conversión de bosques a pastos, principalmente para la actividad ganadera. Otro objetivo fue conocer si la intervención humana puede acelerar los procesos de recuperación de bosque en los tres sitios.

Los pastos en su mayoría son cultivados con *Setaria sphacelata*, una especie exótica que es preferida por los propietarios de las fincas en la región. Debido a la técnica de tala y quema usualmente empleada para la conversión de bosques, las tierras quemadas son invadidas por llashipa *Pteridium arachnoideum*, creando tierras denominadas como sitio de Llashipa. Vegetación secundaria (sitio Arbustivo) está también bien representado en el área de estudio, el mismo que ha tenido una progresiva sucesión natural desde que fue abandonado.

En total tres experimentos se llevaron a cabo en este estudio:

1) Experimento de reforestación usando species nativas, y también incluyó el monitoreo de la sucesión natural en tiempo y su respuesta a la remoción de la vegetación competitiva.
2) Experimento de plántulas pretratadas con fertilizante, inoculación con hongos micorrhizicos arbusculares (AMF) y exposición a la sombra.
3) Experimento de Rhizotron, el mismo que evaluó el efecto de la fertilización y la competencia del pasto (*S. sphacelata*) en el desarrollo de la raíz y la producción de biomasa.

La dinámica de **sucesión natural** fue comparada en términos de riqueza y abundancia de especies leñosas en los tres sitios y también la efectividad de la remoción de la vegetación competitiva fue evaluada. El monitoreo fue realizado en 2003, 2005 y 2007 en 16 parcelas (116 m^2) por sitio y la trayectoria sucesional también fue analizada. Los resultados mostrarón que los sitios de Llashipa y Arbustivo llegaron a ser parecidos florísticamente con un efecto de facilitación, esta semejanza puede deberse a su similar historia de uso del suelo y mejor disponibilidad de luz. Estos dos sitios parecen seguir una trajectoria successional paralela siendo el sitio Arbustivo con el más alto número de especies y abundancia, seguido por el sitio de Llashipa. El sitio Pasto, sin embargo, demostró tener un efecto de competencia por el pasto exótico en el reclutamiento de especies leñosas con un número menor de diversidad; la trayectoria sucesional en este caso no es clara todavía.

Reforestación consistió de seis especies nativas correspondientes a media sucesión (*C. montana, T. chrysantaha* and *Juglans neotropica*), y temprana sucesión (*A. acuminata, H. americanus* and *Morella pubescens*), los mismos que fueron plantados durante 2003 y 2004 en los tres sitios con un total de 288 parcelas (10.80 x 10.80 m cada parcela). Sobrevivencia, altura y diámetro del cuello de la raíz fueron monitoreados anualmente hasta 2008 for cada especie con la finalidad de evaluar el rendimiento de las plantas en el tiempo y determinar si la vegetación actual en los tres sitios facilita o suprime el establecimiento de las plántulas. Un tratamiento de deshierbe fue añadido para reducir la competencia por herbáceas usando un machete durante los dos primeros años (tratamiento manual) y tratamiento químico fue aplicado (Glifosato, Ranger 480 g/l al 2% de concentración) a los 48 meses. La mitad de las parcelas fueron expuestas al tratamiento manual y químico y consecuentemente el crecimiento y supervivencia de las plantas fueron evaluadas. Los resultados de este experimento mostraron que ciertas especies se adaptaron bien dependiendo de las condiciones del sitio como es el caso de *A. acuminata* en el Pasto, *M. pubescens* en la Llashipa y *T. chrysantha* en el sitio Arbustivo. Además un efecto de micro-sitio fue observado, lo cuál es un aspecto importante para direccionar futuras recomendaciones. El tratamiento de deshierbe dentro del experimento de reforestación reveló que la mayoría tuvo un efecto positivo en las parcelas tratadas aunque no signifincancia estadística fue encontrada, excepto para *T. chrysantha* que reaccionó bien al tratamiento en todos los sitios pero particularmente en el sitio Arbustivo, donde la sombra y la protección de la vegetación facilitó el crecimiento de las plantas y la competencia for nutrientes y agua pudo ser reducida.

En base al pobre desarrollo de la sucesión natural y el rendimiento de las especies nativas arbóreas, en particular de las especies de media sucesión en el sitio de Pasto, un nuevo experimento fue establecido en 2009 usando **plántulas pretratadas** con cinco diferentes tratamientos. Los objetivos de este experimento fueron primeramente cuantificar los efectos de la fertilización y de AMF sobre la sobrevivencia, incremento de altura y del diámetro del cuello de la raíz de tres especies nativas en el pastizal y en segundo lugar evaluar el efecto de la sombra y el tratamiento sobre los parámetros antes mencionados para *T. chrysantha.* Los tratamientos usados en el experimento fueron 1) alta fertilización, 2) baja fertilización con inóculo de AMF de baja vitalidad, 3) baja fertilización con vital inóculo de AMF, 4) vital AMF y 5) Control. El efecto de los tratamientos fue evaluado dos años después de ser plantados con respecto a la supervivencia, creciemiento y calidad de plantas. Las especies nativas usadas en el experimento fueron *C. montana*, *T. chrysantha* y *H. americanus*. La tendencia de los resultados indican una especificidad de las especies a los tratamientos aunque ninguna significancia ha sido encontrado hasta el momento, más que para la supervivencia de *T. chrysantha*. Esta última especie y *C. montana* reaccionaron positivamente al tratamiento baja fertilización con inóculo de baja vitalidad de AMF para el crecimiento de las plantas mientras que sólo *H. americanus* fue favorecido con el tratamiento de alta fertilización. Es interesante, la efectividad del vital AMF en términos de supervivencia aunque no este acompañado por una mejora en el crecimiento. Además *T. chrysantha* respondió positivamente a la sombra en todos los tratamientos.

Experimento de rhizotron fue llevado a cabo en el invernadero para entender el efecto de la competencia del pasto (*S. sphacelata*) y la fertilización en la densidad de longitud de raíces (RLD) y la producción de biomasa en las plántulas de *C. montana*, *T. chrysantha* y *A. acuminata.* En total 60 rhizotrones fueron usados para el monitoreo del desarrollo de la raíz. Al final del monitoreo todas las plantas fueron cosechadas y secadas para calcular la producción de biomasa aérea y de raíces. Los resultados confirman la agresividad de *S. sphacelata*. Esta especie tuvo una notable capacidad para producir una gran cantidad de biomasa aérea y un gran desarrollo de densidad de longitud de raíces en comparación con las especies forestales. *C. montana* y *T. chrysantha* fueron negativamente afectadas por la competencia del pasto mientras A. *acuminata* fue más exitoso produciendo mejor densidad de longitud de raíces y más alta cantidad de biomasa aérea y de raíces.

En general, los resultados pueden influenciar en la silvicultura y en los esfuerzos de restauración de un bosque tropical de montaña en el Sur del Ecuador. Específicas recomendaciones son dirigidas de acuerdo a las condiciones del sitio.

En el sitio del Pasto, una intervención humana es preferible; *A. acuminata* sería un buen candidato para la plantación debido a su buena adaptación a las condiciones del sitio y a la capacidad de sobrellevar los efectos competitivos del pasto. En el sitio de la Llashipa, donde la sucesión natural esta ocurriendo, perchas naturales o artificiales deberían ser establecidas para atraer agentes de dispersión de semillas o un enriquecimiento a través de una plantación o siembra directa de *Morella pubescens* es una opción para acelerar los procesos de restauración. En el sitio Arbustivo, similares esfuerzos deberían ser llevados a cabo, en el reclutamiento de especies dispersadas por animales junto con un enriquecimiento con especies como *T. chrysantha*, el cuál demostró estar bien adaptado a la vegetación secundaria. Futuros estudios deben ser conducidos usando otras especies arbustivas o árboles nativos con capacidad para fijar nitrógeno, y es recommendable que las características de micro sitio en los tres sitios sucesionales sean investigados con la finalidad de plantar grupos de árboles previamente seleccionados en los sitios correctos para asegurar su buen creciemiento.

Un monitoreo a mediano y largo plazo debería ser realizado para proveer mejor conocimiento de la dinámica de las comunidades de vegetación, así como también considerar las necesidades de la gente local para lograr la restauración de tierras abandonadas y la conservación de la biodiversidad en el valle de San Francisco.

1. General Introduction

1.1 Ecuador faces high land transformation

Ecuador is one of the most diverse countries in the world in terms of absolute number of species and number of species per unit of area (Sierra et al. 2002). To date, a total of 15,306 vascular native species has been documented (Jørgensen & León-Yánez 1999). However, this outstanding biodiversity is threatened by a high deforestation rate and subsequent non-sustainable land use. According to FAO (2010) the annual rate of deforestation between 2005 and 2010 in Ecuador was 1.89 % and Ecuador's Ministry of the Environment (2011), found that the mean annual deforestation rate was 17,009 ha/yr from 2000 to 2008 in the Andes of South Ecuador.

In developing countries around the world the causes of deforestation are related to rapid population growth, expansion of cropland and pastures, and intensive harvesting of forest for fuel wood and wood exports (Allen & Barnes 1985). Montagnini & Jordan (2005) mentioned that deforestation is mainly related to the expansion of agriculture and ranching in the tropics.

Currently, there is a large amount of land in the tropics being converted for agricultural purposes, especially into pasture for cattle ranching (Aide et al. 2000; Günter 2011). Some of this land may be abandoned due to a decrease in productivity through overgrazing or inappropriate cultivation practices using fire and/or the invasion of aggressive weed species (Hobbs & Cramer 2007). These facts lead to serious problems in land degradation and vegetation coverage with increasing amount of secondary forest. In Ecuador, degraded land is estimated at 14.15 % of the territory, being defined as a long-term decline in ecosystem function and measured in terms of net primary production (Bai et al. 2008).

According to Koning et al. (1999), grassland area is widespread in Ecuador and more noticeable along Andean foothills, particularly in the north-west and south-east. The San Francisco valley, the study area, has also been subject to conversion of primary forest to pasture, mainly for cattle ranching. Göttlicher et al. (2009) found in the San Francisco valley that land use below 2.200 m asl is comprised of 45.2 % native forest, 15.4 % pasture in use, 10.6 % bracken fern invaded areas , 21.7 % successional vegetation, 0.3 %

landslides, and 6.9 % with other land uses. This gives a clear picture of how much the original ecosystem, in particularly in lower parts, has been reshaped by human activities (Crespo 2004).

The usual technique for forest clearance employed in this area is slash and burn (Beck et al. 2008a), and the exotic grass *Setaria sphacelata (*Schumach.) Stapf & C.E. Hubb is cultivated for pastoral use. The fires, set by the farmers in the attempt to create grazing for their livestock, frequently get out of control and may burn a whole mountainside and in the long run these fires stimulate the presence of fire-tolerant species such as bracken fern (*Pteridium arachnoideum* KAULF. MAXON), which can overrun the pastures and lead to abandonment (Beck et al. 2008a; Roos 2010).

Overall, there is a large amount of land in different stages of succession after abandonment which can be categorized into three different types of land: freshly abandoned pastures still dominated by grasses; other areas dominated by bracken fern; and shrub areas where succession has already advanced and the first shrub and tree species have established.

Given this situation in the Andes of Ecuador, there is an urgent need for scientists and practitioners to work together to find efficient ways of restoring the different types of degraded/abandoned land. Nevertheless, these activities of restoration must be into the economical system promoting productive activities instead of destructive ones (Knoke et al. 2008; Knoke et al. 2009).

1.2 Why is it important to restore degraded lands?

Restoration is strongly linked to human benefits; the Millennium Ecosystem Assessment (2005) mentioned that a healthy ecosystem promotes well-being through four principal types of ecological services - supporting services (nutrient cycling), provisioning services (food, fresh water, wood and fiber, fuel, etc.), regulating services (climate or flood regulation, disease regulation, etc.), and cultural services (aesthetic, spiritual, educational and recreational). When an ecosystem is restored, it is a potential strategy to reduce the pressure on remnant natural forest (Plath et al. 2011) and it is a potential approach for mitigating global change by improving carbon stocks (Sasaki et al. 2011).

The Constitution of the Republic of Ecuador, in the Article 72, published in the Official Register (2008), stated that nature has the right to be restored and this restoration will be independent of the obligation of the State, individuals, or legal entities to compensate individuals and communities that depend on affected natural systems. Therefore, all action against the integrity of natural ecosystems in Ecuador has to be restored for the common good, although the constitution is not very explicit about what constitutes compensation, saying that "the State shall establish the most effective mechanisms to achieve the restoration and shall adopt adequate measures to eliminate or mitigate harmful environmental consequences."

Landowners can get direct benefits when an ecosystem is restored and they can gain access to the ecosystem's goods and services. Moreover, ecological restoration increases economic opportunities and benefits by enhancing the social, cultural, psychological and spiritual aspects of human welfare (Aronson et al. 2006). Restoration can be made even more attractive for local people if it is integrated into an agroforestry system and/or an agro-successional restoration, which implies using agroecology and agroforestry techniques as a transition phase early in forest restoration (Lamb et al. 2005; Vieira et al. 2009).

However, an effective restoration project requires a deep understanding of social, economic and ecological aspects. Within the ecological context, the history and environmental conditions of the site, the ecology of species and the functional groups of species recruited naturally or planted are decisive in the process of forest recovery. Within the social context, is important the integration of local communities in resource management and conservation efforts (Kainer et al. 2009). There is clear example in Ecuador of why the Restoration might fail: in the Galapagos Islands, 16 from 30 projects of plant eradication programs were unsuccessful due to lack of either from the support of institutions for providing resources or from land owners who were not involved properly in the project (Gardener et al. 2010).

Nevertheless, the information generated by this study might be a starting point for either a biodiversity conservation project or the development of forest as a source of wood production and other purposes. However, combinations of both aims can also be compatible to ecological restoration (Lamb et al. 2005) within a context of sustainable land management.

1.3 Basic concepts in the context of ecological restoration

In this dissertation, following the Society for Ecological Restoration International (SER 2004), restoration is understood as “a process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed.” Moreover, restoration is not only the science of ecology but also includes social perspective, economic policy, planning and other social and philosophical issues (Davis & Slobodkin 2004).

For some authors, restoration means to resemble intact habitat as closely as possible (Corbin & Holl 2012) or “bring back the ecosystem to the original state or condition” (e.g. Evans 2009) but this latter goal is questionable because the ‘original ecosystem’ is hardly likely in terms of equal floristic conditions and structure (Lamb et al. 2005), especially with the megadiverse conditions found in Ecuador. A novel or emergent ecosystem is more likely to arise and species may occur in combinations and relative abundances that have not occurred previously (Hobbs et al. 2006).

Despite these reservations, a “reference ecosystem” (SER 2004) might be suitable to compare and evaluate the success of restoration in the different phases over time because many ecosystem services and certain components of the original biodiversity can be reestablished (Chazdon 2008).

On the other hand, many times restoration is confused with several activities such as reclamation, rehabilitation, mitigation, ecological engineering and other types of resource management, including forestry, that contribute to recovering sufficient biotic and abiotic resources for development to continue without further assistance (SER 2004).

1.4 Objectives of the study

The general aim of this study is to contribute to the understanding of processes of forest recovery at three successional sites in the San Francisco valley. To achieve this, different experiments that are closely related to each other were employed. The largest part was the reforestation experiment and besides the planting, natural succession was monitored and analyzed and also a weed treatment was included as a tool to accelerate restoration processes. A fertilization and AMF inoculation experiment was established to investigate if seedlings previously treated in the nursery can improve restoration success compared to traditional reforestation practices. Additionally, a rhizotron experiment was carried out for a better understanding of the complex below-ground competition interactions between *S. sphacelata* and tree species used in the reforestation experiment.

Based on these experiments, five specific objectives have been postulated in this thesis:

1. To compare the dynamic of natural succession and its trajectory in three different successional sites over time and identify aspects of facilitation and competition.
2. To compare seedling survival and development in five native tree species planted on three different successional sites.
3. To evaluate whether the removal of competitive vegetation facilitates the growth performance of native on three successional sites.
4. To determine the effects of fertilizer application, inoculation with arbuscular mycorrhiza fungi (AMF) and provision of shade on the survival and growth performance of tree seedlings of three species on a recently abandoned Pasture site.
5. To analyze the effects of fertilization and grass competition (*Setaria sphacelata*) on root development and biomass allocation of three native tree species in a rhizotron experiment.

1.5 Research questions

Based on each objective different scientific question have been formulated:

1) Dynamics of natural succession

- What are the effects of time and successional site on development of woody species richness and abundance?
- What are the possible triggers for diversity recruitment?
- Are there differences between successional sites in the dynamics of species composition and do the sites represent a chronosequence?
- What is the effect of competing ground vegetation removal on species richness and abundance?

2) Survival and growth development of five native tree species on the tree plantation

- Are there differences in the survival and growth performance of native species in time (from 0 to 60 months) and between successional sites?

3) Weeding treatment applied within the tree plantation

- What are the effects of removal of competitive vegetation on survival and growth performance of planted seedlings on three successional sites?

4) Fertilization, AMF inoculation and shading on the Pasture site (Seedling pre-treatment experiment)

- What are the effects of fertilization, AMF inoculation and its combination with low amounts of fertilizer on survival, height increment and root collar diameter increment of *C. montana*, *T. chrysantha* and *A. acuminata* two years after planting in the field?
- What is the effect of shading and its interaction with treatments on the growth performance of *T. chrysantha?*

5) Root development of three native tree species with and without competition of *Setaria sphacelata* and fertilization in a rhizotron experiment

- What is the effect of grass competition and added fertilizer on the root length density and biomass allocation of tree species (*C. montana, T. chrysantha and A. acuminata*) and grass *(S. sphacelata)*?

Figure 1 provides an overview on the different elements of the study.

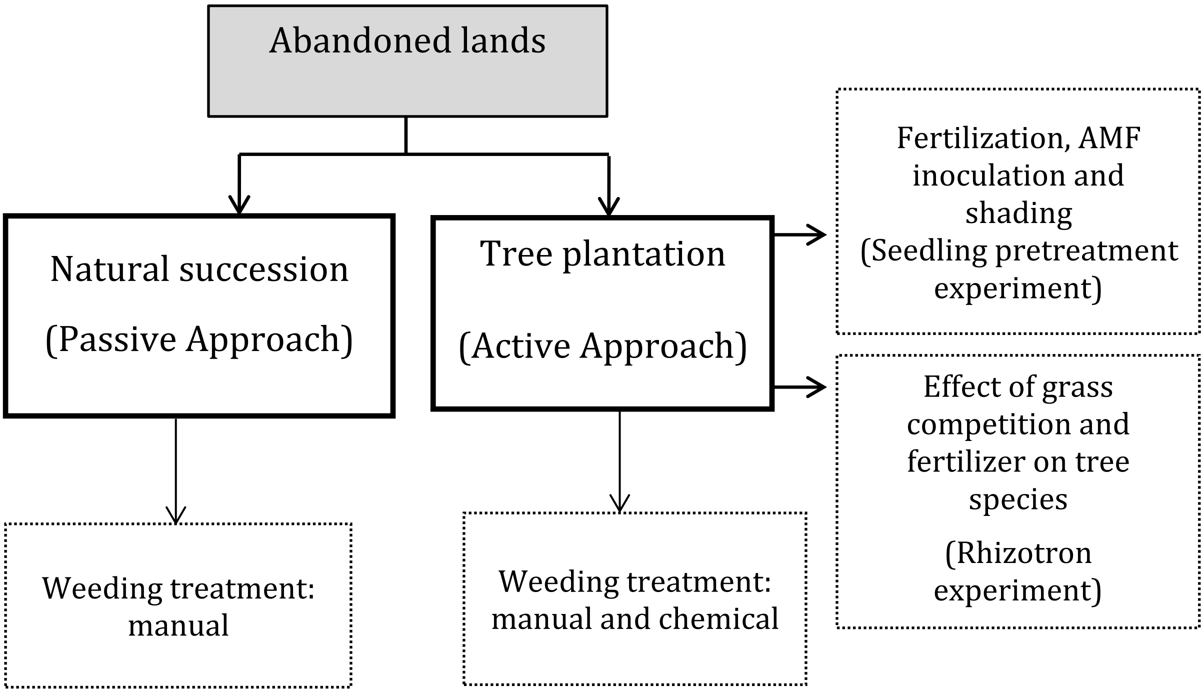


Figure 1. Schematic of the research showing two approaches to forest recovery by natural succession and tree plantation (solid lines) under the same trial in the three successional sites and their associated experiments (dotted lines)

1.6 Background of research

All investigations have been conducted within the framework of the DFG Research Unit (FOR 816) "Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador" financed by the DFG (German Research Foundation). (www.tropicalmountainforest.org).

2. State of the art

2.1 Natural succession and tree plantations as alternatives of restoration

Two well-known restoration approaches, or alternatives, are passive and active restoration (Mclver & Starr 2001; McClain et al. 2010). The first relates to natural succession without any human intervention (Holl & Aide 2011), which is the cheapest way to forest recovery (Hooper et al. 2005; Sampaio et al. 2007), while a higher floristic diversity is expected compared to other methods such as planting trees (Engel & Parrota 2001) where a limited number of tree species may be used. However, there is a risk that degraded land has already crossed an ecological threshold (Lamb et al. 2005) which impedes natural succession reaching an advance stage. In these cases, the succession trajectory of these degraded systems lead to alternative states (Suding et al. 2004). Ecological thresholds may occur due to two types of barriers; biotic interactions, such as invasive weeds preventing forest recovery, and abiotic limitations, such as harsh micro-environments (Whisenant 2002).

The second alternative is reforestation, which refers to the re-establishment of forest through planting and/or deliberate seeding by human intervention and usually the objectives of a plantation are productive and protective (Evans & Turnbull 2004; FAO 2012). It often implies a cost of considerable time and labor (Holl & Aide 2011).

Table 1 presents a comparison of the main characteristics of active and passive restoration approaches.

Table 1. Comparison of attributes of passive and active approaches of restoration

Attributes	**Passive approach**	**Active approach**
Economic investment	minor	major
Provision of Biodiversity	↑	↓
Provision of Goods (e.g. timber)	↓	↑
Provision of Ecological services	↑	↑
Time of forest recovery	Slow*	Faster*

*Depending on successional species status (↑) increasing, (↓) decreasing

Each approach also has limitations, for example, forest recovery through natural succession depends, in part, on the availability of seeds (Wijdeven & Kuzee 2000) and distance from remaining forest (Slocum & Horvitz 2000; Zimmermann et al. 2000; Günter et al. 2007), whereas reforestation (following this is referred to as planted forest or tree plantation) mainly depends on good species–site adaptation (Parrotta 1992; Holl et al. 2000; Evans & Turnbull 2004; Craven et al. 2011). Furthermore, during the phase of tree establishment on degraded lands, the seedlings have to cope with strong abiotic and biotic barriers (Gómez-Aparicio 2009).

Several authors agree that both natural succession and tree plantation success are highly influenced by land-use history (Aide et al. 1995; Chinea 2002; Klanderud et al. 2010) and former land-use intensity (Uhl et al. 1988; Guariguata & Ostertag 2001). However, the best alternative depends on the severity of damage, the goals of restoration and the availability of resources to repair the damage (Lugo 1997; Holl & Aide 2011).

In the context of tree plantation, despite general agreement that the use of indigenous species is the most appropriate for reforestation and the initiation of the recovery process, most projects predominantly use exotic species (Butterfield 1995; Evans & Turnbull 2004). An overriding reason in Ecuador and many other tropical countries, native species plantations are still a major challenge due to a lack of knowledge about their propagation in nurseries, their site requirements and their silvicultural characteristics. As a consequence, in Ecuador for example, reforestation efforts mainly use exotic species such as *Pinus spp*. and *Eucalyptus spp*. (Stimm et al. 2008; Günter et al. 2009; Weber et al. 2011), whose long-term impacts on soil properties, hydrological processes and biodiversity remain uncertain. So far, it is known that the impact of pinus plantation on the ecosystems of the high Andean region of Ecuador vary depending on the region and its properties but the general tendency is to have lower values of moisture content, available water, organic matter content, P retention and texture (Hofstede et al. 2002; Farley et al. 2004).

2.2 Ecological interactions influencing the restoration of abandoned lands

There are many interactions that influence the restoration processes on abandoned and degraded land. The most important ones, which will be explicitly addressed in this thesis, are competition, facilitation and mutualism. Natural interactions are inherently very complex and might enhance or delay the restoration processes by modifying environmental stresses and resource availability (Callaway & Walker 1997; Butterfield 2009).

2.2.1 Competition

Competition can occur within and among species, and can completely exclude species from a community (Falk et al. 2006). The effects might be based on competition for light, nutrients, space, pollinators or water (Brooker et al. 2008). Competition by grasses is among the most important barriers for forest regeneration on former pastures (Aide et al. 1995; Holl 1998a; Ortega-Pieck et al. 2011) and it has been revealed in several studies that some exotic grasses, often used for tropical pastures, are extremely competitive, for example, *Saccharum spontaneum* in Panama (Hooper et al. 2005; Craven et al. 2009; Craven et al. 2011), *Setaria sphacelata* in Ecuador (Rhoades et al.1998; Beck et al. 2008a), *Axonopus scoparius* in southern Costa Rica (Holl 2002), and *Cynodon plectostachyus* in Veracruz, Mexico (Ortega-Pieck et al. 2011). In some cases exotic species can be invasive species with higher rates of carbon assimilation, light–use efficiency, instantaneous nitrogen-use efficiency and instantaneous energy-use efficiency (Funk &.Vitousek 2007) which enables them to be very competitive.

Another aggressive and dominant competitor, widely found in both the tropics and temperate zones is the fern *Pteridium spp.* The high competitiveness of the genus *Pteridium* is attributed to special characteristics such as allelopathy (Dolling 1996; Marrs et al. 2000) and its large and vigorous rhizome system with high carbohydrate reserves (Roos et al. 2010). The widespread invasion of ferns has been observed in many places in the tropics such as Mexico (*Pteridium aquilinum* (L) Kuhn.) (Douterlungne et al. 2008), and Puerto Rico (*Dicranopteris pectinata)* (Lawrence 1994).

In the study area *Pteridium arachnoideum* is considered a suppressor of natural regeneration of indigenous forest (Beck et al. 2008a) although other studies have also reported positive effects of bracken fern (*Pteridium esculentum)* by preventing erosion, suppressing exotic grasses and facilitating forest regeneration (McGlone et al. 2005). There are still gaps in information on how competitive vegetation affects tree species performance under different types of vegetation, although the effects of above-ground competition are more easily explained than below-ground competition due to the difficulty of quantifying competition without disturbing the root systems. A nondestructive method of investigating sub-soil competition is the Minirhizotron technique which permits the recording of root length, specific growth and loss rate data (Böhm 1979; Johnson et al. 2001; Graefe et al. 2008).

For restoration purposes, weed removal has been considered a promising method to reduce high competition for resources. Holl (1998a) and Douterlungne et al. (2008) showed that above-ground clearing had a positive effect on tree seedling height of several species. In agriculture and in plantations, three weeding alternatives can be used to reduce competition: mechanical, manual and chemical (Evans & Turnbull 2004). Herbicide application represents an effective management strategy for reducing competition and thus facilitating seedling growth rates (Griscom et al. 2005; Celis & Jose 2010); the best known herbicide is Glyphosate, which was introduced in the 1970s and represents a significant input in agricultural production (Yamada et al. 2009).

However, in the San Francisco valley it is more common for local farmers to apply manual weeding methods, mainly using machetes in order to maintain the pastures. Therefore, a question to resolve is if manual and/or chemical removal of competition on bracken fern and shrub sites could also support forest recovery.

The other method of suppressing weed competition is through shade by developing a closed tree canopy (Davidson et al. 1998; Hooper et al. 2005; Craven et al. 2009), which reduces the amount of available light that grasses require for their growth. Thus, a planted forest can overtop the invasive species and consequently enhance the natural regeneration of native tree species in its understory and improve tree establishment.

2.2.2 Facilitation

Overall, more attention has been given to competition effects than facilitation effects, although the latter may be an important ally in restoration efforts. Facilitative interactions occur in nature in different ways; e.g. by protecting individual plants from herbivores, potential competitors or extreme conditions of climate in particular in dry ecosystems, or provision of resources by canopy leaching, microbial enrichment, mycorrhizal networks and hydraulic lift (Brooker et al. 2008). In various ecosystems, it has been found that shade from shrubs or trees can facilitate the recruitment of species or improve plant growth performance. Shrubs can act as a nurse plant in the restoration of forest in the tropics and can have a net facilitation effect on the early stages of tree seedling establishment (Holl 2002; Gómez-Aparicio 2009). Several explanations for the facilitation by the shrub life-form in the restoration are related to providing more nutrients and beneficial microclimates for plant establishment (Vieira et al. 1994) and increased seed dispersal by animals (Vieira et al. 1994; Holl 2002).

Depending on the life stage of the vegetation, competition and facilitation can shift, for instance, seedlings benefit from nurse plants whereas adults do not (Callaway & Walker 1997). This shift can be from facilitation in a stressful year, to stronger competition in a productive year (Holmgren et al. 1997; Callaway 2007; Butterfield 2009); for example, it has been shown that in Mediterranean ecosystems there is a higher chance of facilitation in years with strong drought (Gómez-Aparicio et al. 2004). Therefore, environmental conditions can alter the balance between facilitation and competition (Kikvidze & Callaway 2009).

However, as the majority of studies of facilitation effects have been conducted in arid, alpine and high Andean ecosystems, tropical savannas, salt marches, tundras and temperate grasslands and forests (Holmgren et al. 1997; Brooker et al. 2008), little is known about the facilitation aspects in terms of vegetation cover and structure in a tropical mountain forest.

2.2.3 Mutualism

Mutualism is a mutually beneficial interaction between individuals of two species, although the degree of benefit resulting from an interaction depends on if adaptation within the mutualism is considered (De Mazancourt et al. 2005). Mutualism can occur for example between arbuscular mycorrhizal fungi (AMF) and plants. It is well known that AMF play important roles in ecosystems such as supplying inorganic nutrients and water to plants (Entry et al. 2002; Munkvold et al. 2004; Khalvati et al. 2005) and protecting plant roots from pathogens (Smith & Read 2008; Sikes et al. 2009). Basically, the host plant takes advantage of the presence of AMF for the uptake of phosphorus and other nutrients while mycorrhizal fungi require carbon from the host plant to survive (Entry et al. 2002). Several authors mentioned that AMF improved plant performance (Van der Heijden 2004; Ouahmane et al. 2007), particularly in poor soils, due to the ability of infected roots to absorb nutrients (Gerdemann 1968; Hartnett et al. 2002).

In restoration, the inoculation of tree seedlings with AMF may be an effective strategy to improve seedling establishment on abandoned pasture sites (Van der Heijden 2004) but only a few studies have been conducted under field conditions (Renker et al. 2004; White et al. 2008), hence the effects of AMF, for instance, on plantations have still to be evaluated (Martin-Laurent et al. 1999) in field experiments.

Kottke et al. (2004) demonstrated a high degree of colonization by glomalean fungi in the tropical forest in San Francisco valley, but when the natural forest is converted into other land uses, the AMF community and its composition may decrease or get lost from the soil, which may impede good plant functioning (Onguene & Kuyper 2005). Therefore, the re-establishment of vegetation, for instance through reforestation, is not simple because the establishment of tree seedlings may not only depend on the right species in the right place, but also on the soil base where seedlings can match mycobionts (Haug et al. 2010). Currently there is still a gap in the information on specific AMF and associated plant hosts (Anderson 2008).

However, reintroductions of mycorrhizal propagules through natural processes or human intervention might be supportive but the effectiveness of the association depends on plant species and environmental conditions (Frioni et al. 1999). Urgiles et al. (2009) found a high colonization by AMF in two native species (*Cedrela montana* and *Heliocarpus americanus*) from tropical mountain forests in Ecuador with a high growth performance in a nursery experiment.

3. Material and methods

3.1 Study area

3.1.1 General information about Ecuador

The Republic of Ecuador has an area of 256,370 km^2 and it is located in the Northwest of South America. It is bordered by Colombia to the North, by Peru to the East and the South and by the Pacific Ocean to the West. It also includes the Galapagos Islands, located 1,000 km from the mainland (Atlas de la República del Ecuador 2011; Fig. 2).

The population of Ecuador is 14,483,499 people, according to the latest census of population and housing (INEC 2010).

There are three main land regions:

a) Coast region: it is a region located below 1300 m asl between the western slopes of the Andes and the Pacific Ocean

b) Andean Highland region: includes the areas from 1300 m asl up to the top of mountains

c) Amazonia region: located below 1300 m asl on the eastern slopes of the Andes. This region represents 50 % of the total area of Ecuador (Sierra et al. 1999).

Figure 2. Map of the Republic of Ecuador (Bertzky et al. 2010)

The study area is part of the Andean region; accordingly this region is explained in more detail.

3.1.2 Andean Region

During the mid-to late Tertiary (25-2.5 million years ago) intensive volcanic activity on the top of uplifted basal rocks of both the Western and Eastern cordilleras built up the Andes and by the end of the Tertiary, volcanic activity had ceased in the Andes of Southern Ecuador (Jørgensen & León-Yánez 1999). Soils derived from volcanic ash are relatively fertile, as are those with glacial loess or with limestone bedrock (Young 2011). There are a variety of climates throughout the Andes, although temperature is strongly related to altitude. There is a temperature decrease of 0.6 °C per 100 m increase in elevation (Hofstede et al. 2003; Baquero et al. 2004).

The Andean region is a hot spot for biodiversity with high plant endemism (Valencia et al. 2000; Kessler & Kluge 2008). The major floristic diversity in Ecuador is located in the Andes with 64 % of the total of vascular plants (Jørgensen & León-Yánez 1999) and 36 types of remnant vegetation being found (Baquero et al. 2004). Although this region has been subject to human-induced forest clearance for agricultural purposes for the last 10,000 years (Pearsall 1992), land reforms in 1964 and 1973 encouraged the colonization of new areas, which has led to an intensification of land-use transformation in the last few decades (De Zaldívar 2008).

Currently, a high percentage of the population is concentrated in the Andean Region; in the capital city Quito alone, the population is 2´239,191 followed by Cuenca city with 505,585 habitants (INEC 2010). Obviously, this causes an enormous pressure on the natural ecosystems to provide ecosystem goods and services such as water, timber, and food.

3.1.3 The Biological Reserve San Francisco (RBSF)

The RBSF, the study area, is located in the Cordillera Real, an eastern range of the South Ecuadorian Andes, in the area of the Huancabamba depression (Beck & Richter et al. 2008). The RBSF is located at 3° 58' 30" S and 79° 4' 25" W in the San Francisco valley (Beck et al. 2008b) in the Zamora Chinchipe province, 30 km from Loja city (Fig. 3). Elevations range from 1600 m asl at the valley bottom to 3200 m asl at the highest point, del Cerro de Consuelo (Beck et al. 2008b). Due to the high diversity of species present in RBSF, it is considered as an outstanding hotspot of plant diversity (Beck & Richter et al. 2008) and since 2007 the study area has formed part of Podocarpus-El Condor Biosphere

Reserve declared by UNESCO. One of the causes of the high taxonomic diversity is the great topographic heterogeneity of the area. This 1000-hectare of RBSF is a complex system of ridges, steep slopes, valleys and ravines (Homeier 2008). The natural vegetation of the RBSF is evergreen lower and upper mountain rain forest (Beck et al. 2008b) with a surprising quantity of animal and plant species in such a small area (Richter et al. 2009). 1208 species of seed plants (Homeier & Werner 2007) have been found and more than 280 are tree species (Homeier 2008).

The RBSF is made up of two types of ecosystems; 1) undisturbed natural forest covering the NNW-facing slopes of the valley and 2) its anthropogenic replacement ecosystems on the opposite side of the valley (Beck et al. 2008b). The reforestation experiment is located in this latter part (specific study areas in this study). Currently the owner of the RBSF is the NGO "Nature and Culture International" (www.natureandculture.org), which has established a research station (Estación Científica San Francisco, ECSF) with all the facilities for logistic support.

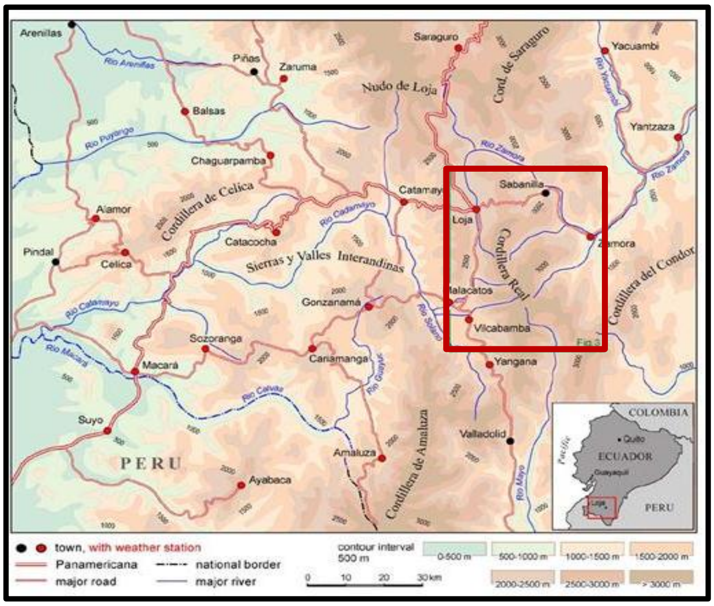


Figure 3. The Biological Reserve San Francisco (BRSF) M. Richter 2008

Soil

The dominant soil type in all altitudinal and slope classes between Loja and Zamora at the northern border of the National Park Podocarpus extending from the San Francisco river to either site is Histosol (Ließ 2011). However, other soil types have been reported in the study area such as Cambisols, Planosols, Umbrisols and Podzols (Wilcke et al. 2008; Bahr 2007).

In the RBSF, two dominant groups of rocks which differ in mineralogical and chemical composition were identified: a) meta-siltstones/sandstones/quartzites and b) slates/phyllites with partly alternating fine layers. According to the Al and K content, all top soils are located in the first group, which means the chemical composition of the different land-use types are similar (Makeschin et al. 2008). By comparing the three successional sites used in this study, P and extractable Mn in the B-horizon differ among the study sites. At the Pasture site the P concentrations are high in the first two horizons with high extractable Ca and K as well. On the Bracken site, Mn, Mg and N were rich but there was poor available P. On the Shrub site, the C and cation values are low in the A-horizon (Günter et al. 2009).

Climate

In a regional context, the climate in the provinces of Loja and Zamora Chinchipe has a seasonal variation of precipitation. There is an extremely wet season from April to July and a less humid period from September to December (Bendix et al. 2006). Apart from the humidity, the rainfall is also a very important input source of inorganic nutrients in the ecosystem of tropical mountain forest (Rollenbeck et al. 2005). The average annual minimum air temperature ranges from 15 °C at the valley bottom (1600 m asl), to a minimum of 5.8 °C at the lower pasture areas. The average annual maximum temperature ranges from 26.2 °C at the valley bottom to 10.8 °C in the upper areas (3200 m asl)(Fries et al. 2009).

In Table 2 the average annual precipitation (mm) and air temperature (°C) at 2 m height at RBSF (1960 m asl) over the 6 years since the beginning of the experiments is shown.

Table 2. Total of annual precipitation (mm) and mean annual temperature (°C) at RBSF

Year	Precipitation	T°
2003	957.8	15.35
2004	1676.6	15.35
2005	1857.7	15.49
2006	1082.6	14.98
2007	1733.9	14.83
2008	1768.3	14.78

Source: Rollenbeck & Peters (2009)

3.1.4 Social aspects and land-use history in the area of RBSF

Zamora Chinchipe province has a population of 91,376 (INEC 2010) and mestizos-colonos are the most dominant ethnic group (Pohle 2008). In the San Francisco valley, ecosystem transformation started with the construction of roads in 1962 connecting the cities of Loja and Zamora (Pohle 2008) and a first impact of colonization was the exploitation of species with high timber value from natural forest such as *Podocarpus oleifolius, Prumnopitys montana, Tabebuia chrysantha, Cedrela montana* (Crespo 2004; Roos 2010). Due to the considerable reduction of the valuable timber, smallholders converted the natural forest into grasslands, the most economically attractive activity for the landowner (Knoke et al. 2009).

3.1.5 Experimental sites

As already mentioned, the landscape of the San Francisco valley is made up of different categories of abandoned land. In the area adjacent to the RBSF, three successional sites are present and were used for the establishment of experiments. A description of the successional sites follows:

Pasture site (Fig. 4a) (elevation 1,800 – 2,100 m asl): The area is dominated by *Setaria sphacelata,* an introduced species from tropical Africa. This species has been cultivated since the initial clearing (slash and burn).

Other, less dominant grasses such as *Melinis minutiflora* P. Beauv and sparse patches of *Pteridium arachnoideum* (Bracken fern) can also be found. According to aerial photography, the natural forest was cleared over 36 years ago. The slope ranges from 15 – 38°. Before the experiment started in 2003, the site was actively used for milk production. At the beginning of the experiment, the site was fenced off to prevent cattle invasion.

Bracken site (Fig. 4b) (elevation 1,900 – 2,100 m asl): This site is covered by Bracken fern (*Pteridium arachnoideum),* which, as mentioned, is well known as a fire-tolerant species. In the last 23 years the whole site has been burnt at least 4 times but never cultivated with *S. sphacelata*. The last fire event was approximately 12 years ago and aerial photography tells us that the forest was originally cleared over 23 years ago as well. The slope ranges between 23 and 43°.

Shrub site (Fig. 4c) (elevation 2,100 – 2,200 m asl): This site, originally cleared over 50 years ago, is considered secondary forest as it has been under natural succession without human intervention for over 25 years since the last fire event. It is also the result of recurrent fires without *S. sphacelata* cultivation. Several woody species are present but the most abundant are *Ageratina dendroides* (Spreng.) R.M. King & H. Rob. and *Myrisine coriacea* (Sw.) R. Brown. The slope ranges between 5 – 43°.

3.2 Experimental design

Although the tree plantation experiment is the main trial in this study, permanents plots for monitoring natural succession were also established on the same three successional sites 'Pasture, Bracken and Shrub'. Tree plantation and natural succession follow a randomized block design and each site represents a block. A second factor in the design is the treatment (control and repeated clearing) (Figure 5). The plot size was 10.8 × 10.8 m. The total area of experiment comprises 12 hectares (four ha each site), located on the same side of the valley 3km from each other, which means all the sites have the same climatic conditions. More details about the methods and removal techniques for each restoration alternative are given in the following sections.

Shrub site

Bracken site

Pasture Site

Figure 4. Three successional sites in the San Francisco Valley, from the bottom (a) Pasture, (b) Bracken and (c) Shrub

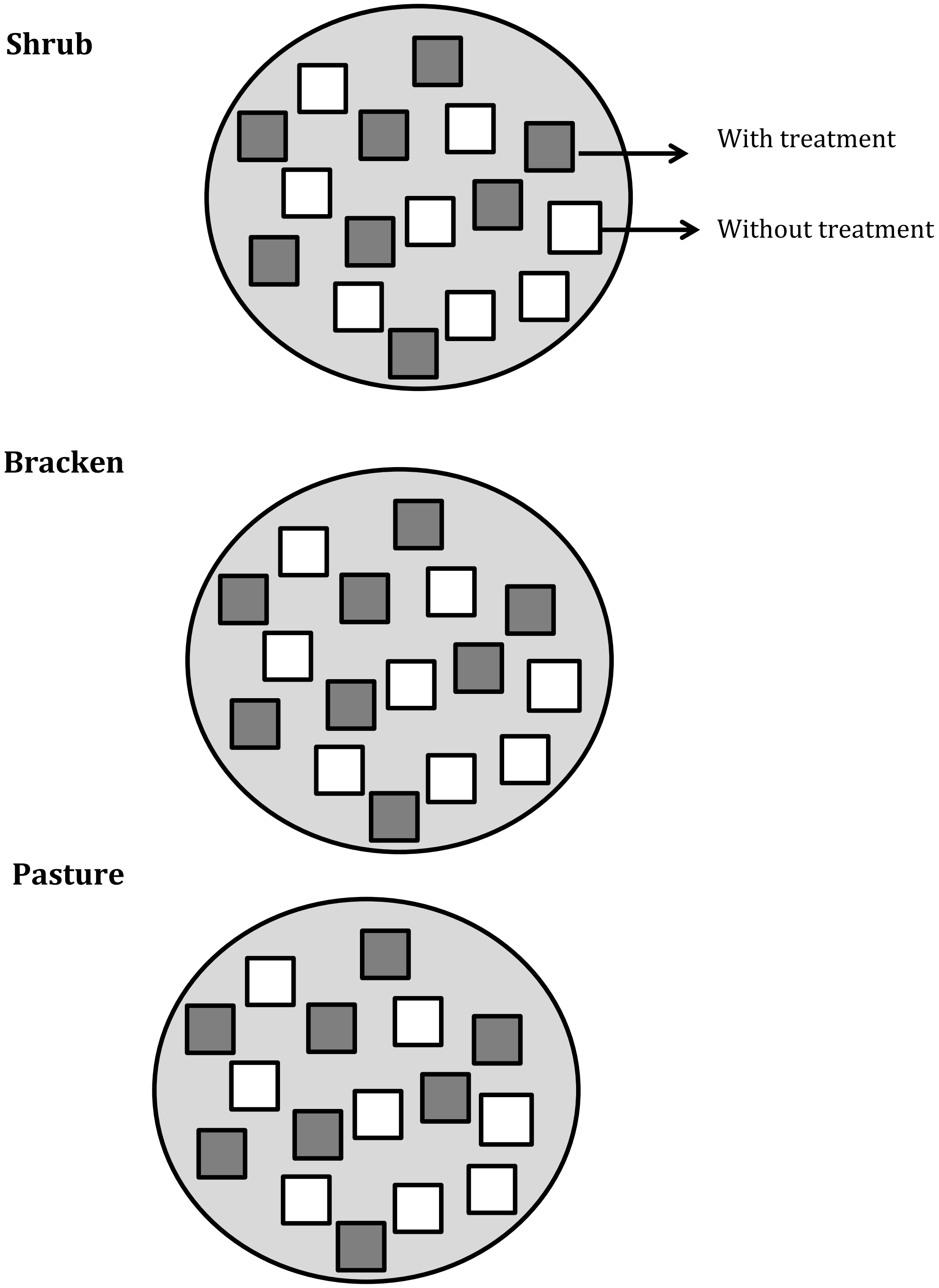


Figure 5. Scheme of experimental design, representing the three successional sites and the plots randomly distributed in the field. Gray squares represent the eight treated plots and white squares represent the control plots. This method was applied for both tree species planted and natural succession. The total area of monitoring is 12 hectares

3.2.1 Monitoring of dynamic of natural succession

In 2003, sixteen randomly selected plots were established on each of the three successional sites to monitor natural succession. Half of the plots were manually treated by cutting back all competing herbaceous species with a machete every four months from 2003 to 2005. The total area sampled at each site was 1866 m^2. Manual treatment was chosen as the preferred method of treatment as it is the common practice of the farmers in the region.

Data Collection in natural succession plots

In 2003, 2005 and 2007, hereafter referred to as “0 months”, “24 months”, and “48 months” respectively, all woody species were registered and identified. However, due to the dense vegetation cover by the end of the monitoring, only the plants with a height >30 cm were included. Species were categorized as shrub, treelet or tree based on field observations and based on the Catalogue of Vascular Plants of Ecuador (Jørgensen & León-Yánez 1999). For each plant, species name, height (cm), root collar diameter (cm) and number of stems was registered. Additionally an identification tag was attached.

Furthermore, abiotic factors such as slope and altitude were measured as well as biotic factors like Leaf Area Index (LAI), density (ind/ha) and Woody Volume Index ($\pi*0.5*(\text{basal diameter})^2/4*\text{height}$) (see Wishnie et al. 2007) on a plot basis at 48 months. LAI (LAI 2000, Licor, Nebraska, USA) was measured at 30 cm, and above the vegetation at forty points regularly distributed in each plot under cloudy conditions following the manufacturer’s guidelines (LI-COR 1992). To avoid excessive influence of slope, the data of rings 4 and 5 were excluded.

The neighboring pristine forest of the RBSF was considered the reference ecosystem. It has been intensively studied and checklists of biological diversity for different groups of organisms are available (Homeier & Werner 2007; Beck et al. 2008). The comparison of the floristic composition between the study sites and old growth forest was based on studies of several research groups at RBSF (e.g. Dislich et al. 2009; J. Homeier 2010, Georg-August University Göttingen, personal communication).

3.2.2 Survival and growth development of tree species in the tree plantation

A total of 288 plots were established (6 species × 3 successional sites × 2 weeding treatment × 8 repetitions), 96 plots randomly distributed per successional site. On each plot 25 seedlings were planted with a spacing of 1.8 x 1.8 meters. Before planting the seedlings, the herbaceous ground vegetation was removed manually by machete. The native species are *Cedrela montana, Tabebuia chrysantha, Juglans neotropica*, *Alnus acuminata*, *Heliocarpus americanus* and *Morella pubescens.* More information about the species planted is given in table 3 and appendix 1. The plantation was done from March to October 2003 except for *A. acuminata* and *M. pubescens* which were planted in July 2004 and March 2005 respectively.

The data set corresponds to 48 months for *A. acuminata* and 60 months for the remaining species.

Table 3. Native tree species used in the reforestation experiment

Species	Family	Common name	Year of planting	Successional Status
Early-successional				
Heliocarpus americanus L.	Tiliaceae	Balsilla	2003	Light demanding
Alnus acuminata H.B.K.	Betulaceae	Aliso	2004	Light demanding
*Morella pubescens (Humb. & Bonpl. ex Willd.) Wilbur **	Myricaceae	Laurel de cera	2005	Light demanding
Mid- successional				
Juglans neotropica Diels	Juglandaceae	Nogal	2003	Shade tolerant
Cedrela montana Moritz ex Turcz	Meliaceeae	Cedro	2003	Shade tolerant
Tabebuia chrysantha (Jacq.) Nichols	Bignoniaceae	Guayacán	2003	Shade tolerant

* *Morella pubescens* could not be included in the survival and growth development analysis due to the logistic limitations in the soil sampling. However, this species was used to compare the final performance

3.2.2.1 Tree species selection and seedlings production

The selection of the native species for the tree planting experiment was based on their different successional status, timber value and capacity to provide services. The seeds for the propagation of the species were collected in the natural forest adjacent to the study area except for *A. acuminata* and *J. neotropica* which were collected in the forest close to Loja city. The material was collected from different healthy mother trees according to the fruiting season of each species. All the seeds were pooled, mixed and raised in the nursery at the Universidad Nacional de Loja (UNL). Before the seedlings were planted they passed through an acclimation phase at RBSF (see more details in Aguirre 2007; Günter et al. 2009).

3.2.2.2 Soil sampling

In 2006 three soil samples were randomly selected within each experimental plot (Fig. 6) using a "Pürckhauer" soil core with a length of one meter. Every soil sample was related to the four nearest tree seedlings. A soil sample was taken 0.9 m from each plant. Each horizon was described applying the guidelines of the Arbeitskreis Standortskartierung (2003). A total of 432 soil samples were taken for the five species and several parameters (e.g. thickness of horizons (cm), proportion of sand, lime, clay, and rocks (%) were recorded in the field. More details of methods are given in Günter et al. (2009). The proportion of sand, clay, and organic matter was also used to estimate the water holding capacity of soil with the program '*Soil Water Characteristics*' of Saxton and Rawls (2006). In Appendix 2 the values of the parameters used are shown.

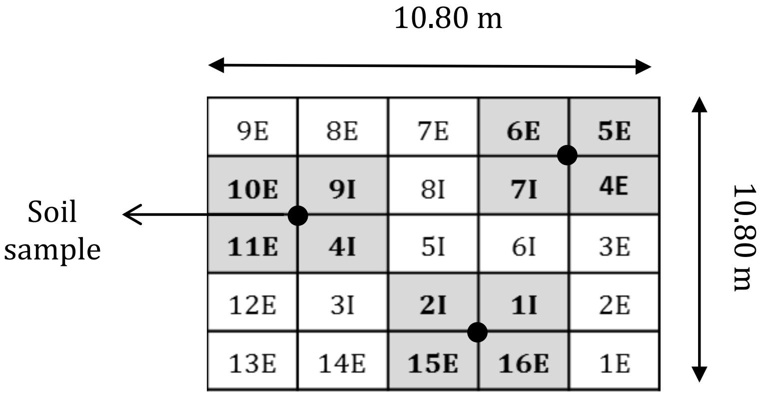


Figure 6. Scheme of the sampling of the soil cores (Full circles) in the plots and the related tree individuals included in data analysis (I= inner and E= edge)

3.2.2.3 Seedlings measurement

Since the establishment of the tree plantation, survival, total stem height (cm) and root collar diameter (RCD)(cm) were recorded annually in the same month as the seedlings were planted. Stem height was measured from soil surface to the highest apical. The growth development considers five measurements for *C. montana, T. chrysantha, J. neotropica* and *H. americanus* and four measurements for *A. acuminata*. Hereafter, 0 represents the initial measurement (1 month after planting), 1= 12 months, 2 = 24 months, 3 = 36 months, 4=48 months, 5=60 months.

3.2.3 Manual and chemical weed control in the tree plantation

As a method to assist the plant establishment in tree plantation, in the first two years a manual treatment with a machete for removing above-ground weed vegetation was conducted every 6 months in the selected plots (50% of all plots). Because of the very intensive development of the competitive ground vegetation, an additional chemical treatment with Glyphosate (commercial name 'Ranger' in a 2% concentration was applied to the emergent vegetation at 48 months age (Fig. 7) in a 1 m diameter area around each tree individual. Three weeks before the application, the weed species were topped by machete to reduce weed density and height, especially *S. sphacelata* and *P. arachnoideum*. To avoid any damage to tree seedlings from the chemical product, every single tree was protected with a plastic shield during the application of the product. The data set to evaluate the manual and chemical treatment was at 60 months.

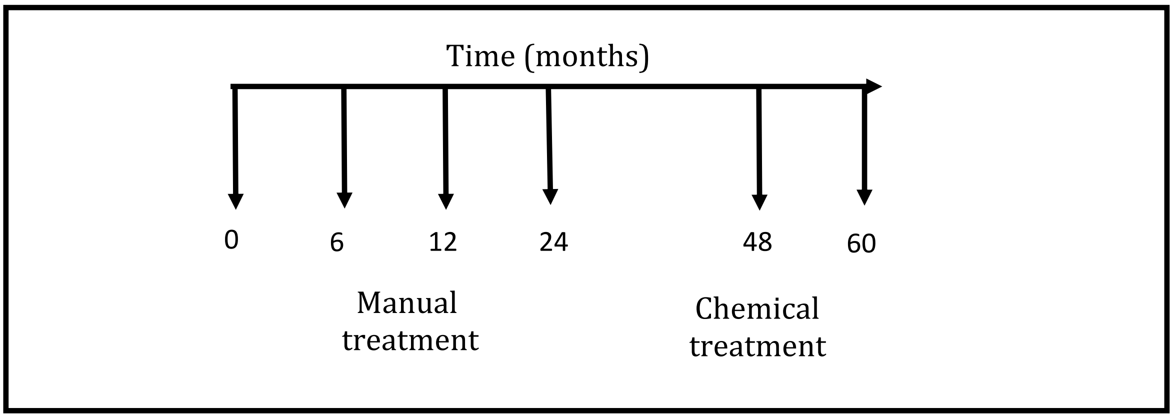


Figure 7. Sketch of application of manual and chemical treatment over time on treated plots

3.2.4 Seedling pretreatment experiment

Based on the first results presented in Aguirre's dissertation (2007) demonstrating low plant performance of tree species on the Pasture site and the promising results of Urgiles et al. (2009) with high AMF colonization of two native species from the study area in the nursery, a new experiment with the previous addition of fertilizer and AMF inoculum to seedlings in the nursery was conducted to investigate if seedling performance is improved by the different nursery treatments.

3.2.4.1 Seed Collection and seedling production

For this experiment, the seeds of the tree species used in this experiment (*C. montana, T. chrysantha* and *H. americanus*) were collected in the natural forest at RBSF. A total of 15 good quality mother trees for *T. chrysantha* and 15 for *H. americanus* were chosen and their seeds collected in August and December 2007 respectively. In the case of *C. montana,* the seeds originated from only 6 good quality mother trees and were harvested in July 2007. The seedlings were raised in the nursery at Universidad Nacional de Loja. The AMF were cultivated at the laboratory of Genetics, Biocenter of the Ludwig-Maximilians-Universität (LMU) and the finished inoculum was provided to the nursery. The preparation of the AMF inoculum was based on the roots from the well-growing tree seedlings in the experiment conducted in Ecuador by Urgiles et al. (2009). The first trap was cultured on fresh roots, which were subsequently isolated in the laboratory. The inoculum consisted of an AMF-cocktail, in addition to roots and substrate of *Plantago lanceolata.* A total of 24 kg of inoculum was produced (Krüger C. LMU, personal communication). The fertilizer used for the experiment was Osmocote composed of N-P-K (15 + 9 +15) with Magnesium and Sulfur (+2+3) with inorganic traces of Boron, Copper, Iron, Manganese, Molybdenum and Zinc. The fertilizer application and the inoculation of the seedlings were conducted in the nursery with the goal of producing seedlings of high vigor and quality with the ability to resist adverse conditions in the plantation on the Pasture site. In the nursery, a total of 3150 seedlings were distributed in 5 treatments (Table 4). The experimental design in this phase was a randomized treatment design (Fig. 8). All of the tree seedlings were irrigated with the same amount of water and a physical barrier (plastic wall) was installed to avoid cross-contamination between the treatments.

This work was done in cooperation with the research group of Prof. Dr. Arthur Schüßler, Narcisa Urgiles and Claudia Krüger.

Table 4. Description of the five different treatments applied on tree seedlings in the nursery

Code	Description
FF	Full fertilizer (½ Osmocote, 0.5g/individual)
LF –AMF	Low fertilizer (¼ Osmocote, 0.25g/individual) + devitalized AMF Inoculum
LF +AMF	Low fertilizer (¼ Osmocote, 0.25g/individual) + living AMF Inoculum
+AMF	living AMF inoculums (8.5 g)
C	Nursery standard sterilized soil

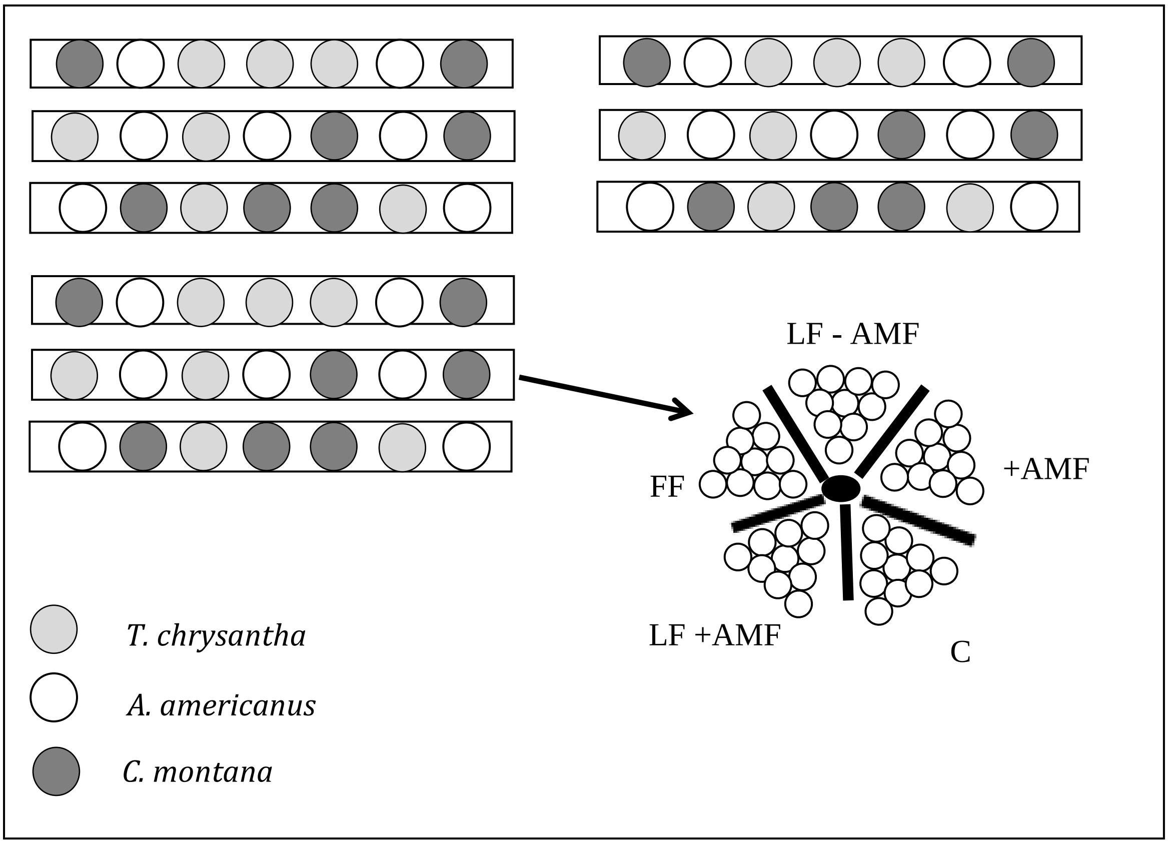


Figure 8. Display of tree species and five treatments in the nursery phase, randomly distributed and separated by mechanical barriers. Total number of seedlings 3150

3.2.4.2 Experimental design of the outplanting

The field experiment (only at the Pasture site) was set up in 2009. The plots were arranged in a randomized design (Fig. 9). For *T. chrysantha,* 2 factors could be tested (treatment and light), while for *C. montana* only treatment was tested because not enough seedlings were available to test under different light conditions. Therefore, mirroring their successional status, *C. montana* was only planted under shade (black shade cloth with 50% light intensity) and *H. americanus* without shade. Each factor combination was tested in 6 replicated plots of 16 m^2 with 9 seedlings each. Thus, in total 270 seedlings of *H. americanus*, 270 seedlings of *C. montana* and 540 *T. chrysantha* seedlings (50% with shade and 50% without) were planted. Each seedling was protected against rabbit browsing with wire netting. Site preparation before planting was done via manually eliminating the ground vegetation by machete.

Figure 9. Representation of distribution of plots with and without shade on the Pasture site

The evaluation of the above mentioned treatments on plant performance was measured in terms of survival (%), height increment (HI) and RCD increment (RCDI). In addition, at the end of monitoring the quality of each seedling was classified into three categories 1 (good), 2 (regular) and 3 (bad). Good quality meant a healthy seedling, green leaves without any kind of damage (<30%); regular seedlings meant that seedlings presented damage between 30 and 60% in the whole visible plant, and bad quality meant that seedlings presented clear signs of lack of nutrition, diseases and/or pests (>60%).

3.2.4.3 Seedlings measurements of the outplanting

The increment of seedlings was calculated by measuring the difference between the initial dimensions and the dimensions at two years of age. The percentage of survival included all individuals remaining at the final measurement compared with the initial number of seedlings. Two individuals per plot were dug up to study fungal colonization and their subsequent molecular analysis (Krüger C. personal communication).

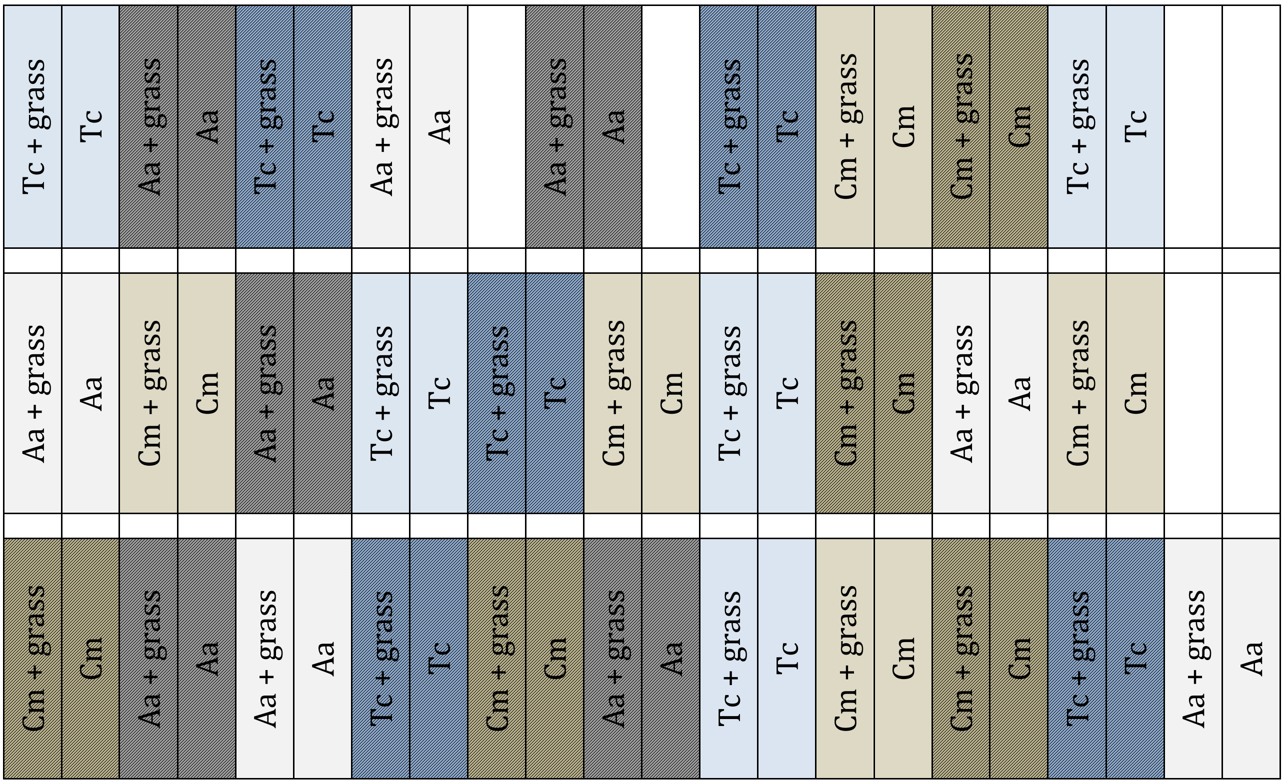
3.2.5 Rhizotron experiment

A better understanding of the root competition processes between the tree species and the grass *S. sphacelata* is needed as this may be determinant in the early phase of a tree plantation. Thus, a mini-rhizotron experiment was set up in June 2008 and monitored over a 31-week period. Three species were chosen which corresponded to mid-successional species (*C. montana* and *T. chrysantha*) and early-successional species (*A. acuminata*).

The experiment used a completely ramdomized design (Fig. 10). It consisted of 4 treatments × 5 replicates × 3 tree species. A total of 60 rhizotrons were established in the nursery of DFG/UNL in Loja. The treatments are detailed in table 5.

Table 5. Description of treatments used in the rhizotron experiment

Treatment	**Code**	**Description**
Competition	Competition	Grass competitor with no fertilizer
Fertilizer	Fertilization	No grass competitor with fertilizer added
Competition plus fertilizer	Comp.+ Fert.	Grass competitor with fertilizer added
Control	Control	Without competitor and fertilizer



Tc + grass	Tc	▨ Aa + grass	▨ Aa	▨ Tc + grass	▨ Tc	Aa + grass	Aa		▨ Aa + grass	▨ Aa		▨ Tc + grass	▨ Tc	Cm + grass	Cm	▨ Cm + grass	▨ Cm	Tc + grass	Tc		
Aa + grass	Aa	Cm + grass	Cm	▨ Aa + grass	▨ Aa	Tc + grass	Tc	▨ Tc + grass	▨ Tc	Cm + grass	Cm	Tc + grass	Tc	▨ Cm + grass	▨ Cm	Aa + grass	Aa	Cm + grass	Cm		
▨ Cm + grass	▨ Cm	▨ Aa + grass	▨ Aa	Aa + grass	Aa	▨ Tc + grass	▨ Tc	▨ Cm + grass	▨ Cm	▨ Aa + grass	▨ Aa	Tc + grass	Tc	Cm + grass	Cm	▨ Cm + grass	▨ Cm	▨ Tc + grass	▨ Tc	Aa + grass	Aa

No fertilizer

□ *A. acuminata*
□ *C. montana*
□ *T. chrysantha*

Fertilizer

▨ *A. acuminata*
▨ *C. montana*
▨ *T. chrysantha*

Figure 10. Experimental design of the rhizotron experiment in the nursery

The experiment was divided in three phases:

1. **Adaptation phase:** one individual tree seedling was planted in each of the 60 rhizotrons and in half of those rhizotrons one individual of *S. sphacelata* was planted next to tree seedlings. This phase of 15 weeks was needed until the roots of tree seedlings were visible in the glass of the rhizotron.
2. **Competition phase:** Once the roots of the tree seedlings and grass became visible, the monitoring started.
3. **Competition plus fertilizer phase**: along with competition phase, the fertilizer was applied to half of the plants with competition (15 rhizotrons) and to the other half of the plants (15 rhizotrons) that were kept without competition. The fertilizer used was Osmocote in a dose of 1.58 gr, applied at 19th week. This dose corresponds to a full fertilizer treatment used in the nursery explained in the previously mentioned (Seedling pretreatment experiment). The plant analysis (e.g. root length density) was given within 24 weeks (every four weeks).

The seeds of *C. montana* and *T. chrysantha* were collected in the pristine forest in the RBSF and raised in the nursery. In the case of *A. acuminata*, the seeds were collected 5 km from Loja – Zamora, however due to the high mortality of this species, new seedlings were bought from a nursery in Loja city. Grass clones of *S. sphacelata* were collected from the plots of the reforestation experiment. All the seeds were germinated in trays in the nursery in sand and black soil substrate (1:1). Once the seedlings reached an average height of 15 cm, they were transplanted into the rhizotron.

3.2.5.1 Construction and manipulation of rhizotron

Each rhizotron was manually constructed. It consisted of two sheets of transparent 3 mm thick glass held in an 80 cm × 50 cm × 2.6 cm aluminium frames. The substrate for the filling of the rhizotron was randomly collected from the plots at the Pasture site in two layers (organic and mineral) which were then mixed and steam sterilized at 120 °C.

Each rhizotron was filled with an organic layer of 30 cm depth and a 50 cm layer of mineral soil (Fig. 11a). The substrate was carefully filled and slightly compacted in each rhizotron. Moreover, tensiometers were installed at depths of 10, 30 and 60 cm to control soil moisture. A black cloth covered both sides of the rhizotrons to achieve the natural darkness for roots. In the nursery, the rhizotrons were placed in a wooden structure with a 74° inclination to quicken the adhesion of roots to the glass (Fig. 11b).

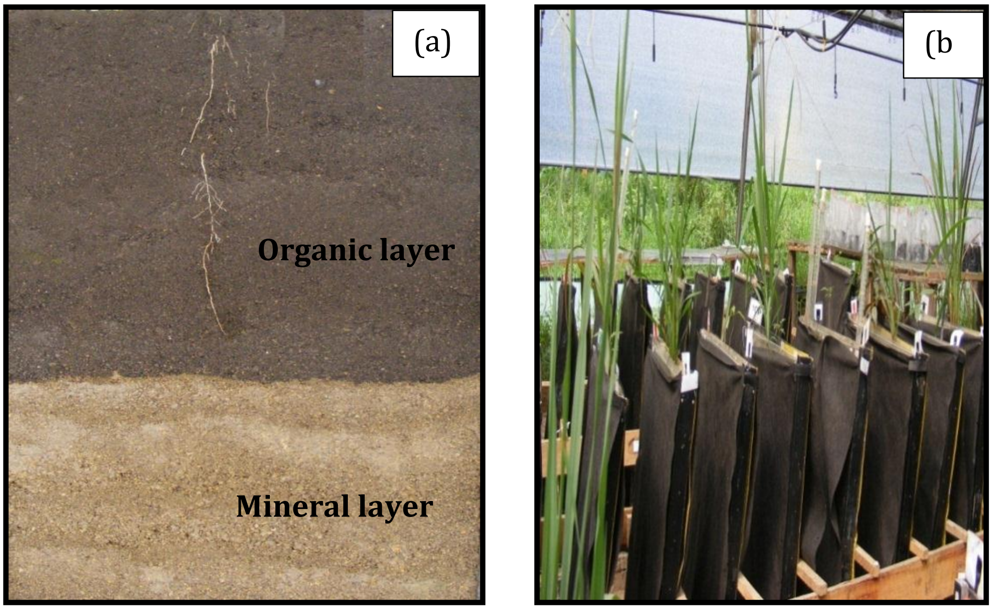


Figure 11. Rhizotron experiment: a) two layers of substrate and b) overview of rhizotrons with the black cover in the nursery

3.2.5.2 Roots monitoring and biomass samples

Weekly, roots were marked in permanent ink onto a transparent sheet (50 × 80 cm) and photographed at a resolution of 7-megapixel; all dead roots were removed from the acetate sheets when they ceased to be visible. At the end of monitoring period, the surviving tree seedlings were harvested to measure their above- and below-ground biomass allocation by separating roots, stems, leaves, and inflorescences (in the case of *S. sphacelata,* which had a reproductive phase in the rhizotrons). The roots were gently washed out and all the samples were oven-dried at 70 °C for 48 hours and then weighed.

The acetated sheets were processed using the image analysis software WinRHizo, which is especially designed for root measurement (WinRHIZO Pro version 2003b, Regent Instruments, Canada). The variable measured was root length density. This last process was done for the master's thesis of Loiza (2011).

3.3 Data analysis

An overview of data analysis according each objective is given in the Figure 12.

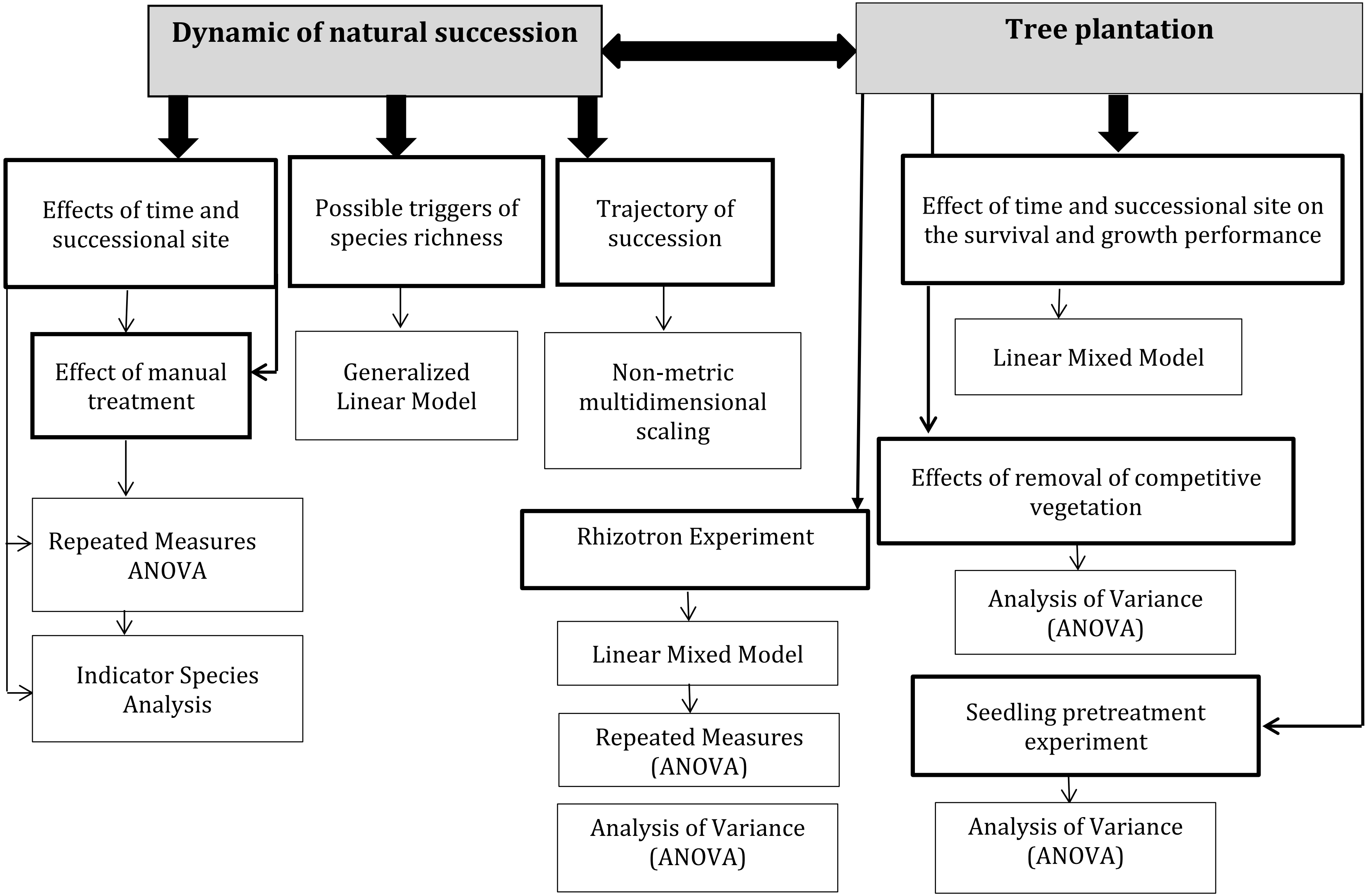


Figure 12. Diagram of all statistical analyses according to each experiment and their respective research questions

3.3.1 Dynamic of natural succession

Repeated Measures ANOVA (RMA) was used to test the temporal changes of species richness and abundance per site. Time was the repeated measures factor and treatment was considered as another factor between subjects. The interaction between time and treatment was also included in the analysis.

Species accumulation curves were used to make equal sampling efforts based on sample individuals and these were calculated across time for each successional site in Ecosim version 7.0 (Gotelli & Entsminger 2009). The Evenness and Shannon indexes were computed at plot level for each study site over time and the results were statistically tested using One-way ANOVA followed by a Tukey comparison test considering time as a factor. Data transformations were made to meet the assumptions of ANOVA.

Chao's Sørensen based on abundance was also used to compare between each pair of sites (Pasture-Bracken, Bracken-Shrub, and Shrub-Pasture) over time to confirm similarity using EstimateS 8.2.0 (Colwell 1999; Chao et al. 2006).

A Generalized Linear Model (GLM) procedure was used because the dependent variable is linearly related to the factor via a specific link function. Also, it allows for the variable to have a non-normal distribution (Field 2009). The predictors of the model were sites and treatment as factors and all plot parameters as covariates. The type of model had a Poisson distribution with log link which is typical for count data. This type of distribution is used to model the probability of different numbers of seedlings per plot, assuming independent sampling (Quinn & Keough 2002). The variables were selected until the goodness of fit was close to 1 because GLM models explain a proportion of deviance that range from 0.15 (weak fit) to 0.90 (high fit) (Guisan et al. 1999). The statistical analyses were performed in SPSS 16.0.

Furthermore, a non-metric multidimensional scaling (NMS) based on species richness and abundance at 0 and 48 months was conducted using Sørensen (Bray–Curtis distance) to determine the successional trajectory of the three successional sites. An autopilot mode was chosen to make multiple runs, finding the best solution at each dimensionality and to test significance.

Indicator Species Analysis was used to observe species change on each site at the beginning and end of the monitoring to better understand some of the ecological processes over time. Indicator values were calculated according to Dufrêne & Legendres (1997) (see also Mc Cune & Grace 2002). Two groups (0 and 48 months) were formed and the indicator values were tested for statistical significance using a Monte Carlo technique. The last two analyses were carried out in PC-ORD 5.14.

3.3.2 Survival and growth development of tree species in the tree plantation

Survival and plant growth development were analyzed for each species using a linear mixed model in InfoStat software with an R interface* (Di Rienzo et al. 2010). Only the 12 plants involved in the soil sampling per plot (in total 96 seedlings per species) were included in the analysis. The mixed models approach was chosen due to the ease of modeling the data set, which included a nested factor (soil core within plot) and repeated measures analysis. In this model, successional site and time were fixed effects and soil core data within plots were considered as a random factor; water holding capacity of the soils was included as covariate.

The method for estimating parameters was REML (Restricted Maximum Likelihood) and it is an alternative way of estimating the covariance parameters in 0 (West et al. 2007). It was necessary to assess different correlation functions such as compound symmetry, unstructured, and AR(1) to model the lack of independence shown in the repeated measures. Moreover, due to the tendency of increasing variance across time, the co-variance matrix structure was taken into account in the model.

Model selection was based on AIC (Akaike information criterion) and BIC (Bayesian information criterion) where the best model was given when the lowest values of AIC and BIC were found.

Assumptions of homogeneity of variance and normality were tested. For the proportion of survival an arcsine square root transformation was applied.

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* InfoStat software was used only for the Linear Mixed Model, which was done at CATIE (Costa Rica) in cooperation with statistician Dr. Fernando Casanoves

Statistical model

$y_{ijkl} = \mu + S_i + plot(S)_{j(i)} + T_k + ST_{ik} + C(plot^*S)_{l(ji)} + Cov + \varepsilon_{ijkl}$

Where:

S= site

T= time

C= soil core

Cov = covariance

y_{ijkl} = response variable

μ= overall mean value

S_i = effect of *i*th site

$plot(S)_{j(i)}$ = error of site (error A)

T_k = effects of k-th time of measure

ST_{ik} = interaction between site and time of measure

$B(plot^*S)_{l(ji)}$ = random effect of soil core within the plot

Cov = WHC

εijkl= random error

3.3.3 Weeding treatment within the reforestation experiment

Analysis of Variance (ANOVA) was conducted using treatment and successional site as factors and survival, height and RCD as dependent variables. According to the assumptions of ANOVA, a normal distribution and homogeneity of variance is needed and the observations should also be independent (Field 2009). In consequence, a logarithmic transformation was carried out for plant growth variables and an arcsine square root transformation of proportion of survival was needed to meet the assumptions of ANOVA. Levene's test and Shapiro-Wilk test were used to confirm the homogeneity of variance and normal distribution respectively (Field 2009). Moreover a Post Hoc (Tukey) was chosen to make comparisons between sites.

3.3.4 Seedling pretreatment experiment

Analysis of Variance (ANOVA) was used for each species and logaritmic transformations were done for height increment and RCD increment. The percentage of survival was converted to proportions and an arcsine square function transformation was done in order to satisfy the assumptions of normality and homogeneity of variance. The same conditions as mentioned previously are applied in this section.

3.3.5 Rhizotron experiment

A linear mixed model using Infostat (Di Rienzo et al. 2010) was used to test the differences in the root length density over time between treatments. Fixed effect was the treatment and weeks, while the seedling or individual code was a random factor. Also, two repeated measure analysis of variance was conducted to analyze the root length density of *S. sphcelata* (dependent variable), with the fixed factor being 1) only competition and 2) fertilizer and its interaction with fertilizer, and the repeated measure being age (weeks). The assumption of sphericy (Mauchly´s test) was checked, which refers to the equality of variances of the differences between treatment levels (Field 2009). Greenhouse-Geisser correction was used in the case of the violation of the sphericity. Analysis of variance (ANOVA) was used to compare the above- and below-ground biomass allocation in the tree species and the grass competitor. The dependent variable used was biomass (g). The fixed factor was treatmetmet and the co-variable was the age in terms of replaced plants (1) and no replaced plants (2). All of Analysis of Variance was performed using SPSS 16.

4. Results

4.1 Dynamic of natural succession

4.1.1 Influence of time and successional site on the recruitment of species richness and abundance

Table 6 shows the development of species richness and abundance in the three successional sites over time. The Pasture site demonstrates a markedly lower increase in species richness and abundance in comparison with Bracken and Shrub sites, particularly in the last period of monitoring. According to repeated measures analysis (RMA), there was no significance in the second observation period (Table 7), confirming that species richness and abundance increased at all sites, except the recently abandoned pasture, where it increased only in the first 24 months and then stagnated. As expected, an increase in woody species richness and abundance over time on the Bracken and Shrub sites was found, with time being highly significant (Table 7). Surprisingly, the Bracken site had a high increase in both total number of species, from 18 to 53 between 24 and 48 months, and in abundance, from 737 to 1967 individuals (Table 6). In the same periods, the Shrub site also showed growth in species richness, from 44 to 64, while abundance increased from 2237 to 3075 individuals (Table 6).

Table 6. Total of species richness and abundance on the three successional sites in three periods of monitoring

	Time of monitoring		
	0 months	**24 months**	**48 months**
Species richness			
Pasture	12	17	28
Bracken	13	18	53
Shrub	37	44	64
Abundance			
Pasture	85	353	344
Bracken	297	737	1967
Shrub	1081	2237	3075

Table 7. Influence of time on species richness and abundance of seedlings per successional site (Pasture, Bracken and Shrub). Summary of within-subjects contrasts, according to repeated measures analysis of variance

	0- 24 months			24-48 months		
	MS	F	Sig.	MS	F	Sig.
Species richness						
Pasture	8.167	29.153	<0.001	0.874	2.350	0.148
Bracken	0.492	18.375	<0.001	1.899	61.482	<0.001
Shrub	7.582	386.384	<0.001	2757.089	308.912	<0.001
Abundance						
Pasture	95.119	45.769	<0.001	0.019	0.008	0.928
Bracken	22.154	143.243	<0.001	3.522	141.094	0.001
Shrub	207.239	414.470	<0.001	73.874	13.259	0.003

MS= Mean square and F-value

The diversity indices (Table 8) demonstrate that the Bracken and Shrub sites both show marked increases in comparative diversity, with the Shrub site showing the highest Shannon index although dominated by two main woody species *Ageratina dendroides* (Asteraceae) and *Myrsine coriaceae* (Myrsinaceae). Diversity on the Pasture site shows little change in the second observation period, which suggests that there is little succession occurring whereas the Bracken site was characterized by the highest dynamics. The evenness values comparing Pasture with Bracken and Shrub confirm these findings. By the end of the study, Shannon, Evenness and Chao's Sørensen index (Table 9) indicate that the Bracken site had almost reached a diversity level comparable to that of the Shrub site. However, despite higher dynamics in species recruitment on the Bracken site, the floristic similarity between Bracken and Shrub has not increased suggesting differential recruitment of species.

Table 8. Mean (± Standard Deviation) Shannon (H') and Evenness (E') indexes per successional site (Pasture, Bracken and Shrub). Different letters correspond to significant differences (P < 0.05) according to Tukey HSD comparison between times

	0 months		24 months		48 months	
Successional site	**H´**	**E´**	**H´**	**E´**	**H´**	**E´**
Pasture	0.19a (±0.21)	0.18a (±0.19)	1.03ab (±0.55)	0.71a (±0.31)	1.06b (±0.64)	0.63a (±0.33)
Bracken	0.25a (±0.21)	0.18a (±0.14)	0.81a (± 0.40)	0.51ab (±0.24)	1.63b (± 0.37)	0.68b (± 0.13)
Shrub	0.57a (±0.09)	0.27a (±0.04)	1.67b (± 0.29)	0.66a (± 0.10)	1.83b (± 0.19)	0.66a (± 0.06)

Table 9. Comparison of floristic composition among sites at 0, 24 and 48 months of observation period according to Chao Sørensen Est –abundance per successional site (± Standard Deviation)

Successional site	**0 months**	**24 months**	**48 months**
Pasture vs. Bracken	0.29 ±0.37	0.54 ±0.34	0.38 ±0.31
Pasture vs. Shrub	0.32 ±0.39	0.55 ± 0.31	0.41 ±0.34
Bracken vs. Shrub	0.63 ±0.29	0.71± 0.23	0.70 ±0.19

In order to compare diversity among communities, species accumulation curves were used at 0, 24 and 48 months. The results indicated that the Pasture site will likely need several decades to reach similar diversity as is found on the Bracken and Shrub sites due to its slow increase in species richness and abundance over time (Fig. 13a) which affected the shape of the curve, while on the Bracken site the difference between 48 and 60 months is clear, which predicts further increase in the recruitment of species over the next few years (Fig. 13b). The recruitment of diversity on the Shrub site has been highly dynamic as well with an evident increase in species richness and abundance in the last period of monitoring (Fig. 13c).

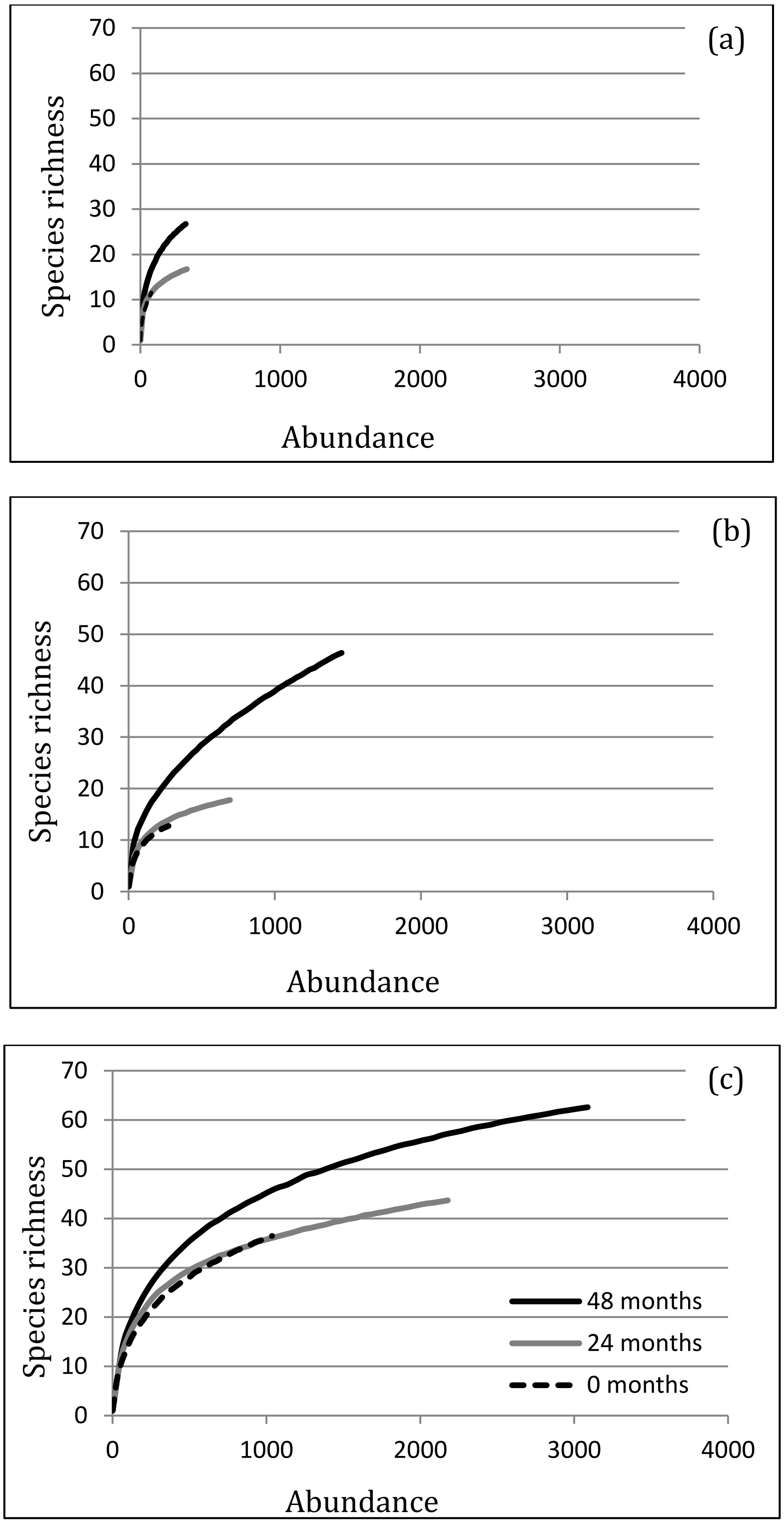


Figure 13. Species accumulation curves per site over time: (a) Pasture site, (b) Bracken site and (c) Shrub site. Sampling area per site is 1866 m^2

4.1.2 Potential triggers for woody diversity

The next task was to identify the factors that influence the recruitment of woody species. Using the generalized linear model it was found that the recruitment and establishment of new species was influenced by the availability of light, with higher light intensities being favorable for species richness. Thus the truly significant biotic factor on species richness was LAI (P=<0.001). Woody volume index (P=0.056) and density (P=0.058) also showed some positive effect on species richness although not statistically significant.

On the other hand, the interaction of successional site with LAI (P=0.060; Fig. 14a) and woody volume index (P=0.053; Fig. 14b), suggests that the type of vegetation present on each successional site, with its respective amount of light, may influence woody richness, while at the same time a well-developed vegetation structure (presence of treelets and trees) may benefit the arrival of further woody species. A gradient of available light at ground (30 cm) from Pasture to Bracken and Shrub could be identified on LAI basis, although opposite to what was expected with pasture having the highest shade due to dense vegetation of *S. sphacelata.*

The treatment as second factor of analysis (P=0.942) and its interactions such as LAI and woody volume index could not explain any effect on the dependent variables. Likewise, slope did not produce any effect on species richness either (P=0.888). Altitude was not included in the model due to low differences in the altitude among plots, therefore the goodness of fit of the model was improved, these values were χ^2 = 1.012 and Deviance = 1.065.

It has to be highlighted that no factors or variables could explain any effect on abundance due to the lack of goodness of fit using Generalized Linear Model.

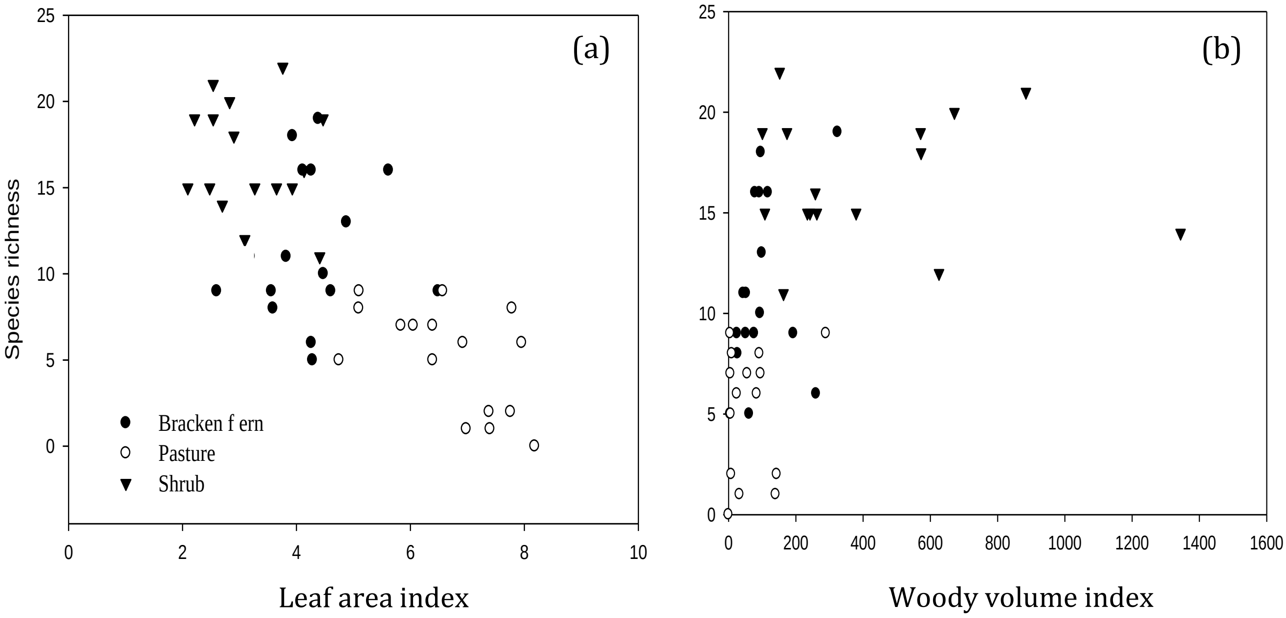


Figure 14. Relationship between species richness and a) Leaf area index and b) Woody volume index. Pasture site (open circles), Bracken site (solid circles) and Shrub site (triangles)

4.1.3 Indicator species analysis

In Table 10, only species with the highest significance ($P<0.05$) at 0 months and 48 months according to the indicator species analysis are presented. The Pasture site maintained the same indicator species (*Baccharis latifolia*) in the two observations although a new species (*Ageratina* sp.) became significant by the end of the monitoring. On the Bracken site, more species became significant by the end of monitoring (*Baccharis brachylaenoides, Baccharis* sp., *Baccharis tricuneata*, *Vernonia* sp., *Escallonia paniculata*, *Monochaetum lineatum, Roupala montana*), although it should be noted that all of these have wind-dispersed seeds. On both of these sites a high dominance of pioneer species and shrub life–forms was evident.

In contrast, at the Shrub site, the proportion of seed-dispersal mechanism of the dominant species shifted from predominantly wind-borne to animal vectors. The dominating life-forms at 48 months are treelets and trees and were probably recruited from seed dispersed by birds or bats. Furthermore, some species were added to the list of indicator species with the highest significance at 48 months (*Ilex* sp., *Baccharis macrantha*, *Baccharis* sp., *Viburnum pichinchensis*, *Clethra fagifolia*, *Clusia* spp., *Macleania poortmani*, *Vaccinium floribundum*, *Alchornea pearcei*, *Macrocarpaea* sp., *Persea* sp., *Palicourea* sp., *Hesperomeles obtusifolia*, *Palicourea anceps).*

The floristic composition at all sites was compared to the adjacent old forest in terms of presence (P) or absence (A). The results revealed that of the 32 woody species with highest significance registered in the adjacent old growth forest only 13 species were present in the sites, the majority of which were found on the Shrub site (Appendix 2).

Table 10. Comparison of indicator species ($p<0.05$) among successional sites and between initial and final observation period of woody indicator species: Dispersal syndromes, Presence in adjacent old growth forest and woody species form

	Pasture		**Bracken**		**Shrub**	
Months	**0**	**48**	**0**	**48**	**0**	**48**
Total	2	2	1	7	6	19
Dispersal mechanism (animal/wind)	0/2	0/2	0/1	0/7	3/3	12/7
Presence in reference forest (present/absent)	0/2	0/2	0/1	1/6	4/2	9/10
Life form (tree/shrub)	0/2	0/2	0/1	1/6	1/5	8/11

4.1.4 Ordination of the three sites at 0 months and at 48 months

To determinate the successional trajectory as useful tool for monitoring restoration progress of the three successional sites, 1463 individuals of 43 species and the 5386 individuals of 92 species present at 0 and 48 months respectively were ordered by non-metric multidimensional scaling (NMS). The first three axes explained 71.9% of the variation. Figure 15 shows that Bracken and Shrub sites form almost parallel, or slightly convergent successional trajectories, while at the Pasture site no clear successional pathway could be identified due to point-cloud range along a multidimensional space, or in other words, the floristic composition of each plot is disperse and shows no clear pattern of successional trajectory.

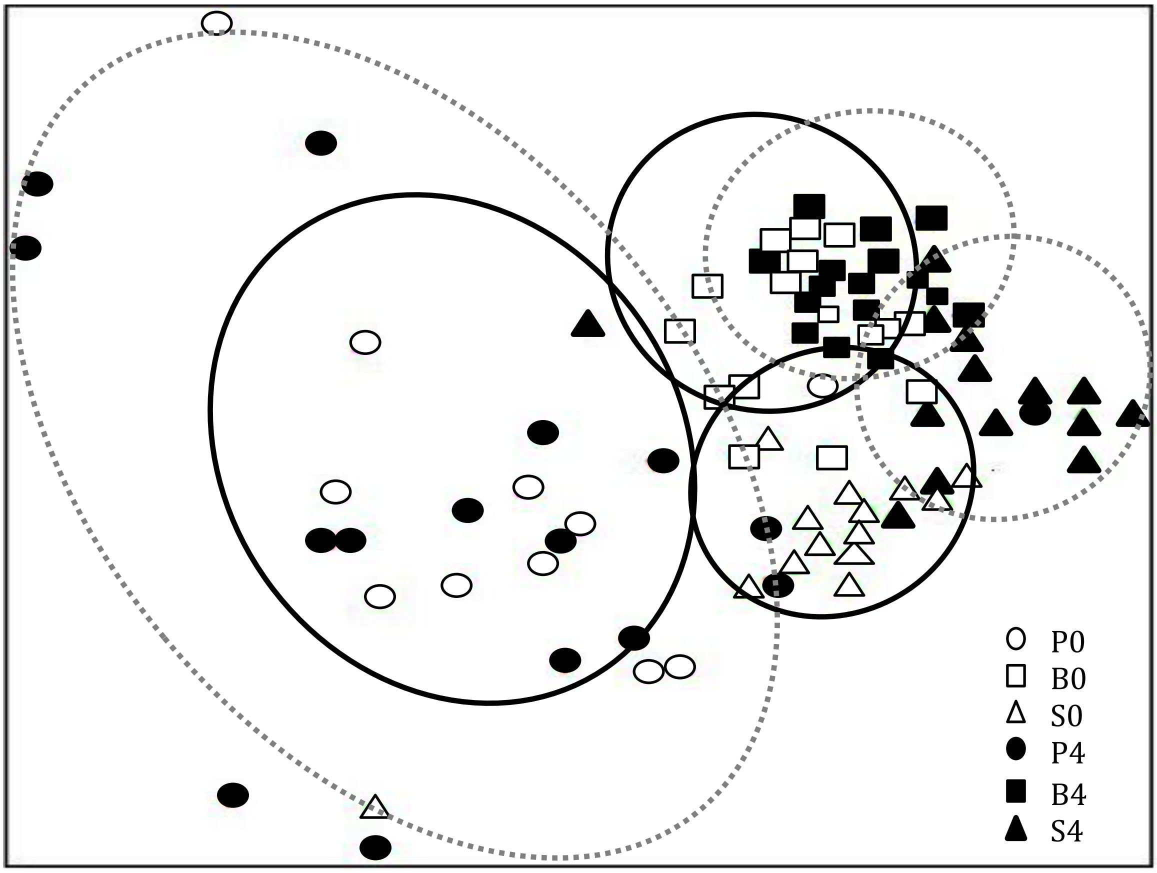


Figure 15. Non-metric multidimensional scaling ordination based on species richness and abundance of woody regeneration on three sites: P= Pasture, B = Bracken and S= Shrub, at 0 months (open symbols) and 48 months (full symbols). The full circles indicate the conditions at 0 months, the dashed circles those at 48 months. The Monte Carlo p-value is 0.0040 and the final stress is 16.14 in regard to the first three axes

4.1.5 Effect of manual weeding on species richness and abundance across time

We expected manual weeding to enhance species recruitment and abundance by reducing competition. However, it had no positive effect on species richness or abundance on the Pasture site (Figs. 16a & b), as revealed by the interaction between time and treatment used in the RMA (Table 11) and somewhat surprisingly, on the Bracken and Shrub sites this treatment showed even a negative effect on species richness. The statistics reveal that the treated plots had significantly lower species richness on the Bracken site between 24 and 48 months (P=0.047; Fig. 16c); the same tendency was found on the Shrub site (P=0.072; Fig. 16e).

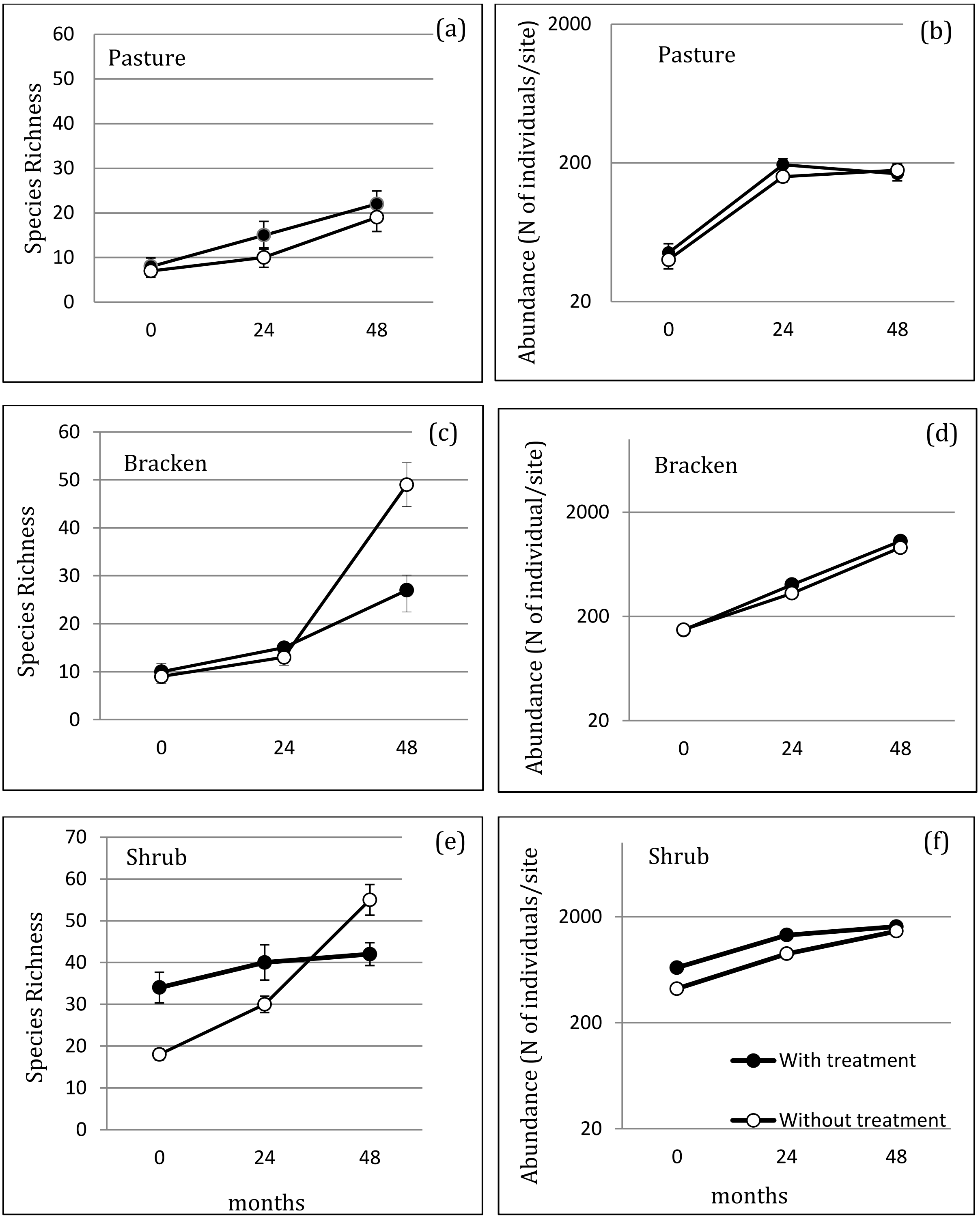


Figure 16. Effects of mechanical treatment on species richness and abundance at 0, 24 and 48 months per successional site: Pasture (a-b); Bracken (c-d) and Shrub (e-f). Open circles correspond to without treatment and full circles correspond to with treatment

*SD is not seen in the graphs of abundance due to the logarithmic scale.

Table 11. Effect of interaction between time and treatment on species richness and abundance per successional site. Summary of within-subjects contrasts, according to repeated measures ANOVA (p<0.05)

	0-24 months			24-48 months		
Time × treatment	MS	F	Sig.	MS	F	Sig.
Species richness						
Pasture	0.132	0.470	0.504	0.353	0.950	0.346
Bracken	0.027	0.996	0.335	0.146	4.727	0.047
Shrub	0.005	0.236	0.276	10.572	1.184	0.098
Abundance						
Pasture	0.452	0.217	0.648	2.280	0.991	0.336
Bracken	0.004	0.293	0.597	0.019	0.762	0.397
Shrub	0.678	1.357	0.242	20.627	3.702	0.072

MS= Mean square and F-test

4.2 Survival and growth development of the tree species in the tree plantation

4.2.1 Survival

4.2.1.1 Effects of time and site on survival for mid-successional species

During the monitoring periods, the survival rate differed among species and sites, although as expected the general pattern of survival was decreased over time. In some cases no excessive losses appeared, for example *C. montana* on the Bracken site, whose survival shifted from 59.4 % at 48 months to 56.3% (n=96) at 60 months but in other sites such as the Pasture site, a huge decline of individuals was found from 90.6% to 57% between 12 and 24 months (Fig. 17a). *T. chrysantha* was the most successful species over time in all three sites with more than 80 % (n=96) of survival at 60 months age (Fig. 17b), thus there is an evident stability in the number of surviving individuals particularly on the Shrub site. The most notable species among all mid-successional species tested in the tree plantation was *J. neotropica.* This species has shown the poorest adaptation to all three sites from the beginning of plantation and at the end of monitoring the percentage of survival was below 18% (Fig. 17c). The losses of individuals over time was highly significant for all species (*P*<0.0001).

On the other hand, site did not reveal any effect on survival for all mid-successional species and consequently the pattern of survival per each species seems to be similar among sites over time. However, by comparing between the initial and final measure of survival, the tendency revealed that on the Bracken and Shrub sites *T. chrysantha* presented the highest percentage of survival with 83 % and 97 % respectively at the end of monitoring. Likewise, on the Bracken site, *C. montana* had better survival (56%) than on other successional sites (Table 12).

The interactions time × site showed that survival on the different sites varies according to the different periods of monitoring. This interaction was highly significant for all mid successional species (Table 17).

Table 12. Survival (%) of mid-successional species after 60 months, ± Standard Deviation. P (Pasture), B (Bracken) and S (Shrub)

	P	B	S
C. montana	34.4±27.6	56.3±30.8	35.4±30.8
T. chrysantha	80.2±19.4	83.3±17.3	96.9±8.8
J. neotropica	13.5±21.3	18.8±12.4	9.4±12.9

4.2.1.2 Effects of time and site on survival for early-successional species

A. acuminata and *H. americanus* showed a high mortality in the first years of the plantation. However, after 1 year the rate of loss became lower for *A. acuminata*, while for *H. americanus* the losses continued over time. At the Pasture site the losses are highest but the individuals of *A. acuminata* that survived the first two years had a lower rate of mortality. In the last monitoring periods, the losses of individuals of *A. acuminata* reduced from 58% to 53% at 36 months and 48 months respectively on the Pasture site (Fig. 17d). In the case of *H. americanus,* survival consistently decreased, showing a poor adaptation to all the sites and average survival at the end of monitoring was below 25% (Fig. 17e). On the Pasture site, *H. americanus* had a marked loss of individuals by its third measurement where only 13 % (n=96) survival was shown, and 6% survived to the end of monitoring (Table 13; Fig. 17e). Statistically time had a highly significant negative effect for both early successional species (*P*=<0.0001).

Site negatively affected the percentage of survival of *H. americanus* (*P*=<0.0001), showing a consistent loss of individuals on all the three sites. In the case of *A. acuminata* survival was similar among sites, with an initial high mortality tapering off. There is a tendency for lower mortality on the Pasture site (53%, n= 96) with respect to the other two sites (Fig. 17d). The interaction of site × time for *H. americanus* and *A. acuminata* showed a high significance (*P*=<0.0001). This indicates that survival on the different sites changes over time.

Table 13. Survival (%) of early-successional species after 48 months for *A. acuminata* and 60 months for *H. americanus,* ± Standard Deviation. P (Pasture), B (Bracken) and S (Shrub)

	P	B	S
A. acuminata	53.1±20.4	37.5±36.7	40.6±38.9
H. americanus	6.3±9.7	21.9±18.9	30.2±33.3

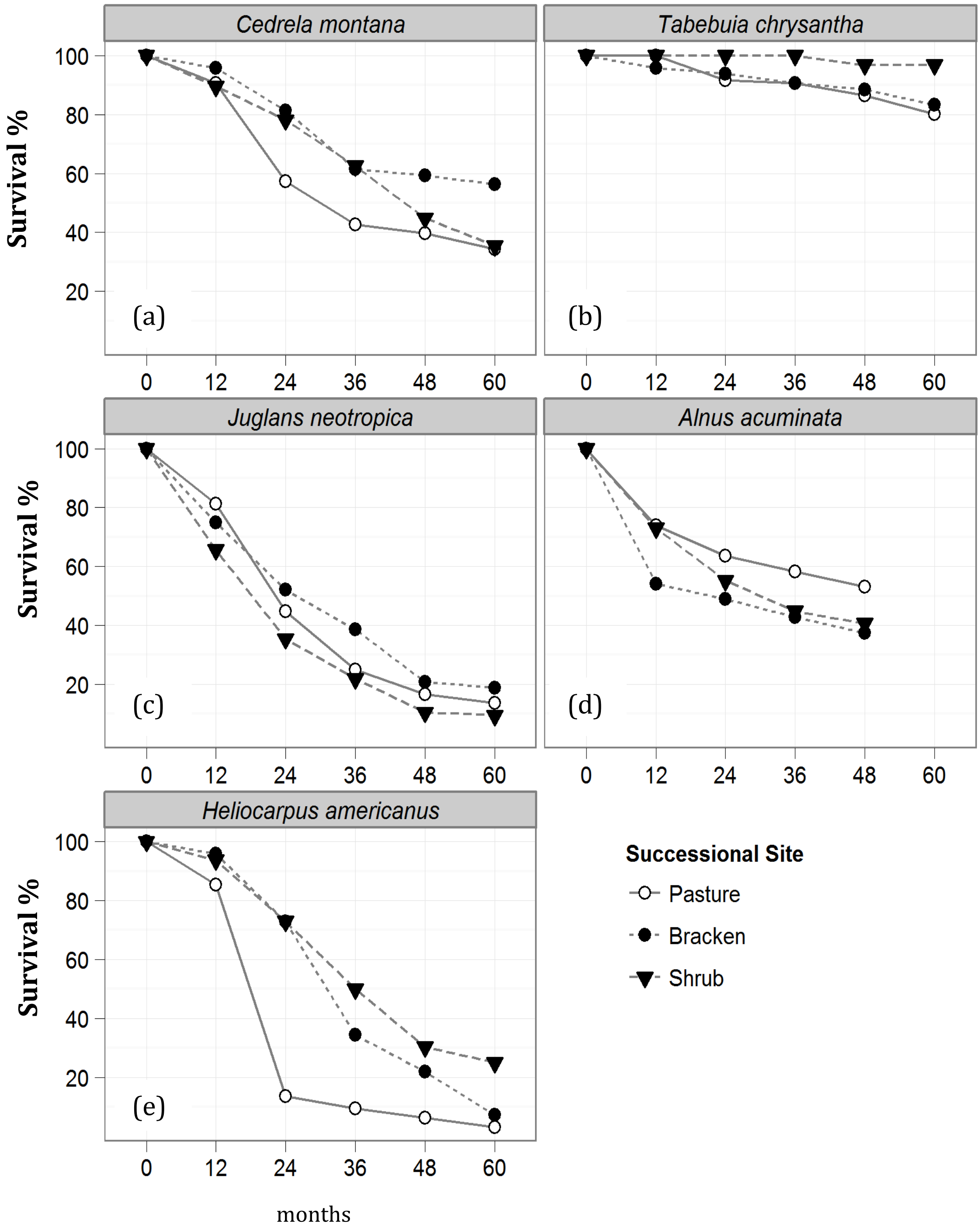


Figure 17. Survival (%) of planted species at the different sites during the monitoring period from 0 to 60 months

In order to better understand the survival performance of species within the plots across sites, three categories of plots were created: less than two surviving individuals (<2), between three and six individuals (3-6) and more than six individuals (>6). Each plot was analyzed for number of individuals of each species (see Table 14). The important result was that the majority of surviving plants for *H. americanus* and *J. neotropica* in the last period of monitoring are mostly concentrated in an individual plot and in the case of *C. montana,* only 8 plots retained more than 6 individuals. Exceptionally, *T. chrysantha* kept more than 6 individuals per plot over time. There was a high standard deviation for most of species over time with the exception of *T. chrysantha*, which explains the high heterogeneity in the landscape.

Table 14. Total percentage survival of all species ±SD and number of plots according to surviving individuals and each period of observation (n=24 plots)

Species	Age	Survival	Number plots with surviving individuals			Total plot
			<2	3-6	>6	24
C. montana	0	100			24	24
	12	92.4±8.6			24	24
	24	76±18.6	2	7	15	24
	36	61.8±23	2	7	15	24
	48	51.4±25.8	5	7	12	24
	60	44.8±25.4	7	9	8	24
T. chrysantha	0	100			24	24
	12	98.61±11.2			24	24
	24	97.57±7.29			24	24
	36	97.57±7.29			24	24
	48	92.71±10.44			24	24
	60	89.93±12.11			24	24
J. neotropica	0	100			24	24
	12	74±11.4			24	24
	24	44.1±18.4	3	13	8	24
	36	26.4±11.8	8	16		24
	48	15.3±13.9	16	7	1	24
	60	5.6±18	22	1	1	24
A. acuminata	0	100			4	24
	12	65.6±24.9	2	8	4	24
	24	50.3±27.5	5	8	1	24
	36	47.6±28.9	7	8	9	24
	48	43.8±28.2	7	7	0	24
H. americanus	0	100			24	24
	12	91.7±9.41			24	24
	24	53.5±21.63	5	7	12	24
	36	28.8±18.40	11	7	6	24
	48	21.9±24.18	15	5	4	24
	60	3.8±31.45	23		1	24

4.2.2 Growth development

4.2.2.1 Effect of time and site on growth for mid-successional species

The dynamic of growth development varies among species according to site conditions and their own intrinsic abiotic and biotic needs. Nevertheless, time variably showed positive and negative effects depending on the species and significant results for plant height and RCD for all species was found. For instance, for *T. chrysantha* on all sites, the plant growth development increased over time (Fig. 18b; Fig. 19b), while mean height of *C. montana,* kept small mainly on the Shrub site and even a slight decrease at 48 months of age was registered (Fig. 18a); this is probably the result of accumulative plant stress which resulted in the observed apex damage.

For *J. neotropica* a clear dieback was observed at all sites in the first year, suggesting either planting shock or poor adaptation to the environmental conditions. However, while the individuals on the Pasture and Shrub sites since month 36 could increase its height again, those at the Bracken could not regenerate, thus the mean height continued to decrease (Fig. 18c).

Analyzing site as another factor showed that *C. montana*, once established, grew better on Pasture than on Bracken and Shrub sites based on the few remaining seedlings as mentioned before in the survival section. The plant growth of *T. chrysantha* is higher on the Shrub site, its final plant growth had a mean height of 52 cm and a RDC of 1.8 cm (Fig. 18b; Fig.19b); the biggest individual was 1.29 m. In contrast, the smallest plants were found on the Pasture site with an average height of 26 cm. In the case of *J. neotropica*, the few individuals in the last periods of monitoring showed a constant plant growth over time on the Pasture site (Fig. 18c; Fig. 19c). Statistically the site factor was significant for all the parameters tested (see Table 17). The interaction of site × time also had significance for all species for stem height and RCD, indicating that the plant growth development over time differs among sites (Table 17).

In general, the mid-successional species did not even reach a mean height of one meter on any of the three sites (Figs. 18a, b & c). Table 15 shows a comparison between initial and final measures for each species with their respective standard deviation.

The generally higher standard deviation at the end of monitoring clearly indicates the high heterogeneity in plant growth within successional site with the exception of *J. neotropica*, which showed negative mean growth anyway. Therefore, the plants of greatest height could be concentrated in certain micro-sites or clustered in certain plots.

Table 15. Comparison between initial (I) and final measures (F) of mean height and root collar diameter (RCD) of mid-successional species ± SD. P (Pasture), B (Bracken), S (Shrub)

	Initial P	Final P	Initial B	Final B	Initial S	Final S
Height (cm)						
C. montana	26.1±6.7	91.7.2±65.5	26.9±6.6	65.7±51.4	26.0±6.4	27.2±16.4
T. chrysantha	18.2±2.9	26.2±11.0	15.5±3.4	37±32.2	16.4±3.8	51.5±27.5
J. neotropica	64.6±17.7	81.7±31.2	45.5±13.5	21.4±12.8	50.4±20.9	48.2±26.1
RCD (cm)						
C. montana	0.7±0.1	2.8±2	0.7±0.2	2±1.1	1.2±0.2	1.2±0.2
T. chrysantha	0.6±0.1	1.2±0.2	0.6±0.1	1.6±0.7	0.6±0.1	1.8±0.6
J. neotropica	0.8±0.1	2.5±0.8	0.8±0.1	1.2±0.3	0.8±0.1	1.4±0.5

4.2.2.2 Effects of time and site on growth for early-successional species

A. acuminata was the most successful species on the Pasture site over time. This species had a mean height of 3.9 m and an RCD of 6.9 cm at 48 months (Fig. 17d; Fig. 18d), with a mean height of 2 m on the Bracken site and 1.5 m on the Shrub site (Fig. 17d). The results for *H. americanus* show growth development over time on all the sites, although this masks the poor survival rate and the development of only a few individuals can be shown. At 12 months *H. americanus* had a reduction in height compared to the initial measurement due to a stem dieback effect and a second decrease event at 48 months. Time as factor of analysis was statistically significant per each species (P=<0.0001) (Table 17).

Table 16 compares the initial and final height and RCD of the early successional species, indicating that *A. acuminata* had the greatest increment in height (4 m) and RCD (7 cm) on the Pasture site and mirrored to a lesser extent on the other sites. The effect of site was statistically significant for plant growth of *A. acuminata* (Table 17*)* but the opposite trend was found for *H. americanus*. It is not possible to state that this species has been successful due to its significant site specific mortality rate.

The interaction site × time had also high statistical significance and positive response for plant growth for the two species (Table 17). This shows that besides site and time having an effect individually, growth development across time is different between sites.

Table 16. Comparison between initial and final measures of mean height and RCD of mid-successional species ± SD. P (Pasture), B (Bracken) and S (Shrub)

	Initial P	Final P	Initial B	Final B	Initial S	Final S
Height (cm)						
A. acuminata	40.9±18.4	398.2±112	61.35±13.6	204.02±112	41.7±12.8	149±81.4
H. americanus	35.8±9.4	93.2±33	26.5±5.7	61.8±55.2	36.4±9.5	71.7±67.7
RCD (cm)						
A. acuminata	0.6±0.2	6.9±4.3	0.5±0.1	4.8±2.2	0.5±0.1	2.8±1.2
H. americanus	0.6±0.1	1.4±0.4	0.5±0.1	1.8±0.9	0.6±0.2	1.4±0.7

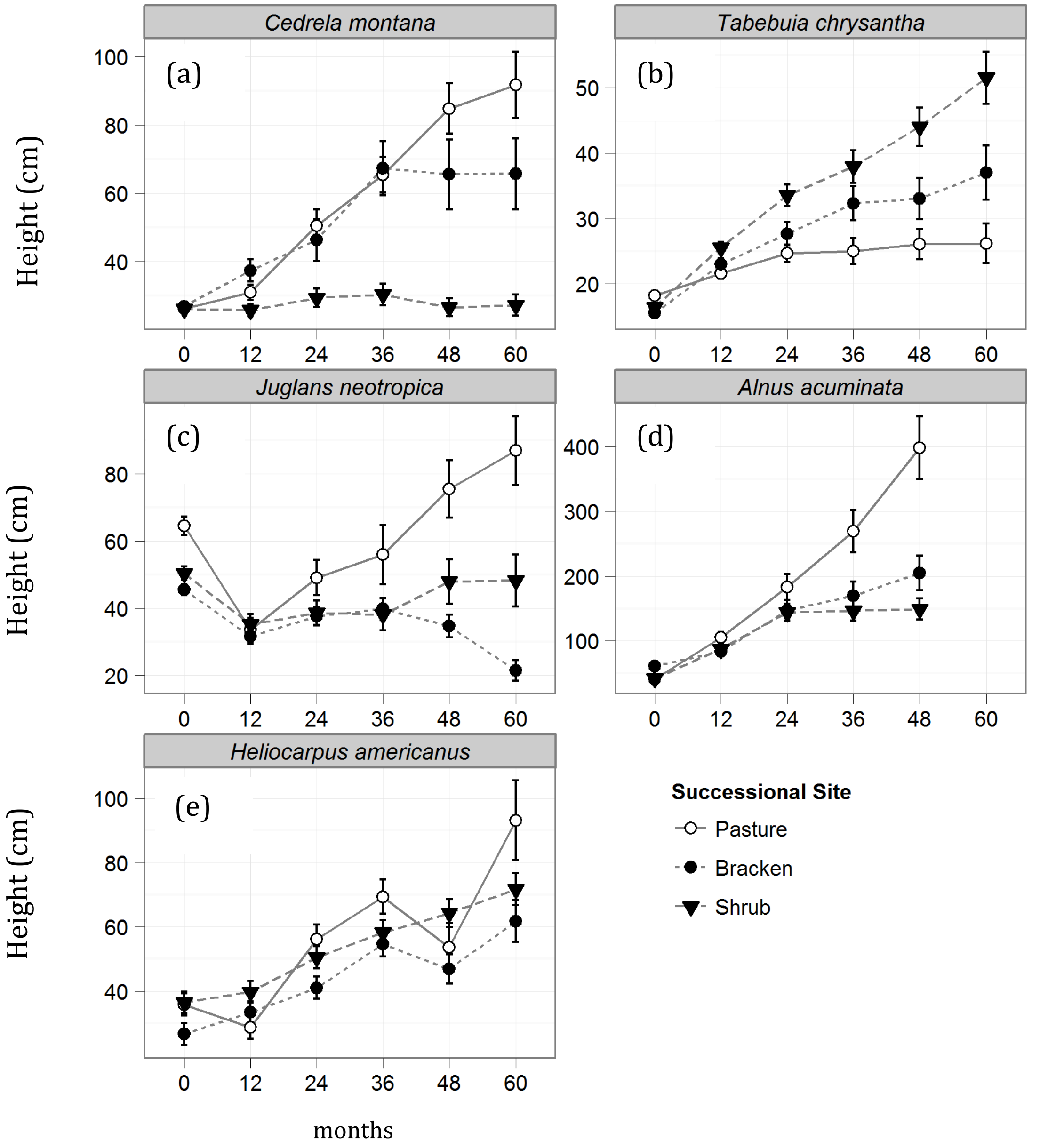


Figure 18. Development of the mean height at the different sites during the monitoring period from 0 to 60 months (Bars = Standard Error)

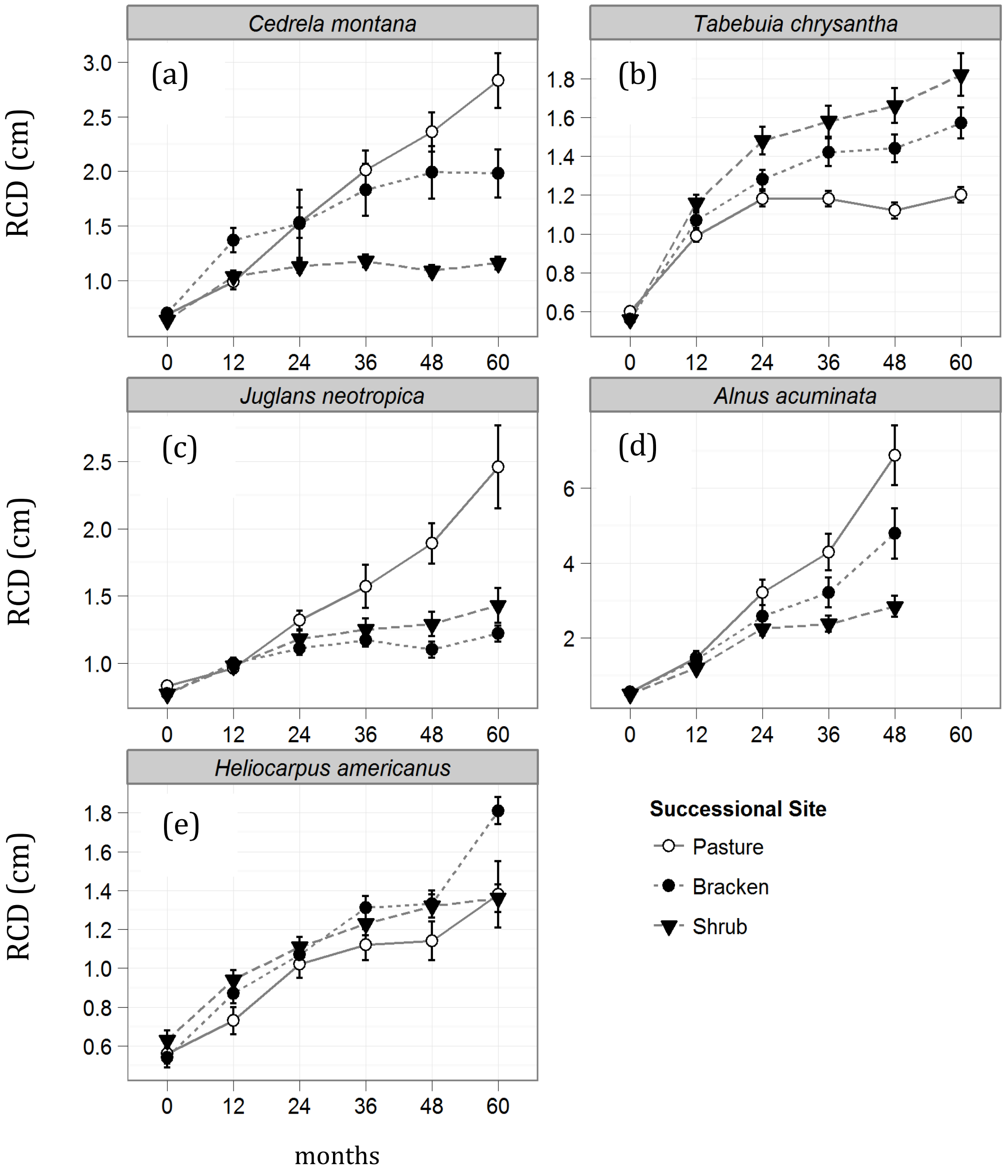


Figure 19. Development of the mean root collar diameter during the monitoring period from 0 to 60 months (Bars = Standard Error)

4.2.2.3 Effect of Water holding capacity (WHC) on survival and growth plant performance

The WHC included as a covariate in each model did not reveal any statistical effect on survival, growth of height and RCD (Table 17). Only *T. chrysantha* seems to respond positively to WHC for RCD (*P*=0.0375). At 24 months and 36 months-age a correlation of R^2 0.18 and 0.40 respectively was found between water holding capacity and RCD.

Table 17. Statistical significance for early-and mid-successional species for survival, height and RCD using Linear mixed models

	Mid successional			Early successional	
	Cm	Tc	Jn	Aa	Ha
Survival					
Site	0.1578	0.2994	0.1861	0.5261	<0.0046
Time	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
WHC	0.4641	0.9380	0.8917	0.6526	0.4929
Site × time	0.0067	0.0005	0.0452	0.0501	0.0808
Height					
Site	0.0021	0.0010	0.0018	0.0027	0.5000
Time	<0.0001	<0.0001	<0.0001	<0.0001	0.0001
WHC	0.7096	0.9339	0.8325	0.4935	0.2160
Site × time	0.0027	<0.0001	<0.0001	<0.0001	<0.0001
RCD					
Site	0.0037	0.0001	0.0039	0.0015	0.2497
Time	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
WHC	0.2328	0.0375	0.5700	0.6692	0.2097
Site × time	0.0017	<0.0001	<0.0001	<0.0001	<0.0001

Species: Cm (*Cedrela montana*), Tc (*Tabebuia chrysantha*), Jn (*Juglans neotropica*), Aa (*Alnus acuminata*), Ha (*Heliocarpus americanus*).

WHC: Water holding capacity

4.3 Weeding treatment within the reforestation experiment

The results presented in this section represent the current status of the tree plantation at 60 months of age, except for *A. acuminata* which is 48 months.

4.3.1 Effect of treatment on survival and growth of species

There is no clear evidence of a positive effect of the treatment on survival and plant performance over time with the exception of *T. chrysantha.* Nevertheless, the tendency for most species revealed a higher survival on treated plots although *J. neotropica* and *M. pubescens* had the opposite performance. Likewise, overall plant performance with the application of treatment showed a slight improvement.

Mid-successional species

For survival, *C. montana* showed no significant difference between plots with and without treatment (*P*=0.439; Fig. 20a) although survival on treated plots was slightly superior than without treatment; most evident on the Shrub site. The tallest plants were on untreated plots, although statistically there was no difference (*P*=0.532; Fig. 20b). However, the RCD was significantly improved by the application of treatment (*P*=0.014; Fig. 20c).

The survival of *T. chrysantha* was slightly improved with the application of treatment (*P*=0.073; Fig. 21a), with the highest survival percentage being registered on the treated Shrub site (98 %) (n=200). This species reacted positively to treatment for height and RCD with high statistical significance (*P*=0.000; Figs. 21b & c).

J. neotropica had a poor survival (<20%) at all the sites. From the few remaining individuals in all the sites the results showed that survival was better beneath untreated plots than treated ones; and a marked difference was evident on the Pasture site, although no statistical significance was found (Fig. 22a). The highest plants are on the Pasture site in untreated plots with similar results on the Bracken site and smaller plants on the Shrub site (Fig. 22b). The highest RCD was found on the Pasture site in untreated plots, while on the Bracken site the plants had better RCD beneath treated plots and on the Shrub site the treatment did not favor the RCD performance (Fig. 22c).

For all the species, the interaction treatment × site did not have a significant effect on the survival parameter (Table 18). The interaction did not explain the plant growth either, except for *J. neotropica* (Height, *P*=0.049 and RCD, *P*=0.035), indicating that treatment varies according to the successional site, for instance, the plants only grew better on the Pasture site without treatment.

Early-successional species

In the case of *A. acuminata*, the application of treatment contributed slightly to improve the survival percentage in particular on the Pasture and Shrub sites (Fig. 23a) although no statistical significance was found (Table 18). Also the treatment did not significantly improve the growth performance of this species; however, by comparing the difference between treated and untreated plots on the Bracken site, a difference in mean height (84 cm) and RCD (1.8 cm) was observed under treated plots (Figs. 23b & c).

H. americanus showed a low survival percentage in all the sites (<32%) (P=0.006; Fig. 24a). In spite of the few remaining individuals, there is a trend of plants to respond better in treated plots. In the case of the plant growth, the application of treatment favored the final height on the Pasture site while the Bracken and Shrub sites showed similarly poor plant performance (Fig. 24b). Treatment had no significant effect on survival or stem height (Table 18) while RCD is highly improved by treatment, which was most evident on the Pasture site (*P*=0.041; Fig. 24c)

M. pubescens, revealed that it survives better without treatment, except on the Shrub site (Fig. 25a). However, statistically there is not difference between treated and untreated sites (Table 18). Although survival was higher without treatment, growth (height and RCD) has better effect with treatment (Figs. 25b & c; Table 18).

4.3.2 Effect of site on the survival and growth performance

Mid-successional species

C. montana showed that site influenced its survival (*P*=0.049; Fig. 20a). However, the lowest survival percentage (35%, n=200 with treatment and 200 without treatment) is given on the Pasture site, while a higher survival percentage above 55% was observed on the Bracken site. Particularly, the best plant growth occurred on the Pasture site although as mentioned, the surviving individuals were very low, while at the Bracken site the survival was higher. A pattern of contrast was observed on the Bracken and Shrub sites, where the survival was high but the growth performance was lower (Figs. 20b & c).

T. chrysantha, which showed that site affected its survival (*P*=0.000; Fig. 21a), established itself particularly well on the Shrub site with a 98 % survival rate (n=200 with treatment and 200 without treatment). Likewise, for stem height (*P*=0.067; Fig. 21b) and RCD (*P*=0.013; Fig. 21c) there was an important difference between sites with the Shrub site again showing the best performance with a mean height of 72 cm and 2.9 cm of RCD. Plant growth performance was the lowest on the untreated Pasture site.

J. neotropica demonstrated itself to be poorly adapted to all the sites because its survival rate was below 18%, although site did not affect survival (*P*=0.078; Fig. 22a), although a slightly improved survival rate on the Bracken site was found. In spite of the low representation of seedlings of this species, on the Pasture site it was observed that both parameters of plant growth had more success than other sites (Figs. 22b & c), for instance, the mean height on the Pasture was 73 cm and 2cm of RCD without treatment. Furthermore the combination of treatment and site was found to have a significant effect on height and RCD while site alone had no significant effect on plant growth (Table 18).

Early-successional species

A. acuminata did not show a significant relationship between site and survival, although it had a higher percentage survival on the Pasture site 49% (without treatment) and 63% (with treatment) compared to the other sites (Fig. 23a). Site significantly affected its growth, doing much better on the Pasture site (height of 4.3 m) followed by the Bracken (2.8 m) and Shrub sites (1.4 m), all of them with treatment; a high significance for height and RCD was found (*P*=0.000; Figs. 23b & c).

H. americanus was not well adapted to all the successional sites with survival below 31.5% but there were significant differences among sites with survivorship being highest on the Shrub site followed by Bracken then Pasture (*P*=0.006; Fig. 24a).

There is an important role of the site given by the plant performance mainly on the Pasture site (height 1.5 m and RCD 5cm) (*P*=0.023; Fig. 24b) (*P*=0.082; Fig.24c). The Bracken and Shrub sites had similar results for plant growth.

M. pubescens was strongly influenced by site conditions with both plant growth and survival being significant (*P*=0.000; Figs. 25 a, b & c). This result can be seen from the superior survival and growth on the Bracken site with treatment (Height of 2.4 m and RCD of 7.6 cm) when compared to its relatively poor showing on the Pasture and Shrub sites. The interaction site × treatment did not reveal any significance for all the parameter tested (Table 18).

Cedrela montana

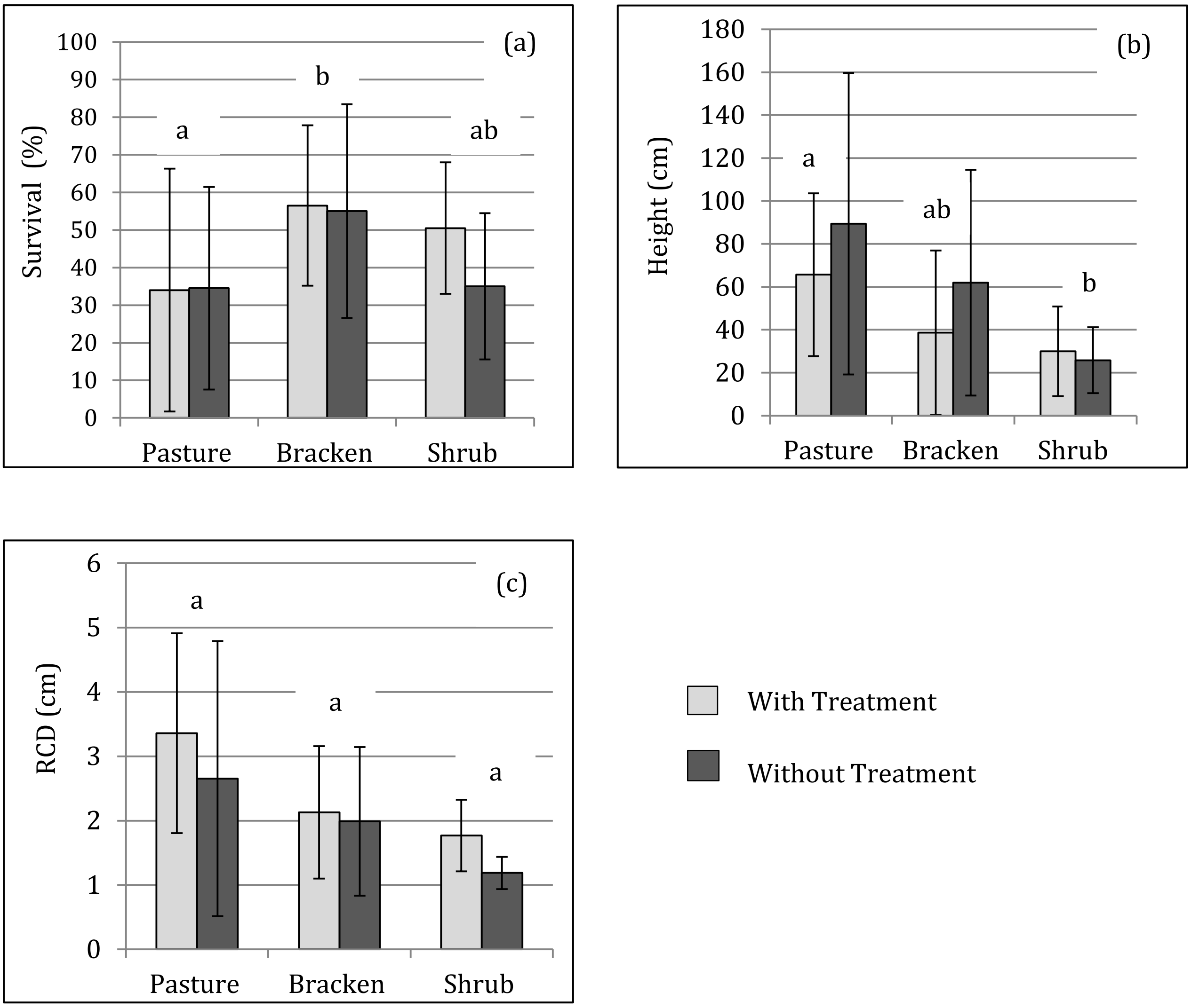


Figure 20. Survival (a) Height (b) and RCD (c) of *Cedrela montana* at 60 months of plantation. The different letters correspond to significant differences according Tukey HSD ($p<0.05$)

Tabebuia chrysantha

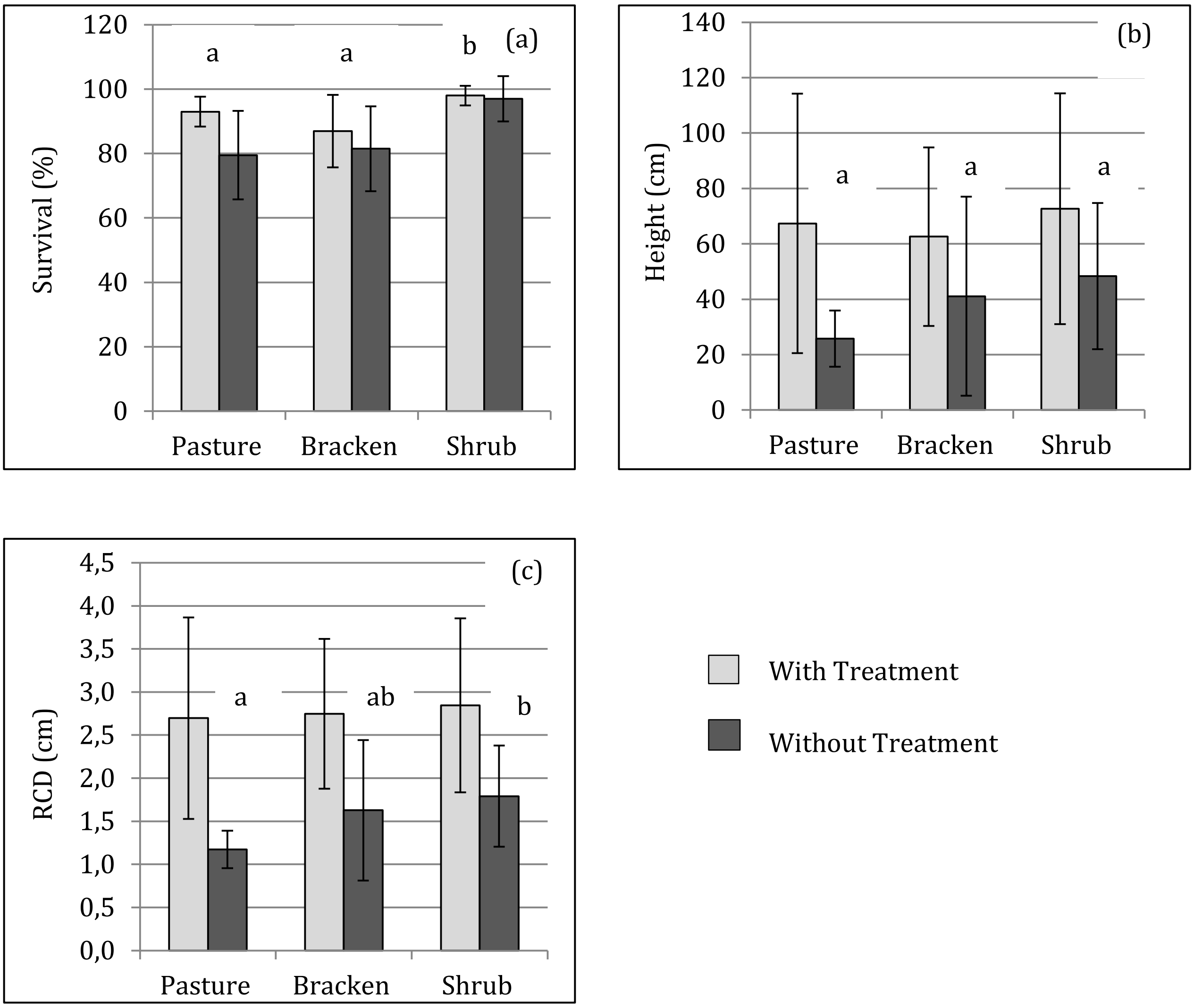


Figure 21. Survival (a) Height (b) and RCD (c) of *Tabebuia chrysantha* at 60 months of plantation. The different letters correspond to significant differences according Tukey HSD (p<0.05)

Juglans neotropica

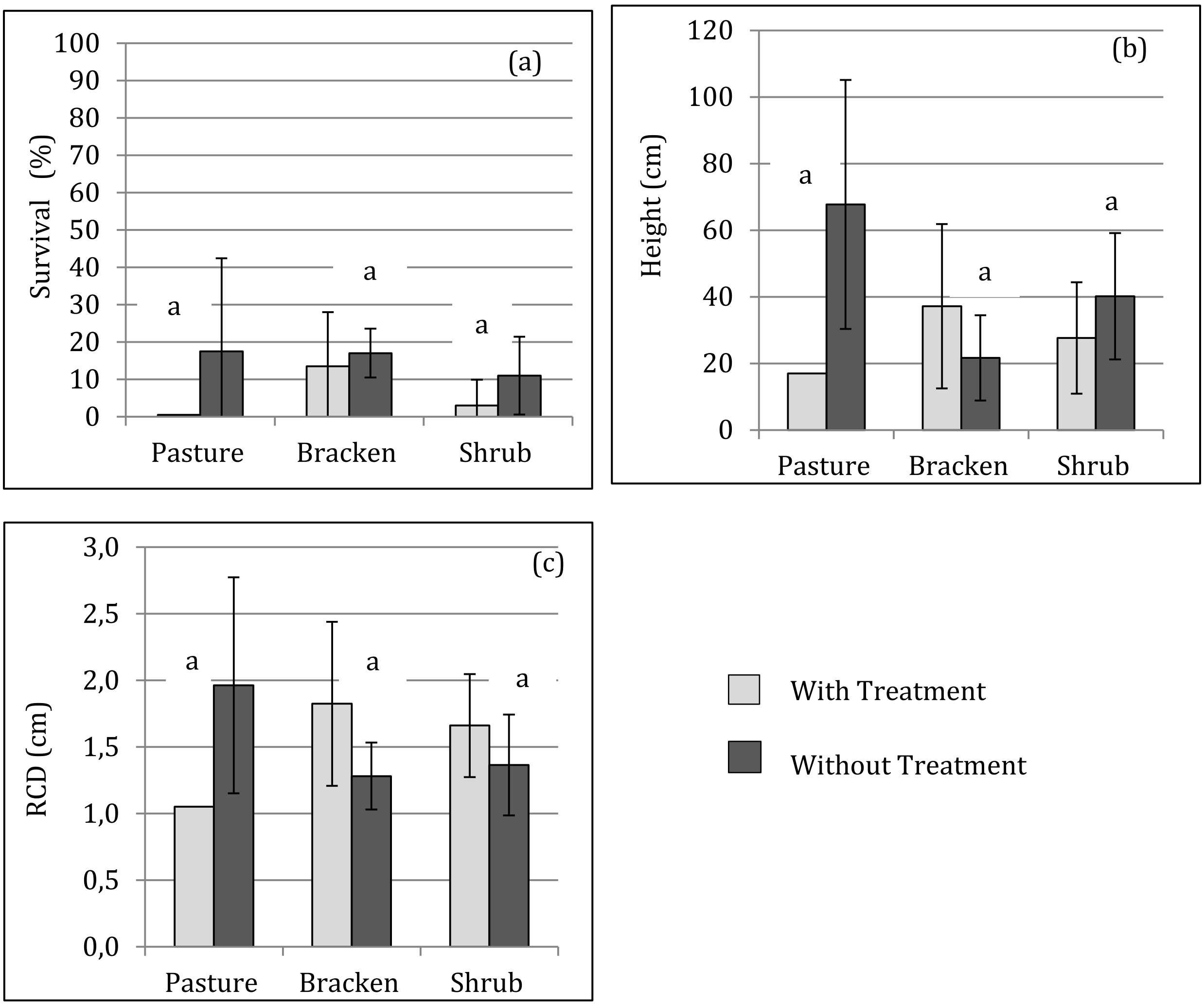


Figure 22. Survival (a) Height (b) and RCD (c) of *Juglans neotropica* at 60 months of plantation. The different letters correspond to significant differences according Tukey HSD ($p<0.05$)

Alnus acuminata

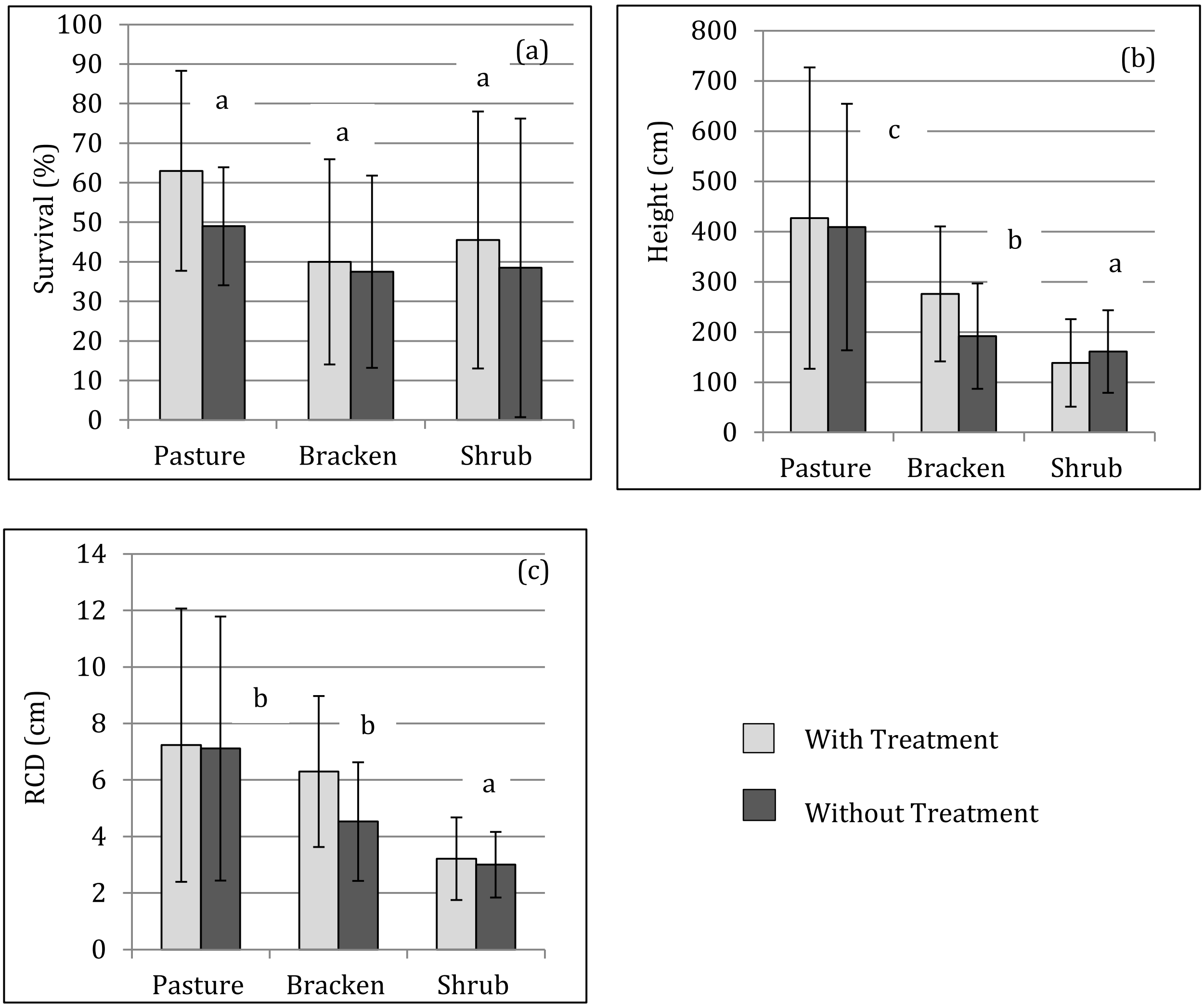


Figure 23. Survival (a) Height (b) and RCD (c) of *Alnus acuminata* at 60 months of plantation. The different letters correspond to significant differences according Tukey HSD ($p<0.05$)

Heliocarpus americanus

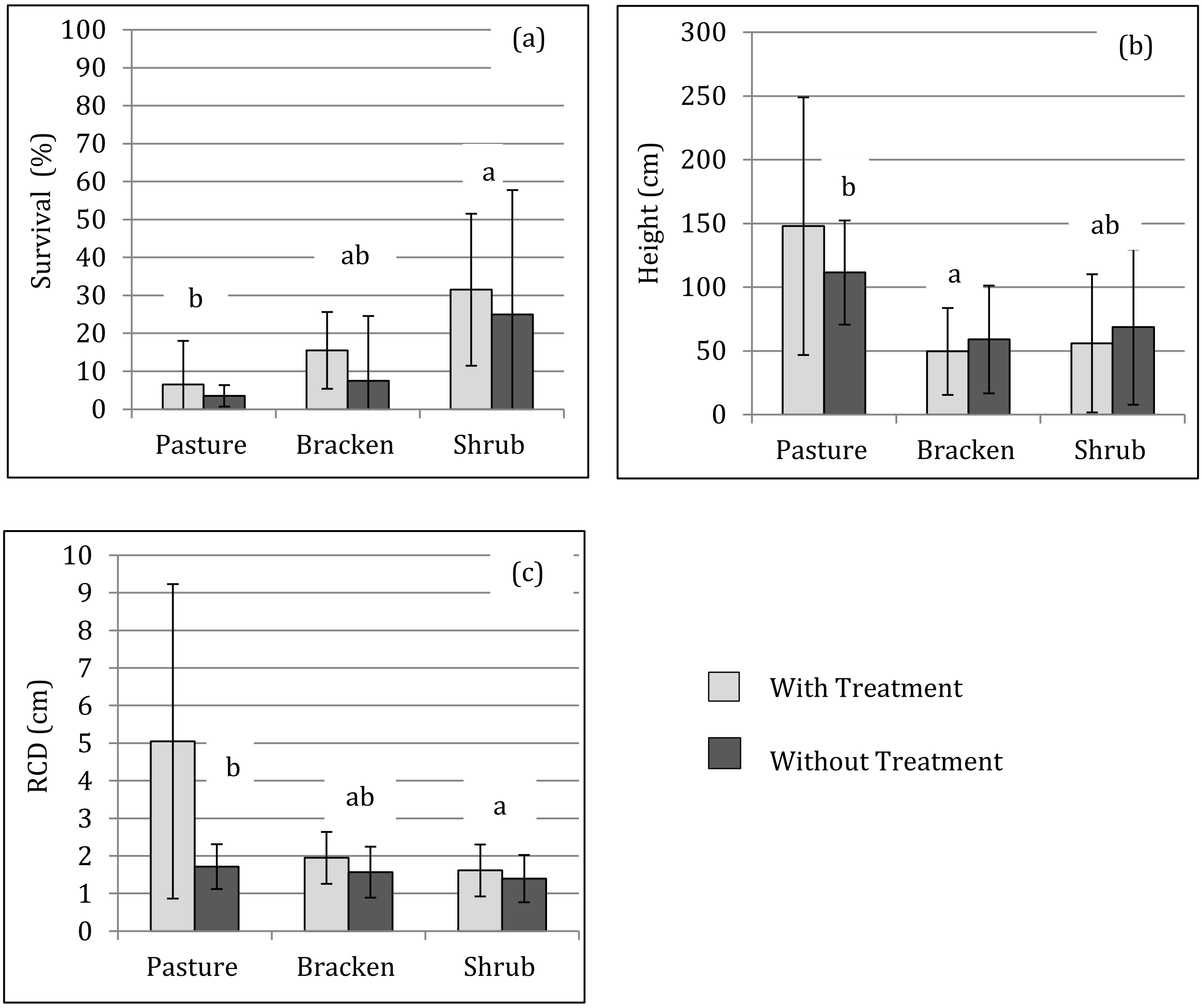


Figure 24. Survival (a) Height (b) and RCD (c) of *Heliocarpus americanus* at 60 months of plantation. The different letters correspond to significant differences according Tukey HSD ($p<0.05$)

Morella pubescens

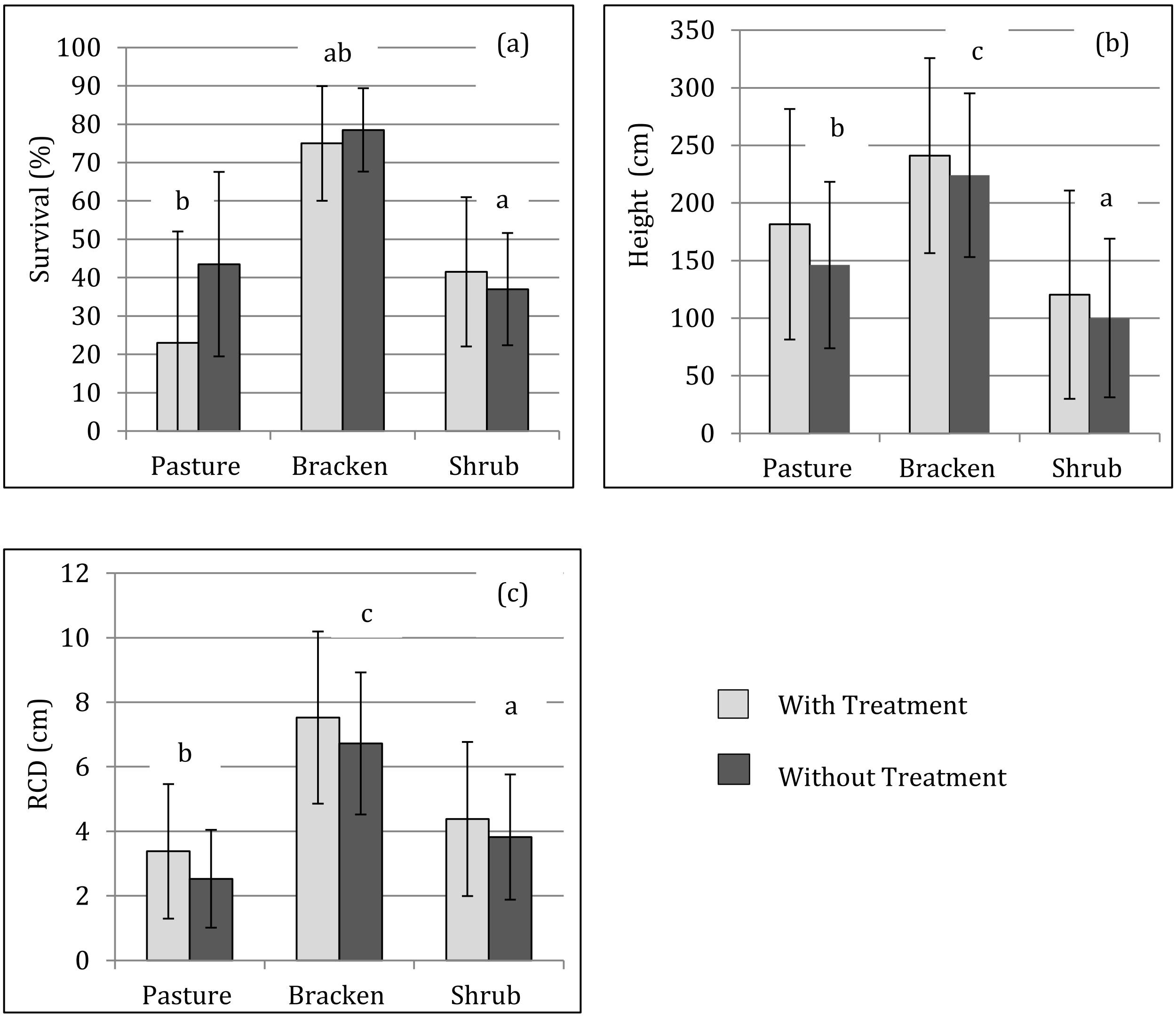


Figure 25. Survival (a) Height (b) and RCD (c) of *Morella pubescens* at 60 months of plantation. The different letters correspond to significant differences according Tukey HSD ($p<0.05$).

Table 18. ANOVA for each species and for survival, height and root collar diameter (RCD)

	P- value					
	Cm	Tc	Jn	Aa	Ha	Mp
Survival						
Treatment	0.439	0.073	0.010	0.256	0.121	0.174
Site	0.049	0.000	0.078	0.180	0.006	0.000
Treatment × Site	0.538	0.258	0.398	0.977	0.795	0.118
Height						
Treatment	0.532	0.000	0.143	0.872	0.875	0.462
Site	0.020	0.067	0.548	0.000	0.023	0.000
Treatment × site	0.531	0.360	0.049	0.756	0.603	0.940
RCD						
Treatment	0.014	0.000	0.684	0.341	0.041	0.412
Site	0.105	0.013	0.566	0.000	0.082	0.000
Treatment × site	0.947	0.132	0.035	0.547	0.710	0.968

Species: Cm= *Cedrela montana*, Tc = *Tabebuia chrysantha*, Jn= *Juglans neotropica*, Aa= *Alnus acuminata*, Ha = *Heliocarpus americanus*, Mp= *Morella pubescens*

4.4 Seedling pretreatment experiment

The species investigated in this experiment did not show clear evidence that tree seedlings reacted significantly under any treatment after two years of plantation. Overall, there were species-specific signs and behavioral responses to the treatments which agree with species traits such as early-successional species (*H. americanus*) and mid-successional species (*T. chrysantha* and *C. montana*).

4.4.1 Effect of fertilization on survival, height increment and root collar diameter increment of tree species two years after planting

The results showed a high percentage of survival for treatments with fertilizer, above 93% for seedlings of *C. montana* (Fig. 26a), although it did not show statistical significance (Table 19). However the full fertilizer treatment showed one of the highest survival rates among treatments (98.1%), although this treatment showed much lower performance for both plant growth parameters in comparison with Low fertilizer with devitalized AMF, the latter treatment had an height increment of 36 cm and a RCD increment of 0.57cm (Figs. 26b & c).

T. chrysantha was subjected to treatments with and without shade. Treatment was found to be a significant factor in plant survival (*P*=0.001) with similar results between full fertilizer and low fertilizer with devitalized AMF (Fig. 27a). In general, plants with shade slightly outperformed those without shade with a notable exception for full fertilizer treatment and low fertilizer treatment with devitalized AMF in RCD increment.

The performace of *T. chrysantha* without shade revealed that low fertilizer with devitalized AMF was more successful for stem height increment (18cm) and RCD increment (0.43cm) (Figs. 27b & c). As for *C. montana,* full fertilizer treatment showed the lowest growth, particularly for height increment (7cm), among all the treatments. In terms of plant quality the treatments with fertilization followed a similar pattern to *C. montana* with a dominance of regular plant quality but the plants without shade treated with low fertilizer with devitalized AMF had 30% good quality plants, which was higher than other treatments.

H. americanus was the only species to show its maximum height and RCD increment under the full fertilizer treatment 12.5 and RCD of 0.45 cm, respectively (Figs. 28b & c), although this treatment had the lowest percentage for survival (70.3%), which was less than the control treatment (76%) (Fig. 28a). It demonstrated that the most successful treatment for plant growth may not be the same one as for survival. The control treatment for plant growth was less successful than other treatments; the height increment was even negative (minus 5.8 cm), due to stem dieback, likewise the RCD increment was lower than other treatments (0.05 cm). This species contains similar proportion between bad and regular categories within the treatments with fertilization. The results of Low fertilizer with devitalized AMF had a slight stem dieback of -0.35 cm (Fig. 28b) and the survival percentage in this treatment was the highest (87 %) (Fig. 28c).

4.4.2 Effect of AMF on survival, height increment, and root collar diameter increment of tree species two years after planting

As previously mentioned, *C. montana* under Low fertilizer with devitalized AMF responded most positively with respect to plant growth; however, the next most successful treatment was Low Fertilizer accompanied by living AMF with a height increment of 21.2 cm but in terms of RCD increment the living AMF treatment without fertilizer was slightly better with 0.21 cm. Plant growth did not respond well to the living AMF alone, the 14.4 cm increase was less than the control group (Fig. 26b). The quality of the treated seedlings in general were predominantly in the regular category and only low fertilizer with living AMF treatment had a higher percentage of good quality (28%) in comparison to the others – although lower than the control seedlings. (Fig. 26d).

Similar results were found for *T. chrysantha* exposed to full sunlight where again the best treatment was Low fertilizer with devitalized AMF followed by Low Fertilizer in combination with living AMF for height increment with 12 cm. The remaining treatments had similar results for height increment; full Fertilizer (7 cm), control (6.9 cm) and living AMF (6.4 cm) in descending order (Fig. 27b). RCD increment showed similar results, Low fertilizer with living AMF (0.29 cm), living AMF (0.26 cm) and Control (0.18 cm) (Fig. 27c). Among all the treatments, the percentage of survival is above 70% but interestingly the living AMF treatment contributed to the highest percentage of survival (94.4%)(Fig. 27a).

On the other hand, low fertilizer with devitalized AMF had 30% of good plants (without shade), the only treatment with high plants quality in comparison with other treatments (Fig. 27d).

The results were contrary in the case of *H. americanus* as full fertilizer had a positive effect. Interestingly, living AMF treatment was the next best for height (8.7 cm), however, RCD increment was best under low fertilizer with living AMF treatment (0.31 cm) after full fertilizer. As this last treatment had 23% of good plants, the only treatment with plants quality in comparison with other treatments (Fig. 28d), this indicates that in spite of taller individuals with full fertilizer treatment the quality of plant increases in combination with living AMF.

4.4.3 Effect of shading and its interaction with treatments on survival and growth performance of *T. chrysantha*

The shade seems to improve the plant growth performance, mostly under all the treatments, although it did not show a high statistical significance neither for height increment (P=0.095,$_{\text{Ms 2.347,F 2.890}}$) nor RCD increment ($P$=0. 725,$_{\text{Ms 0.074,F 0.125}}$). However, the tendency of seedlings exposed to shade showed that the maximum height increment was beneath low fertilizer with devitalized AMF (20 cm) but the lowest values even with shade were given beneath full fertilizer treatment, while for RCD increment the Low fertilizer with living AMF treatment produced the highest performance (0.4 cm), although similar results was produced among all the treatments (Figs. 27 b & c).

The interaction shade × treatment did not improve height and RCD increment, which was not statistical significant either (P=0.988, $_{\text{MS 0.065, F 0.081}}$) height increment; P=0.525 $_{\text{MS 0.479, F 0.809}}$ RCD increment). It is interesting that under the effect of living AMF and combination with shade, the survival percentage was higher 96.3 % in comparison to all the treatments and slightly superior of those plots without shade 94.4% (Fig. 27a).

In regard to plant quality, in general, all the treatments with shade are dominated by regular category. However, seedlings under Low fertilizer with living AMF had a 31% of good plants (Fig. 27e). It demonstrated that low doses of fertilization and living AMF may contribute to increment the quality of plants on the Pasture site.

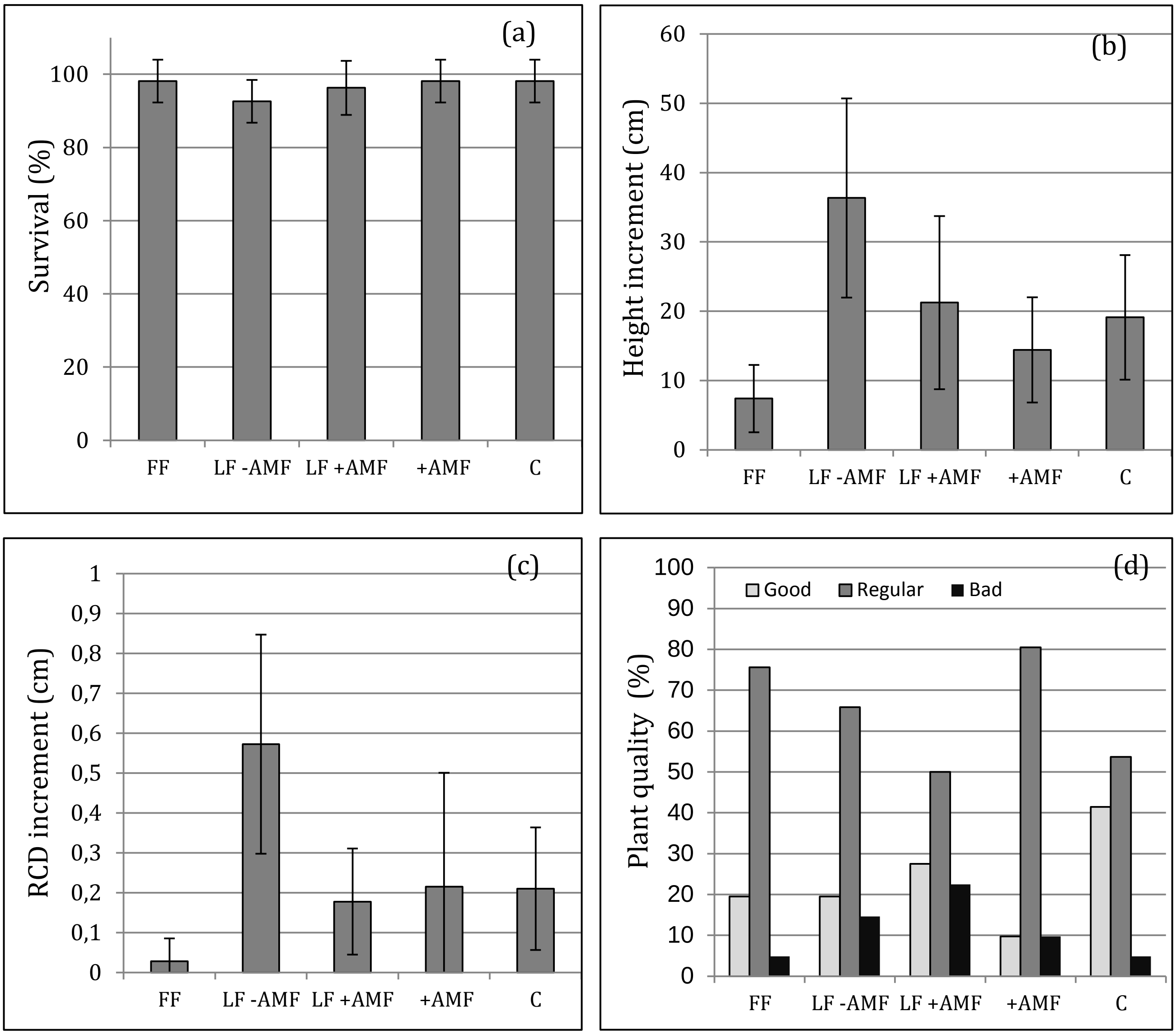


Figure 26. Effect of five treatments on (a) survival, (b) height increment, (c) RCD increment and (d) plant quality two years after planting without shade for *Cedrela montana.* FF (Full fertilizer), LF –AMF (Low fertilizer with devitalized AMF), LF +AMF (Low fertilizer with living AMF), +AMF (living AMF), and C (control) ± SD

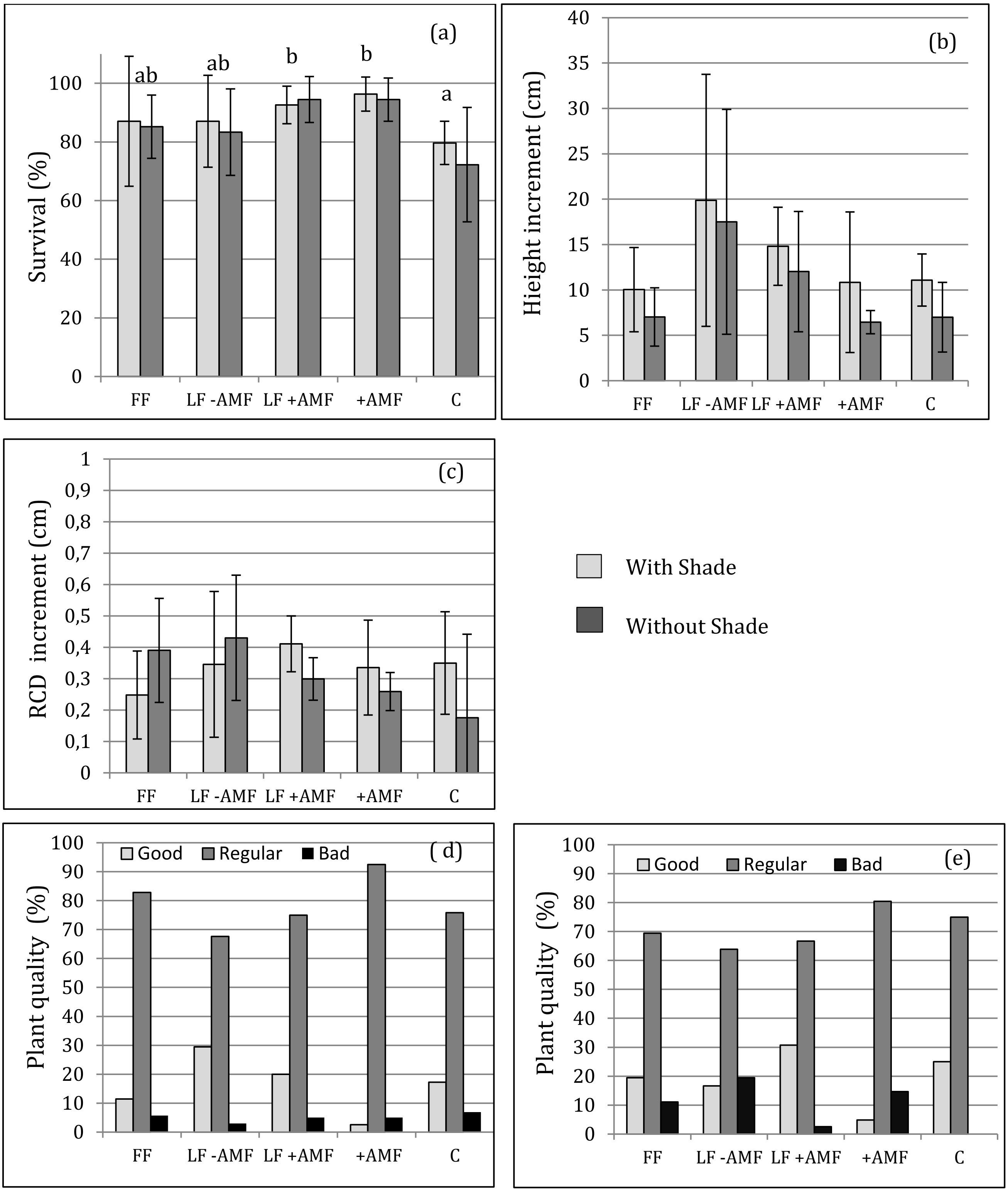


Figure 27. Comparison between five treatments of (a) survival, (b) height increment, (c) RCD increment, (d) percentage of plant quality without shade and (e) with shade after two years of planting for *T. chrysantha.* FF (Full fertilizer), LF –AMF (Low fertilizer plus devitalized AMF), LF +AMF (Low fertilizer plus living AMF), +AMF (with AMF), and C (control). ± SD. The different letters correspond to significant differences according Tukey HSD ($p<0.05$)

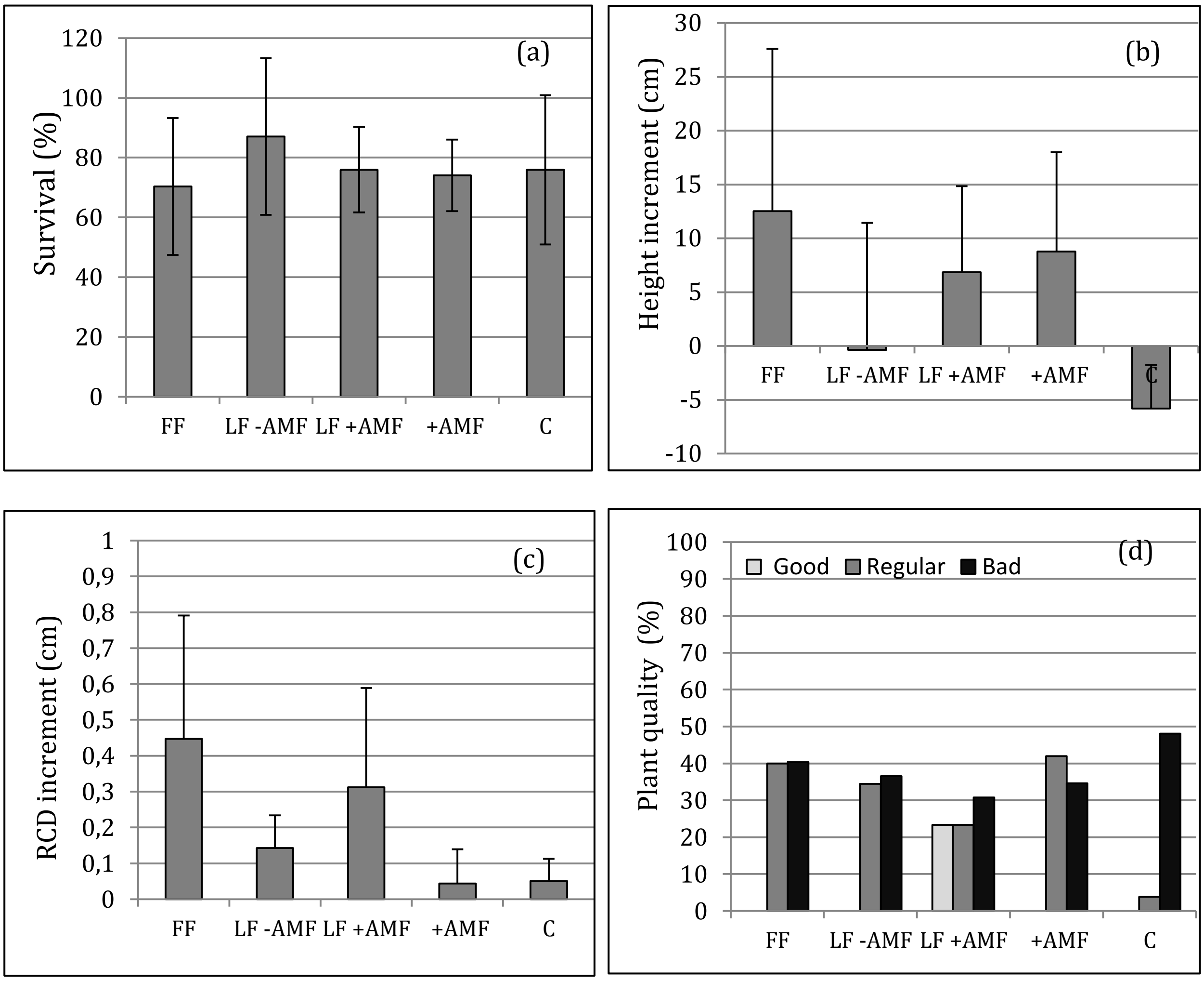


Figure 28. Efffec of five treatments on (a) survival, (b) height increment, (c) RCD increment and (d) plant quality two year after planting without shade for *Heliocarpus americanus*. FF (full fertilizer), LF-AMF (Low fertilizer with devitalized AMF), LF + AMF (Low fertilizer with living AMF), + AMF (living AMF), and C (control) ± SD

Table 19. Analysis of Variance per species using treatment as factor of analysis

	MS	F	Sig.
Height increment (cm)			
C. montana	2.046	0.828	0.520
T. chrysantha	0.557	0.686	0.605
H. americanus	32.677	0.221	0.924
RCD increment (cm)			
C. montana	6.154	2.802	0.059
T. chrysantha	0.596	1.006	0.413
H. americanus	0.185	0.483	0.748
Survival (%)			
C. montana	0.006	0.187	0.943
T. chrysantha	0,234	5,531	0.001
H. americanus	0.063	0.568	0.688

MS= Mean square and F-value
RCD= Root collar diameter

4.5 Rhizotron experiment

The results from this experiment have certain particularities that are important to clarify; for example, the grass competitor was well established in the rhizotron conditions from the beginning of the experiment, thus the replacement of tree seedlings due to mortality has already been done in competitive conditions

4.5.1 Root Length density (RLD) of *S. sphacelata*

The grass *S. sphacelata* was the most successful species producing the greatest RLD over time in combination with all tree species, with being time statistically significant when the plants where growing with competition and fertilization (P=0.000; Table 20). A pattern of height increment from 16 to 24 weeks was observed across species, more likely related to suitable environmental conditions in the nursery which could influence in such increment. The maximun RLD (0.12 cm/cm^3) of the grass was observed at 24 weeks with fertilization when it was accompanied by *T. chrysantha* and *A. acuminata*. Under the combination of grass plus tree species, the addition of fertilzer seemed to improve the RLD with exception of *C. montana* at 24 weeks. The interaction time × Fertilizer was not significant for *T. chrysantha (P*=0.250; Fig. 29b) and *A. acuminata (P*=0.839;Fig. 29c), except for *C. montana* which was slightly significant *(P*=0.054; Fig. 29a). The latter result indicates the effect of fertilization vary according to time.

Table 20. Repeteated measures for the root length density for grass species *S. sphacelata* under competition and application of fertilizer

	Competition (4-24 week)			Application of fertilizer (16-24 week)		
	MS	F	Sig.	MS	F	Sig.
C. montana						
Time	4.822	44.552	0.000	3.511	92.039	0.000
Time × Fertilizer				0.138	3.608	0.054
T. chrysantha						
Time	2.365	4.707	0.009	7.196	41.537	0.000*
Time × Fertilizer				0.280	1.618	0.250*
A. acuminata						
Time	4.276	14.052	0.000	2.605	31.196	0.000
Time × Fertilizer				0.015	0.178	0.839

*Greenhouse-Geisser correction
MS= Mean square and F-value

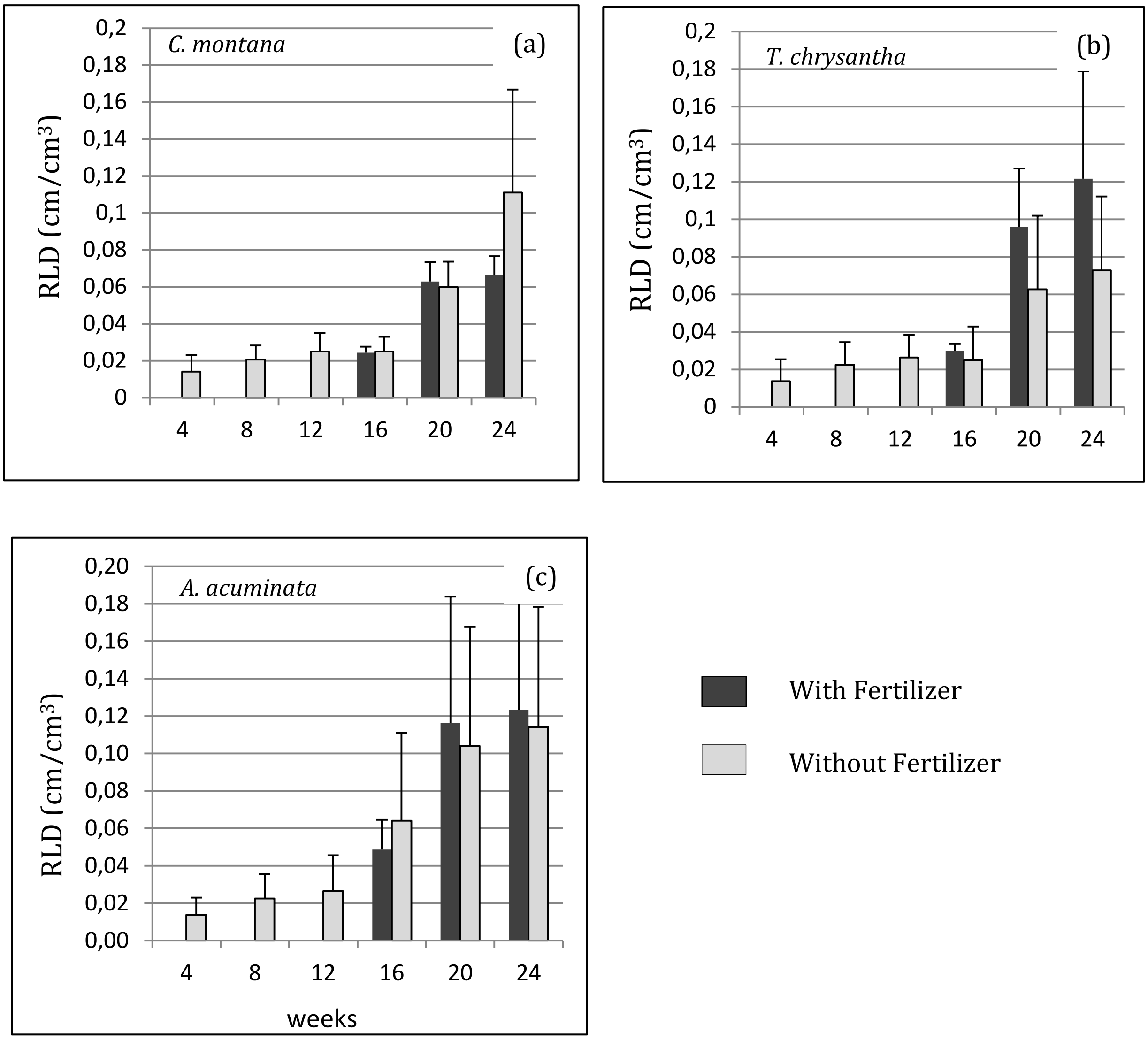


Figure 29. Effect of fertilizer over time on root length of S. sphacelata in combination with (a) *Cedrela montana*, (b) *Tabebuia chrysantha* and (c) *Alnus acuminata*

4.5.2 Root length density (RLD) of tree species

Table 21 shows that there was a reduction of individuals over time during the experiment; hence the results are in some cases based on one individual seedling, particularly at the end of monitoring. This is due to either the roots were not visible in the glass even if the seedlings were alive, or the roots did not present any development over time.

Table 21. Total number of individuals per each species under the effects of competition, fertilization and its combination from 4 to 24 weeks

		weeks					
Species	**N**	**4**	**8**	**12**	**16**	**20**	**24**
Cedrela montana							
Competition							
Fertilizer	5	4	3	2	2	1	1
Without fertilizer	5	4	3	3	2	2	1
No competition							
Fertilizer	5	5	5	4	3	2	1
Without fertilizer	5	4	4	4	4	3	3
Tabebuia chrysantha							
Competition							
Fertilizer	5	4	3	3	2	2	2
Without fertilizer	5	5	4	3	3	3	2
No competition							
Fertilizer	5	4	4	4	3	2	2
Without fertilizer	5	5	4	4	4	2	1
Alnus acuminata							
Competition							
Fertilizer	5	4	4	3	2	1	
Without fertilizer	5	5	4	4	2	2	2
No competition							
Fertilizer	5	5	5	3	1	1	1
Without fertilizer	5	4	4	4	3	2	2

In general, a similar pattern across species was found where RLD decreased at 16th week, particularly in the treatments such as competition and competition with fertilizer (Figs. 30a, c & e). This fact may be associated to the fast mortality of roots in such small seedlings in the period of high temperature and low relative humidity registered in December (2008) and March (2009) in the nursery (Loaiza 2010). However, the effects on RLD of the tree seedlings seem to be stronger under competition.

Another pattern is given for *C. montana* and *T. chrysantha,* which had poorer RLD development over time in all the treatments in comparison with *A. acuminata*. *C. montana* under competition showed that the RLD decreased over time, it seems that during the phase of adaptation, seedlings of *C. montana* produced roots whose consequent mortality can explain the decreasing of RLD. However, between 16 and 20 weeks a slight increment was observed (Fig. 30a). The addition of fertilizer did not improve the RLD of the tree seedlings, therefore it is assumed that the grass takes advantage of the nutrients at least at 16 and 20th week as showed in Fig. 29a. On the other hand, seedlings without competition also reacted negatively over time although the maximum value was registered at 8th week; here the application of fertilizer seems to enhance the RLD (Fig. 30b). In general, there are significative differences among treatments (*P*=0.008) but not among weeks (Table 22). Thus, beyond the stress of competition for *C. montana*, this species was not well adapted to the rhizotron conditions and the application of fertilization without competition may support root development, however in pastures sites dominated by *S. sphacelata* the total control of grasses will require enormous efforts.

T. chrysantha showed an increment of RLD under the effect of competition from 4th to 12th week, which may be a sign that competition stimulated the root length density of tree seedlings, although at 16th week a rapid decrease occurred although a recovery of RLD was subsequently observed. The addition of fertilizer to the seedlings with competition showed an enhancement of the RLD (Fig. 30c). The seedlings without competition (control) had similar values of RLD from 4th to 12th week but in the following weeks this parameter decreased. The addition of fertilizer to seedlings without competition caused a slight improvement of RLD mainly at the beginning (16th week) (Fig. 30d). The factor treatment did not show significance (Table 22) but the factor week showed a high significance (*P*=0.0002).

A. acuminata, on the other hand, seems to be stimulated by competition to produce a better RLD than other species; an increment of RLD has been observed from 4 to 12 weeks. In spite of its decrease in the 16th week, a subsequent development of root length was observed. Nevertheless, the addition of fertilizer contributed notably to increasing the root length density (Fig. 30e). In general, this indicates the capacity of *A. acuminata* to face root competition.

Surprisingly, seedlings without competition (control) and with further addition of fertilizer responded with the lowest values of RLD (Fig. 30f) suggesting that the roots obtained the required nutrients without further growth. Overall, the treatment factor was significant (*P*=0.002) as was the interaction treatment × week (*P*=0.001).

Table 22. Linear Mixed Model analysis for the root length densitiy of tree species

	p-value		
	C. montana	*T. chrysantha*	*A. acuminata*
Treatment	0.0008	0.2604	0.0002
Week	0.1620	0.0002	<0.0001
Treatment × week	0.9603	0.6229	<0.0001

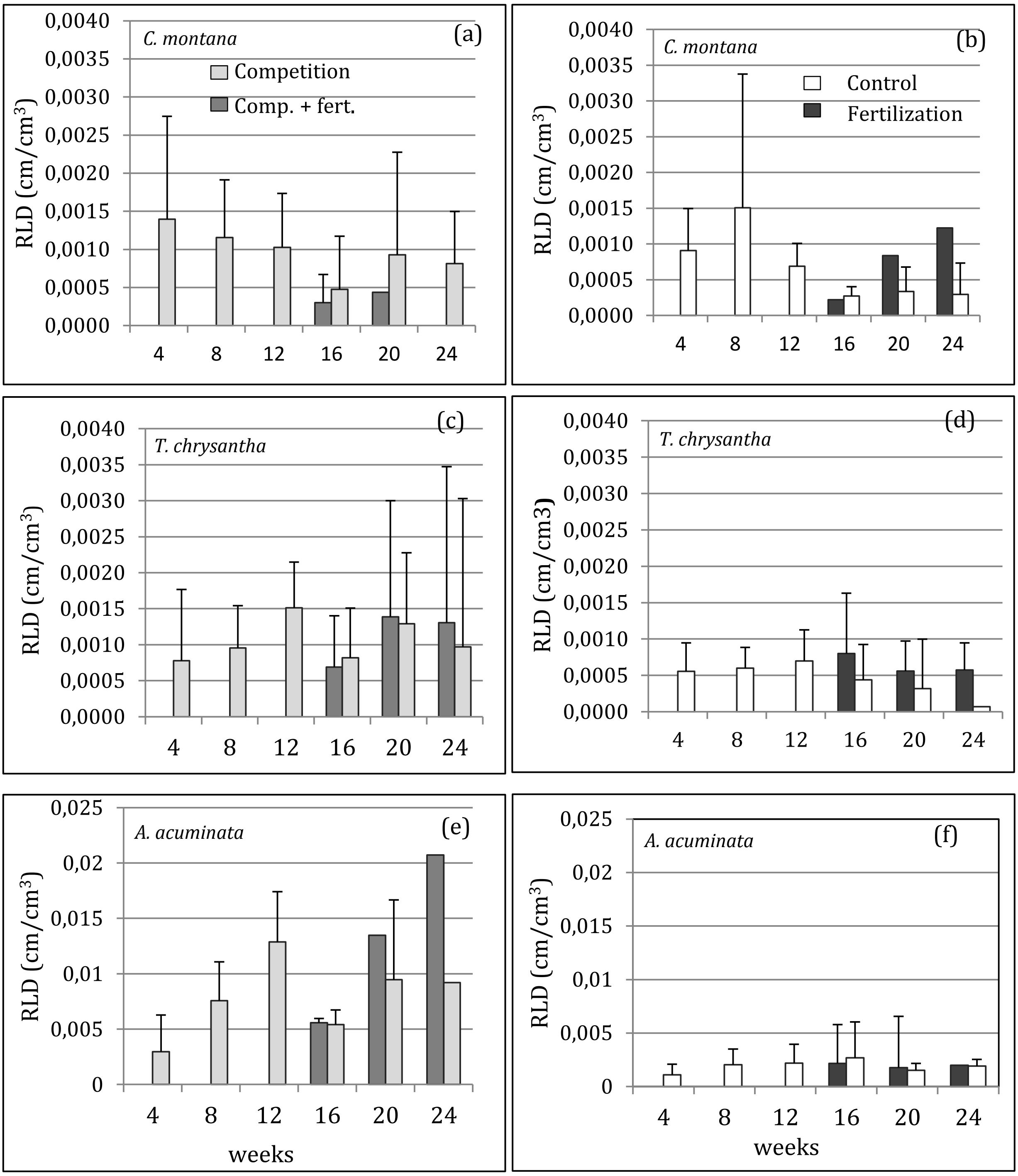


Figure 30. Root lenght density (RLD cm/cm³) with and with out competition, and addition of fertilizer (a-b) *Cedrela montana*, (c-d) *Tabebuia chrysantha*, (e-f) *Alnus acuminata*

4.5.3 Above- and below-ground biomass allocation for *Setaria sphacelata*

As expected the amount of above- and below-ground biomass allocated by *S. sphacelata* was higher in comparison to tree species. Nevertheless, a clear tendency has been observed to produce more above-ground biomass than below-ground biomass in combination with each tree species tested in the experiment (Figs. 31a & b) although not statistically significant (Table 23). Furthermore, there is no difference of biomass allocation neither above nor below-ground biomass across species (Table 23). The addition of fertilizer seems to lead to more on above-ground biomass allocation particularly in combination with *T. chrysantha* and *A. acuminata* (Fig 31a; Table 23). In regard to above-ground biomass allocation, the maximum value has been observed when the grass was associated with *A. acuminata* (18 g) under fertilizer while for below-ground biomass the maximum value of the grass has been registered accompanied by *C. montana* (10 g). The interaction between species × fertilizer did not show statistically significance either (Table 23). Overall the results indicate that the biomass allocation of grass does not depend on the tree species combination or fertilization (Figs. 31 a & b).

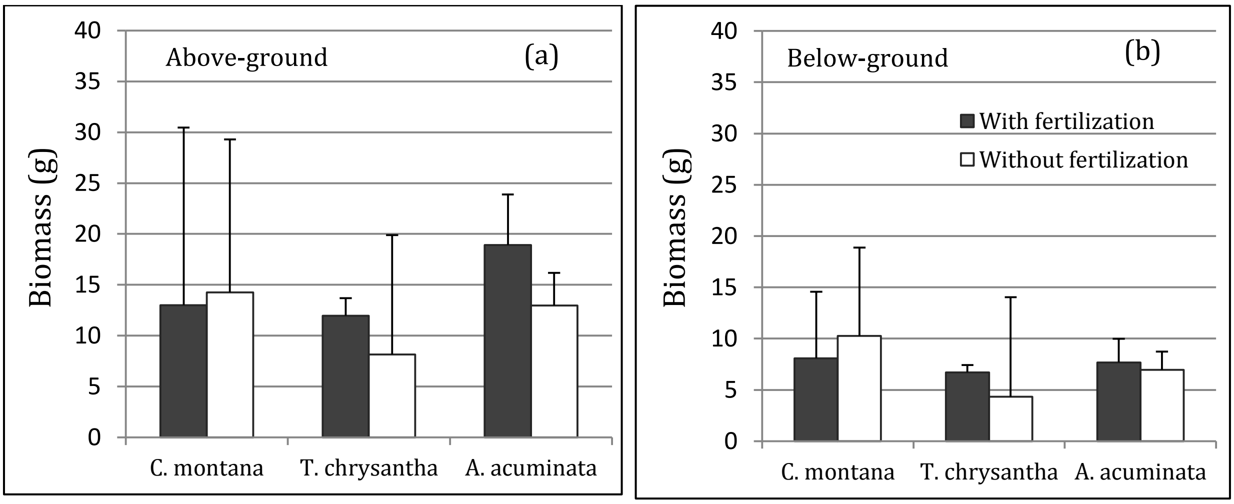


Figure 31. Biomass allocation of *S. sphacelata* (a) above-ground, and (b) below-ground

Table 23. Summary of ANOVA for the above- and below-ground biomass allocation of *S. sphacelata*

	Above-ground			Below-ground		
	MS	F	Sig.	MS	F	Sig.
Species	0.057	0.061	0.941	0.158	0.193	0.826
Fertilizer	1.163	1.253	0.277	0.768	0.936	0.346
Species × Fertilizer	0.022	0.024	0.977	0.013	0.016	0.984

MS= Mean square and F-value

4.5.4 Above- and below-ground biomass allocation of tree species

Tree species showed a similar pattern of biomass allocation mainly above-ground, therefore the biomass ratio between above and below-ground seems to be unbalanced (Figs. 32 a, b & c). However, special features among treatments were observed, for example, *C. montana* had the poorest above- and below-ground biomass allocation beneath competition and competition plus fertilization treatments (Fig. 32a). It may indicate that the competition with *S. sphacelata* might be detrimental for growth of *C. montana.* The fertilizer and control treatments lead to slightly more allocation of above-ground biomass than the first two treatments described. The maximum value for biomass allocation was given in the control treatment (above 0.06 g and below 0.02 g) whereas the lowest values were registered under competition treatment (above 0.01 g and below 0.01 g).

T. chrysantha showed a similar negative effect as shown for *C montana* for both treatments, (single competition and competition plus fertilizer) (Fig. 32b). These treatments had the lowest values of biomass allocation both above- and below-ground in comparison to fertilizer and control treatments (Fig. 32b). The latter treatments were more successful in the production of biomass indicating that seedlings without competition have the capacity to produce more biomass. This clearly shows that *S. sphacelata* has the capacity to inhibit the development of *T. chrysantha* seedlings.

Interestingtly, *A. acuminata* demonstrated that its tree seedlings under the effect of fertilization produced a high amount of above-ground biomass (0.07g), followed by Competition treatment (0.05 g). These two treatments produced better biomass performance than the combined treatment (Competition + fertilizer) and control (Fig. 32c).

Analysis of variance did not show a significant effect of treatment on the above- and below-ground biomass for any of the tree species. The replacement of individuals did not have any effect on the biomass allocation either (Table 24).

Table 24. Analysis of Variance (ANOVA) for the biomass allocation above- and below-ground for the tree species

	Above-ground			**Below-ground**		
	MS	F	Sig.	MS	F	Sig.
C. montana						
Treatment	2.421	1.840	0.210	3.361	3.057	0.084
Replacement	0.101	0.077	0.788	0.184	0.167	0.692
Treatment × replaced	1.847	1.404	0.304	2.611	2.376	0.138
T. chrysantha						
Treatment	0.079	0.072	0.931	1.371	2.090	0.170
Replaced	1.846	1.685	0.223	3.975	6.059	0.032
Treatment × replaced	0.093	0.085	0.919	1.471	2.242	0.152
A. acuminata						
Treatment	0.027	0.019	0.981	0.060	0.026	0.974
Replacement	0.907	0.639	0.439	0.673	0.292	0.599
Treatment × replaced	0.243	0.171	0.845	0.183	0.080	0.924

MS= Mean square and F-value

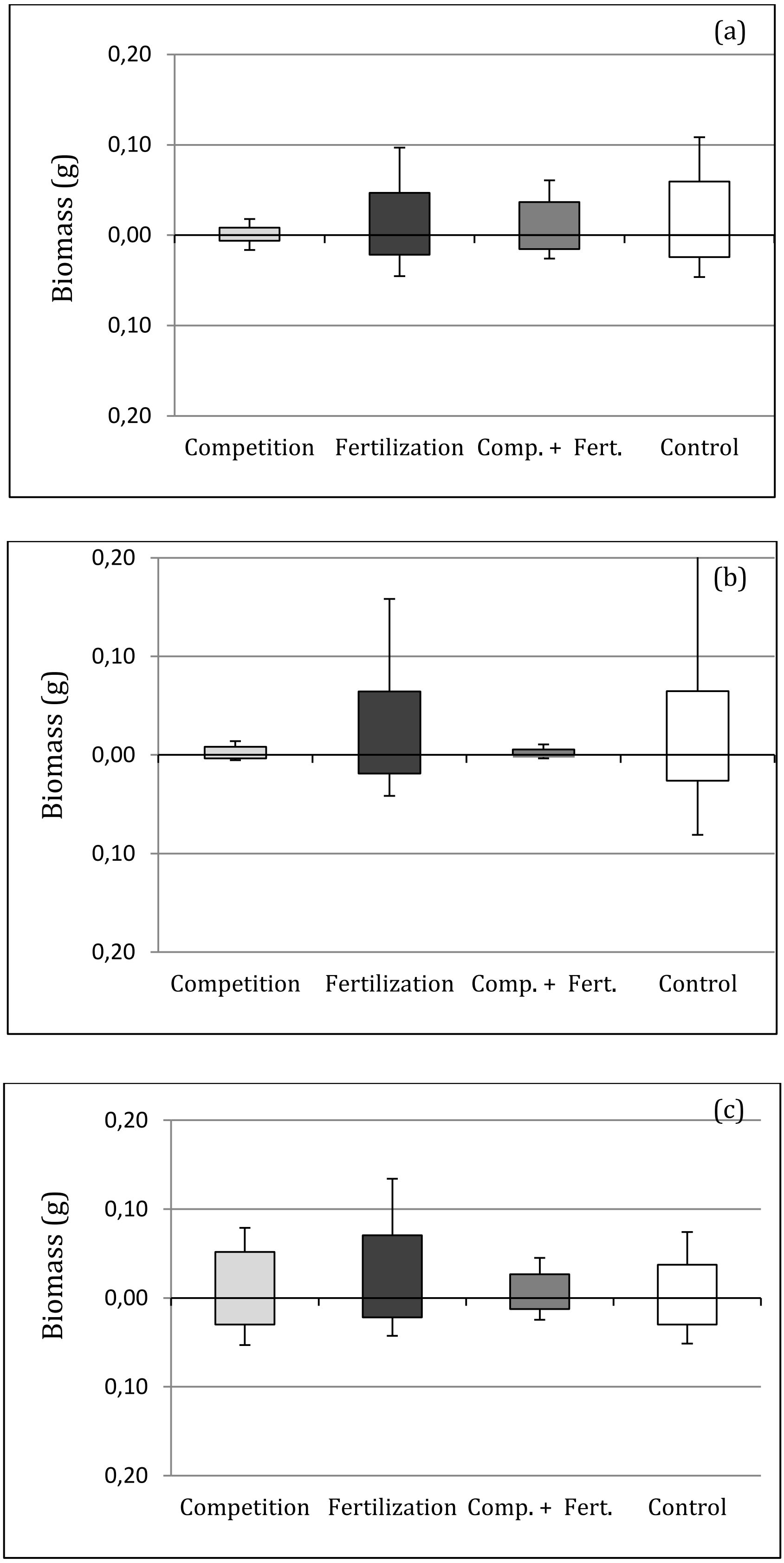


Figure 32. Above- and below-ground biomass allocation (a) *Cedrela montana* (b) *Tabebuia chrysantha*, (c) *Alnus acuminata*

5. Discussion

5.1 Methodology

5.1.1 Limitations of the experiments

In Aguirre's dissertation (2007) the problems associated with limited knowledge of tree species for reforestation programs in the Andes and low availability of seedlings of native species in the nurseries for reforestation purposes in the region has been addressed very well. However, a concern about pseudoreplication in the experimental design for the reforestation experiment of each successional site representing a single block has not been mentioned before. The corresponding answer is that the three areas are large enough (4 ha each) and the plots were sufficiently widely and randomly distributed to alleviate concerns of pseudoreplication. In addition, the same soil types are represented in all the three sites.

In this study, the behavior of species has been analyzed in a context of pure plantation in spite of the fact that the original experimental design also contained a mixed plantation. However, this data set has to be treated in different analyses due to species such as *A. acuminata* having already developed shade canopy and consequently affected the growth performance of other species. In any case, it is encouraged to diversify the species and combine them properly for restoration purposes.

Yet, many questions remain unanswered in the field experiments; for instance, do different levels of insect herbivores and reduced soil nutrients have negative impacts on planted seedlings and naturally recruited woody species? Gonzales and Ordóñez (2009) identified that *A. acuminata* were attacked by leaf cutting ants (*Acromymex sp.)* and an insect of the family Chrysomelidae (*Chrysochus sp*. and *Agelastica sp*.) produced tree damage. Several studies mentioned that various means of seedling predation (mammals, gopher, rabbit and insects) is another clear factor influencing seedling establishment (e.g. Holl et al. 2000; Alvarez-Aquino et al. 2004). On the other hand, according to personal observation, *T. chrysantha* had leaf yellowing, which could be attributed to nutritional deficiencies or photoinhibition.

In the fertilization and AMF inoculation and shading experiment it was not possible to know beforehand neither spore density nor composition of AMF inoculum. At the same time it was not possible to access the information of removed plants used for the molecular detection of all AMF at species level, and matching plants – AMF, which has been done by Krüger (2012, unpublished data). Therefore, in the respective discussion section it was not possible to address whether the roots were infected or not.

With respect to the rhizotron experiment, a high mortality of plants was found; probably due to the small size of seedlings and their low capacity to resist high temperatures and the low relative humidity in the nursery, particularly in the dry season. To counteract these extreme conditions, the irrigation of plants was increased to daily and the floor surface was kept moist. Based on this experience it is recommended to plant bigger seedlings into the rhizotron to avoid the need for replacements which directly influenced the homogeneity of the experiment, defined by different life span of plants and on the balance of experimental design. Furthermore, in the experimental design more replicates have to be considered in order to get more information because the results showed that the seedlings can stop their root development or even be invisible in the rhizotron over time.

5.1.2 Strengths of the experiments

The first part of the study (Natural succession) explores changes in species diversity and composition both on the three successional sites over time (from 2003 to 2007) in a mountain ecosystem in the Andes. The reforestation experiment shows the development of tree species over 4 or 5 years depending on the species, hence problems such as stem die-back and high mortality in a certain year could be distinguished.

Moreover, the analysis of the current status of the reforestation experiment at 60 months of age is another contribution along with manual and chemical treatment for the future reforestation programs in the San Francisco valley. The inclusion of new species such as *M. pubescens* in the data analysis had an important output for restoration purposes due to the success of this species on the Bracken site. In the Andes of Southern Ecuador, it is probable that this is the only experiment carried out where two restoration alternatives were used.

The experiment of fertilization, AMF inoculum and shading conducted in the field advances restoration techniques. Allen et al. (2001), already suggest that field restoration experiments are an opportunity to understand mycorrizhal responses, particularly in disturbed areas.

5.2 Discussion of the results

5.2.1 Natural succession and tree plantation

5.2.1.1 Dynamic of natural succession

Effects of time and successional sites on the natural succession processes

The Bracken and Shrub sites showed a strong relationship between time, woody species richness and woody species abundance while the Pasture site showed little change over the 48 months period. If we consider the time since the lands were abandoned (0, 12, and 25 years for Pasture, Bracken and Shrub respectively), the rapid increase in woody species diversity on the Shrub site, and especially the Bracken site should be considered surprising; however, this is in line with previous studies; Aide et al. (1995), for example, demonstrated that pasture sites show little development in the first 10 years, and need a full fifteen years to show significant woody development, which explains both the poor development on the Pasture site and the seemingly incongruous development on the Bracken site. Other studies have shown similar trends (e.g. Pascarella et al. 2000; Chinea 2002), which suggest that these two sites may have crossed a threshold and are now following relatively fast successional trajectories. The Pasture site, on the other hand, seems to be in a very slow transitional phase, or may even be non-successional.

Competition or facilitation as triggers of natural succession?

The combination of the successional dynamics of the Shrub and Bracken sites, along with the negative effect of the manual cutting treatment, reveal a strong facilitation effect associated with these two sites as demonstrated by woody volume index.

The negative effect of the manual weeding shows that the supposed competitive species actually provide microhabitat amelioration, possibly through providing the appropriate combination of light and shade for the germination, establishment and survival of seedlings of different species (Vieira et al. 1994; Martinez 2003; Gómez-Aparicio et al. 2008; Dupuy & Chazdon 2008).

Bracken fern has been considered a barrier to regeneration due to its phytotoxic effects (Gliessman & Muller 1978; Dolling 1996; Marrs et al. 2000); however, these results reveal that it is beneficial to the establishment and growth of woody species as demonstrated by Günter et al. (2009) and Douterlungne et al. (2008), who showed that seedlings of *Cedrela montana* Moritz ex Turcz (cedro) in the study area, and *Ochroma pyramidale* (Cav. ex lam.) (balsa) in Chiapas, southern Mexico, developed well under bracken fern. The speculative issue is that the bracken fern provided seedlings protection from high irradiation, rain and wind, as well as shade.

The Pasture site, on the other hand, showed little natural succession over time, thus demonstrating completely different dynamics from the previous two sites. This site had a much lower species richness and abundance and recruitment was very poor. As LAI was shown to be a significant factor for species recruitment, we would expect slower regeneration on this site; however, the cutting back of the dominant grass species *S. sphacelata,* which can reach an average height of 70 cm in only 18 months (Roos et al. 2010), did not have a significant effect on species recruitment. This suggests that competition for light is not significant and there must be alternative explanations for the effect; one reason could be root competition due to the high below-ground biomass of *S. sphacelata* (Eckert 2006) which is better explained in the rhizotron experiment. Moreover, it has been demonstrated in the northwest Ecuador that *S. sphacelata* has an impact on soil nitrogen processes (Rhoades C.C:, unpublished data in Rhoades et al. 1998) which prevents the establishment of other species, or it may be a simple lack of seed dispersal, although if this were the case, more wind-dispersed species should still be present.

It would appear that *S. sphacelata* pastures are highly stable transitional communities and if we wish to promote rapid forest recovery, appropriate treatments need to be found. There are several possible methods to lower the competitive strength of *S. sphacelata* through treatments; for example, by establishing shelter tree systems, using light demanding or pioneer species in order to shade the pastures and consequently reduce or eliminate the strong competition (Celis & Jose 2011). Günter et al. (2009) and Aguirre et al. (2011) suggest that *A. acuminata* could be a suitable species for this process while also acting as a nurse species and perch species thus further facilitating the recruitment of new species.

Dynamics of the floristic compositional change on the three successional sites and their successional trajectory

Over the four years of monitoring, the floristic composition of the Shrub and Bracken sites have become more similar according to the Chao's Sørensen index despite there being a large difference in time since the last anthropogenic impact (fire); ordination seems to show that the two sites, rather than following exactly the same successional trajectories, are following parallel ones. So far it is still not clear whether the vegetation at the different sites is converging towards a common 'final state'.

Historically, the Pasture site has received very different influences from the Bracken and Shrub sites: The Pasture site was cultivated with *S. sphacelata,* followed by intensive grazing and probably suffered soil compaction through cattle trampling as on other pasture sites in the tropics (e.g. Martinez & Zinck 2004). Moreover, due to the strong competition of *S. sphacelata*, the Shannon index of the Pasture site changed little between 12 and 48 months which may indicate an alternative stable state - a degraded non-successional community with only a few species having been able to establish themselves on the open area and reassemble the community (Verdú et al. 2009), although there is evidence that slow transient successional change is occurring.

The results do not support the hypothesis of a chronosequence of succession as none of the successional trajectories on the sites are linear. The Pasture site shows no clear trajectory at all which means it could either follow an inhibition model (Connell & Slatyer 1977) or a model of deflection or arrested succession generated by *S. sphacelata* (Sarmiento 1997).

Overall, the results agree with Bakker et al. (1996) in that the greatest influences on successional pathways and the dynamics and speed of recovery are inextricably linked to site history. The evidence suggests that the Shrub and Bracken sites are following different, yet equally fast successional pathways.

Removal of competing ground vegetation

The weed-removal technique applied in this study was found to have a negative effect on species richness. Although in most of cases it was not statistically significant, there was an obvious difference in the species richness on the Bracken and Shrub sites.

These differences could be due to the facilitation effect of the dominant species on the Bracken and Shrub sites being in fact far greater than first suspected, while the regrowth rate of *S. sphacelata* on the Pasture site may have been too vigorous to significantly assist the recruitment of woody species.

These findings are in line with studies in Brazil (Sampaio et al. 2007) and Panama (Hooper et al. 2005), which also suggest that a significant factor may be that naturally regenerating seeds suffer morbidity due to treatments, and that seed availability may also be a significant factor in recruitment.

Is competition a major limiting factor on these sites?

The indicator species analysis revealed differences between the sites regarding species richness and abundance. There is evidence that the structural complexity of vegetation on the Bracken site is still behind the Shrub site as the area is still dominated by wind-dispersed pioneer species. This suggests that animal seed dispersers are less attracted to this site, probably due to lower abundance of perch trees and food (Guevara et al. 1986; Slocum 2001). The same analysis showed that on the Shrub site, species reliant on vertebrate seed dispersal became more prominent over time, suggesting that the presence of woody life-forms stimulated the activity of birds and thus facilitated seed dispersal as previously described in other studies (Vieira et al. 1994; Holl 1998b). This seed-dispersal mechanism is probably limited to birds, and possibly bats, as the physical barriers of the river and the road would likely prevent small mammals from migrating to the recovering areas.

These seed-dispersal syndromes may provide us with some insight into the limiting factors for woody-species recruitment. On the Pasture and Bracken sites, the species are exclusively wind-borne, while the majority of significant species on the Shrub site are dispersed by animals. This would suggest that a limiting factor, which also affects community structure, is seed availability. The sites would appear to have differential attractiveness to seed dispersers, which may be an effect of less complex vegetation structure, thus limiting seed dispersal on the Pasture and Bracken sites. Other studies have shown that seed availability is a major limiting factor in forest recovery (Wijdeven & Kuzee 2000) along with distance from primary forest (Holl 1999). To assist succession on these sites, it might be appropriate to make them more attractive to seed dispersers with the addition of perch trees or planting of trees to artificially increase the attractiveness of these sites. This has been shown to be effective in many cases (Hooper et al. 2005; Holl et al. 2000)

It can be concluded that manual treatments are definitely inappropriate for these sites. However, it should be added that other treatments might be effective as, for example, herbicides have proven to be apt for reducing competition stress in other cases (Griscom et al. 2009), although in restoration, only herbicides with relative low toxicity and low persistence are acceptable (Davy 2002). Glyphosate, for example, used successfully in a reforestation experiment in the research area, was found to be the most appropriate grass-elimination treatment to improve tree growth on pastures (Weber et al. 2008).

Overall, the natural regeneration on the three sites is ongoing, although somewhat hindered on the areas cultivated with *S. sphacelata.* It appears that the Shrub and Bracken sites will reach secondary forest stage without human interference relatively quickly, although physical barriers may prevent the establishment of a community comparable to the reference forest. The results for the Pasture site remain less conclusive, although restorative actions would be required if fast recovery is desired.

5.2.1.2 Reforestation experiment

Aspects of facilitation and competition

The influence of different land use history and intensity on each site may be reflected by their current environmental conditions (floristic composition, availability of light, organic matter content, etc). In the three study areas Aguirre (2007), Weber et al. (2008) and Günter et al. (2009) have already mentioned that there is a species–specific adaptive capacity for responding to intrinsic conditions in each site in the first three years of plantation. The success of tree plantation depends on the strategies of tree species to cope with dominant and aggressive exotic species such as *S. sphacelata* and *P. arachnoideum* on the Pasture and Bracken sites, respectively. Many authors concur with negative effects of grasses on tree establishment (e.g. Rhoades et al. 1998, Holl et al. 2000) which can produce high above-ground competition (Celis & Jose 2011) and below-ground competition causing stress and consequently disadvantaging tree species (Loaiza 2011). *S. sphacelata* can also contribute to soil carbon loss and presumably nitrogen and phosphorus loss (Makeschin et al. 2008).

On the other hand, many native species, in particular mid-successional species, may have problems due to different aspects such as; low seedling quality inherent from their genetic pool, poor seedling cultivation in the nursery, and applying inappropriate planting techniques. The synergy of all of these, or even the effect of just one of them, may be responsible for the success or failure of plantation. These aspects are little known or studied in the Andes region of Ecuador (Stimm, personal communication).

P. arachnoideum has already mentioned as an aggressive weed, and in studies conducted by Roos et al. (2010), it was revealed that its complete removal was not possible on the Bracken site in the study area using various treatments. With its aggressive nature, and allelopathy or phytotoxic effects on other plants (Marrs et al. 2000; Dolling 1996), it should interfere in the development of tree species and therefore no species should have high performance under the cover of bracken fern. However, in the weeding experiment, where *M. pubescens* was studied, the results showed a good adaptation to the Bracken site conditions at 60 months.

Based on previous findings, the vegetation structure present on the Shrub site is an indicator of facilitation; providing a favorable habitat for the development of other species such as *T. chrysantha*. However, for other tree species (e.g. *C. montana*) the presence of neighboring vegetation may produce suppression of growth due to the liberation of chemical compounds into the environment (Lambers et al. 2008).

By examining the behavior of species such as *C. montana*, which have a high growth performance on the Pasture site but a poor survival rate, a new prediction for micro-site effect arises from this study: Specific tree species grow better in specific micro-sites. This has also been shown by Carpenter et al. (2004), who found a spatial heterogeneity in growth of trees where species grew well in less degraded areas. The topography in the Andes is irregular and generates a variety of habitats; hence in the natural forest in the San Francisco valley (Reference forest) with the incidence of land-slides promotes high habitat heterogeneity on a small scale (Wilcke et al. 2003). Furthermore, it has been proved that one of the causes for high tree diversity is the existence of topographic gradients with a small-scale mosaic of edaphically different habitats (Homeier et al. 2009); likewise, the topographic position contributes to the quantity and quality of epiphytic biomass in the same natural forest (Werner et al. 2012). If the same criterion can be transferred to the three successional sites in the context of tree species adaptation and their relationship with micro-site and nutrient concentration, then reforestation on a landscape level has to be carried out by planting specific groups of trees according to topographic or soil characteristics to create favorable conditions. A cluster of trees has been recognized as a forest restoration strategy (Guevara et al. 1986; Corbin & Holl 2012) and generates a lower cost in comparison to plant seedlings in large areas (Holl et al. 2011). It should be also borne in mind that a species mosaic agrees with the general idea of placing species into the landscape (Lamb 1998).

Differences between early- and mid-successional species

Early successional species

Although *H. americanus* theoretically requires high light intensities to grow, this species showed little adaptation to the open areas, although only the few remaining and best individuals are on the Pasture site. The high mortality of *H. americanus* coincides with the study of Holl (2002) who examined *Heliocarpus appendiculatus* Turcz in three types of abandoned pastures in seasonal montane wet forest in southern Costa Rica. From this it can be surmised that *H. americanus* not only requires light to establish in open areas, but its growth may also be associated with other abiotic factors such as well-drained soils and nutrients sources (Paul et al. 2010).

A. acuminata can cope with the aggressiveness of grass due to its better root length density in comparison with *C. montana* and *T. chrysantha* shown by the rhizotron experiment. Ortega-Pieck et al. (2011) also found that in the mountain region in Mexico *A. acuminata* planted on sites dominated by exotic grass (*Cynodon plectostachyus*) grew better in stem height but had lower survivorship than on sites dominated by native grass. This behavior has been documented as a reaction to notably competitive environments. This species is also associated with nitrogen-fixing bacteria and fungi species (Becerra et al. 2007) which contributes to its ability to establish well on degraded lands. This promising growth performance of *A. acuminata* on grasslands has made it a species frequently requested by landholders for reforestation and watershed conservation programs in Andean countries, although a study of an alder plantation in Colombia showed low efficacy for the establishment of species diversity (Murcia 1997).

Consequently, in the San Francisco valley, the biodiversity and recruitment of the understory of areas planted with *A. acuminata* on the Pasture site are continuously monitored and compared to the diversity of the adjacent natural forest (Reference ecosystem).

Mid-successional species

Overall, the response of mid-successional species in the experimental plantation showed a slower growth performance and lower survival than early-successional species as was expected. This finding is in line with other studies (Menalled et al. 1998; Davidson et al. 1998). In spite of *J. neotropica* being considered a multipurpose species (Gerique 2010), thus being thought a promising species for reforestation programs in the highlands in Ecuador due to its high performance; it did not show good adaptation to any of the three successional sites. There are two main reasons that might explain this finding. Firstly, field observations showed that this species was attacked by the insect *Gretchena garai* Miller especially on the Pasture site. This insect has been described as a new species near Loja and injures the leader shoot of *J. neotropica* (Miller 1987). These negative effects of insect attacks or fungus on the plantations have been demonstrated by several other authors as well (e.g. Plath et al. 2011; Garen et al. 2009). Secondly, the presence of *J. neotropica* in the nearest natural forest has not been registered yet according to the checklist of vascular species (Homeier & Werner et al. 2007). It is possible that this species does not fit the specific environment conditions of the reforestation site. Pedraza & Willimans-Linera (2003) also found a poor performance for *Juglans pyriformes* in terms of height growth in degraded and grass-dominated sites in a Mexican cloud forest area. This may indicate a sensitivity of *Juglans* to critical climatic factors, insect attacks and adaptation to degraded lands.

On the Shrub site where shelter species are supposed to provide shade, *C. montana* was not as successful as expected. Even an apical-dieback was registered, which may be caused by biotic or abiotic stress, for instance by mineral or water deficiencies (Zech et al. 1989 cited in Zech & Drechsel 1991). A better survival was detected on the Bracken site (up to 60%, n=96), although the plants had a smaller size compared to the Pasture and Shrub sites. In this same line, Plath et al. (2011) found that *Cedrela odorata* in pasture-afforestation in the lowlands of Panama had low survival rates (48%, n=140).

They suggested that high competition of grasses or shrubs may be detrimental to seedling growth.

T. chrysantha had notably better growth performance over time on the Shrub site. It may be assumed that there is protection of shelter shrubs or trees which create positive microclimatic conditions and support by adding organic matter to the soil (Viera et al. 1994). The survival of this species was high in all the successional sites; the same high survival trend was found for *Tabebuia rosea* (98%, n=294) after two years of plantation in the lowlands in Panama (Plath et al. 2011). Similar results were found in the lowland of Puerto Rico for *Tabebuia heterophylla,* which has been the most abundant species in a reforestation trial over 55 years in a Pasture site (Silver et al. 2004). It suggests an inherent ability of the genus Tabebuia to resist and adapt to a wide range of land degradation.

If the best growth development and survival occur on the Shrub site, this gives an idea of the importance of silvicultural contributions such as enrichment using late-successional species in the Andes of southern Ecuador with the aim of protecting and managing large areas of secondary or regrowth forest (Lamb 2005).

Undoubtedly, the fast growth increment of early successional species has an advantage over mid-successional species, although an adequate combination of different species in different stages of development may not only facilitate the growth of valuable trees but also enhance native species richness and community structures, which are important attributes of biodiversity (Clewell et al. 2000). A good choice of species must be based on their ecological status, the land-use of degraded lands, as well as stakeholder's requirements.

Relationship between water holding capacity and growth performance and survival

The study revealed that WHC could not be correlated with any effect on the growth and survival of native species. A possible explanation could be related to the high amount of rainfall and high atmospheric humidity typical of the study area which negated any effect, although the water status of a seedling is not dependant only on soil water, but also on its transpiration demands and thermal stress (Holmgren et al. 1997).

This finding is in line with Holl (1999), who found on an abandoned pasture in a seasonal montane wet forest of Costa Rica that seedlings were apparently not limited by available water in the short period of the study. In another study in Puerto Rico soil moisture was tested under fern cover (Dicranopteris *pectinata);* these results indicated higher moisture beneath that vegetation than in open areas (Lawrence 1994).

In spite of favorable climate conditions in San Francisco Valley, on the Pasture site (same study area) Podzols have been found as one type of soil, in the majority of cases sandy substrates encourage the formation of Podzols (Bahr 2007). This could indicate rapid drainage and the successive removal of calcium, manganese, iron and humus compounds as has been found in the tropical lowlands of Malaysia by Andriesse (1970). Likewise, fire events occurred in November 2010 and October 2011 burning several hectares of the Bracken and Shrub sites, respectively (www.tropicalmountainforest.org), which gives an idea of the severity of the dry season. Thus, competition between tree seedlings and invasive vegetation for water resources over a short period of time in any given year could cause water stress and limit plant growth or even cause mortality (Hau et al. 2003; Kursar et al. 2005). Therefore, several measurements of available moisture are needed during the dry season and throughout the year due to the climate variation between years with their respective number of days without rain and high temperatures, which is characteristic in the San Francisco valley.

On the other hand, density, salinity and gravel data were not available for inclusion in the Soil Water Characteristics model, but the variables available can still yield results since soil texture has the dominant effect on soil water with the additional variable of Organic Matter (Saxton & Rawls 2006).

With reference to the analysis of root biomass in the rhizotron experiment, *S. sphacelata* had the highest above- and below-ground biomass allocation compared to tree species and it consumes a high amount of water according to tensiometer measurements (unpublished data). Bracken fern species seem to be tolerant to dry soils and intermittent drought (Cartledge & Carnahan 1971), therefore the competition for water source may be lower and may highlight the facilitation process on the Bracken site.

5.2.1.3 Weeding treatment within the reforestation

Effects of treatment on survival and growth performance

There is a pattern of positive response for most tree species at 60 months age in terms of height performance due to the removal of competitive vegetation although not significantly, only *T. chrysantha* showed a strong positive effect on height and RCD growth on treated plots. As the herbicide application killed the whole weed plant and completely eliminated even the roots due to the translocation of the product within the plant, this indicates that *T. chrysantha* is more sensitive to below-ground rather than above-ground competition because, as mentioned above, this species may need shelter species for its development. During the first 24 months of manual treatment, *T. chrysantha* did not show any response (Aguirre 2007), although Günter et al. (2009) found a positive reaction at 36 months. These results lead to two conclusions; 1) manual treatment is shown to be effective in the third year while 2) the chemical treatment has a more rapid effect on plant performance. Graven et al. (2009) also found that herbicide application significantly improved growth for height and basal diameter for *Terminalia amazonia* and *Tectona grandis* in Panama.

The opposite result was found for *C. montana* because it reacted better in terms of height on untreated plots, thus competition seems not to be the dominant factor in the study area for this species.

The effect of treatment on the root collar diameter for *C. montana, T. chrysantha and H. americanus,* was also positive, while the opposite result was seen for *J. neotropica* in terms of survival because the impact was significantly negative on treated plots; however, this interpretation has to be taken with caution due to the few remaining individuals on the three sites.

The positive tendency of treated plots on basal diameter for *H. americanus* and *C. montana* may be explained by above-ground competition, which is one source of plant stress caused by weed species (Holl 1998a; Archibald et al. 2011), suppressing the development in height but improving the basal diameter growth. This result has been observed since the beginning of the plantation (Aguirre 2007). This finding coincides with results for *Schefflera heptaphylla* (L.) D.G. Frodin (Araliaceae) planted on degraded grassland in Hong Kong (Hau et al. 2003).

J. neotropica showed a poor adaptation to all successional sites, and the application of treatment could not contribute to reducing biotic stress produced by the high interspecific competition and its percentage survival was low as well. This suggests that above-ground competition plus a high irradiance typical in the Cordillera Real (Emck & Richter 2008) is too much for this species due to its trait as a shade tolerant species. In any case, this species seemed poorly adapted to the environmental conditions of the San Francisco Valley, while in other areas of the south of Ecuador (e.g. Saraguro) this species grows in wild and cultivated fields and is used by local people (Gerique 2010).

Even though a non-selective herbicide was applied, there are still certain specifications depending on the target weed species to be controlled. As expected, the poor impact of fertilizer on the survival and plant growth of tree species on the Bracken site is attributed to the low effectiveness of Glyphosate in controlling bracken fern. Some studies have reported that Asulam herbicide is more efficient for bracken fern than other herbicides (Davy 2002; Roos et al. 2010). However, on sites dominated by grasses Glyphosate herbicide is widely used to abolish annual and perennial weeds (Davy 2002).

Some authors recommend a land preparation especially on sensitive soil types, before or during the first years of plantation with the aim of guaranteeing successful plant performance which subsequently compensates high initial labour cost (e.g. Du Toit et al. 2010; Onyekwelu et al. 2011). From the results, this study does not suggest applying any treatment for eliminating weed competition posterior to the establishment of a plantation as significant improvement in the growth performance of trees did not occur with the exception of *T. chrysantha* on the Pasture site with additional features such as natural or artificial shade. Another reason not to recommend pretreatment is that a smallholder in the San Francisco valley most likely cannot afford such a high cost when the perceived benefits are low. Therefore, this study was focused on finding the right species to be planted according to different vegetation types present. However, this study encourages to investigate other promising native species for reforestation as for example *Inga spp.* which are also N-fixing species.

Effect of successional site on survival and plant growth performance

The current stage of the reforestation experiment taking into account all surviving plants clearly shows that early-successional species had a good performance and in some plots they had already formed a canopy at 60 months of age, especially in open areas, where *A. acuminata* could cope with the aggressiveness of *S. sphacelata*. It is also known that early-successional species resist high insolation and consequently higher temperatures (Alvarez-Aquino et al. 2004) although the survival rate is very low, especially for *H. americanus*. This directly contradicts the results of survival in the lowlands of Ecuador where the percentage was above 75% measured at 2.5 years of age (Davidson et al. 1998). This suggests that *H. americanus* requires other characteristics such as high humidity, soil nutrition or a specific AMF associations not found in the study area to survive well. A cause of mortality of seedlings in open areas is desiccation due to increased insolation, high temperatures, and lower relative humidity (Alvarez-Aquino et al. 2004; Holl et al. 2002).

As it is mentioned in the previous section, of the early-successional species *A. acuminata* resulted more suitable to the Pasture site as shown by survival and plant growth while *M. pubescens* showed good performance on the Bracken successional site attributed to its shrub life-form, and its abiotic and biotic requirements fitting well to bracken fern coverage. It is possible that *P. arachnoideum* may share the same habitat with other species without producing strong competition or its presence helps to reduce other negative effects as for example high insolation. This shrub is an effective species for restoration purposes because several *Morella* or *Myrica* species form actinorhizal plant symbioses with *Frankia,* which consequently helps N-fixing capabilities (Grayston et al. 1996). Furthermore, the rapid growth of *M. pubescens* can counteract erosion due to the steep topography, as presented by the Bracken site.

This shrub species produced a mean of 3200 fruits/tree, although the percentage of germination is low 8.3 % (Encalada & Alvarado 2010). However, due to its bird seed-dispersal syndrome, *M. pubescens* easily spreads out and grows naturally and consequently may enhance soil nutrients and facilitates the arrival or establishment of mid-successional species according to the theory postulated by Connell and Slatyer (1977).

Thus, planting or direct seeding this species in areas dominated by bracken fern are some suggested methods for restoration of these areas. On the Shrub site, *T. chrysantha* has been the most successful species in all the tested parameters, as mentioned in a previous section of this thesis and also presented by Aguirre (2007), Weber et al.

(2008), Günter et al. (2009) and Aguirre et al. (2011). The surrounding vegetation on the Shrub site acted as facilitator for *T. chrysantha,* which is in line with Holl's (2002) argument that shrubs have a net facilitation effect on the early stages of tree seedling establishment compared to areas of grass without shrubs in Costa Rica.

Based on the growth performance of species and taking in account the task of reconversion from pasture to forest, this study suggest that *A. acuminata* and even *T. chrysantha* can be recommended for Pasture site according the results of the first 48 and 60 months respectively, although latter species needs shade to grow better. The survival and growth of the latter species can be enhanced by applying methods to reduce the below-ground competition and through artificial shading as protection to avoid photo-inhibition.

5.2.2 Seedling pretreatment experiment

- Fertilization

Full fertilizer treatment had a positive effect on *H. americanus* for height and RCD increment on the Pastures site. It has mentioned before that this species had a faster growth capacity on the Pasture site. Urgiles et al. (2009) found similar results with the application of moderate fertilization (0.50 g Osmocote^R per seedling) in this species, which plant height was superior in comparison with other treatment such as: Not inoculated, no fertilizer, inoculated with mycorrhizal roots from *H. americanus,* no fertilizer; Mixed inoculum, no fertilizer; mixed inoculum, Osmocote^R fertilizer 0.25 g; Inoculated with mycorrhizal roots from *H. americanus,* Osmocote^R fertilizer 0.25 g and No inoculated, Osmocote^R fertilizer 0.50 g, after 6 months in a nursery experiment. The favorable response to the fertilizer may be related that *H. americanus* could make better use of added nutrients (Urgiles et al. 2009) and its ability to allocate resources to the shoot system (Shukla & Ramakishnan 1984; Holl et al. 2002).

Fertilization is an efficient restoration tool because it enhances soil nutrient availability in the early stages of secondary succession (García-Palacios et al. 2011). In addition, a good root biomass allocation is not discarded based on the finding of similar species like *A. acuminata* in the rhizotron experiment. This species successful competed with grass through a high below-ground biomass allocation and long root length. The negative effect of the control treatment and the slight improvement of seedlings with Low fertilizer and living AMF suggests that the establishment of *H. americanus* seedlings has to be accompanied with fertilizer or AMF inoculum, although supplied mineral nutrients have to be at the proper rate and balance (Landi et al. 2005). The low success of *C. montana* and *T. chrysantha* under full fertilizer treatment could suggest a complete independence of added nutrients or it may be that the quantity was still not enough to produce a substantial effect on their performance or another explanation is due to the insufficient root formation and/or soil conditions do not allow to the plant to absorb the fertilizer.

On the other hand the factors influencing in the high percentage of bad quality plant in all the treatments are still unclear; therefore further investigations in this topic have to be conducted to understand the limiting factors in the growth development of *H. americanus.*

- AMF Inoculation and its combination with fertilizer

Results revealed that seedlings pretreated with living AMF inoculum, two years after planting on a Pasture site, had improved survival for *T. crhysantha* and *C. montana,* although for HI and BDI the treatments did not show a clear positive effect.

In general, most studies related to AMF are conducted under controlled conditions and the results usually exhibit a positive effect on plant performance, for instance, shoot biomass using mycorrhizal inoculation (Onguene & Kuyper 2005; Urgiles et al. 2009) The latter authors found in the nursery experiment using a mixed inoculum from four tree species that the biomass production of *C. montana* was increased, also the inoculation by mycorrhiza from *H. americanus* improved plant performance of *H. americanus*, which did not coincide with the results of the experiment in the field. Therefore, the pattern of tree species behavior may differ considerably between nursery and field conditions, where other factors such as light, water stress, and competitive interactions may interact and influence growth performance. Some authors have mentioned that specific initial conditions at time of planting might be more important than a diverse inoculum (Allen et al. 2005; Anderson 2008). Nevertheless, the findings of this ongoing experiment may shift in the next few years and a new interpretation may be required; hence the effects of these treatments have to be discussed with caution.

Low fertilizer with devitalized AMF treatment seemed to contribute to plant growth of *C. montana* and *T. chrysantha*, most likely a low dose of fertilizer is enough to produce positive effects. It is stated that in many situations high soil P concentrations reduce or eliminate mycorrhizal colonization (Smith & Read 2008). The lack of a clear effect of living AMF treatment may be due to it requires a long period of time for a relevant and positive effect on plant growth to materialize as seedlings inoculated with AMF are still developing their root system in the first years of the plantation which may be limited in the nursery phase. The fungus also requires a high amount of C and consequently represents a cost for the plant for producing roots to maintain the symbiosis (Smith & Read 2008) and the pattern of allocation will influence above-ground plant productivity (Koide & Elliott 1989). Another explanation for the low growth performance with the application of AMF treatment might be due to poor root infection rates with its specific fungal symbiont or a very low specificity to their hosts (Harley 1989). The types of AMF are most likely adapted to specific conditions (Carpeter et al. 2001) and for instance, the soil properties in the pasture differ from container grown plants in the nursery (Smith & Read 2008). The results are also associated with the findings of Haug et al. (2010) in the same study area, where only one sequence type common between pristine forest and nursery was found, which suggest difficulties in cultivating forest AMF. If this is the case, further investigations have to be conducted for re-establishment of the AMF community on the Pasture site. Perhaps, a direct application of soil substrate from natural forest into the soil surrounding seedlings would improve inoculation of roots of tree species and consequently improve plant growth performance although in a landscape context this would be difficult to do.

The results of the low effectiveness of AMF inoculation are in line with White et al. (2008), who showed that AMF colonization did not result in a positive plant establishment on a roadside prairie restoration site; probably, the fungi selected to achieve colonization in the nursery are not competitive in the field (Smith & Read 2008).

In conclusion, due to the unclear effect of AMF on the plant performance three suggestions emerge of this study 1) a long- term effect may be expected due to the time required for seedlings to allocate below-ground biomass for promoting the reproduction of AMF, 2) the specificity and effectiveness of AMF may shift from nursery to the field due to complete different environmental conditions, and 3) the root competition of

S. sphacelata might also delay the AMF function and consequently affect the growth performance of plants at the beginning of the plantation.

- Shading of *Tabebuia chrysantha*

Results for *T. chrysantha* under shading demonstrated a better height increment in all treatments than when seedlings were directly exposed to high irradiation on the Pasture site. This agrees with the findings of tree performance in the secondary forest in the San Francisco valley. Low fertilizer with devitalized AMF and living AMF plus shade conditions responded well with respect to plant height and percentage survival, respectively. This suggests that the addition of fertilizer and arbuscular micorrhiza fungi inoculum will allow this species to cope with competitive grass and permit tree establishment on the Pasture site when shade is present.

5.2.3 Rhizotron experiment

Grass competition and root development

In spite of the low number of observations at the end of monitoring, the results revealed differences between early- and mid- successional species' root length density. This concurs with some authors that the investment of root biomass in the production of root length varies among species (Eissenstat 1992; Craine 2006). *A. acuminata* presented the longest roots in comparison with other species and the addition of fertilizer in competitive conditions improved the production capacity of RLD. High competition of *S. sphacelata* may stimulate the root length growth of tree species as a defense mechanism against the aggressiveness of the grass and for better nutrient uptake. Craine (2006) explained that a high RLD of temperate grasses might be either due to a slow rate of diffusion of inorganic N in soils or interplant competition. In a practical context, the degree of success of *A. acuminata* on the Pasture site is in part due to the capacity of increasing the RLD.

As shown in other sections of this thesis, *T. chrysantha* and *C. montana* have low plant growth in pastures, one of the reasons is their own inherent traits as mid-successional species. However, another explanation, revealed by the rhizotron experiment, is due to their low RLD when accompanied by *S. sphacelata.* This confirms the poor response of these species to below-ground competition. For tree species such competition implies considerable carbon expenditure for below-ground processes as mentioned by Eissenstat (1992) and Leuschner et al. (2007). The addition of fertilization slightly improved the RLD for *C. montana* without grass competition which further indicates a sensitiveness to below-ground competition with *S.* sphacelata and the consequent incapacity to access nutrients. This suggests that in field conditions an intensive control of the grass would have to be done along with the addition of fertilizer in order to improve plant performance.

The highest RLD was found in *S. sphacelata* along with a high percentage of fine roots (<2mm) making up the total below-ground biomass and a high water demand according to soil moisture measurements by tensiometers (unpublished data). Altogether, this converts the grass into a potential competitor for any woody species. In this context, another main constraint arises; water capture for plants with small roots under grass competition.

Within the parameters of the root system, root length is a more sensitive measure for dynamic root properties than root number (Johnson et al. 2001). Also, thinner roots are more efficient for water and nutrient uptake from the soil (Finér et al. 2011), although at this time the root diameter images have yet to be analyzed which means it is not possible to discuss the water and nutrient uptake efficiency of tree species.

Biomass allocation of tree species and *S. sphacelata*

A general pattern was observed in that tree species showed lower below-ground than above-ground biomass allocation. This indicates that the species tested in this experiment, under all treatments tried to improve their competitiveness by allocating more biomass to the shoot for better light interception in nursery condition.

Also, in tree species accompanied by exotic grass, the root biomass production was even lower; therefore competition aside from nutrients, water and space inside the rhizotron is evident. Due to the results revealed that plants without competition produced lower root biomass in comparison with shoot biomass, this is not in line with Wilson (1988), who found that the root competition is usually more important than shoot competition in determing competitive balance. Therefore, it supports the idea the allocation pattern between above- and below-ground biomass may arise from different degrees of phenotypic plasticity of species in response to different ranges of environmental conditions or competition for resources (Aerts et al. 1991).

The response of *A. acuminata*, which allocated more biomass to the shoot, coincides with other studies using similar species as for example early successional species (Shukla & Ramakrishnan 1984; Paz 2003). This may be explained by the need to maximize allocation to the shoot system for intercepting high energy (Shukla & Ramakrishnan 1984). The results for *C. montana* in this experiment and the findings in the experimental plots on the Pasture site at two years of plantation carried out by Eckert (2006) agree about the allocation of more biomass above-ground. However, it differs from the results of a study in Panama testing *Cedrela odorata,* which invested more in roots under field conditions (Coll et al. 2008). It suggests that the behavior of *C. montana* differs according to specific soil and environmental conditions.

In the case of *T. chrysantha,* the result does not match with Eckert as he found a better below-ground than above-ground biomass allocation. This last fact gives an idea of the high resistance of *T. chrysantha* on the Pasture site observed by its high survival in the reforestation experiment. However, the ability to face the competition does not only depend on the biomass allocation pattern but also on morphological characteristics as specific leaf area and specific root length (Aerts et al. 1991).

In this study the addition of fertilizer aided tree species to increase the above-ground biomass slightly, particulary for *A. acuminata*, therefore the seedlings took advantage of available soil nutrients to produce more leaves and increase their stem. Hence, plants have higher relative growth rates when they are under higher nutrient status (Eissenstat 1997).

The grass produced the highest amount of biomass both above- and below-ground in comparison to the tree species. The successful performance of this grass and its strong competitively may be explained by it being a C4 grass with a higher photosynthetic capacity than C3 grasses (Rhoades et al. 2000; Marques da Silva et al. 2004), greater nitrogen (N) use efficiency, particularly on sites low in N (Waller & Lewis 1979), and a better water-use efficiency than trees (Günter et al. 2009). The interaction of the greater root length, high below-ground biomass allocation, and the physiological adaptations make *S. sphacelata* a robust competitor. In the line with the results of tree species, the grass also produced higher above-ground than below-ground biomass allocation. This indicates that the nursery conditions with high temperatures and low relative humidity, particularly in certain months of the year act as a driver to increase the shoot biomass allocation and improve photosynthesis.

6. Conclusions and recommendations

The general conclusion of this study is that both alternatives to restoration, natural succession and tree plantation, can be compatible with each other on abandoned lands in the San Francisco valley because seed dispersal can increase after trees are planted due to the attraction of dispersal agents. At the same time native tree species may offer other benefits such as shade or adequate habitat for recruitment of woody species in the understory. Nevertheless, the tree species have to be planted in the right site according to their ecological requirements and if possible, to recognize conditions at a micro-site scale. Thus, in the greater context of landscape and in a mid-and long-term scale, the goals of restoration, conservation of biological diversity or production can be achieved in a tropical mountain forest by a mixture of artificial and natural regeneration.

Overall, there is little information about the dynamics of natural succession, ecology of native tree species and their performance over time in different types of vegetation in the Andes; therefore this investigation is advancing the field of silviculture and restoration in Ecuador. This research might represent one of the few studies in a tropical mountain forest that deals with questions related to restoration, which differs substantially from the northern Andes of Ecuador where soils are formed in recent volcanic material and thus have completely different characteristics (Hofstede et al. 2002). Nevertheless, valid comparisons were done using studies from the Americas, mostly carried out in Central America, Mexico and Brazil. The knowledge generated by this thesis contributes both to the general literature and the results can be directly applied by landowners in the San Francisco valley and/or in similar areas. Furthermore, the results also may support the Ecuadorian government over the next few years when it instigates the National Forestation and Reforestation Plan (PNFR), integrating plantations for industrial, agroforestry purposes and re-establishment of forest for protection and conservation (ITTO 2009; Dirección Nacional Forestal, 2011).

Restoration planning on abandoned lands in the San Francisco valley must be based on a sound analysis of natural succession and development of plant growth. Specific conclusions and recommendations follow.

6.1 Dynamic of natural succession

Based on the differences in speed of natural succession and the type of the functional vegetation recruited naturally on the three successional sites, it can be stated that the successional trajectory on the Pasture site is slow and not yet clear. The Bracken and Shrub sites showed highly similar trajectories, although they are parallel in nature and therefore do not represent a chronosequence. Nevertheless, this study highlights the mechanism of facilitation observed on the Bracken site, where the natural succession increased particularly at the end of monitoring (48 months). Manual weed removal did not improve the recruitment of woody species and consequently its use is not recommended on abandoned lands.

This study demonstrates that pastures need human intervention. The recommendation is planting native tree or shrub species that provide shelter and are well adapted to the aggressiveness of *S. sphacelata*. On the Bracken and Shrub sites, an enrichment planting or direct seeding is needed, although the selection of species has to be done carefully with special emphasis on animal-dispersed woody species (*Hyeronima asperifolia, Myrsine coriacea, Persea sp.*) to further enhance biodiversity recruitment.

6.2 Tree plantation

This study has shown that *A. acuminata* and *M. pubescens* are well adapted to the Pasture and Bracken sites respectively, which emphasizes the important role that nitrogen fixing species can have in the early phases of restoration. These two types of successional sites represent the most recently stages of abandoned lands. On the other hand, *T. chrysantha* showed a noteworthy growth development and high survival on the Shrub site. Here, the results revealed treatment of ground vegetation might be helpful. However, in the sites with high dominance of species such as *S. sphacelata* and *P. arachnoideum,* manual and chemical treatment is not recommended at the same frequency as performed in this experiment; the high cost of labor is not compensated by a better growth performance of remaining species.

Additional experiments using species specific herbicide (e.g. Asulam to control bracken fern) should be tested as a tool to control biotic stress for some tree species, although for many restorationists this is not a very attractive method. Another investigation, given the high growth rate and rapid canopy development of *A. acuminata,* would be to measure the effect of shade on *S. sphacelata* as a technique to reduce the strength of the grass and enhance woody species recruitment. As the results showed microsite adaptions of some species, e.g. *C. montana*, are extremely important, this effect has to be studied more deeply to understand the effect of soil properties and other vegetation indicators.

Further investigations integrating rainfall interception and evaporation are also recommended to create a more precise soil water storage model in the study area. Also, a long term correlation of survival, plant growth and root development in function of length and intensity of the dry months could be very helpful in order to evaluate the future dynamics with regard to the adaptation of vegetation to climate change.

6.3 Seedling pretreatment experiment

From the seedlings pretreatment experiment it can be concluded that the treatment must be adapted to a plant's successional status; therefore this experiment recommends that *H. americanus* may require full fertilizer to enhance stem height and root collar diameter on the Pasture site, while *C. montana* and *T. chrysantha* need a combination of low fertilizer and devitalized AMF as shown by the improvement of the plant performance observed on the Pasture site.

However, these results may be preliminary and a long-term monitoring of seedlings is required due to the unclear effects of AMF on plant performance under field conditions. Time might be a crucial factor for the symbiosis; the roots may need to be better developed and colonized with AMF, which may shift plant performance in the future. Additionally, it is recommended to link root colonization rate with plant growth.

6.4 Rhizotron experiment

This experiment clarified the aggressiveness of *S. sphacelata,* which in terms of restoration can be critical for the establishment of woody species through natural succession and/or tree plantation. Nevertheless, this experiment concludes that *A. acuminata* can cope with the grass competition much better than *C. montana* and *T. chrysantha.* The success of *A. acuminata* on the Pasture site in the tree plantation experiment confirms this ability and emerges as a good candidate for restoration purposes.

Below-ground competition between tree species and *S. sphacelata* could only partially analyzed in this rhizotron experiment, leaving questions open about effects of morphological characteristics such as specific leaf area, root architecture and specific root length, which are important to fully understand the ability of tree species to compete for resources (e.g. nutrients) on abandoned lands. Therefore, it is recommended to continue investigating physiological and ecological aspects of native species in the tropical mountain forest.

6.5 Further recommendations

1. This study recommends the integration of an adaptive management strategy in the context of restoration processes in the San Francisco valley. Adaptaive ecosystem management may be a useful tool for decision making of land use management as well in a larger time - space (Heinimann 2010) because either farmer's requirements or ecological factors like the speed of restoration can shift over time. Thus, ecological, social and economic indicators have to be previously formulated for a subsequent systematic monitoring over time. In ecological terms, the neighboring natural forest can act as a reference ecosystem. In socioeconomic terms, the provision of constant income based on sustainable land management satisfying the true needs of local people might be a fundamental indicator (Fig. 33).
2. In the last decades, the nature is facing the effects of global climate change, therefore restoration has to be considered as a key aspect in the formulation of goals, strategies, politics and planning future restoration projects.
3. The relationship between academia or research and practitioners has to be improved in order to achieve restoration of degraded lands in the different ecosystems in Ecuador. A clear example of this missing link is given in a report of a global study in the forestry sector (ITTO 2009).

A brief summary of results and recommendations per each successional site in regard to both alternatives of resotarion is given in the Figure 34.

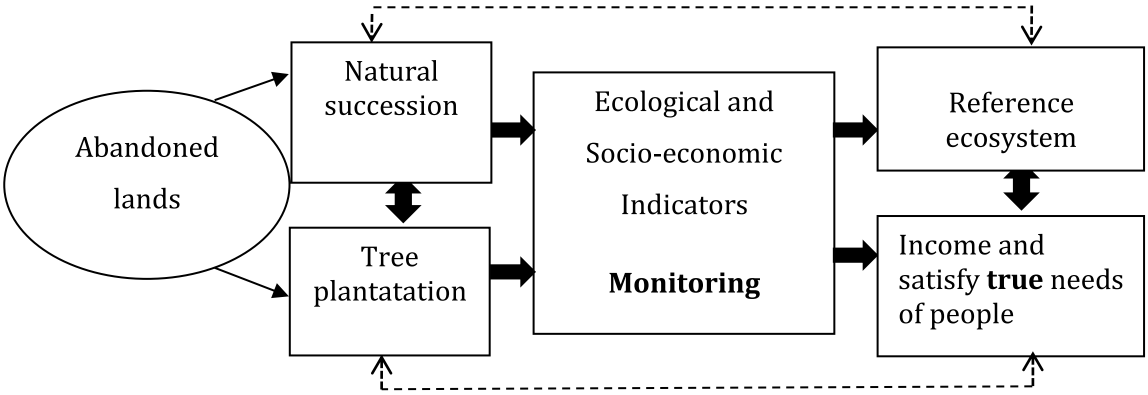
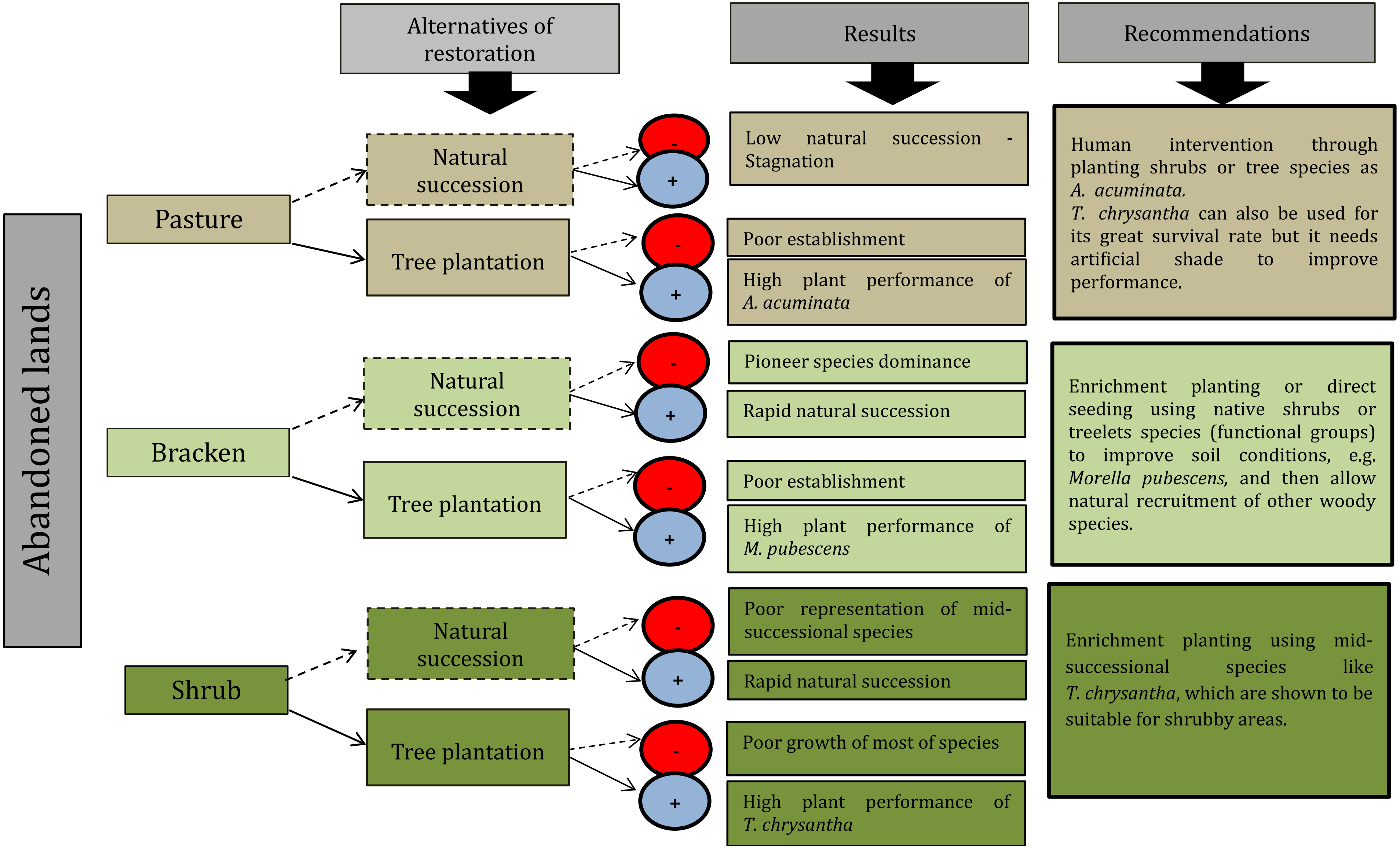


Figure 33. Adaptive management in the process of restoration



Human intervention through planting shrubs or tree species as *A. acuminata.*
T. chrysantha can also be used for its great survival rate but it needs artificial shade to improve performance.

Enrichment planting or direct seeding using native shrubs or treelets species (functional groups) to improve soil conditions, e.g. *Morella pubescens,* and then allow natural recruitment of other woody species.

Enrichment planting using mid-successional species like *T. chrysantha*, which are shown to be suitable for shrubby areas.

Figure 34 Summary of results and recommendations for Natural succession and tree plantation on the three successional sites

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Appendices

Appendix I. Description of the native tree species in the reforestation experiment

Cedrela montana Moritz ex Turcz

Taxonomy and nomenclature
Family: Meliaceae
Local name: cedro (Zamora, Ecuador)

Description: a slow-growing tree reaching 25 to 30 m in height and 30 cm d.b.h. The leaves are alternate, compound, and paripinnate with whole margins. This species grows in soils with good drainage and fertility. *C. montana* grows at elevations between 1600 and 2800 m, with an average annual temperature between 10 and 20ºC (Nieto & Rodriguez 2002). Currently, it is possible to find this species in pristine forests remnants in the South of Ecuador. The root system belongs to dichotomous topology (Loaiza et al. 2011, unpublished data).

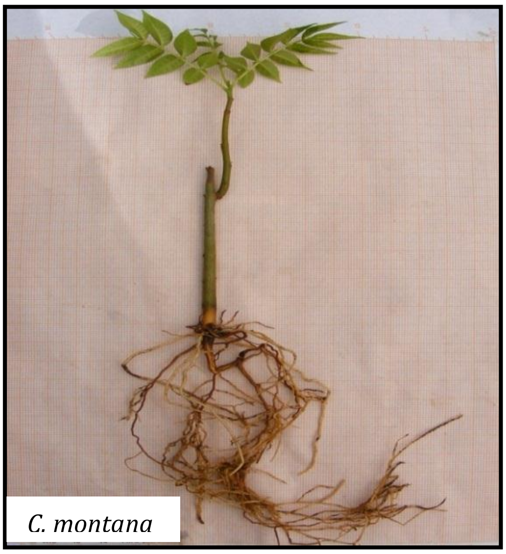
Uses: *C. montana* is one of the most valuable neotropical timber trees (Gentry 1993). It is highly appreciated in carpentry and for furniture due to its color, grain and workability. The species is characterized by its hardness and high durability (Nieto & Rodriguez 2000). Gerique (2010) found that the wood of *C.* cf *montana* is used for Bow yokes, swivels and plough handles in Southern Ecuador.

Phenology and harvest: The peak flowering event in the RBSF is in December (Encalada & Alvarado 2010). The fructification is biannual (Armijos 2008) and the maximum period of fructification is in August (Encalada & Alvarado 2010). The fruits are preferably collected from the trees just before they split open or from the ground immediately after seed fall.

Ecology of seeds:

Germination in petri dishes:	8.5 ±14.8 %
Moisture content:	13.3 %
Purity:	78.3 ±1.2 %
Weight of 1000 seeds:	15.6±0.6 g

Source: Encalada & Alvarado (2010)
The percentage of germination on substrate in the nursery is above 60 % (Briceño 2005)



C. montana

Tabebuia chrysantha *Jacq. G. Nicholson*

Taxonomy and nomenclature
Family: Bignoniaceae
Local name: Guayacán (Zamora, Ecuador).

Description: Reaches 35 m height and 60 cm diameter, deciduous (CATIE 2000a). Many of the trees of this genus are an important source of timber (Gentry 1992; Gentry 1993). This species grows in the remnants of pristine forest.

Uses: Currently, in the South of Ecuador, this species is used mainly for construction of houses and fences (Gerique 2010). Its timber has high market value due to its aptness for furniture. Moreover, it is used as an ornamental plant due to the yellow color of the flowers.

Phenology and harvest: It flowers between August and September and fruits from September until November (Encalada & Alvarado 2010). Seed production of this species in the RBSF was registered in individuals with greater than 22 cm DBH (Armijos 2008). Once harvested they are placed under the shade until they split open naturally (CATIE 2000a).

Ecology of seeds:

Germination in petri dishes:	28.6±15.5 %
Moisture content:	13.1±0.5%
Purity:	76.2 ±3%
Weight of 1000 seeds:	23.1±0.9 g

Source: Encalada & Alvarado (2010).
The percentage of germination on substrate is above 60 % (Briceño 2005)

Juglans neotropica Diels

Taxonomy and nomenclature
Family: Juglandaceae
Local name: nogal or tocte (South of Ecuador), Walnut (English)

Description: This species is native to Ecuador, Colombia, Perú and Bolivia. It is a slow growing tree reaching 25 m in height and 40 cm d.b.h. It needs deep and fertile soils with a loose, loamy, or loose-sandy texture. The range of elevation is between 1600 and 2500 m, with an average of temperature that ranges between 14 and 22 °C (Nieto & Rodriguez 2000). *J. neotropica* grows in the wild and as a cultivated species (Gerique 2010)

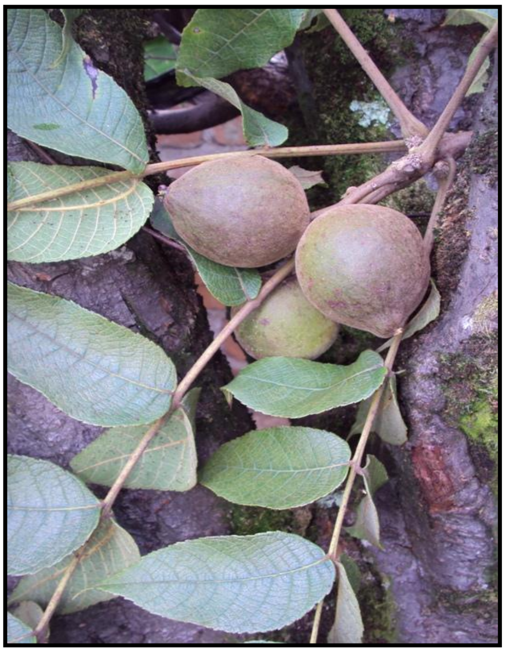
Uses: The seeds are edible, the leaves have medicinal uses, the timber is used for construction, and the fruits are used to dye textiles and wool (Gerique 2010).

Phenology and harvest: In Loja city (Parque Universitario de Educación Ambiental y Recreación "Francisco Vivar Castro") the peak of flowering is December and January. Fruiting was registered in March and April (Díaz & Lojan 2004). According to CATIE (2000b), this species may produce fruits after 8 years of being planted. The fruits are collected from the ground or from the crown of the tree when they have turned yellowish.

Seed information:
Percentage of germination: above 70% in substrate

Moisture content:	50.6 %
Purity:	100 %
Weight of 1000 seeds=	20152 g

Source: Díaz & Lojan (2004)



Alnus acuminata *Kunth in H.B.K.*

Taxonomy and nomenclature
Family: Betulaceae
Local name: Aliso

Description: The natural distribution is from Mexico to Peru. It is widely cultivated in its natural range in plantations and in agroforestry systems (Fournier 2002). In natural conditions in Ecuador individuals reach between 15 m and 30 m, although in some places over 30 m and 60 cm DBH (Añazco 1996). The trees thrive in poor and degraded soils due to its nitrogen fixing capability in roots nodules.. It grows over a wide elevational range from 1300 to 3000 m (Fournier 2002). The root system belongs to dichotomous topology (Loaiza et al. 2011, unpublished data).

Uses: This species is used in construction for window parts, doors, boxes, and musical instruments (Salaza & Jøker 2000). In Southern Ecuador, this species is usually used to make living fences and firewood (Gerique 2010). It is also attributed as medicinal and as useful species for agroforestry (Añazco 1996).

Phenology: In the Forest of San Pedro de Vilcabamba, the peak flowering season is in October and November. Fruiting is from January until April (Díaz & Lojan 2004). The seed collection in Ecuador will depend on the site (province). At km 7 between Loja – Zamora road, for example, seed can be collected in June and July (Añazco 1996).

Seed Harvest: Seeds should be collected when the cones turn dark brown and are close to dehiscence. The cones are collected from trees and placed on blankets until they open and seeds come out.
The seed is considered orthodox (Salazar & Joker 2000).

Seed information:
Percentage of germination varied: one tree had a maximum of 73 % but a second tree produced only 3% of germination
Purity: 91 (%)
Moisture content: 14 (%) (Díaz & Lojan 2004).

Morella pubescens (Humb. & Bonpl. ex Wild) Wilbur

Taxonomy and nomenclature
Family: Myricaceae
Local name: Laurel de cera

Description: *M. pubescens* is a shrub, reaching 12 m in height depending on the site conditions. This species develops well at altitudes of between 1500 and 4500 m (Jorgensen & León 1999). The distribution of species is in the Andean regions of Colombia, Ecuador, Peru, Bolivia and other Central American countries (Luna 2011).

Uses: This is species is known in agroforestry, the wax of fruits and oil of the leaves are promising for the pharmaceutical industry (Luna 2011) which may be an economic alternative for local people as well. This species is also used for watershed conservation (Muñoz & Luna 1999).

Phenology and harvest: In the RBSF**,** the period of maturation of fruits starts in December. From January to March this event is at its peak (Jara & Romero 2005; Encalada & Alvarado 2010).

Ecology of seeds:

Germination in petri dishes:	8.5±13 (%)
Moisture content:	15.8 (%)
Purity:	66.1 ±1.3 (%)
Weight of 1000 seeds:	12.4±0.6 (g)

Source: Encalada & Alvarado (2010)

Heliocarpus americanus L.

Taxonomy and nomenclature
Family: Tiliaceae
Local name: Balsilla or Balsa blanca

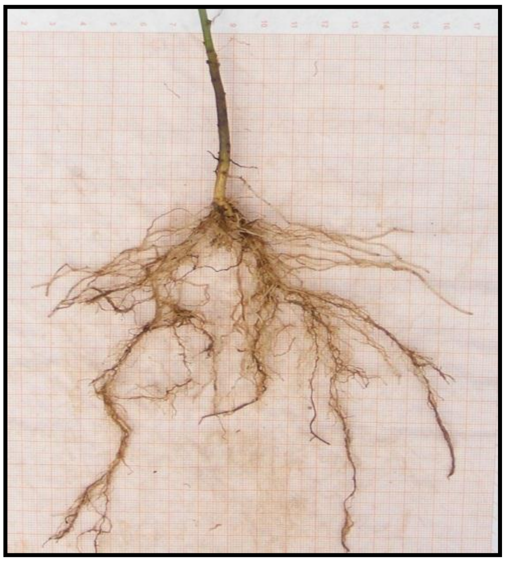
Description: This species is native in America meridional (Tropicos 2012), and in Ecuador it is distributed in the three continental regions from sea level to 2.500 m asl (Jorgensen & Leon 1999). Trees can reach 18 m height and 20 cm DHB. This species grows in soils with low fertility (Aguirre 2002). *H. americanus* grows in the wild (Gerique 2010).

Uses: In the south of Ecuador, this species is used for crafts, construction, fibers, fuel and veterinary medicine (Gerique 2010) and for making crates (Davidson et al. 1998). In Colombia the white balsum (from the bark) is the most used species in the "panela" clarification processes" (Restrepo et al. 2006).

Phenology and harvest: In the RBSF the flowering season is from February to June (Cabrera & Ordoñez 2004).

Fruiting starts at the end of May until the end of October, however, the peak period is July and August (Jara & Romero 2005). Once collected the seeds is possible to store them for few months.

Seed information:
Percentage of germination:
16 % (Cabera & Ordoñez 2004),
25 % (Jara & Romero 2005).
Weight of 1000 seeds (g):
1.86 (Cabrera & Ordoñez 2004),
1.38 (Jara & Romero 2005).
Purity : 89.9 (%) (Cabrera & Ordoñez 2004),
92.4 (%) (Jara & Romero 2005).
Moisture content:
28.5 (%) (Cabrera & Ordoñez),
10.41(%) (Jara & Romero 2005).



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Appendix II List of woody indicator species showing a comparison between 0 and 48 months per site with highest significance (p<0.05)

					p value					
					0 months			48 months		
Family	Species	Dispersal	Life-form	Natural forest	P	Bf	S	P	Bf	S
Aquifoliaceae	*Ilex* sp.	bird	treelet	P						0.011
Asteraceae	*Ageratina dendroides* (Spreng) R.M. King & H. Rob	wind	shrub	A			0.001			0.004
Asteraceae	*Ageratina sp*.	wind	shrub	A				0.001		
Asteraceae	*Baccharis brachylaenoides* DC.	wind	shrub	A					0.04	
Asteraceae	*Baccharis macrantha* Kunth	wind	shrub	A						0.021
Asteraceae	*Baccharis latifolia* (R&P) Pers.	wind	shrub	A	0.001			0.009		
Asteraceae	*Baccharis* sp.	wind	shrub	A						0.009
Asteraceae	*Baccharis obtusifolia* Kunth	wind	shrub	A		0.002				
Asteraceae	*Baccharis* sp1	wind	shrub	A					0.001	
Asteraceae	*Baccharis tricuneata*	wind	shrub	A					0.002	
Asteraceae	*Vernonia* sp2	wind	shrub	A					0.024	

Caprifoliaceae	*Viburnum pichinchensis* Benth	bird	tree	A				0.003
Clethraceae	*Clethra fagifolia* Kunth	wind	tree	A				0.003
Clusiaceae	*Clusia* sp1	bird	tree	P				0.013
Clusiaceae	*Clusia* sp2	bird	tree	P				0.008
Cyatheaceae	*Cyathea* sp.	wind	treelet	P		0.004		
Ericaceae	*Macleania poortmannii* Drake	bird	tree	A				0.001
Ericaceae	*Vaccinium floribundum* H.B.K.	bird	shrub	A				0.001
Euphorbiaceae	*Alchornea pearcei* Britton ex Rusby	wind	tree	P				0.008
Gentianaceae	*Macrocarpaea* sp.	bird-bat	treelet	P				0.001
Grosilariaceae	*Escallonia paniculata* (Ruiz & Pav.) Roem. & Schult.	wind	treelet	A			0.022	
Lauraceae	*Persea* sp.	bird	tree	P				0.03
Melastomataceae	*Brachyotum campanulare* (Bonpl) Triana	wind	shrub	A	0.019			0.001
Melastomataceae	*Monochaetum lineatum* (D. Don) Naudin.	wind	shrub	A			0.002	
Melastomataceae	*Tibouchina laxa* (Desv.) Cogn	wind	shrub	A		0.003		0.032
Melastomataceae	*Miconia* sp.	bird	tree	P		0.044		
Myrsinaceae	*Myrsine coriacea* (Sw.) R. Br. Ex Roem. & Schult.	bird	treelet	P		0.001		0.001
Rubiaceae	*Palicourea* sp1.	bird	treelet	P				0.001

Rubiaceae	*Palicourea* sp2.	bird	treelet	P	0.001		
Proteaceae	*Roupala montana* Aublet	wind	tree	P		0.004	
Rosaceae	*Hesperomeles obtusifolia* Pers.	bird	tree	A			0.007
Rubiaceae	Palicourea anceps Standl	bird	treelet	P			0.001

The reference ecosystem (RBSF): P= present, A= Absent.

Successional sites: P (Pasture) Bf (Bracken) and S (Shrub)

Appendix III. Values of sand (%), clay (%) and organic matter (%) per site, species and soil samples

Site	Species	Soil samples	Sand %	Clay %	Organic matter %
Pasture	*A. acuminata*	1	29.1	33.04	2.5
		2	19.8	39.1	2.8
		3	21.6	37.7	2.7
	H. americanus	1	45.5	28.3	3
		2	41.9	29.6	2.9
		3	43.5	27.1	3.1
	C. montana	1	35.4	34.42	3
		2	34.2	34.4	3
		3	40.8	33	3
	T. chrysantha	1	28.7	35.8	3.1
		2	30.7	36.2	3.1
		3	37.2	32.6	3.2
	J. neotropica	1	29.7	32.7	2.9
		2	30.2	31.2	3.1
		3	32.9	31.6	2.7
Bracken	*A. acuminata*	1	15.8	42.0	2.9
		2	11	43	3.1
		3	12.2	46	3.6
	H. americanus	1	33.9	35.4	3
		2	31	36.1	3
		3	33.2	35	3.1
	C. montana	1	28	39.9	3.2
		2	37.6	32.2	3.1
		3	32.8	35	3.4
	T. chrysantha	1	34.7	33.8	3.1
		2	38	29.6	2.9
		3	34.3	33	3.3
	J. neotropica	1	36.4	29.8	2.9
		2	41.7	30.2	3.2
		3	45.1	28.9	3.1
Shrub	*A. acuminata*	1	30.4	35.3	3
		2	30.4	36.1	2.7
		3	26	36.9	2.7
	H. americanus	1	20.8	42.1	3.1
		2	18.1	43.8	2.9
		3	21	41	3.1
	C. montana	1	17.7	42.1	2.9
		2	19.4	42	3.3
		3	19.4	40	3
	T. chrysantha	1	21.4	40	2.9
		2	24.1	35.7	2.6
		3	23.3	41.9	2.9
	J. neotropica	1	24.2	36.6	2.9
		2	24.4	35.6	2.5
		3	25.9	34	2.5

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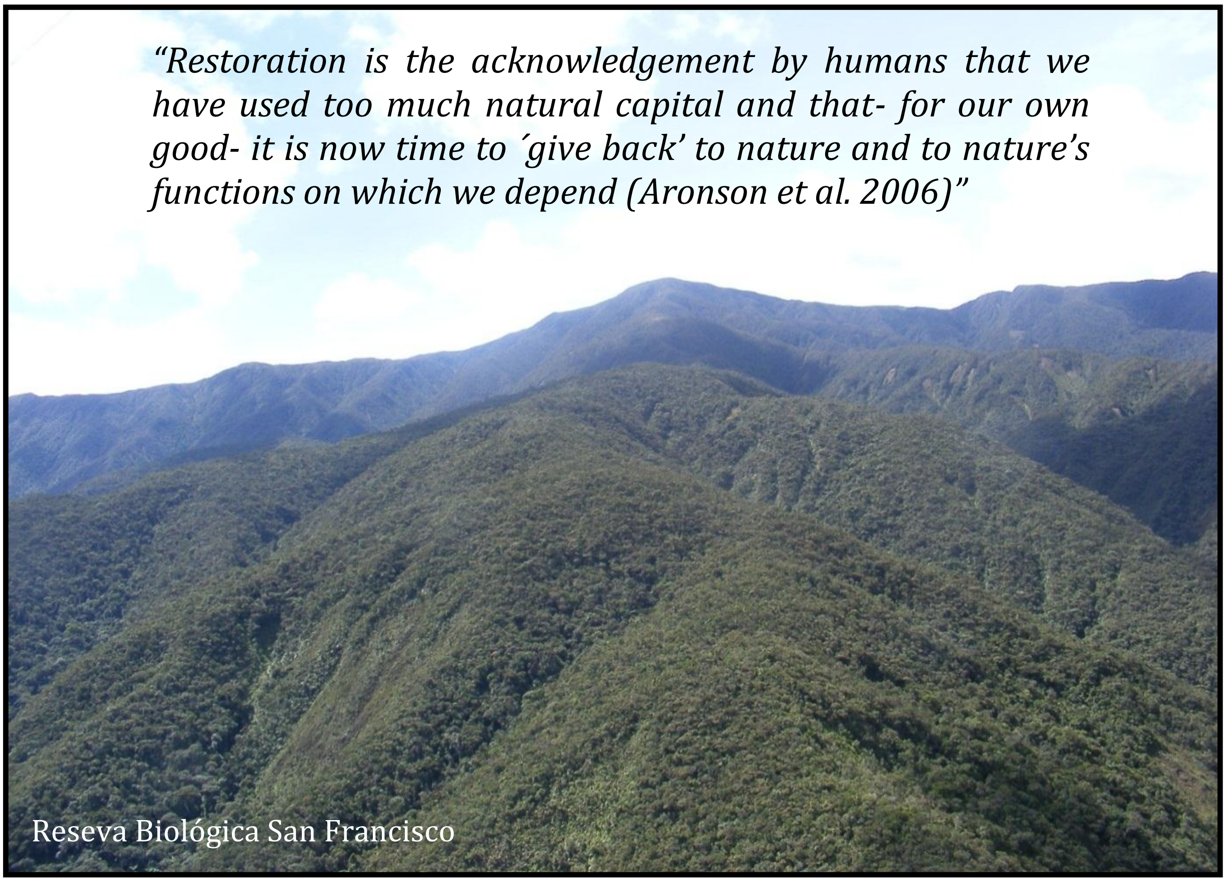

“Restoration is the acknowledgement by humans that we have used too much natural capital and that- for our own good- it is now time to ´give back’ to nature and to nature’s functions on which we depend (Aronson et al. 2006)”

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