CATIE

Solutions for environment and development
Soluciones para el ambiente y desarrollo

TROPICAL AGRICULTURAL CENTER FOR
RESEARCH AND HIGHER EDUCATION

GRADUATE SCHOOL

Litterfall dynamics and nutrient cycling under different tropical forest restoration strategies in southern Costa Rica

by

Danielle Camargo Celentano Augusto

Thesis submitted for consideration by the School of Graduate Studies as a
requirement for choosing the degree of

Magister Scientiae in Management and Conservation of
Tropical Forests and Biodiversity

Turrialba, Costa Rica, 2010

This thesis has been accepted in its present form by the Education Division and the Graduate School of CATIE and approved by the Advisory Committee of the student as partial requirement for eligibility for the degree of

MAGISTER SCIENTIAE IN MANAGEMENT AND CONSERVATION OF TROPICAL FORESTS AND BIODIVERSITY

SIGNERS:

Bryan Finegan, Ph.D.
Major Advisor

Fernando Casanoves, Ph.D.
Advisory Committee Member

Diego Delgado, M.Sc.
Advisory Committee Member

Ima Celia Guimarães Vieira

Ima Celia Vieira, Ph.D.
Advisory Committee Member

Rakan A. Zahawi, Ph.D.
Advisory Committee Member

Glenn Galloway, Ph.D.
Dean, Graduate School

Danielle Camargo Celentano Augusto
Candidate

"Um dia a Terra vai adoecer. Os pássaros cairão do céu, os mares vão escurecer e os peixes aparecerão mortos na correnteza dos rios. Quando esse dia chegar, os índios perderão o seu espírito. Mas vão recuperá-lo para ensinar ao homem branco a reverência pela sagrada Terra. Aí, então, todas as raças vão se unir sob o símbolo do arco-íris para terminar com a destruição. Será o tempo dos Guerreiros do Arco-Íris."

(Prophecy made more than 200 years by "Eyes of Fire", an old Cree indian woman*)*

DEDICATORY

To the future generations.

ACKNOWLEDGMENTS

I am grateful for the Organizations of American States (OAS) for the scholarship I received during the last two years and for paying my academic fees. My research project was supported financially by the International Tropical Timber Organization (ITTO), the Wildlife Conservation Society (WCS) through the Conservation Leadership Programme (CLP), The Nature Conservancy (TNC) through an Organization for Tropical Studies (OTS) restoration workshop grant, and by the Tropical Agricultural Centre for Research and Higher Education (CATIE).

I am indebted to my committee members Bryan Finegan, Rakan (Zak) Zahawi (OTS), Diego Delgado, Fernando Casanoves, and Ima Celia Vieira (Museu Paraense Emilio-Goeldi) for all their support. Bryan provided great support for me to come study at CATIE, I also appreciate his unconditional confidence in my work. I have special gratitude for my advisor and friend Zak for all the time he invested in my project (proposals, experimental set up …), thanks a lot!

My “non-official” advisors Karen Holl (University of California in Santa Cruz) and Rebecca Ostertag (University of Hawaii) provided invaluable support and guidance. My research proposal received important contributions from Suzanne Brais (Université du Quebéc) and Gabriela Soto. Rebecca Cole (University of California in Santa Cruz) provided greatly appreciated assistance in setting up my experiment in Coto Brus and in many other logistical and scientific issues. Darryl Cole (Finca Loma Linda) was very supportive during all stages of my project. Thanks Don Darryl for opening the doors of your house to me! Your Loma Linda is Linda!

Juan Abel Rosales and Roman Gomez Meza were spectacular field assistants in Coto Brus and the completion of my project would have been impossible without them. Esthefanie Daniela Rodrigues Cerdas was also great assisting me in the lab to sort litterfall. I thank all my assistants very much! I had a great time with them. Other help in the field was provided by Paulo Rosales for litterfall, Allen Llama for stand litter sampling and Guillaume Rousseau for soil sampling. Victor Milla (OTS) and Christian Brenes (CATIE) provided me with shape files from the study area for my maps. Gabriela Soto provided me with litterbags for the decomposition study. Susan G. Letcher and Federico Oviedo (both OTS) helped me with the taxonomic identification of canopy species. Carl Schmitt also helped during the experimental set up. I thank Patricia Leandro for her support in the lab and Fernando Casanoves for his assistance with data analyses.

Preliminary results of my thesis were presented and discussed at the Restoration Institute (University of Victoria, Canada) and in the Iberoamerican Congress of Ecological Restoration (Brazil). I am thankful to Dr. Eric Higgs (UVIC) for his enthusiatic support concerning my participation in the Restoration Institute, for CATIE and OAS for their assistance with travel costs, and for my friend Kate Proctor for receiving me in her house. Conservation International (CI) through the Conservation Leadership Programme (CLP) financed my participation in the Iberoamerican Congress of Ecological Restoration in Brazil.

I thank everybody at Las Cruces Biological Station. Rodolfo Quirós, Doña Emilce Ramírez and Xenia Barrantes for logistical assistance. The cooks for their great meals! Nana (and Africa) for her lovely friendship. I miss you all! I thank all landowners in Coto Brus that allowed the restoration experiment to be setup on their lands. I thank the red truck for transporting me safely!

I thank everybody at CATIE! Special gratitude to Noyli Navarro, Jeanette Solano and Aranjid Valverde in the Graduate School, Wendy Ditel, Hugo Brene and Leonel Coto (Leo) in the Department of Natural Resources, Douglas Navarro, Carlos Castillo Guerrero and Arthur Ramírez (Arturito) in the lab. My friend Adriana Arciniegas reviewed my Spanish paper. I thank Marie Eve Laudry pour l'amitié and for lending me a computer for data entry. I am fortunate, during the last two years I made very good friends from Costa Rica and many other countries, including from Brazil! Pura vida!

Finally, I have special gratitude for my husband Guillaume Rousseau for his partnership, transcendental patience, comprehension, gentleness and unconditional support and love. Obrigada meu amor.

CONTENT

SUMMARY

Tropical forests protect the world's greatest biodiversity and maintain critical ecosystem services. However, deforestation is still widespread in most tropical countries, particularly in Latin America. Deforestation provokes changes in global nutrient cycles with high environmental and social costs. In turn, restoration strategies to facilitate tropical forest recovery in degraded areas may accelerate the reestablishment of nutrient cycling. My Msc. project evaluated litterfall and nutrient dynamics under four recovery treatments: plantation (entire area planted), islands (planting in six patches of three sizes), control (natural regeneration), and young secondary forest (7 – 9 yr). Treatments (plots of 50 × 50 m) were established in June 2004 at six replicate sites in southern Costa Rica. Planted species included two native timber-producing hardwoods (*Terminalia amazonia* and *Vochysia guatemalensis*) intercropped with two nitrogen-fixing species (*Inga edulis* and *Erythrina poeppigiana*). Litterfall production did not differ significantly ($F = 129.4$, $p < 0.0001$) between secondary forest (7.3 Mg ha^{-1} $year^{-1}$) and plantation (6.3 Mg ha^{-1} $year^{-1}$), whereas islands presented intermediate values (3.5 Mg ha^{-1} $year^{-1}$), and control (1.4 Mg ha^{-1} $year^{-1}$) had the lowest production. Leaves represented >75% of total litterfall. *Inga edulis* contributed 70% of leaf fall in plantations. Nutrient concentrations for Ca, Mg, K, Zn and Mn were significantly higher in secondary forest than other treatments, and this was correlated positively with higher species diversity. Nitrogen concentration in leaves was higher in treatments where nitrogen-fixing species were planted. Sites presented very high variability in plant productivity and nutrient inputs. Plantations had greater accumulation of litter on the forest floor (9.4 Mg ha^{-1}) than other treatments (4.5 - 6,2 Mg ha^{-1}). No statistical differences were found in a 5 month long leaf decomposition study among treatments; likewise, similar results were found for soil nutrient concentration and stock, although sites did vary. Both planted restoration strategies recovered the function of litter production more quickly as compared to the control, but that does not imply the reestablishment of nutrient cycles. Litter quality indicators (nutrient concentration and C:nutrient ratios) were better in secondary forest. The dominance of litter from one species is not desirable for restoration practice as it can dictate nutrient availability and may negatively affect successional pathways. Accordingly, restoration strategies with more heterogeneous planting designs, such as the island methodology, may promote a more rapid increase in plant diversity and litter quality, which could in turn accelerate the reestablishment of nutrient cycling.

Key words: Costa Rica, decomposition, ecological restoration, leaf litter, litterfall dynamics, nutrient cycling, soils, tropical forest.

RESUMEN

Los bosques tropicales protegen la mayor biodiversidad del planeta y mantienen servicios ecosistémicos vitales. Sin embargo, la deforestación sigue intensa en la mayoría de países tropicales, en particular en América Latina. La deforestación provoca cambios en los ciclos de nutrientes que presentan altos costos ambientales y sociales. Estrategias de restauración ecológica tienen el potencial de acelerar el restablecimiento del ciclo de nutrientes en áreas degradadas. En mi proyecto de Maestría, se evaluó la dinámica de la hojarasca y nutrientes bajo cuatro tratamientos: Plantación (toda la superficie plantada); Islas (árboles sembrados en parches de tres tamaños), Control (regeneración natural) y Bosque Secundario joven (7-9 años). Los tratamientos (parcelas de 50 x 50m) fueron establecidos en junio de 2004 en seis sitios en el sur de Costa Rica. Las especies plantadas fueron dos nativas maderables (*Terminalia amazonia* y *Vochysia guatemalensis*) intercaladas con dos fijadoras de nitrógeno (*Erythrina poeppigiana* e *Inga edulis*). La producción de hojarasca no difirió ($F = 129{,}4$; $p < 0{,}0001$) entre el bosque secundario (7,3 Mg ha^{-1} $año^{-1}$) y la plantación (6,3 Mg ha^{-1} $año^{-1}$), mientras que las islas presentan valores intermedios (3,5 Mg ha^{-1} $año^{-1}$), y el control (1,4 Mg ha^{-1} $año^{-1}$) la producción más baja. Hojas representaran > 75% de la hojarasca. Inga edulis aportó el 70% de las hojas en las plantaciones. La concentración de Ca, Mg, K, Zn y Mn en la hojarasca fue significativamente mayor en los bosques secundarios que otros tratamientos, y esto se correlacionó positivamente con la mayor diversidad de especies. La concentración de nitrógeno en las hojas fue mayor en los tratamientos donde se plantaron especies fijadoras de nitrógeno. Se encontró alta variabilidad en la productividad y aporte de nutrientes entre los sitios. La acumulación de hojarasca en el suelo fue mayor en las plantaciones (9,4 Mg ha^{-1}) que otros tratamientos. No se identificó diferencias estadísticas entre tratamientos en el estudio de descomposición, así como para la concentración y contenido de nutrientes en el suelo. Las estrategias de restauración recuperaran la función de producción de hojarasca más rápidamente en comparación con el control, pero eso no implica el restablecimiento de los ciclos de nutrientes. Los indicadores de calidad de hojarasca son mejores en los tratamientos recuperando naturalmente. La dominancia de hojas de una especie no es deseable para la práctica de la restauración una vez que determina la disponibilidad de nutrientes y puede afectar negativamente la sucesión. En consecuencia, las estrategias de restauración que presentan un diseño de plantación más heterogéneos, como el método de islas, pueden promover un incremento más rápido de la diversidad vegetal y la calidad de la hojarasca, y luego acelerar el restablecimiento de los ciclos de nutrientes.

Palabras-claves: Restauración ecológica, bosques tropicales, dinámica de la hojarasca, ciclo de nutrientes, suelos, Costa Rica

INDEX OF TABLES

INDEX OF FIGURES

LIST OF ACRONYMS

AOAC	Association of Official Agricultural Chemists
BB	Bambú (study site)
BN	Bernie (study site)
CLP	Conservation Leadership Program
CATIE	Tropical Agricultural Centre for Research and Higher Education
CD	Cedeño (study site)
FAO	Food and Agriculture Organization of the United Nations
FLR	Forest Landscape Restoration
IMN	Instituto Meteorológico Nacional de Costa Rica
ITTO	International Tropical Timber Organization
IUCN	International Union for Conservation of Nature
LCBS	Las Cruces Biological Station
LL	Loma Linda (study site)
MEA	Millenium Ecosystem Assessment
MM	Melissa (study site)
NPP	Net Primary Productivity
OTS	Organization for Tropical Studies
SER	Society for Ecological Restoration
SG	San Gabriel (study site)
WCS	Wildlife Conservation Society

1 INTRODUCTION

Tropical forests protect the world's greatest biodiversity and provide ecosystem services at local, regional and global scales. Human societies are sustained by ecosystem services and their degradation impacts human well-being worldwide, especially for future generations (MEA 2005). However, deforestation is still widespread in most tropical countries, particularly in Latin America where forests are being logged and rapidly converted to agricultural use (FAO 2006). Indeed, incentives for commodities markets alongside the intangible value of ecosystem services of standing forest, make conservation a less attractive economic option (Angelsen 1999, Laurence 1999a, Nepstad *et al.* 2006). Besides the negative impacts on habitats, biodiversity, and natural resources (Laurence 1999a, Fearnside 2005), tropical deforestation releases 20% of all anthropogenic greenhouse gases (Gullison *et al.* 2007), which is a major global concern of our time. Moreover, it provokes key changes in global nutrient cycles, which have high environmental and social costs (MEA 2005).

Protecting remaining tropical forests is the main goal for conservation. However, conventional protection has proven to be insufficient due to the increasing isolation of existing protected areas (DeFries *et al.* 2005), and the high rates of forest loss and fragmentation (Laurence 1999b). Conservation efforts must be associated with connectivity establishment through biological corridors (Bennett 2004), conservation practices in agricultural lands (Daily *et al.* 2001, Vandermeer and Perfecto 2007, Harvey *et al.* 2008) and restoration strategies (Finegan 1996, Holl *et al.* 2003, Lamb *et al.* 2005, Chazdon 2008).

In this context, secondary forests play a key role in mitigating human impacts; they represent an important forest type in the tropics, and their area is increasing in some regions due to agricultural land abandonment led by policy and economic forces (Arroyo-Mora *et al.* 2005, Grau *et al.* 2003) and soil fertility exhaustion (Alfaiai *et al.* 2004, Arima *et al.* 2005). Secondary forests reestablish habitat, conserve biodiversity, supply goods (Finegan 1992), and restore ecosystem services such as atmospheric carbon fixation (Marin-Spiotta *et al.* 2007) and nutrient cycling through litterfall (Ostertag *et al.* 2008).

Secondary forest recovery rates differ greatly at the stand scale both within and between regions (Van Breugel *et al.* 2007). Among several factors identified as affecting recovery patterns and dynamics are the lack of seed dispersal, seedling competition with grasses, and a lack of soil nutrients (e.g. Uhl *et al.* 1988; Nepstad *et al.* 1996, Holl 1999, Holl

2002). Human induced strategies to overcome barriers for forest restoration are needed in the tropics considering the current scale of deforestation and the large areas of degraded lands (Lamb *et al.* 2005). Different methods have been proposed to facilitate recovery of tropical forests as reviewed in Lamb and Gilmour (2003) and Lamb *et al.* (2005).

Recently, a well replicated research project was established in southern Costa Rica to answer theoretical and practical questions about tropical forest recovery in abandoned pastures at local and landscape-levels (Fink *et al.* 2009, Holl *et al.* in press). This project, which compares natural regeneration to two active restoration strategies (uniform mixed-tree plantation and planting "tree islands"), may represent a viable model for restoration in other tropical regions. Considering the high costs of establishing plantations and the restricted budget of restoration initiatives (Holl and Howart 2000), tree islands may be a more cost effective restoration strategy (Zahawi and Augspurger 2006). This method mimics the natural regeneration process known as nucleation, where patches of succesional vegetation create microhabitat favorable to late-successional species (Yarranton and Morison 1974). Both restoration strategies (plantation, island) use two native timber-producing hardwoods (*Terminalia amazonia* and *Vochysia guatemalensis*) intercropped with two nitrogen-fixing species (*Erythrina poeppigiana* and *Inga edulis*). The latter two have been shown to increase soil nutrient availability through litterfall, enhance tree cover and habitat complexity, and thereby create better conditions for seedling establishment (Nichols *et al.* 2001, Nichols and Carpenter 2006). Moreover, *Inga* produces fruits that attracts birds (Fink *et al.* 2009).

More than restoring habitat for biodiversity, the proposed system potentially accelerates the reestablishment of ecosystem services, such as carbon sequestration (both in plant biomass and soils) and nutrient cycling when compared to natural succession. Also, considering that the reestablishment of the N-cycle in a succesional pathway in abandoned tropical areas can take several decades (Davidson *et al.* 2007), introducing N-fixers may accelerate this process. These assumptions can be addressed through litterfall, decomposition and soil studies that focus not only on the whole system but also on the role of the introduced species. Indeed, species composition has been shown to affect nutrient availability and successional pathways (Vitousek and Walter 1989). Litterfall and decomposition are the main carbon and nutrient transfer processes from vegetation to soil (Vitousek and Sandford 1986) and are a measure of system net primary productivity (NPP; Clark 2001a). Therefore, the study of litterfall dynamics, decomposition and nutrients inputs will provide us with information to compare the re-establishment of ecosystem services among restored systems, natural regeneration, and young secondary forests.

1.1 Objectives of the study

1.1.1 Overall objective

To contribute practical and theorical knowledge for tropical forest ecological restoration by studying the restablishment of nutrient cycles under two different restoration strategies (uniform mixed-tree plantation and tree islands), and compare them with similar-age areas under natural regeneration, and young secondary forests.

1.1.2 Specific objectives

- To quantify and classify the diversity, quantity, and quality of litterfall and nutrient return to soil among the two restoration strategies, early natural regeneration, and young secondary forests.

- To assess the litter decomposition rate under different restoration strategies.

- Evaluate soil chemical characteristics among treatments and identify if there is a restoration effect.

1.2 Hypotheses

H_1. Mixed-tree plantation, tree islands, and control will present differences in litterfall production, nutrient inputs from litterfall, and soil organic-C content. Given that litterfall production is proportional to tree density and canopy closure (Zou *et al.* 1995, Oelbermann and Gordon 2000) and that the organic-C content of soils responds rapidly to changes in vegetation cover and soil management (Schroth *et al.* 2003a), we predict that litterfall production (measured as dry weight), its nutrients inputs (measured by litterfall production and its chemical contents) and soil organic-C content will be greater in the mixed-tree plantation followed by tree islands and ultimately control.

H_2. Litterfall production will be similar in the mixed-tree plantation and young secondary forest. Prior studies have found that in systems with a closed canopy, there is no obvious trend in litterfall production with increasing forest age (Bray and Gorham 1964, Giese *et al.* 2003, Ostertag *et al.* 2008), species richness (Scherer-Lorenzen *et al*. 2007) or species diversity (Wardle *et al*. 1997). Considering that plantation (4 to 5 yr) and secondary forest (7-9 yr) systems had closed canopy at the beginning of this study, we predict that litterfall production (measured as dry weight) will not differ.

H_3. The two restoration strategies will have higher soil and litterfall nitrogen content when compared to natural regeneration and young secondary forest. Given that the re-establishment of the N-cycle in a succesional pathway in degraded areas can take on the order of decades (Davidson *et al*. 2007), we expect that nitrogen contents in both litterfall and soil will be higher in the restoration systems as compared to natural regeneration and young secondary forest because N-fixers (*Erythrina poeppigiana* and *Inga edulis*) were planted in these systems.

To test my hypotheses I collected and weighed litterfall twice a month during one year in all four treatments and performed four litterfall chemical analyses spread evenly over the 1 yr sampling period. Also, I analyzed soil chemical contents in the different systems. Moreover, to assess additional information about the litter dynamic, I pursue a preliminary study on leaf litter decomposition.

2 CONCEPTUAL FRAMEWORK

"*Everyone in the world depends completely on Earth's ecosystems and the services they provide, such as food, water, disease management, climate regulation, spiritual fulfillment, and aesthetic enjoyment. Over the past 50 years, humans have changed these ecosystems more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fiber, and fuel. This transformation of the planet has contributed to substantial net gains in human well-being and economic development. But not all regions and groups of people have benefited from this process—in fact, many have been harmed. Moreover, the full costs associated with these gains are only now becoming apparent"* (Millennium Ecosystem Assessment, MEA 2005).

Tropical forests play a vital role providing ecosystem services, especially those that support life on Earth (*supporting ecosystem services*) like primary production and nutrient cycling. These services have been drastically altered by human activities (especially agriculture and industry) over the past two centuries and that has had undoubted negative impacts on human well-being (MEA 2005). Vitousek *et al.* (1986) warned about human appropriation of the products of photosynthesis; twenty years ago they estimated that nearly 40% of potential terrestrial NPP is used directly, co-opted, or foregone because of human activities and that this could drastically affect the Earth's long-term carrying capacity.

The cycles of several key elements (e.g. P, N, S, C, and Fe) have been altered due to human activities, increasing ecosystem "leakiness" with respect to nutrients (MEA 2005). For example, the concentration of atmospheric CO_2 is greater than any other period in human history (IPCC 2007), and is accelerating due to the emissions from burning fossil fuels and the conversion of high C-density ecosystems (i.e. forests) to low C-density agroecosystems. This is a key factor affecting global climate change (IPCC 2007). For nitrogen, the use of synthetic N fertilizer, expanded planting of N-fixing crops, and deposition of N-containing air pollutants, have created an additional flux of 200 Tg a year and only part of it is denitrified (MEA 2005).

Even though many nutrients are being oversupplied (as N, P and S), some regions of the Earth, particularly Africa and Latin America, have a net depletion of soil fertility and high degradation because nutrients are not replaced; a process that has serious consequences for human nutrition and the environment (MEA 2005).

Tropical forest restoration has the potential to mitigate some of those negative impacts on supporting ecosystem services, as it plays an important role in both nutrient cycles and the NPP budget. My research thesis focused on evaluating litterfall dynamics under different tropical forest restoration strategies at the site level. Litterfall is a key indicator of both primary productivity and nutrient dynamics.

2.1 Supporting ecosystem services of tropical forests

Tropical forests cover less than 10% of Earth's territory but sustain between 50 and 90% of the planet's terrestrial species (WRI 1992). Moreover, they provide ecosystem services at different scales. However, these forests are threatened by logging, agricultural expansion, and other direct and indirect drivers of deforestation. Deforestation of tropical forests was estimated at 15.2 million ha year^{-1} between 1990-2000, while in the same period a relatively small increase in forest lands was registered as secondary regrowth (1 million ha year^{-1}) and plantations (1.9 million ha year^{-1}) (FAO 2001). Between 2000 and 2005, tropical deforestation was even greater (around 19 million ha year^{-1}; FAO 2006). Tropical deforestation contributes 20% of global greenhouse gas emissions (Gullison *et al.* 2007), and has a huge negative impact on the delivery of ecosystem services, such as NPP and nutrient cycling.

2.1.1 NPP in tropical forests

Plants are the main primary producers in terrestrial ecosystems; they use sunlight, water, atmospheric carbon dioxide and inorganic nutrients (minerals) to produce organic compounds via photosynthesis. This organic compound production is called Primary Production, and it is a crucial part of the C-cycle in the biosphere. Net Primary Production (NPP) is the difference between total photosynthesis (Gross Primary Production, GPP) and total plant respiration in an ecosystem (Clark 2001b); NPP provides the basis for the maintenance, growth, and reproduction of all heterotrophs and represents the total food resource on Earth (Vitousek *et al.* 1986). NPP is usually measured as mass of carbon per area and time (g C/m^2/yr).

Tropical forests are extremely important for the balance of carbon exchange (inputs and losses) between reservoirs or pools (the "global carbon budget"), and can function as both a source or sink of carbon depending on their age, disturbance, stress, and other factors (Lewis

2006). Clark *et al.* (2001a) show that tropical forests represent around 59% of the global carbon pool in forests and that these areas have between 32% and 43% of the world's terrestrial NPP potential. However, NPP cannot be directly measured in forests (Clark *et al.* 2001b). Instead, NPP is evaluated as the total amount of carbon fixed by the forest during a specified interval, which includes all new above- and below-ground organic matter that was both fixed and retained, as well as that lost by the plants, such as leaves and flowers (Figure 1; Clark *et al.* 2001b). Most field studies focus on aboveground components (fine litterfall and biomass increment) considering the difficulties of evaluating belowground components.

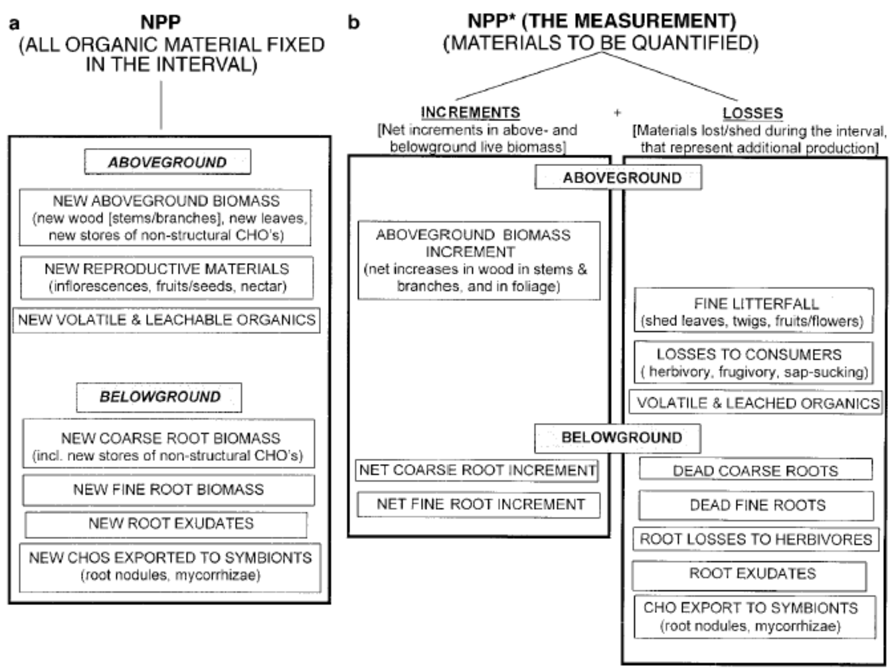

Figure 1. The components of (a) forest NPP and (b) NPP, the sum of all materials that together represent: (1) the amount of new organic matter that is retained by live plants at the end of the interval, and (2) the amount of organic matter that was both produced and lost by the plants during the same interval. CHO = carbohydrates. (Extract from Clark et al. 2001b).*

Litterfall amounts to the majority of aboveground NPP in old growth tropical forests, and reflects a forest's productivity (Lowman 1988). Clark *et al.* (2001a) found that litterfall ranges from 0.9 to 6.0 *t* C-ha^{-1}yr^{-1} in mature tropical forests while tree biomass increment (the second in importance) ranged from 0.3 to 3.8 *t* C-ha^{-1}yr^{-1}. Variation in litterfall is mainly due to differences in rainfall, temperature, elevation and soil fertility (Vitousek and Sanford 1986). Clark *et al.* (2001a) also found a predictive relationship between annual litterfall and aboveground biomass increment (R^2=0.69).

Litterfall in early successional forests shows a large increase in the first years; however once a canopy is closed there is no obvious trend in litterfall production with increasing stand age (Zou *et al.* 1995, Ostertag *et al.* 2008), species richness (Scherer-Lorenzen *et al*. 2007) and diversity (Wardle *et al.* 1997). Ewel (1976) found great differences in litterfall during the first 14-years of succession in Guatemala; they registered an increase of 55% in litterfall. Zou *et al*. (1995) in Puerto Rico found no difference in litterfall production between a mid-succesional forest and a mature forest. Ostertag *et al.* (2008) found similar results and conclude that young secondary forests (10 to 20 years) have the potential to recover litter-cycling functions and provide some of the same ecosystems services of primary forest.

In plantations, litterfall production varies according to the species planted, plantation density, cultivation system, and stand age. Cuevas and Lugo (1998) evaluated 26-years old stands of ten species, grown under similar climatic and edaphic conditions in Puerto Rico and found a mass of litterfall ranging from 8.1 to 14.3 t $ha^{-1}yr^{-1}$, with significant differences among species. In Costa Rica, *Erythrina poeppigiana* has been shown to produce 9.6 t $ha^{-1}yr^{-1}$ (CATIE 2003), exactly the same litterfall production found by Di Stefano and Fournier (2005) for a 10-years-old *Vochysia ferruginea* plantation. *Terminalia amazonica* litterfall production can be 7.5 t $ha^{-1}yr^{-1}$ in homogeneous plantation system (Mora 2005). Lugo (1992) compared tropical tree plantations of two species with secondary forests of similar age and found that plantations had higher total litterfall as well as aboveground biomass production.

2.1.2 Nutrient dynamics in tropical forests

Chemical elements and molecules operate in a closed system. The biogeochemical cycle is their circuit in Earth; including transfers among the living biosphere (*Bio*), and the nonliving lithosphere, atmosphere, and hydrosphere (*Geo*) (Ricklefs 1996). All elements are being recycled constantly; this mechanism occurs at different scales and elements can be accumulated for long ("reservoirs") or short periods (“exchange pools”). Forests are considered exchange pools for almost all elements. Biogeochemical cycles are called “nutrient cycles” if elements concerned are essential to life, since a nutrient is a chemical or substance that is vital to an organism’s metabolism.

Around 77% of the worlds biologically rich tropical forests are sustained by soils with moderate to low fertility (Vitousek and Sanford 1986). A high proportion of total site nutrient capital (the total amount of nutrients in all pools that are potentially available to the biota) is held in the biomass (50-90%) and plants have developed highly adaptive mechanisms for the acquisition and retention of nutrients (Walker and Reddell 2007). This factor makes tropical forests very vulnerable to high intensity anthropogenic disturbance (e.g. forest fire and clearing); where not only the site capital is directly removed but the tight, biotically bound nutrient cycles are disturbed, increasing nutrient leakage from the landscape (Walker and Reddell 2007).

Nutrient cycling in tropical forests (Figure 2) involves a complex set of direct and indirect feedback mechanisms between the soil and vegetation, and can be thought as transfers of nutrients between a number of compartments or pools (Bruijnzeel 1991). The distribution and cycling of elements include inputs by means of precipitation, mineral weathering, and gas absorption (including biological N fixation), and outputs by losses as solutes (leaching) and through volatilization (Vitousek and Sanford 1986). The nutrient status and availability of a site depend on the balance between nutrient inputs and outputs.

The factors that affect nutrient cycles in tropical forests are climate, species composition, successional phase, and soil fertility (Vitousek and Sanford 1986). In addition, patterns of nutrient cycling in tropical forests differ depending on soil type. Vitousek and Sanford (1986) found that moderately fertile soils support productive forests that cycle large quantities of nutrient elements, whereas forests on wide-spread oxisol/utisol soils have tight cycles of P and Ca, although they are rich in N. Forests on sandy spodosol/psamment soils cycle small quantities of N (also P in some cases), and they present high root/shoot ratios. Finally, they found that montane tropical forests in general appear to have low N. They conclude that these patterns affect the physiology, community ecology, and population biology of tropical forests. Moreover, nutrient concentrations in individual tissues reflects the influence of soil fertility; and the photosynthetic capacity of leaves is highly correlated to leaf nutrient concentration (mainly N) (Vitousek and Sanford 1986).

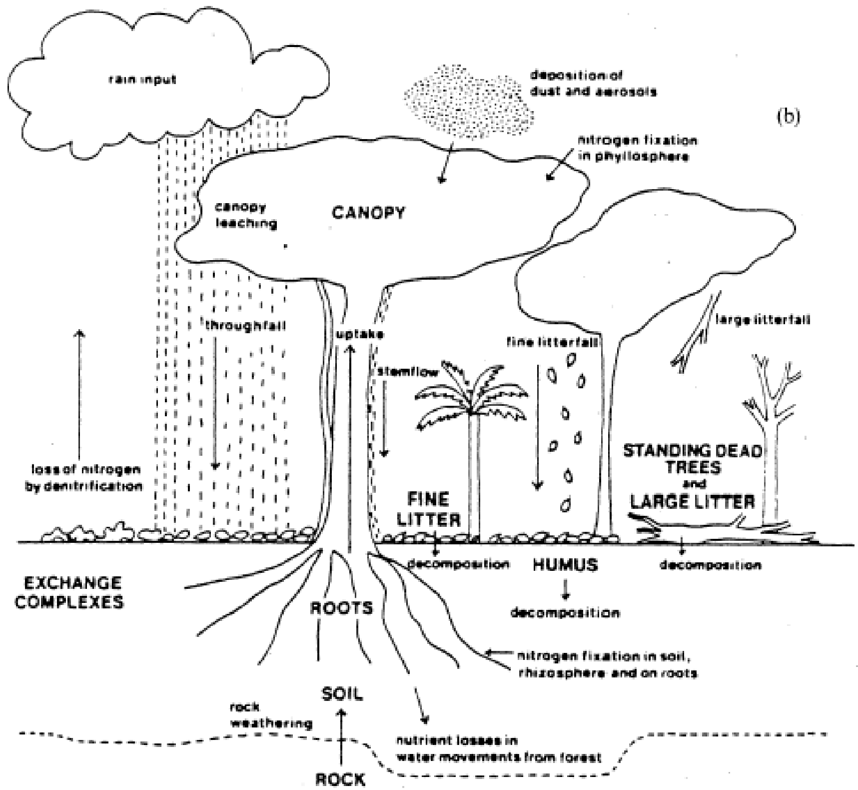

Figure 2. Nutrient cycling pathways in tropical forests (from Bruijnzeel 1991).

2.1.2.1 Nutrient input through litterfall

Litterfall is a fundamental process in nutrient cycling as it represents the main transfer of organic matter and mineral elements from aboveground vegetation to the soil surface (Vitousek and Sanford 1986). Litterfall is composed of leaves (leaflets and petioles), woody materials (< 1 cm), reproductive parts (flowers, fruits and seeds), and miscellaneous material (indeterminate plant material). Nutrient concentration of N, P, K, Ca and Mg in litterfall generally follows the pattern of miscellaneous > reproductive parts > leaves > total litter > fine wood (Cuevas and Lugo 1998). However, more than seventy-five percent of litterfall consists of leaves (Clark *et al.* 2001b) and so leaf fall represents the main determinant of the 'seasonality' of nutrient return to the soil (Moraes *et al.* 1999). The ratio between litterfall mass and litterfall nutrient content is called nutrient use efficiency (NUE; Vitousek 1982). The litter dynamic comprises litterfall, litter deposition on soils, and litter turnover into inorganic nutrients though decomposition, mineralization, and humification processes (Figure 3). It is followed by plant nutrient uptake from soils and its accumulation as plant biomass. The amount and pattern of litterfall are determinants of nutrient availability.

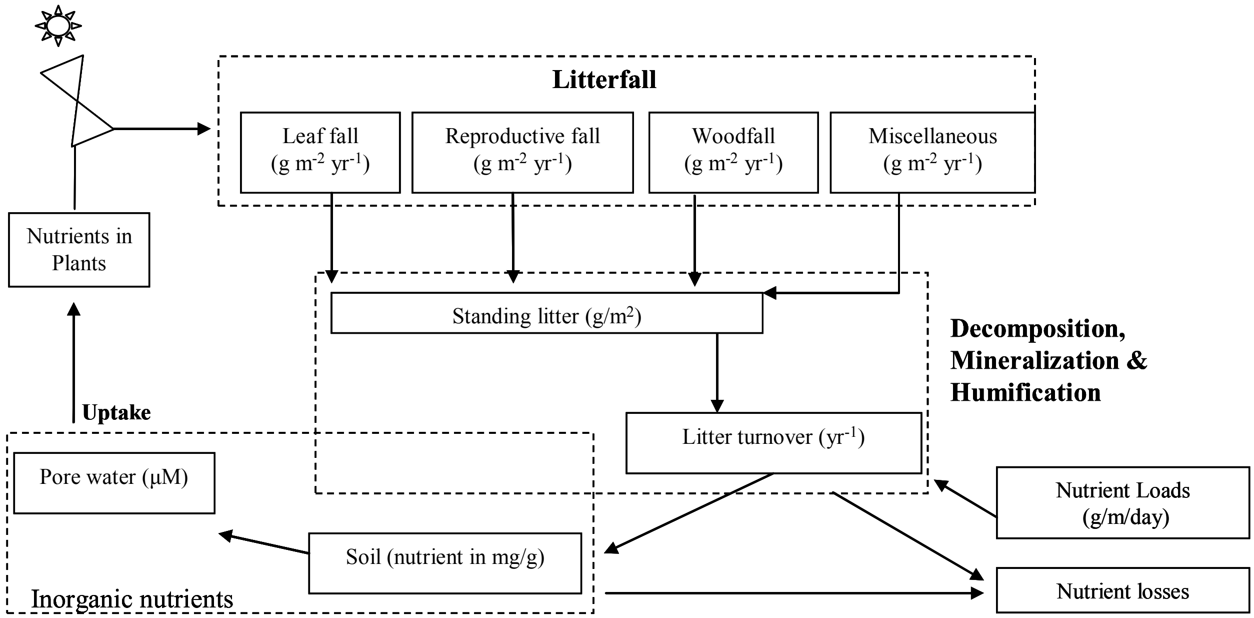

Figure 3. Nutrient cycle in tropical forests (adapted from different sources).

Litterfall quantity is proportional to tree density and canopy closure (Zou *et al.* 1995; Oelbermann and Gordon 2000). It is affected by a complex set of environmental variables such as temperature, rainfall (quantity and periodicity), soil and elevation, as well as potential and actual evapotranspiration and latitudinal position (Meentmeyer *et al.* 1982). Litterfall can be very seasonal depending on the region and forest species composition; the highest deposition of litter usually occurs in the dry season (Klinge 1977).

Tree species composition alters leaf litter chemistry and decomposition processes (Zou *et al.* 1995); it has been shown to affect nutrient availability and accordingly, successional pathways (Vitousek and Walter 1989). Soil fertility also plays an important role in litterfall nutrient content. Tropical forests in infertile sites present low nutrient concentrations, while moderately fertile soils support productive forests that cycle large quantities of nutrient elements (Vitousek and Sanford 1986).

In young secondary forests (5 yr) following hurricane Hugo in Puerto Rico, Scatena *et al.* (1996) found that N, P, K, Ca and Mg concentration in litterfall increased with forest age. However, only K recovered its "original" concentration after five years. They observed that the nutrient cycling strategy consisted of rapid accumulation of aboveground nutrients during stand closure and rapid turnover and cycling of nutrients through litterfall as the stand matured (Scatena *et al.* 1996).

Lugo (1992) compared N and P annual nutrient return to forest floor through litterfall between tree plantations and secondary forests of similar age. Plantation had greater nutrient return when compared to secondary forests. This was reflected in higher litterfall production in plantations, because he also found that plantation litterfall had lower nutrient concentration than secondary forests. Moreover, he found that litter of secondary forests had faster nutrient turnover than plantation, though plantations re-translocated more nutrients before leaf fall than did his secondary forests.

2.1.2.2 Litterfall decomposition, soil organic matter, and soil fertility

The litter layer protects the soil surface from erosion, releases nutrients, replenishes soil organic matter and provides a carbon substrate for soil biota (Schroth *et al.* 2003a). Soil organic matter includes all organic substances in soil, both living (<5% of total soil organic matter) and dead (~95%). According to Schroth *et al.* (2003a), the organic matter content of a soil influences a wide range of soil properties (chemical and physical) and processes, and is considered one of the most important components of soil fertility. Fertility is defined as "*the potential of a soil to supply nutrient elements in the quantity, form, and proportion required to support optimum plant growth*" (MEA 2005). Soil organic matter functions either as a source or a temporary sink of nutrients, and is affected by plant inputs as well as uptake. More than providing nutrients, organic matter regulates water movement into the subsoil and improves soil moisture retention, improving the functions of soil biota in regulating many ecosystem functions (Walker and Reddell 2007).

Litterfall decomposition involves a series of interactions between organic matter, soil microbial (fungi and bacteria) and invertebrate communities, and environmental conditions. The faunal communities in soil and litter are influenced by the quantity and quality of litter and its distribution; and these fauna not only influence the dynamic of decomposition and nutrient release, but also soil properties (Schroth 2003b). When biomass decomposes in or on the soil, nutrients may either remain in the soil in mineral form, be incorporated into soil biomass or soil organic matter (immobilization), be taken up by plants, or be lost from the system by leaching or as a gaseous form (Schroth 2003b). The relative importance of these pathways depends on the nutrients, the decomposing material, and biotic and abiotic conditions (Schroth 2003b).

Decomposition of litter is influenced by the seasonality of rainfall and plant composition; the rate is faster during the wet season when conditions for growth and activity of soil microorganisms are optimal (Xuluc-Tolosa *et al.* 2003). Different tropical species have different decomposition rates, and litter quality, especially C/N and lignin/N ratios, have been proposed as good predictors of decomposition rates. Xuluc-Tolosa *et al.* (2003) found that litter quality explains more of the variability in decomposition rate than the environmental variables; greater nutrient content favors more rapid decomposition in young forests. Ostertag *et al.* (2008) also show correlation between litter quality and decomposition rates.

Decomposition of litter and soil organic material releases nutrients into forms available to plants, which completes the nutrient cycle (Vitousek and Sanford 1986). However, availability of nutrients in soils is not only a function of its chemical form, but also of the capabilities of the plants growing in that soil to mobilize and absorb it (Lamber *et al.* 2007). Plants have different nutrient-acquisition strategies, which have been shown to depend on landscape age and soil nutrient status (Lamber *et al.* 2007). Lamber *et al.* (2007) found that the diversity of nutrient-acquisition strategies explained a major component of the observed plant species richness in south-western Australia. Indeed, plants have been adapting to overcome nutrient limitations (especially N and P); adaptations include mechanisms of reabsorption, and internal recycling and re-allocation for use in growth (Lamber *et al.* 2007).

2.2 Tropical forest ecological restoration

The degradation of natural resources, ecosystems, and the services they provide has been growing exponentially worldwide, especially in the tropics, and it has direct negative impacts on human well-being (MEA 2005). Land degradation is defined by the UNEP as "*a human induced or natural process which negatively affects the land to function effectively within an ecosystem, by accepting, storing and recycling water, energy, and nutrients*". According to Daily (1995), 35% of the world's land degradation is a result of overgrazing, 30% is due to deforestation and 28% to other agricultural practices. The ultimate land degradation step is the removal or loss of soil physical components; but other soil processes such as acidification, increased salinity, organic depletion, compaction, nutrient depletion, chemical contamination, and erosion are also considered degradation, and are linked to inappropriate land use practices (Marques *et al*. 2007).

Ecological Restoration attempts to reverse the negative effects of land degradation caused by human actions. It is defined by the Society for Ecological Restoration (SER 2004) as "*the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed*". In other words, it is an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its integrity, functionality and sustainability. Ecosystems in need of restoration are those that are degraded, damaged, transformed, or entirely destroyed as a direct or indirect result of human activities (SER 2004; Falk *et al.* 2006); although they can also be caused or aggravated by natural agents (SER 2004).

2.2.1 Concepts and thoughts

Restoration *sensu stricto* aims to re-establish an ecosystem's original form, including taxonomic composition as well as pre-existing basic functions (Lévêque and Mounolou 2004). Restoration *sensu lato* attempts to return an ecosystem to its historic trajectory when the restored site will not necessarily recover its former state without some form of intervention (SER 2004). Functions and processes of restored environments should be similar to the original ecosystem over time. Lamb and Gilmour (2003) consider that in the future it will be more appropriate to seek the restoration of "resilient natural vegetation" and its desired functions for the restablishment of desired ecosystem services. Indeed, the establishment of a self-sufficient ecosystem that requires minimal to no continued human input is the ultimate goal of ecological restoration (Hobbs *et al.* 2007a; Walker *et al.* 2007). SER (2004) propose that restoration is achieved when an ecosystem moves towards its historic trajectory of development. Trajectory and boundaries are defined according to studies of comparable intact ecosystems, and other referential information. Some aspects of biodiversity, structure, and functioning may change and/or fluctuate as all normal ecosystem development responds to natural, directional change (i.e. non-cyclic) such as stress and disturbance events (SER 2004).

The terms reclamation, rehabilitation, and reforestation are frequently confused with restoration, but have different meanings as defined by Lamb and Gilmour (2003) and SER (2004). **Reclamation** is the re-establishment of productivity and ecological processes in degraded sites (amelioration), but not necessarily the original biodiversity. It is usually achieved with a few species only. This practice is often used in the context of mined lands and can employ exotic species. **Rehabilitation** is the re-establishment of productivity, ecological processes and some portion of the original biodiversity. Due to ecological and economic reasons, the new ecosystem often represents species not previously found in the original system. Finally, **reforestation** is the restocking of an existing forest for ecological and/or economical benefits. Even though this can be done by ecological restoration, the term is mostly used for productive purposes where monocultures and exotic species are frequently used. It is important to highlight that these three activities can restore ecosystem functions completely or partially. At the site-level, the selection of the most appropriate method depends on the initial state of degradation of the area, the desired outcomes, and the available budget (Figure 4).

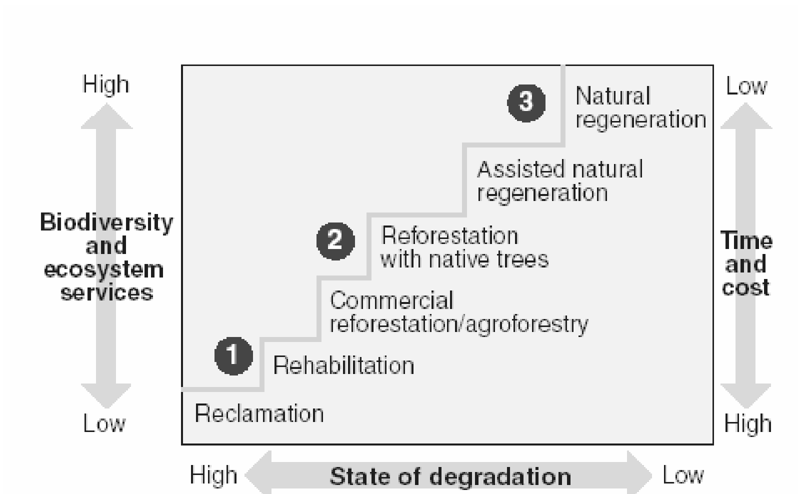

Figure 4. The restoration staircase. Depending on the state of degradation of an ecosystem, different approaches can be taken to restore some level of biodiversity and ecosystem service. The expected results are (1) restoration of soil fertility for agricultural or forestry use, (2) production of timber and non-timber, and (3) restoration of biodiversity and ecosystem services (from Chazdon 2008).

Recently a more holistic concept of restoration was proposed termed "Forest Landscape Restoration" (FLR), which is defined as the process that aims to restore ecological integrity and enhance human well-being in deforested or degraded forest landscapes (ITTO and IUCN 2005, Mansourian *et al.* 2005). This approach considers the dynamic and complex interactions between people, natural resources and land use on a landscape scale. According to ITTO and IUCN (2005), FLR differs to most other restoration approaches because: (1) it takes a landscape-level view where site-level restoration decisions take into account landscape-level objectives and impacts; (2) it operates on the 'double filter' condition where restoration efforts must result in both improved ecological integrity and enhanced human well-being; (3) it is a collaborative process involving a wide range of stakeholders; (4) it does not necessarily aim to return a landscape to its original forested state – rather it aims to fortify the resilience of forested areas while maintaining options for optimizing the delivery of forest-related goods and services; and (5) it can be applied to secondary forests, forested lands, and even agricultural lands.

To achieve these interdisciplinary objectives, the FLR approach proposes an ensemble of complementary practices in addition to ecological restoration including: the rehabilitation and management of degraded primary forests, management of secondary forests, restoration of primary forests and their functions, promotion of natural regeneration in degraded areas and marginal sites, reforestation and forest plantations, and agroforestry and other configurations of on-farm tree plantings (ITTO and IUCN 2005).

Lamb *et al.* (2005) also suggest different strategies in their review of restoration in tropical forest landscapes. They conclude that moving restoration from a site-based level activity to a landscape-level activity is the biggest challenge in this field. Indeed, only landscape-level restoration can complement existing protected area networks, and working at a landscape-level makes it possible to balance biodiversity restoration and production (Lamb *et al.* 2005).

In addition to considering scale, restoration must be thought of as a multi-dimensional process in which different factors interact over space and time. The main aspects to be considered are: (1) biological (at both site and landscape scales, e.g. the integrity of the surrounding ecosystem and natural processes such as dispersal and colonization); (2) physical (soil condition, climate, natural resources); (3) social (e.g. demography, human well-being); (4) economic (e.g. fund availability, sustainability, potential new markets such as environmental services payments and carbon credits); (5) technical (e.g. practical methods at the site-level, use of machinery); (6) cultural (e.g. local habits, traditions, beliefs, values); (7) legal (e.g. land tenure, laws, ordering plans); (8) production (e.g. long term objectives, commercial species introductions for timber and non-timber products); (9) institutional (e.g. governmental, local organization, coordination); and (10) political (e.g. national and international policies, governability, stakeholder participation).

Considering these multi-dimensional factors at the landscape level is vital to successful restoration practice, especially in the tropics where poverty is wide-spread. Like conservation and degradation, restoration is also a social process and human beings have to play a major role. For example, if an ecosystem has no more resilience and natural processes cannot maintain it, humanity has an ethical responsibility to restore at least part of it. Our present situation is in part due to the lack of environmental ethics in our society, which can also explain the collapse of many ancient societies (Diamond 2005. Thus, restoration depends on the altering of human "development" systems (in terms of energy supply, consumption, waste, transportation, and business) and reorienting this relationship with respect to nature. As noted by Higgs (2005), scientific and technological acumen is insufficient for restoration; it is necessary to respect other kinds of knowledge besides science, and especially to recognize a moral center that is beyond the scope of science.

2.2.2 Ecological principles

2.2.2.1 Restoration ecology

There is a common misconception between the terms ecological restoration and restoration ecology. Higgs (2005) warns that they are frequently interchanged or considered synonyms, although they have fundamentally different meanings. According to Higgs, restoration ecology is the set of scientific practices that form a subdiscipline of ecology (i.e. with hypotheses, conjectures, experimentation, publication); while ecological restoration is the ensemble of practices that constitute the entire field of restoration, including restoration ecology as well as the participating human and natural science, politics, technologies, economical and cultural factors (Higgs 2005). SER (2004) summarises "*ecological restoration is the practice of restoring ecosystems and restoration ecology is the science that provides concepts, models, methodologies and tools for practitioners*".

The science of restoration ecology is based on broad areas of ecological theory as presented in Falk *et al.* (2006): (1) Population and ecological genetics; (2) Ecophysiological and functional ecology; (3) Demography, population dynamics and metapopulation ecology; (4) Community ecology; (5) Evolutionary ecology; (6) Fine-scale heterogeneity (enhancing diversity); (6) Food webs; (7) Ecological dynamics and trajectories; (8) Biodiversity and ecosystem functioning; (8) Modeling and simulations; (9) Invasive species and community invisibility; (10) Macroecology (influence of a larger spatial context); and (11) Paleoecology and climate change (planning restoration according to expected global change). Moreover, it also employs concepts from other ecological disciplines, such as conservation biology, disturbance ecology, ecological succession, island biogeography, and landscape ecology (Walker *et al.* 2007).

Palmer *et al.* (2006) state that ecological restoration provides *exciting* opportunities to conduct large-scale experiments and test basic ecological theory, both of which have the potential to build the science of restoration ecology. Ecological restoration is *the ultimate "acid test" of our understanding of ecosystem functioning* (Bradshaw 1987). However, according to Palmer *et al*. (2006) there is also a large part of ecological restoration that will never be guided by restoration ecology; instead, contextual constraints and societal objectives, such as co-opting natural resources or modifying ecological systems for human use, will determine restoration objectives and potential much of the time.

2.2.2.2 Linkages between restoration and succession

There is an intrinsic link between succession and restoration (Table 1); both comprise species composition, ecosystem functions, substrate and microclimate change over time (Walker *et al*. 2007). Succession is a key ecological process whose concepts underly many ecological restoration efforts (Hobbs *et al*. 2007a). However, succession is a natural process; whereas restoration is an assisted or manipulative process more focused on specific outcomes (Walker *et al.* 2007). Nevertheless, the principles of ecological restoration and ecological succession are the same (Bradshaw 1987). Accordingly, succession can offer significant contributions to restoration, whereas the outcomes of restoration activities could serve as practical tests of succesional theory (Walker *et al.* 2007). Indeed, succession and restoration are limited by a similar group of abiotic and biotic constraints (such as seed dispersal, seedling establishment and growth, and microclimate). Thus, overcoming these barriers is a substantial goal of any restoration project (Walker *et al.* 2007), and the results of basic research on successional patterns must guide the development of practical techniques for restoration (Janzen 1988; Finegan and Delgado 2000).

According to Del Moral *et al.* (2007) the application of the lessons of succession to restoration practice will improve restoration program efficiency and quality, and assure that both structure and function develop well. They enumerate some of the lessons to restoration from successional studies; suggesting that restoration tactics should focus on site amelioration, improving establishment success, and protecting desirable species from herbivory and competition during development (Del Moral *et al.* 2007). Moreover, the incorporation of structural heterogeneity at early stages will promote mosaics of vegetation that better mimic the natural landscape (Del Moral *et al.* 2007).

Table 1. Topics that link succession and restoration (adapted from Walker et al. 2007).

Topic	Shared information
Disturbance	Loss of biological legacy, disturbance intensity
Ecosystem function	Energy flow, carbon accumulation and storage, nutrient dynamics, soils properties, water cycle
Community structure and composition	Biomass, vertical distribution, leaf area index, species richness, diversity, species density, spatial aggregation
Community dynamics	Facilitation, inhibition, dispersal, sustainability
Species attributes	Life history characteristics (pollinization, germination, establishment, growth, longevity)
Trajectories	Rates and targets
Models	Generalizations about processes

Assembly rules (principles and predictions about the mechanisms of community organization) and disturbance are other important ecological theories to consider with degraded ecosystem restoration in addition to succession (Hobbs *et al.* 2007a). Finally, climate change studies play a major role in restoration by shifting references. Restoration must follow the new knowledge in this field and use models that contribute to mitigating climate change impacts on terrestrial biodiversity.

2.2.3 Technical strategies at the site-level

Ecological restoration can be achieved through unassisted succession (once perturbation is removed), as well as through technical restoration strategies (Prach *et al.* 2007). The simplest restoration technique is the removal of a perturbation source to allow an ecosystem to recover naturally. Prach *et al.* (2007) argue that unassisted succession can take longer than technical strategies, but this can be compensated for by higher structural and functional diversity and higher natural and conservation value of the resulting ecosystem. However, abandonment will not always lead to the development of desired successional stages (Schrautzer *et al*. 2007) and recovery may present many barriers (Holl 2002). Thus, the choice of better ecological restoration strategies at the site level (passive/unassisted or active/assisted) will depend on the state of degradation, the project objectives, and the budget.

2.2.3.1 Ecological restoration through secondary succession (passive)

Passive (or unassisted) restoration is the most appropriate method when financial resources are scarce, or the state of degradation is not excessive. In this case it is necessary to protect the area to be restored from any type of exogenous disturbance (e.g. fire mitigation, grazer exclusion/inclusion), to enable the processes of colonization and succession to occur naturally.

Patterns and dynamics of succession differ greatly at the stand scale within and between regions (Van Breugel *et al.* 2007) and its development depends on different abiotic and biotic factors (Figure 5). Among factors identified as affecting recovery are: climate and microclimate, water stress, soil and site conditions, previous land-use history (management, timing, and intensity), size of a given area and distance to seed source, seed dispersal, seed bank, seedling establishment success, competition with aggressive grasses and remnant trees (Uhl 1987, Uhl *et al.* 1988, Nepstad *et al.* 1991, Nepstad *et al.* 1996, Finegan 1992, Vieira *et al.* 1994, Holl 1999, Holl *et al.* 2000, Holl 2002, Finegan and Delgado 2000, Chazdon *et al.* 2007). Socioeconomic factors also play an important role in the increase of secondary forests (Grau *et al.* 2003). In Costa Rica, for example, there has been a net increase of forest cover in abandoned lands, a result of conservation policies and associated market forces such as a decrease in the price of rural commodities (Arroyo-Mora *et al.* 2005, Sánchez-Azofeifa *et al.* 2007).

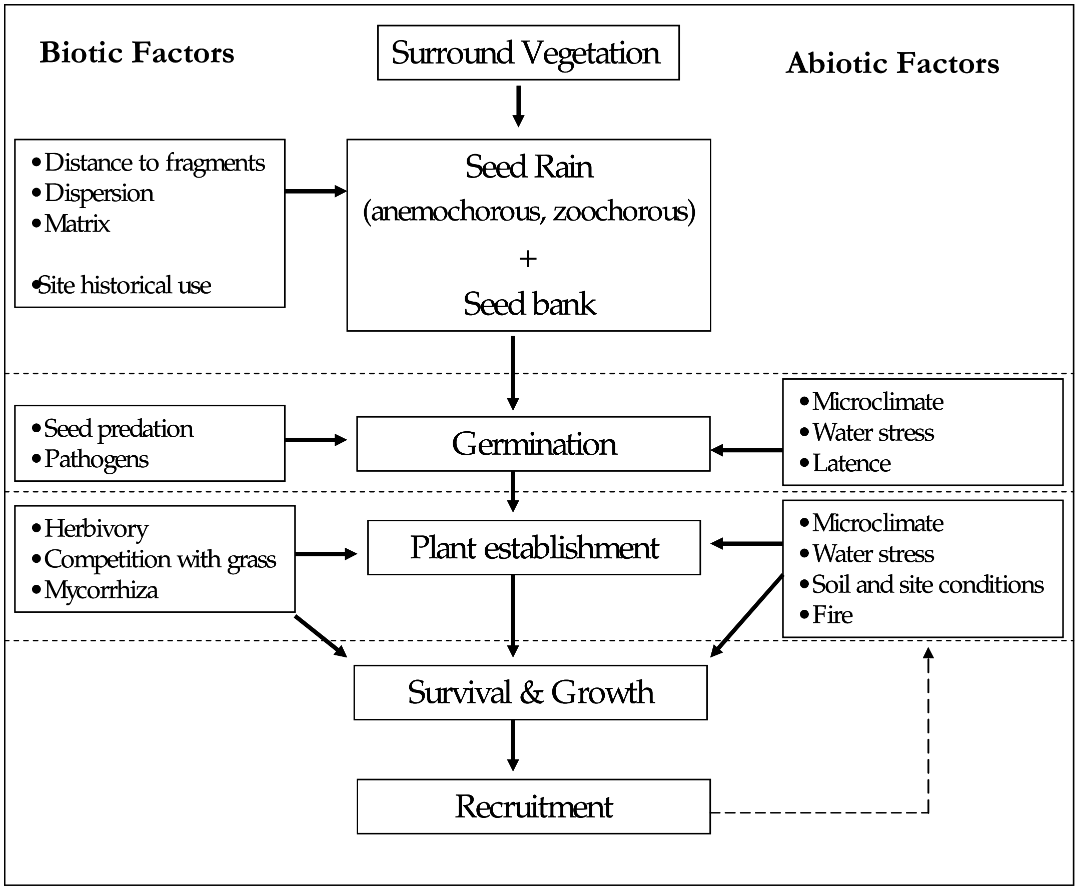

Figure 5. Factor limiting forest recovery in degraded sites. Right: abiotic factor. Left: biotic factors (adapted from Meli 2003 and Holl et al. 2000).

2.2.3.2 Active restoration

Considering the scale of deforestation and degradation in many regions of the tropics, human interventions to restore biodiversity and ecological services are also needed (Lamb *et al.* 2005). Manipulation of both the physical environment and the biota have been considered; and these manipulations may reduce the length of time needed for recovery (Prach *et al.* 2007).

Facilitation is the process by which established plants improve conditions for the establishment of other plants by attracting dispersal fauna, improving soils and microclimatic variables (Del Moral *et al.* 2007). Different methods have been proposed to facilitate recovery in the tropics as reviewed in Lamb and Gilmour (2003) and Lamb *et al.* (2005). Among them are enrichment plantating in secondary forests that present low levels of diversity, direct seeding, planting scattered trees, planting tree islands, dense plantings of a few species, intensive high density and diversity planting, and intensive ecological reconstruction after mining. There is a high range of costs and benefits among techniques, and soil and site conditions, the choice of species, the surrounding environment of the area to be restored, and many other biotic and abiotic factors can affect the gains to both biodiversity and ecosystem services

A plantation of a few species is one of the most common methods. This strategy requires a high density of planted trees per hectare and clearing maintenance in the first years. Early successional species can get established quickly and create better conditions for the arrival of a more diverse community (Reay and Norton 1999). Species should be chosen according to site tolerance or because they are attractive to wildlife (Lamb and Gilmour 2003). Once trees are established, they can suppress shade-intolerant grasses and weeds, attract seed dispersers and improve establishment conditions. When an area is near an intact forest (source of seeds and faunal dispersers) the recruitment of new species may be faster (Lamb and Gilmour 2003). Intercropping species with nitrogen-fixing species can increase soil nutrients and create better conditions for seedling establishment (Nichols *et al.* 2001, Carpenter *et al.* 2004). According to Lamb *et al.* (2005), a plantation of a few species primarily benefits ecological services although it can also supply some goods depending on the species planted.

Dense plantations present high initial costs and maintenance labor. Most restoration initiatives have very restricted budgets and their main obstacles are high costs and competing land uses (Holl and Howarth 2000). Accordingly, other techniques can be more attractive to farmers. For example, planting tree islands may be a more cost effective restoration strategy (Zahawi and Augspurger 2006).

Planting tree islands aims to create a structural complexity that can facilitate recovery. It mimics the natural regeneration process known as *nucleation*, where patches of successional vegetation create a microhabitat favorable to late-successional species establishment (Yarranton and Morison 1974), by reducing temperature and light extremes (Zahawi and Augspurger 2006). Moreover, it attracts seed-dispersing birds and frugivores (Zahawi and Augspurger 2006). This "island" design requires fewer trees to be planted per hectare and is cheaper than the traditional plantation. Establishing tree islands can be very appropriate in abandoned agricultural areas dominated by grasses. However, Lamb and Gilmour (2003) caution that the existence of seed sources and animal dispersor vectors in the landscape is crucial issue to the success of this type of technique. It may not be successful in very large disturbed areas.

2.2.3.3 Choice of species

The introduced species in active restoration strategies play a very important role in subsequent processes towards the restoration of biodiversity and/or ecosystem services. These species should be chosen based on prior ecological research carried out in the area and it is important to use healthy and phenotypically desirable mother-trees (Lamb and Gilmour 2003). Species choice depends largely on the restoration strategy and desired outcomes; species can provide better physical (structural heterogeneity) or chemical conditions (improving soil properties through mychorrizae and/or litterfall), or have biological functions (such as attracting fauna or enhancing diversity); they can also have economical purposes (introduce species for future economical use).

Lamb and Gilmour's (2003) recommendations for species choice are: (1) to initially use fast-growing species that would shade out aggressive weeds and grasses, (2) to introduce species that are not being naturally dispersed (eg, those with large seeds) or late-successional species, (3) species that are important for wildlife (food, nesting and protection), (4) locally-rare and endangered species, and (5) species that farmers like (e.g., hardwoods). The use of exotic species should be limited to cases where degradation is extreme, and it is important to control reproduction of these species and eliminate them as soon as possible. Nitrogen-fixing species are recommended for very degraded soils; they can ameliorate soil conditions and reduce the need for fertilizers (Meli 2003). Cuevas and Lugo (1998) suggest that species selection should be determined based on their effectiveness of resource utilization and the degree of nutrient limitation in the system.

If a future goal is to manage the restored area for economical purposes, valuable species both for timber and non-timber forest products must be planted in the early stages and silvicultural treatments performed in order to improve development. However, in cases where species are being introduced to directly enhance diversity, ensuring genetic variability is a vital issue to the success of the restoration in the long term (McKay *et al.* 2005). Also, seeds should come from trees in located in the landscape that indicate they receive pollen from many potential fathers, to avoid inbred or selfed seeds (Aldrich and Hamrick 1998).

2.2.4 Restoring supporting ecosystem services

Restoration strategies have an important role in re-establishing ecosystem services such as NPP and nutrient cycling. Active techniques may have the potential to accelerate this recovery, but it will depend on the introduced species and site management. Aboveground biomass increment, litterfall dynamics, and nutrient cycling characteristics of a species are important selection criteria for this purpose. NPP (measured by aboveground biomass increment and litterfall) increases rapidly as a system develops. The vegetation composition (natural dispersed species and introduced) have important consequences for NPP and nutrient availability. Cuevas and Lugo (1998) provide evidences that species selection play an important role in the rate and timing of growth, litterfall and nutrient return to forest floor. Nevertheless, it is important to state that these variables will not necessarily be associated with biodiversity enhancement.

Species composition has been shown to affect nutrient availability and successional pathways (Vitousek and Walter 1989). Homogeneous plantations can grow very fast (high NPP) but can produce poor litter quality (i.e. high carbon to nutrient ratios) that will slow decomposition and mineralization processes (Wardle and Peltzer 2007) and may affect forest restoration. For example, Kato *et al.* (2006) found a negative correlation between density of tree planting and native plant species diversity in Eastern Amazon. Therefore, restoration strategies with a more heterogeneous structure as the "tree island design" may have the potential to guarantee greater diversity. The comparison of litterfall and nutrient dynamics under different restoration strategies is poorly documented in the literature. It is very important to understand how these processes develop under different methods to facilitate tropical forest restoration. Comparing these systems to natural processes in different succesional stages may provide us with indicators of success of a particular strategy and assist worldwide restoration efforts.

3 BIBLIOGRAPHY

Aldrich, P.R.; and Hamrick, J.L. 1998. Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. Science 281:103-105.

Alfaiai, A. S.; Ribeiro, G. R.; Nobre, A. D.; Luizão, R. C.; and Luizão, F. J. 2004. Evaluation of soil fertility in smallholder agroforestry systems and pastures in western Amazonia. Agriculture Ecosystems and Environment 102:409–414.

Angelsen, A. 1999. Agricultural expansion and deforestation: modelling the impact of population, market forces and property rights. Journal of Development Economics 58: 185–218.

Arima, E.; Barreto, P.; and Brito, M. 2005. Cattle ranching in the Amazon: trends and implications for environmental conservation. Belém: Imazon. 75p.

Arroyo-Mora, J.P.; Sanchez-Azofeifa, G.A.; Rivard, B.; Calvo, J.C.; and Janzen, D.H. 2005. Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. Agriculture, Ecosystems and Environment 106: 27–39.

Bennett, A.F. 2004. Enlazando el paisaje: el papel de los corredores y la conectividad en la conservación de la vida Silvestre. International Union for Conservation of Nature and Natural Resources (IUCN). 276p.

Bradshaw, A.D. 1987. Restoration: an acid test for ecology. In: Jordan, W.R.; Gilpin, M.E.; and Aber J.E. (Eds.) Restoration ecology. A synthetic approach to ecological research. Cambridge University Press. Cambridge, England.

Bray, J.R.; and Gorham, E. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101-157.

Bruijnzeel, L.A. 1991. Nutrient input-output budgets of moist tropical forest ecosystems: a review. Journal of Tropical Ecology 7:1-24.

Carpenter, F.L.; Nichols, J.D.; Pratt, R.T.; and Young, K.C. 2004. Methods of facilitating reforestation of tropical degraded land with the native timber tree, *Terminalia amazonia*. Forest Ecology and Management 202: 281-291.

CATIE. 2003. Árboles de Centroamérica: un manual para extensionistas. OFI/*CATIE*. 1079 p. Avaiable at: http://herbaria.plants.ox.ac.uk

Chazdon, R.L.; Letcher1, S.G.; Van Breugel, M.; Martínez-Ramos, M.; Bongers, F.; and Finegan, B. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philosophical Transactions of the Royal Society 362: 273–289.

Chazdon, R.L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320: 1458-1460.

Clark, D.A.; Brown, S.; Kicklighter, D.W.; Chambers, J.Q.; Thomlinson, J.R.; Ni, J.; and Holland, E. A. 2001a. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications 11:371-389.

Clark, D.A.; Brown, S.; Kicklighter, D.W.; Chambers, J.Q.; Thomlinson, J.R.; and Ni, J. 2001b. Measuring net primary production in forests: concepts and field methods. Ecological Applications 11:356–370.

Cuevas, E.; and Lugo, A.E. 1998. Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. Forest Ecology and Management 112:263-279.

Daily, G.C. 1995. Restoring value to the world's degraded lands. Science 269 (5222): 350-354.

Daily, G.C.; Ehrlich, P.R.; and Sanchez-Azofeifa, G.A. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica Ecological Applications 11 (1): 1–13.

Davidson E.A.; de Carvalho, C.J.; Figueira, A.M.; Ishida, F.Y.; Ometto, J.P.; Nardoto, G.B.; Sabá, R.T.; Hayashi, S.N.; Leal, E.C.; Vieira, I.C.; and Martinelli, L.A. 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. Nature 447: 995-998.

DeFries, R.; Hansen, A.; Newton, A.C.; and Hansen, MC. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. Ecological Applications 15(1):19-26.

Del Moral, R.; Walker, L.R.; and Bakker, J.P. 2007. Insights gained from succession for the restoration of landscape structure and function. In Walker, L. R.; Walker, J.; Hobbs, R. J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.19-44.

Di Stefano, J.F.; and Fournier, L.A. 2005. Caida de hojarasca y tasas de descomposicion de las hojas de *Vochysia guatemalesis* en un plantación de 10 años, Tabarcia de Mora, Costa Rica. Agronomia Costarricense 29(1): 9-16.

Diamond, J. 2005. Colapso: como as sociedades escolhem o fracasso ou o sucesso. Sao Paulo. Editora Record, 686 p.

Ewel, J.J. 1976. Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. Journal of Ecology 64:293-308.

Falk, D.A.; Palmer, M.A.; and Zedler, J.B. (eds.). 2006. Foundations of restoration ecology. Society for Ecological Restoration International. Island Press, Washington.

FAO. 2006. Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management, FAO Forestry Paper 147. Food and Agriculture Organization of the United Nations, Rome. Available on the Internet www.fao.org/forestry/fo/fra/index/jsp.

FAO. 2001. Global Forest Resources Assessment 2000—Main Report. FAO Forestry Paper 140, Food and Agriculture Organization of the United Nations, Rome, 482 pp. Available on the Internet www.fao.org/forestry/fo/fra/index/jsp.

Fearnside, P.M. 2005. Deforestation in Brazilian Amazonia: history, rates and consequences. Conservation Biology 19 (3): 680-688.

Finegan, B. 1992. The management potential of neotropical secondary lowland rain forest. Forest Ecology and Management 47(2): 295-321.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends in Ecology and Evolution 11(3): 119-124.

Finegan, B; and Delgado, D. 2000. Structural and floristic heterogeneity in a 30- year-old Costa Rican rain forest restored on pasture through natural secondary succession. Restoration Ecology 8 (4):380-393.

Fink, R.D.; Lindell, C.A.; Morrison, E.B.; Zahawi, R.A.; and Holl, K.D. 2009. Patch size and tree species influence the number and duration of bird visits in forest restoration plots in Southern Costa Rica. Restoration Ecology 17:479-486.

Giese L.A.B.; Aust, W.M.; Kolka, R.K.; and Trettin, C.C. 2003. Biomass and carbon pools of disturbed riparian forests. Forest Ecology and Management 180 (1): 493-508.

Grau, H. R.; Aide, T. M.; Zimmerman, J. K.; Thomlinson, J. R.; Helmer, E.; and Zou, X. M. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. BioScience 53: 1159-1168.

Gullison, R.E.; Frumhoff, P.C.; Canadell, J.G.; Field, C.B.; Nepstad, D.C.; Hayhoe, K.; Avissar, R.; Curran, L.M.; Friedlingstein, P.; Jones, C.D.; and Nobre, C. 2007. Tropical forests and climate policy. Science 316: 985 – 986.

Harvey, C.A.; Komar, O.; Chazdon, R., Ferguson, B.G.; Finegan, B.; Griffith, G.M.; Martínez-Ramos, M.; Morales, H.; Nigh, R.; Soto-Pinto, L.; van Breugel, M.; and Wishnie, M. 2008. Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican Hotspot. Conservation Biology 22 (1): 8-15.

Higgs, E. 2005. The two-culture problem: ecological restoration and the integration of knowledge. Restoration Ecology 13 (1): 159-164.

Hobbs, R.J.; Walker, L.R.; and Walker, J. 2007a. Integrating restoration and succession. In Walker, L.R.; Walker, J.; Hobbs, R.J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.168-179.

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

Holl, K.D.; Loik, M.E.; Lin, M.E.; and Samuels, I.A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology 8 (4):339-349.

Holl, K.D.; and Howarth, R.B. 2000. Paying for restoration. Restoration Ecology 8: 260-267.

Holl, K. D. 2002. Tropical moist forest restoration. In Davy A. J.; and Perrow, M. Handbook of Ecological Restoration, vol. II. Cambridge University Press: Cambridge. pp.539-558.

Holl, K.; Crone, E.E.; and Schultz, C.B. 2003. Landscape restoration: moving from generalities to methodologies. BioScience 53: 5.

Holl, K.D.; Zahawi, R.; Cole, R. J.; Ostertag, R.; and Cordell, S. *In press*. Planting seedlings in plantations versus tree islands as a large-scale tropical forest restoration strategy. Restoration Ecology.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.

ITTO and IUCN. 2005. Restoring forest landscapes: An introduction to the art and science of forest landscape restoration. Technical Series No 23. Yokohama: ITTO.

Janzen, D.H. 1988. Management of habitat fragments in a tropical dry forest: growth. Annals of the Missouri Botanical Garden 75: 105-116.

Kato, O.R.; Kato, M.d.S.A.; Carvalho, C.J.R.d.; Figueiredo, R.O.; Camarăo, A.P.; Sá, T.D.d.A.; Denich, M.; and Vielhauer, K. 2006. Uso de Agroflorestas no Manejo de Florestas Secundárias. In: Gama-Rodrigues A.C.d., Barros N.F.d., Gama-Rodrigues E.F.d., Freitas M.S.M., Viana A.P., Jasmin J.M., Marciano J.G.d.A.C. (eds): Sistemas Agroflorestais - Base Cientificas para o Desenvolvimento Sustentável. Universidade Estadual do Norte Fluminense Darcy Ribeiro, Campos dos Goytocazes, p. 119-138.

Klinge, H. 1977. Fine litter production and nutrient return to the soil in three natural forest stands of eastern Amazonia. Geo-Eco-Trop 1:159-167.

Lamb, D.; Erskine, P.D.; and Parrotta, J.A. 2005. Restoration of degraded tropical forest landscapes. Science 310:1628-1632.

Lamb, D.; and Gilmour, D. 2003. Issues in forest conservation. Rehabilitation and restoration of degraded forests. International Union for Conservation of Nature and Natural Resources (IUCN) and The World Wide Fund for Nature (WWF). 122p.

Lamber, H.; Raven, J.A.; Shaver, G.R.; and Smith, S.E. 2007. Plant nutrient-acquisition strategies change with soil age. Trends in Ecology and Evolution 23 (2): 95- 102.

Laurance, W.F. 1999a. Reflections on the tropical deforestation crisis. Biological Conservation 91: 109-117.

Laurance, W.F. 1999b. Introduction and synthesis. Biological Conservation 91: 101-107.

Lévêque, C.; and Mounolou JC. 2004. Biodiversity. John Wiley and Sons, Hoboken, New Jersey. 295 pp.

Lewis, S.L. 2006. Tropical forests and the changing earth system. Philosophical Transactions of the Royal Society 361: 195–210.

Lowman, M.D. 1988. Litterfall and leaf decay in three Australian rainforest formations. Journal of Ecology 76: 451-465.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs 62:1-41.

Mansourian, S.; Vallauri, D.; and Dudley, N. (Eds.). 2005. Forest Restoration in Landscapes: Beyond Planting Trees. WWF and Springer, New York, NY. 437

Marin-Spiotta, E.; Ostertag, R.; and Silver, W.L. 2007. Long-term patterns in reforestation of tropical pastures: plant community composition and aboveground biomass accumulation. Ecological Applications 1:828-839.

Marques, M.J.; Jimenez-Ballesta, R.; Alvarez, A.; and Bienes, R. 2007.Spanish research on soil damage Science of The Total Environment 378: 1-4.

MEA. Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being. A framework for assessment. Island Press. 948p.

Meentmeyer, V.; Box, E.O.; and Thompson, R. 1982. World patterns and amounts of terrestrial plant litter production. BioScience 32:125-128.

Meli, P. 2003. Restauración ecológica de bosques tropicales: veinte años de investigación académica. Interciencia 28 (10): 581-589.

McKay, J.K.; Christian, C.E.; Harrison, S.; and Rice, K.J. 2005. ‘‘How local is local?’’—A review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13 (3) 432–440.

Mora, V. 2005. La producción de biomasa y el almacenamiento de carbonoen los bosques tropicales, plantaciones forestales y sistemas agroforestales. Costa Rica Forestal.

Moraes, R.M. de; Delitti, W.B.C.; and Struffaldi de Vuono, Y. 1999. Litterfall and litter nutrient content in two Brazilian Tropical Forests. Revista Brasileira de Botanica 22: 9-16.

Nepstad, D; Uhl, C; and Serrao, E.A.S. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio 20: 248-255.

Nepstad, D.; Uhl, C.; Pereira, C.A.; and Da Silva, J.M.C. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76: 25-39.

Nepstad, D.; Stickler, C.; and Almeida, O.T. 2006. Globalization of the Amazon soy and beef industries: opportunities for conservation. Conservation Biology 20 (6): 1595-1603.

Nichols, J.D.; Rosemeyer, M.E.; Carpenter, F.L.; and Kettler, J. 2001. Intercropping legume trees with native timber trees rapidly restores cover to eroded tropical pasture without fertilization. Forest Ecology and Management 152: 195-209.

Nichols, J.D.; and Carpenter, F.L. 2006. Interplanting *Inga edulis* with *Terminalia amazonia* yields nitrogen benefits to the timber tree. Forest Ecology and Management 233: 344-351

Oelbermann, M.; and Gordon, A.M. 2000. Quantity and quality of autumnal litterfall into a rehabilitated agricultural stream. Journal of Environmental Quality 29:603-611.

Ostertag, R.; Marin-Spiotta, E.; Silver, W.L.; and Schulten1, J. 2008. Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. Ecosystems 11: 701-714.

Palmer, M.A.; Falk, D.A.; and Zedler, J.B. 2006. Ecological theory and restoration ecology. In Falk, D.A.; Palmer, M.A.; and Zedler, J.B. (eds.). 2006. Foundations of Restoration. Ecology. Society for Ecological Restoration International. Island Press, Washington. p.1-13.

Prach, K.; Marrs, R.; Pysek, P.; and Van Diggelen, R. 2007. Manipulation of succession. In Walker, L. R.; Walker, J.; Hobbs, R. J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.121-149.

Reay, S.D.; and Norton, D.A. 1999. Assessing the success of restoration plantings in a temperate New Zealand forest. Restoration Ecology 7: 298-308.

Ricklefs, R.E. 1996. A economia da natureza. Terceira Edição. Editora Guanabara Koogan S.A., Rio de Janeiro. 470p.

Sánchez-Azofeifa, G.A.; Pfaff, A.; Robalino, R.A.; and Boomhower, J.P. 2007. Costa Rica's payment for environmental services program: intention, implementation, and impact. Biological Conservation 21(5):1165–1173.

SER. 2004. The Primer on ecological restoration. Society for Ecological Restoration International. Science and Policy Working Group. Avaiable at www.ser.org

Scatena, F.N.; Moya, S.; Estrada, C.; and Chinea, J.D. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28: 424-440.

Schrautzer; J.; Rinker, A.; Jensen, K.; Muller, F.; Schwartze, P.; and DierBen, C. 2007. Succession and restoration of drained fens: perspectives from northwestern Europe. In Walker, L.R.; Walker, J.; Hobbs, R.J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.90-120.

Scherer-Lorenzen, M.; Bonilla, J.L.; and Potvin, C. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment Oikos 116: 2108-2124.

Schroth, G.; Vanlauwe, B.; and Lehmann, J. 2003a. Soil organic matter. In: G. Schroth and F.L.Sinclair (eds.). Trees, Crops and Soil Fertility: Concepts and Research Methods. CAB International, Wallingford, UK.

Schroth, G. 2003b. Decomposition and nutrient supply from biomass. In: G. Schroth and F.L.Sinclair (eds.) Trees, Crops and Soil Fertility: Concepts and Research Methods. CAB International, Wallingford, UK.

Uhl, C.; Buschbacher, R.; and Serrao, E.A.S. 1988. Abandoned pastures in eastern Amazonia I. Patterns of plant succession. Journal of Ecology 75: 663-681.

Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. Journal of Ecology 75: 377-408.

Van Breugel, M.; Bongers, F.; and Martínez-Ramos, M. 2007. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover . Biotropica 39 (5): 610–619.

Vandermeer, J.H.; and Perfecto, I. 2007. The agricultural matrix and a future paradigm for conservation. Conservation Biology 21 (1): 274–277.

Vieira, I.C.G.; Uhl C.; and Nepstad, D. 1994. The role of the shrub *Cordia multispicata* Cham. as a "succession facilitator" in an abandoned pasture, Paragominas, Amazonia. Vegetation 115:91-99.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119: 53-72.

Vitousek, P.M.; and J. Sanford, R.L. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137-167.

Vitousek, P.M.; Ehrlich, P.R.; Ehrlich, A.H.; and Matson, P.A. 1986. Human appropriation of the products of photosynthesis. BioScience 36: 368-373.

Vitousek, P.M.; and Walter, L.R. 1989. Biological invention of *Myrirca faya* in Hawaii: plant demography, nitrogen fixation and ecosystem effects. Ecological Monographs 59 (3): 247-265.

Wardle, D.A.; Bonner, K.I.; and Nicholson, K.S. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness affects ecosystem function. Oikos 79: 247-258.

Wardle, D.A.; and Peltzer, D.A. 2007. Aboveground-Belowground linkages, ecosystem development, and ecosystem restoration. In Walker, L. R.; Walker, J.; and Hobbs, R. J. (Eds.). Linking restoration and ecological succession. Springer Series on Environmental Management. pp.45-68.

Walker, L.R.; Walker, J.; and Del Moral, R. 2007. Forging a new alliance between succession and restoration. In Walker, L.R.; Walker, J.; Hobbs, R.J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.1-16.

Walker, J.; and Reddel, P. 2007. Retrogressive succession and restoration on old landscapes. In Walker, L.R.; Walker, J.; Hobbs, R.J. (Eds.). Linking restoration and ecological succession. Springer Series on Environmental Management. p.1-16.

WRI. World Resources Institute. 1992. World Resources 1992–1993. A Guide to the Global Environment. Oxford University Press, New York and Oxford, 382 pp.

Xuluc-Tolosa, F.J.; Vester, H.F.M.; Ramirez-Marcial, N.; Castellanos-Albores, J.; and Lawrence, D. 2003. Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. Forest Ecology and Management 174: 401-412.

Yarranton, G.A.; and Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. Journal of Ecology 62: 417-428.

Zahawi, R.A.; and Augspurger, C. K. 2006. Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. Ecological Applications 16 (2): 464–478.

Zou, X.; Zucca, C.P.; Waide, R.B.; and McDowell, W.H. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. Forest Ecology and Management 78: 147-157.

4 RESEARCH ARTICLES

ARTICLE 1. Litterfall dynamics and nutrient cycling in different tropical forest restoration strategies[1]

Abstract Active restoration strategies to facilitate tropical forest recovery in degraded areas may accelerate the reestablishment of nutrient cycling when compared to natural forest recovery. We evaluated litterfall and nutrient dynamics under four treatments: plantation (entire area planted), tree islands (planting in six patches of three sizes), control (same age natural regeneration), and young secondary forest (7 to 9 yr-old natural regeneration). Treatments were established in June 2004 in plots of 50 × 50 m at six replicate sites in southern Costa Rica and litterfall was measured from September 2008 through August 2009. Planted species included two native timber-producing hardwoods (*Terminalia amazonia* and *Vochysia guatemalensis*) interplanted with two N-fixing species (*Inga edulis* and *Erythrina poeppigiana*). Both planted restoration strategies recovered litter production function more quickly as compared to the control. Litter production was highest in secondary forests (7.3 Mg/ha/yr) and plantations (6.3), intermediate in islands (3.5), and lowest in controls (1.4). *Inga edulis* contributed 70% of leaf fall in the plantation treatment. Litter quality indicators (nutrient concentration and carbon to nutrient ratios) were higher in secondary forests due to higher plant diversity. The dominance of litter from one planted species may not be desirable for restoration if it drives nutrient availability and strongly affects successional pathways. Accordingly, restoration strategies with more heterogeneous planting designs, such as the tree islands, may promote a more rapid increase in plant diversity and litter quality, which can in turn accelerate the reestablishment of nutrient cycling functions.

Key words: Costa Rica; ecological restoration; litterfall; nutrient inputs; plantations; secondary forest; tree islands; tropical forest.

---

[1] Paper in preparation for Biotropica in colaboration with B.Finegan, R.Zahawi, R.Ostertag, R.Cole and K.Holl.

La dinamica de la hojarasca y los ciclos de nutrients bajo diferentes estratégias de restauración de bosques tropicales

Resumen Estrategias de restauración activa de bosques tropicales tienen el potencial para acelerar el restablecimiento del ciclo de nutrientes en áreas degradadas. En ese estudio se evaluó la dinámica de la hojarasca y nutrientes bajo cuatro tratamientos: plantación forestal (toda la superficie plantada); islas de árboles (árboles sembrados en parches de tres tamaños), control (regeneración natural) y bosque secundario jóven (7-9 años). Los tratamientos fueron establecidos en junio de 2004, en parcelas de 50 × 50 m, y en seis sitios en el sur de Costa Rica, y la hojarasca fue evaluada entre septiembre de 2008 y agosto de 2009. Las especies introducidas fueron dos nativas maderables (*Terminalia amazonia* y *Vochysia guatemalensis*) intercaladas con dos fijadoras de N (*Erythrina poeppigiana* e *Inga edulis*). La producción de hojarasca no difirió entre el bosque secundario y la plantación, mientras que las islas presentan valores intermedios y el control la producción más baja. *Inga edulis* aportó el 70% de las hojas en las plantaciones. Las estrategias de restauración recuperaon la función de producción de hojarasca más rápidamente en comparación con el control. Sin embargo, los indicadores de calidad de hojarasca (concentración de nutrientes y relación carbono: nutrientes) son mejores en los tratamientos recuperados naturalmente. La dominancia de hojas de una especie no es deseable para la práctica de la restauración ya que puede determinar la disponibilidad de nutrientes y afectar negativamente la sucesión. En consecuencia, estrategias de restauración que presentan un diseño de plantación más heterogéneos, como las islas, pueden promover un incremento más rápido de la diversidad vegetal y la calidad de la hojarasca, y luego acelerar el restablecimiento de los ciclos de nutrientes

Palabras-claves: Costa Rica, restauración ecológica, hojarasca, aporte de nutrientes, plantaciones, bosque secundario, islas de árboles, bosque tropical

4.1 Introduction

Tropical forests are among the most important biomes on earth. They house high levels of biodiversity (Losos & Leigh 2004), maintain critical ecosystem services (Noble & Dirzo 1997), and exchange large quantities of carbon and water with the atmosphere (Townsend *et al*. 1992, Field *et al*. 1998). These forests are also threatened by widespread deforestation, particularly in Latin America, where land is being converted rapidly to agricultural uses (FAO 2006). In addition to altering ecosystem structure, tropical deforestation provokes changes in local, regional and global nutrient cycles with high environmental and social costs (MEA 2005).

The majority of tropical forests are sustained by soils with moderate to low fertility (Vitousek & Sanford 1986). Biomass holds a considerable proportion of the nutrients that are potentially available to the biota, and plants have developed highly adapted mechanisms for the acquisition and retention of nutrients (Lambers *et al.* 2007, Walker & Reddell 2007). This characteristic makes some tropical areas especially vulnerable to deforestation, where not only site nutrient capital is removed but nutrient cycles are also disturbed, increasing nutrient leakage from the system (Walker & Reddell 2007).

In this context, secondary forests play an important role in mitigating human impacts. In addition to providing habitat, conserving biodiversity, and supplying material goods, they restore ecosystem services such as nutrient cycling (Ewel 1976, Zou *et al*. 1995, McDonald & Healey 2000, Ostertag *et al.* 2008). Patterns and dynamics of natural succession differ greatly at the stand scale within and between regions (Van Breugel *et al.* 2007), and, in some areas, the recovery of tropical forests can be strongly limited by a range of biotic and abiotic factors. Lack of seed dispersal, seedling competition with introduced pasture grasses, and decreased soil nutrient availability have been identified as important barriers (Uhl 1987, Nepstad *et al.* 1996, Holl 1999, Holl 2002). Indeed, strategies to overcome these barriers to forest recovery are particularly needed in the tropics, given the large areas of degraded lands (Lamb *et al*. 2005) and the need to maintain essential ecosystem functions.

Approaches to forest restoration vary depending on levels of forest and soil degradation, residual vegetation, desired outcomes, and budget (Chazdon 2008). Tree plantation is the most common restoration method, but it is expensive and labor intensive

(Lamb & Gilmour 2003). Planting "tree islands" may be more cost-effective and less labor intensive, as fewer trees need to be planted per hectare (Holl & Zahawi, in press). The tree island design aims to create structural complexity that facilitates recovery by mimicking the natural regeneration process known as nucleation, where patches of successional vegetation create microhabitats favorable to later-successional species establishment (Yarranton & Morison 1974); tree islands reduce temperature and light extremes and can attract seed-dispersing birds (Zahawi & Augspurger 2006, Fink *et al*. 2009, Cole *et al.,* in press). Active restoration strategies may accelerate the reestablishment of ecosystem functions, such as nutrient cycling when compared to areas under natural processes.

Litterfall is a fundamental process in nutrient cycling as it represents the main transfer of organic matter and mineral elements from aboveground vegetation to the soil surface (Vitousek & Sanford 1986). It is a partial measure of NPP (net primary productivity), and is highly correlated to aboveground biomass increment (Clark *et al.* 2001), tree density, and canopy closure (Zou *et al.* 1995, Oelbermann & Gordon 2000). Litterfall is affected by a complex set of environmental variables such as temperature, rainfall, soil fertility and elevation (Vitousek & Sanford 1986), as well as potential and actual evapotranspiration (Meentmeyer *et al.* 1982). In seasonal areas, the highest deposition of litter usually occurs in the dry season (Klinge 1977). Litterfall in early successional forests increases rapidly in the first few years (Ewel 1976); once the canopy is closed, however, there is no obvious trend in litterfall production with increasing stand age (Ewel 1976, Lugo 1992, Zou *et al.* 1995, Ostertag *et al.* 2008), species richness (Scherer-Lorenzen *et al.* 2007), or diversity (Wardle *et al.* 1997). Nevertheless, tree species composition alters leaf litter chemistry and influences decomposition processes (Zou *et al.* 1995, Xuluc-Tolosa *et al.* 2003), which in turn affects nutrient availability and successional pathways (Vitousek & Walter 1989). Low litter quality (i.e., high carbon to nutrient ratios) will retard decomposition and mineralization processes (Wardle & Peltzer 2007) and may affect forest recovery.

In this study, we evaluated nutrient cycling in a large-scale restoration experiment in southern Costa Rica. The project compares natural regeneration to two active restoration strategies (uniform mixed-tree plantation and tree islands; Holl *et al.,* in press) as models for restoration that may be applicable in other tropical regions. Both restoration systems use two native timber-producing hardwoods (*Terminalia amazonia* and *Vochysia guatemalensis*) interplanted with two nitrogen-fixing tree species (*Erythrina poeppigiana* and *Inga edulis*). *Inga* has been shown to increase soil nutrient availability through litterfall, thus creating better conditions for seedling establishment (Nichols *et al.* 2001, Nichols & Carpenter 2006).

Our specific objectives were to evaluate litter production, leaf litter nutrient concentration and input, and soil chemical parameters in the 5-yr old active restoration strategies and compare them with same-aged areas undergoing natural succession and young secondary forests (7-9 yr). We hypothesized that: (1) both active restoration strategies would have higher litter and nutrient inputs than the areas with natural regeneration due to differences in tree density and canopy closure; (2) litter production would be similar in uniform mixed-tree plantation and young secondary forests as a result of comparable canopy cover; and (3) the two active restoration strategies would have higher soil and litterfall N concentration when compared to natural regeneration and young secondary forest due to the planting of N-fixing species.

4.2 Methods

4.2.1 Study sites

This study was conducted from September 2008 through August 2009 at six sites located between Las Cruces Biological Station (LCBS) (8°47’7’’ N, 82°57’32’’ W) and the town of Agua Buena (8°44'42” N, 82°56'53” W) in Coto Brus county in southern Costa Rica (Fig. 6). This region is a fragmented agricultural landscape located within the La Amistad - Osa Biological Corridor, a priority area for conservation aiming to connect the largest remaining primary forests in southern Costa Rica (Céspedes *et al.* 2008). Over the past 60 years, most of the region was cleared and converted to agricultural use, primarily coffee production. In the last 15 years, shifts in the global coffee market led to conversion of coffee plantations to cattle pasture and the fallowing of marginal agricultural lands, resulting in numerous patches of young successional forests (Rickert 2005). Today, around 25 percent of the original forest remains, mostly as small fragments (Daily *et al.* 2001). The forest in this region is classified as a tropical premontane rain forest (Holdridge *et al.* 1975).

Study sites span an elevation range from 1,000 to 1,300 m asl and are mostly steeply sloping. Average temperature in the region (21^{o}C) varies little during the year and annual precipitation averages 3,500 mm with a distinct dry season from December to March. The sites had been used for agriculture for 18 to 50 years prior to the start of the study and most were burned once or twice soon after clearing, but not thereafter (see Holl *et al.* in press for more detailed site description). Sites were either recently abandoned pastures generally dominated (>80% cover) by *Pennisetum purpureum* Schumach and/or *Urochloa brizantha* (Hochst. Ex. A. Rich.) R. D. Webster, or coffee farms dominated by a mixture of forage and non-forage grasses, forbs, and *Pteridium arachnoideum* (Kaulf.) Maxon.

The soils (Inceptisols) are acidic (pH ~ 5.5, Al acidity >0.5 cmol/kg and acid saturation >15% at 5-20 cm depth), and have very low phosphorus (4.09 mg/kg at 0-5 and 1.95 at 5-10 cm depth), low to moderate levels of exchangeable cations (Ca: 9.74 cmol/kg ± 1.54 SE; Mg: 3.41 ± 0.44; K: 0.47 ± 0.08) and very high concentrations of Fe (142.15 mg/kg ± 11.84; Table 2). Bulk density averaged 0.63 g/cm^3 (± 0.03) and organic matter was high (14% at 0-5 cm and 11% at 5-20 cm).

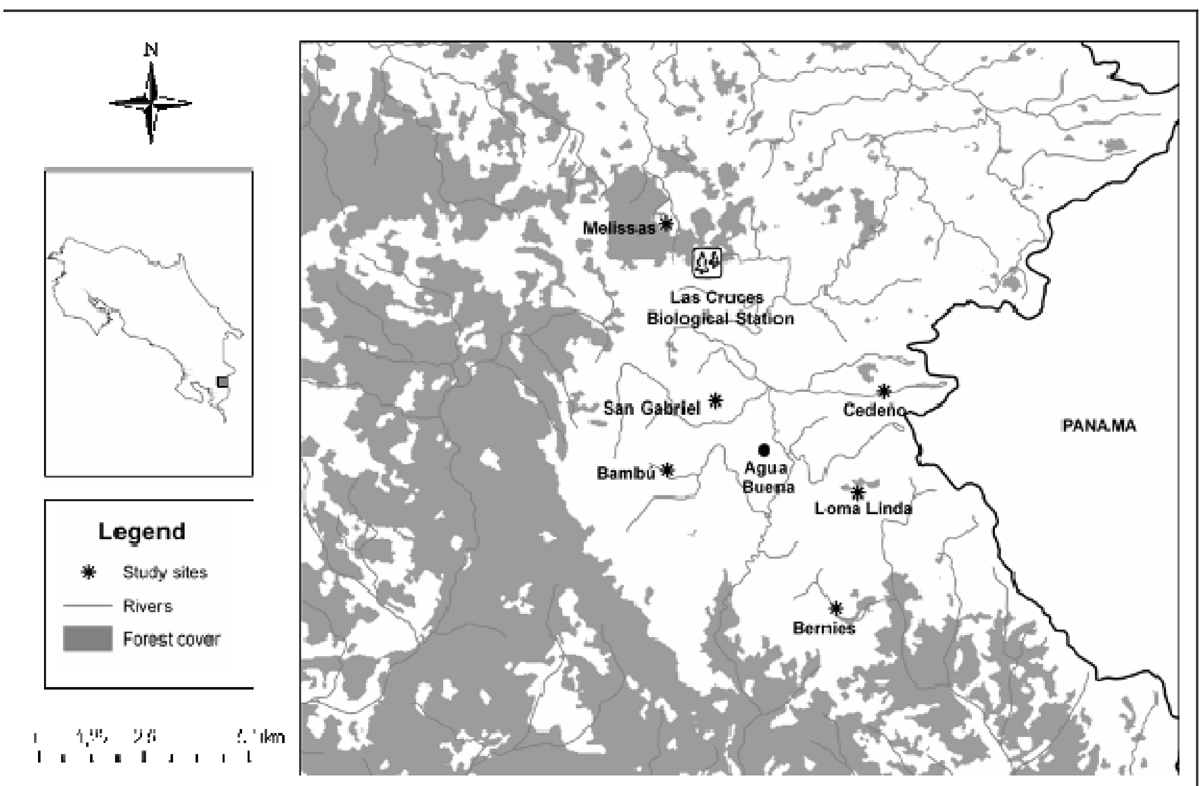

Figure 6. Distribution of study sites in Coto Brus County in southern Costa Rica.

Table 2. Soil nutrient concentrations (mean ± SE and range) at 0-5 cm and 5–20 cm depth averaged across plots (n = 21 total) in all treatments (plantation, island, control, and secondary forest) in Coto Brus, Costa Rica.

Variable	**0-5 cm depth**		**5 – 20 cm depth**	
	Mean ± SE	**Min – Max**	**Mean ± SE**	**Min – Max**
pH (H_2O)	5.60 ± 0.07	5.05 - 6.27	5.51 ± 0.07	5.01 - 6.09
Al acidity (cmol(+)/kg)	1.11 ± 0.21	0.11 -3.38	1.58 ± 0.24	0.16 - 3.40
Acid saturation (%)[a]	12 ± 3	0 -43	19 ± 4	2 - 61
N (%)	0.63 ± 0.05	0.32 - 1.14	0.46 ± 0.03	0.28 - 0.72
C (%)	8.12 ± 0.67	4.40 -15.30	6.17 ± 0.50	3.58 - 10.50
C:N	12.77 ± 0.20	10.72 -14.27	13.17 ± 0.29	10.56 - 14. 75
Organic matter (%)	13.97 ± 1.16	7.57 - 26.32	10.61 ± 0.87	6.16 - 18.06
CEC (cmol(+)/kg)	11.68 ± 1.59	5.31 - 29.21	10.15 ± 1.84	4.51 - 30.07
Ca (cmol(+)/kg)	9.74 ± 1.54	2.15 - 25.19	7.67 ± 1.53	1.42 - 24.27
Mg (cmol(+)/kg)	3.41 ± 0.44	1.24 - 6.70	2.14 ± 0.37	0.53 - 6.14
K (cmol(+)/kg)	0.47 ± 0.08	0.11 - 1.36	0.3 ± 0.06	0.07 - 0.99
P (mg/kg)	4.09 ± 0.63	0.66 - 14.47	1.95 ± 0.22	0.13 - 3.96
Cu (mg/kg)	12.38 ± 1.11	4.20 - 22.33	13.06 ± 1.29	4.79 - 26.42
Zn (mg/kg)	3.70 ± 0.38	1.31 - 6.63	1.29 ± 0.12	0.56 - 2.86
Mn (mg/kg)	23.35 ± 2.26	9.22 - 53.54	17.98 ± 1.71	7.68 - 38.95
Fe (mg/kg)	142.15 ± 11.84	66.74 - 245.24	123.45 ± 10.15	56.38 - 217.41

[a]Acid saturation=(Acidity/CEC)*100

4.2.2 Experimental design

At each site, three treatments in plots of 50 × 50 m were established in June-July 2004. Treatments are plantation (Pl; entire area planted with a mix of four species); islands (Is; planting six tree islands of three sizes 4 × 4 m, 8 × 8 m, and 12 × 12 m); and control (Co; no planting/natural regeneration) (Fig. 7). At three sites an additional representative plot of young secondary forest (SF) was sampled; secondary forests ranged from seven to nine years since abandonment at the start of the study and had a closed canopy. Secondary forest plot design approximated that of restoration treatments.

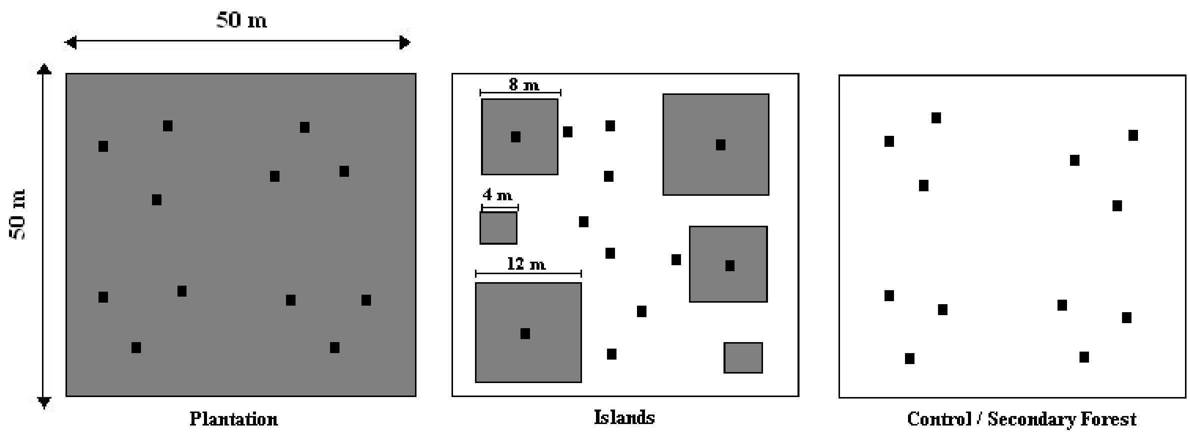

Figure 7. Plot and litter traps (black square) layout. In plantation and control, litter traps are randomly located alongside the permanent vegetation sampling plots. Gray = area planted with tree seedlings; White = unplanted areas.

Plantation and island treatments were planted with four species. Two native timber species, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae) which were interplanted with two naturalized, fast-growing N-fixing tree species, *Erythrina poeppigiana* (Walp.) O. F. Cook (Fabaceae), and *Inga edulis* Mart. (Fabaceae). Species selection was based on: (1) high survival in prior studies in the region (>80%), rapid height growth rates (1-2 m/yr) and broad canopy cover development in the first few years; and (2) availability in local nurseries (Nichols *et al.* 2001; Carpenter *et al.* 2004a; Holl *et al.,* in press). A total of 84 trees were planted in island treatments (344 trees/ha) and 313 trees in each plantation (1,252 trees/ha). Seedlings were planted in alternating rows of *Vochysia/Terminalia* and *Inga/Erythrina*, and were separated by 4 m within rows and 2.8 m across rows (see Holl *et al*., in press for details of experimental layout).

4.2.3 Litterfall sampling

Litter was collected twice monthly from 12 litterfall traps in each 50 × 50 m plot (n = 252) from 1 September 2008 to 30 August 2009 (24 sampling periods). Traps were constructed from fine gauge (0.5 × 0.5 mm) mosquito netting suspended in an inverted pyramid from circular wire hoops and mounted on 60 cm tall legs (area = 0.25 m^2). A rock in the bottom of each trap prevented it from being emptied by the wind. In the island treatment, one trap was installed inside each medium and large island, two were placed within a 2 m perimeter of where trees were planted, and the remaining 6 were located in unplanted areas (≥2 m from the base of trees planted in islands; Fig. 2). In other treatments, groups of three litter traps (separated by 4-10 m) were distributed in each of the four quadrants of the plot.

Litter was sorted into leaves, reproductive parts, woody tissue, and miscellaneous. Mass data were reported as a dry weight (48 hr at 65^{o}C) for every collection. In order to determine the individual contribution of each planted tree species to the litterfall, all leaves and flowers were separated by tree species and vegetation category (four planted tree species, grasses, other dicotyledons, and unidentified plant material) for the first sampling of every month. We did not separate species from the secondary forest treatments.

4.2.4 Leaf litter chemical content and nutrient input

Leaf litter was analyzed for percent concentrations of total C, total N, Ca, Mg, K, P, and mg/kg for Cu, Mn, Zn, and Fe at the onset of the study (October 2008) and for three time periods (Dec-Feb 2009, Mar-May 2009 and Jun-Aug 2009) using bulked samples. Total C and N were analyzed using the combustion method with an automated analyzer (Hermofinigan, Flash EA 1112 Series). Nutrient concentrations (Ca, Mg, K, P, Cu, Mn, Zn and Fe) were determined as follows: plant tissue samples were dried (70°C), milled, sieved using a 1-mm mesh (18/ASTM; Díaz & Hunter 1978; Mills & Jones 1996; AOAC 1984), and analyzed on a Thermo Spectronic (Helios alpha) for P and an Atomic Absorption Spectrophotometer (Perkin Elmer, AAnalysist 100) for other nutrients. Given the low variability in leaf nutrient concentration among sampling periods, we present the mean nutrient concentration for all time periods. Leaf nutrient inputs were estimated using total leaf production for the year and average nutrient concentration.

4.2.5 Climatic, site and canopy variables

Precipitation (mm), temperature (^{o}C), wind speed (m/s) and relative humidity (%) were provided daily by the LCBS meteorological station (Campbell Scientific®; OTS 2009). For each litterfall trap, we measured slope (in degrees) and slope position (valley, hillside and ridge). Canopy cover directly above each trap was determined using a spherical densiometer in February, May and August 2009 and averaged. Individual trees above each litter trap were identified and their height measured. To determine the potential diversity of litter, we estimated a canopy species diversity index (d) per plot according to Margalef diversity index (Margalef 1958): $d = [(S-1)/ \ln N]$; where S is the number of species and N is the total number of individuals. We used all species visible in the densiometer mirror above each litter trap (0 to 4 individuals >2 m tall; Appendix S1) to calculate the index. On average, 17 individuals per plot were used for this estimation.

4.2.6 Soils chemical parameters

In April 2009, we collected soil samples at 0-5 and 5-20 cm depth from ten randomly-selected locations in each plot. For each plot, samples were mixed, air dried, and passed through a 2-mm sieve. We analyzed samples for pH, acidity, total C, total N, Mg, Ca, K, P, Cu, Zn, Mn, and Fe following standard protocols at the CATIE (Tropical Agricultural Centre for Research and Higher Education) soil laboratory (Diaz & Hunter 1978; Olsen & Sommers 1982). We collected five, 4-cm diameter × 10-cm depth bulk density cores from each plot that were dried at 105^{o}C for 48 hr and weighed. We used bulk density and soil chemical concentration information to calculate soil nutrient stocks for each plot by converting the soil chemical concentration from L to a kg basis and multiplying by the soil mass per hectare.

4.2.7 Data analyses

Our experiment was set up as an incomplete block design (the secondary forest treatment was replicated at three of six sites) with site as a blocking factor. Differences in litterfall (total production, each component, and leaf and flower species) among restoration strategies were analyzed using a mixed-model ANOVA with treatments as fixed factors and site as a random factor, and means were compared according to the test of LSD Fisher. The same analysis was used to compare leaf nutrient concentrations and inputs, soil chemical parameters, site conditions, and canopy variables for each treatment. Due to heterogeneous variance for total litterfall and litterfall components, a separate model correcting for heteroscedasticity was run using the function "*varIdent*" of R®. We also analyzed data using a complete block design (four treatments repeated in three sites) and results were consistent with the mixed-model outputs for the incomplete block design. Therefore, we do not report these other model results.

Correlations between litterfall and canopy variables, slope, and soil variables were examined through path analysis. We compared litter production for each position on the slope using an ANOVA (slope position as the independent variable). Correlations between leaf nutrient concentration, canopy species diversity index, and soil nutrients were also assessed using path analysis. Multiple regression models were used to test the relation between litter monthly production and climate variables (rainfall, temperature, and wind), total litter production and soil (pH and nutrients) variables, and nutrients leaf concentration and the number of species (S) and species diversity index (d). In the multiple regression models using total litter production, we used the residual value from the mixed model analyses as the dependent variable to avoid confusion with treatment effects. All statistical analysis and graphics were executed with InfoStat/P® (version 2009; Infostat 2009) and R® (version 2.7.2; R 2008). We report means ± 1 standard error throughout and consider $p < 0.05$ as significant.

4.3 Results

4.3.1 Litterfall production

Litter production was highest in secondary forests and plantations, intermediate in island plots, and lowest in controls (Figure 8, Table 3). Litterfall consisted of mostly leaves in all treatments (Pl = 87%, Is = 88%, Co = 89%, SF = 77%). Leaf and wood fall showed the same pattern as total litter (Table 2), whereas production of miscellaneous material was greatest in secondary forest, intermediate in the planted treatments, and lowest in the control. Production of leaves, wood, and miscellaneous material (Fig. 3) was greater between January and March (drier months) with a peak in February the month of lowest rainfall (6 mm total), lower relative humidity (73%), and higher winds (1.5 m/s). Indeed, climatic variables (rainfall, temperature, and wind) together explained 66 percent of litterfall variation during the year (multiple regression p = 0.0291). Biomass of reproductive parts was higher in secondary forests and peaked in April (Table 3; Fig. 9).

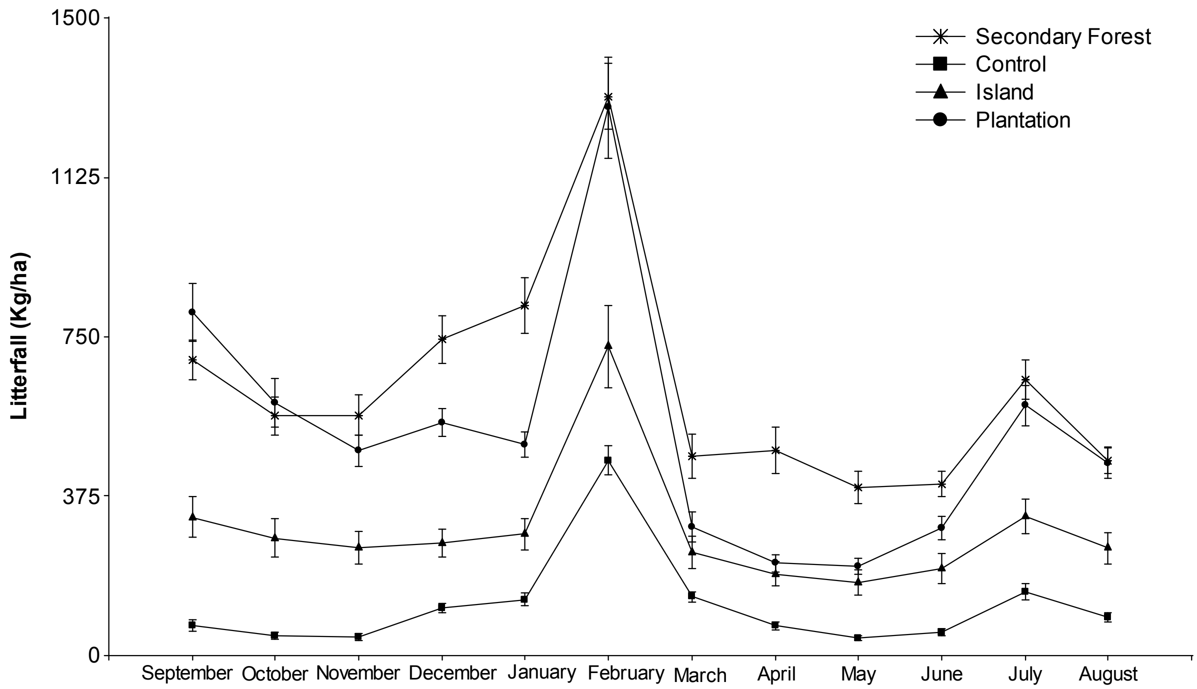

Figure 8. Mean monthly litterfall production (kg/ ha ± SE) between September 2008 and August 2009 in the two active restoration treatments (plantation and island), control and secondary forest) in Coto Brus, Costa Rica.

Table 3. Annual litterfall production (Mg/ ha) between September 2008 and August 2009 (± 1 SE) in plantation, island, control and secondary forest. Values with the same letter are not significantly different (p <0.05) across treatments.

Production (Mg/ ha/ yr)	**Control**	**Island**	**Plantation**	**Secondary forest**	***F***	***p***
Leaves	1.23 ± 0.29^{a}	3.06 ± 0.43^{b}	5.40 ± 0.39^{c}	5.43 ± 0.39^{c}	153.9	<0.0001
Woody	0.07 ± 0.03^{a}	0.22 ± 0.05^{b}	0.48 ± 0.06^{c}	0.65 ± 0.08^{c}	45.8	<0.0001
Reproductive	0.07 ± 0.04^{a}	0.16 ± 0.07^{a}	0.31 ± 0.07^{b}	0.59 ± 0.09^{c}	33.8	<0.0001
Miscellaneous	0.07 ± 0.02^{a}	0.12 ± 0.03^{b}	0.12 ± 0.02^{b}	0.51 ± 0.06^{c}	29.8	<0.0001
Total	1.41 ± 0.36^{a}	3.52 ± 0.52^{b}	6.29 ± 0.48^{c}	7.29 ± 0.53^{c}	129.4	<0.0001

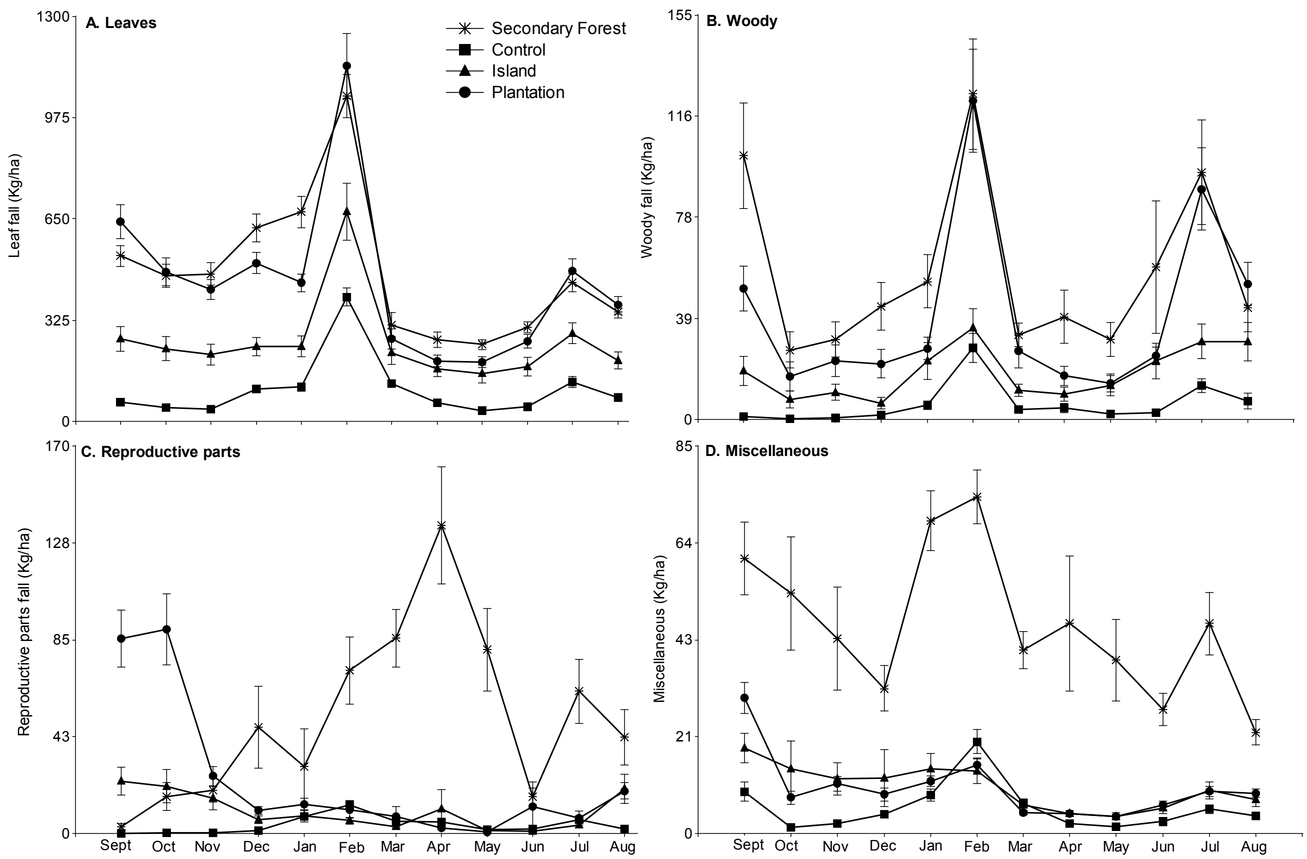

Figure 9. Mean monthly production (kg/ ha ± 1SE) between September 2008 and August 2009 of (A) leaves, (B) wood, (C) reproductive parts, and (D) miscellaneous in the two active restoration treatments (plantation and island), control and secondary forest) in Coto Brus, Costa Rica.

Litter production was negatively correlated with canopy openness (Pl = 35 ± 3%, Is = 62 ± 4, Co = 85 ± 3, SF = 16 ± 1; $r = -0.87$; $p < 0.0001$), and positively correlated with canopy height (Pl = 5.8 m ± 0.2, Is = 4.2 ± 0.24, Co = 3.2 ± 0.2, SF = 7.4 ± 0.4; $r = 0.74$; $p < 0.0001$). Among the planted species, *Vochysia* (5.0 m) was the smaller (*Erythrina*= 6.5 m, *Inga* = 6.4 m, *Terminalia* = 5.9 m; $F = 6.68$; $p = 0.0002$). The number of species (Pl = 4.3 ± 0.2, Is = 4.2 ± 0.7, Co = 3.5 ± 0.8, SF = 7.3± 0.9) was greater in secondary forests than in other treatments ($F = 5.8$; $p = 0.0112$; Appendix S1). The canopy diversity index (d) was also significantly higher ($F = 5.7$; $p = 0.0110$) in secondary forests (2.22 ± 0.30 SE) than in other treatments (Pl = 1.11 ± 0.06, Is = 1.14 ± 0.23, Co = 0.94 ± 0.28). Neither the number of species nor the diversity index, however, correlated with litterfall ($p > 0.1$). *Inga edulis* contributed the vast majority of leaf and flower biomass in plantations (70% and 89%) and islands (47% and 70%;

Table 4). Besides *Inga*, only *Erythrina* produced flowers (small quantities) among the species planted.

Table 4. Proportion (mean ± SE) of total leaf and flower fall grouped by species (October 2008 to August 2009) in plantation, island, control and secondary forest. Values with the same letter are not significantly different (p <0.05) across species composition

	Leaves (%)			**Flowers (%)**		
Species composition [a]	**Control**	**Island**	**Plantation**	**Control**	**Island**	**Plantation**
Inga edulis	1 ± 0^{a}	47 ± 10^{b}	70 ± 5^{c}	2 ± 1^{a}	70 ± 14^{b}	89 ± 2^{b}
Erythrina poeppigiana	4 ± 3^{a}	11 ± 3^{a}	15 ± 4^{b}	1 ± 1^{a}	1 ± 0^{a}	1 ± 1^{a}
Vochysia guatemalensis	0 ± 0^{a}	5 ± 4^{a}	5 ± 2^{ab}	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
Terminalia amazonia	0 ± 0^{a}	2 ± 1^{a}	3 ± 1^{a}	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
Grasses	40 ± 2^{b}	15 ± 11^{a}	2 ± 1^{a}	50 ± 15^{b}	15 ± 12^{a}	5 ± 3^{a}
Other dicot spp. [b]	56 ± 2^{b}	20 ± 6^{ab}	6 ± 1^{ab}	47 ± 15^{b}	14 ± 5^{a}	5 ± 1^{a}
F	6.9	5.4	88.8	8.4	11.9	537.7
p	0.0003	0.0012	<0.0001	<0.0001	0.0012	<0.0001

[a]Unidentified leaf and flower material represented less than two percent in all treatments.

[b]For potential species composition, please refer to the list of canopy species in Appendix 1.

There were large differences in litter production across sites (range 1.1 - 5.7 Mg/ ha) with two sites having significantly lower litter production than the others (F = 31.4, p <0.0001; Fig.10). Site slope (range 8-50%) was negatively correlated with litter production (r = - 0.17; p = 0.0068), but it only explained 3 percent of the variation in the multiple regression (p = 0.007). Litter production was greater in valleys and lower on hillsides within sites, while ridges did not differ from the other positions (F = 2.9; p = 0.051).

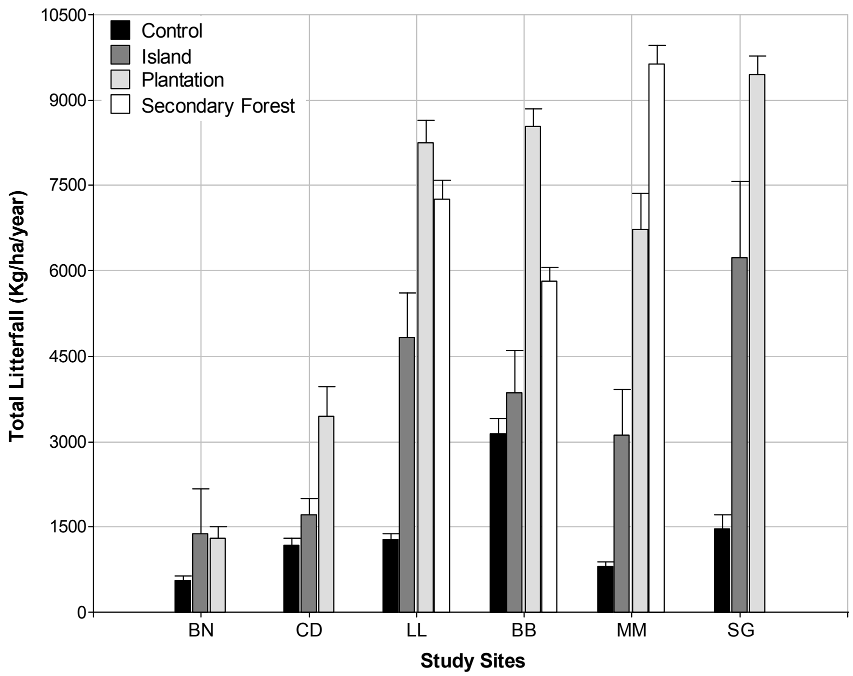

Figure 10. Mean litterfall production (kg ha/ year ± SE) in different restoration treatments (Plantation, Islands, Control) and in secondary forest grouped by site (Bernies/BN, Cedeño/CD, Loma Linda/LL, Bambú/BB, Melissas/MM and San Gabriel/SG) in Coto Brus, Costa Rica.

4.3.2 Leaf litter nutrients content and input

Secondary forests had greater concentrations of Ca, Mg, K, Zn and Mn in leaf litter than did restoration treatments; control and SF did not differ for Mg, Zn and Mn (Table 5). Treatments in which N-fixing species were planted (plantation and island) had greater concentrations of N, higher ratios of C:Ca, C:Mg, and C:K, and lower ratios of C:N than control and secondary forest (Table 4). In turn, leaf C concentration was significantly lower in the control. Other nutrients (P, Cu, and Fe) and the ratio of C:P did not differ among treatments.

Table 5. Mean leaf fall nutrient concentration (± SE) for four periods of analysis in plantation, island, control and secondary forest. Values with the same letter are not significantly different (p <0.05) across treatments.

	Control	Islands	Plantation	Secondary forest	*F*	*p*
Percent						
C	43.13 ± 0.98^{a}	45.85 ± 1.02^{b}	47.67 ± 0.26^{b}	46.03 ± 0.37^{b}	9.7	0.0016
N	1.53 ± 0.15^{a}	2.10 ± 0.17^{b}	2.38 ± 0.12^{b}	1.60 ± 0.09^{a}	10.3	0.0012
Ca	1.58 ± 0.17^{a}	1.45 ± 0.12^{a}	1.36 ± 0.10^{a}	2.14 ± 0.05^{b}	5.5	0.0130
Mg	0.39 ± 0.03^{b}	0.27 ± 0.03^{a}	0.23 ± 0.02^{a}	0.40 ± 0.05^{b}	11.0	0.0009
K	0.50 ± 0.05^{a}	0.46 ± 0.06^{a}	0.42 ± 0.04^{a}	0.84 ± 0.04^{b}	10.0	0.0014
P	0.12 ± 0.01	0.10 ± 0.01	0.10 ± 0.01	0.14 ± 0.02	-	0.2424
mg/ kg						
Cu	12.33 ± 2.18	12.41 ± 1.44	12.13 ± 0.76	9.75 ± 0.08	-	0.5300
Zn	92.37 ± 9.02^{b}	40.45 ± 3.79^{a}	27.77 ± 1.86^{a}	73.32 ± 6.62^{b}	27.7	0.0001
Mn	321.79 ± 43.81^{bc}	267.79 ± 50.11^{ab}	253.58 ± 47.77^{a}	350.92 ± 74.56^{c}	5.8	0.0109
Fe	156.88 ± 22.65	158.58 ± 16.72	144.17 ± 16.19	128.75 ± 7.63	-	0.3005
Ratios						
C:N	29.57 ± 2.83^{b}	22.70 ± 1.99^{a}	20.27 ± 0.97^{a}	28.96 ± 1.46^{b}	7.8	0.0037
C:Ca	28.74 ± 2.74^{ab}	32.61 ± 2.36^{bc}	36.03 ± 2.85^{c}	21.56 ± 0.66^{a}	5.4	0.0140
C:Mg	112.88 ± 7.63^{a}	187.10 ± 23.28^{b}	219.97 ± 15.97^{b}	119.15 ± 12.71^{a}	12.3	0.0006
C:K	88.95 ± 7.10^{ab}	109.01 ± 15.33^{bc}	119.56 ± 9.93^{c}	55.03 ± 2.73^{a}	5.8	0.0110
C:P	388.33 ± 38.65	466.45 ± 30.57	500.24 ± 38.47	358.17 ± 51.69	-	0.0916

Leaf concentration of Ca was positively correlated with both canopy diversity index (d; $r = 0.51$; p = 0.0175) and the number of species (S; $r = 0.44$; p = 0.0454). Together, d and S explained 43% of Ca variation (multiple regression $p = 0.0061$), 28% of Mg ($p = 0.0507$) and 37% of P ($p = 0.0155$). The model was not significant for K ($R^2 = 23$, $p = 0.0966$) and micronutrients ($p > 0.2$). Mn was the only nutrient that was significantly correlated in soil and leaf fall ($r = 0.74$; p = 0.0001).

The total N cycled was highest in plantations, intermediate in islands and secondary forests, and lowest in controls, although the difference between plantations and secondary forests was only marginally significant given high among-site variation in plantations (Table 6). Carbon input was similar in secondary forests and plantations. Secondary forests had greater inputs of Ca, Mg, K, P, Zn and Mn (Pl and SF did not differ for P and Mn). Controls consistently had the lowest input of all nutrients, and islands were slightly higher (plantation and islands did not differ for P, K, Mg, Zn and Mn).

Table 6. Annual leaf fall nutrient input per hectare (± SE) in plantation, island, control and secondary forest. Values with the same letter are not significantly different (p <0.05) across treatments.

	Control	Islands	Plantation	Secondary forest	*F*	*p*
kg/ ha/ year						
C	498.59 ± 127.26^{a}	$1{,}323.90 \pm 301.39^{b}$	$2{,}409.58 \pm 509.65^{c}$	$2{,}485.52 \pm 235.40^{c}$	11.6	0.0007
N	18.70 ± 5.99^{a}	62.06 ± 15.56^{b}	123.04 ± 28.00^{c}	87.90 ± 0.91^{bc}	10.2	0.0013
Ca	18.52 ± 5.61^{a}	41.22 ± 8.84^{b}	66.53 ± 13.65^{c}	117.60 ± 7.34^{d}	22.8	<0.0001
Mg	4.54 ± 1.22^{a}	7.48 ± 1.87^{ab}	10.70 ± 2.29^{b}	21.96 ± 3.68^{c}	10.9	0.0010
K	6.90 ± 2.41^{a}	14.01 ± 3.32^{ab}	23.13 ± 5.34^{b}	48.27 ± 3.54^{c}	18.4	0.0001
P	1.44 ± 0.40^{a}	3.01 ± 0.72^{ab}	5.23 ± 1.24^{bc}	7.53 ± 1.92^{c}	6.3	0.0082
g/ ha/ year						
Cu	15.72 ± 6.81^{a}	38.26 ± 10.44^{a}	64.84 ± 16.19^{b}	53.38 ± 5.82^{ab}	6.3	0.0083
Zn	106.53 ± 25.30^{a}	111.52 ± 19.45^{a}	130.21 ± 24.44^{a}	393.15 ± 4.23^{b}	40.7	<0.0001
Mn	387.78 ± 138.17^{a}	736.36 ± 210.06^{ab}	$1{,}316.52 \pm 452.83^{bc}$	$1{,}862.44 \pm 338.20^{c}$	7.2	0.0050
Fe	185.21 ± 49.08^{a}	442.58 ± 85.15^{b}	718.73 ± 163.84^{c}	702.98 ± 83.23^{bc}	9.0	0.0021

4.3.3 *Soils chemical parameters*

We found no effect of treatment ($p > 0.05$) on soil nutrient concentrations (at both 0-5 cm and 5-20 cm), nutrient stocks per hectare and other soil parameters. Although soil properties varied greatly across sites, no single soil variable was significantly correlated with litterfall production ($p > 0.1$). Soil pH is a key factor for most nutrients availability and uptake. Multiple regression models including pH and nutrients were significant only for P ($R^2 = 0.46$, F = 7.67, $p = 0.0039$) and Fe ($R^2 = 0.63$, F = 15.07, $p = 0.0001$). Moreover, the combination of pH, soil P and Fe (5-20 cm depth) explained 70 percent of litterfall residual variation not explained by the treatments ($F = 13.51$, $p = 0.0001$); the same model for 0-5 cm depth explained a smaller fraction of the variation ($R^2 = 0.41$, $p = 0.0283$).

4.4 Discussion

Degraded areas are widespread throughout the tropics. Developing an understanding of the reestablishment of ecological processes such as nutrient cycling under different tropical forest restoration strategies as compared to natural recovery, is important for the evaluation of proactive methods, and to recommend restoration practices for landowners and public agencies. Although litter dynamics during secondary succession are well studied (Ewel 1976, Zou *et al*. 1995, McDonald & Healey 2000, Ostertag *et al.* 2008), there are very few investigations comparing secondary forests and plantations (Cuevas *et al.* 1991, Lugo 1992) and to our knowledge no publication has examined litter dynamics in tree islands.

4.4.1 *Litter production*

Litter production was much higher in the two active restorations strategies studied (uniform mixed-tree plantation and tree islands) as compared to areas under natural regeneration (controls) after five years. Indeed, most of the control areas were dominated by pasture grasses, which represent an important barrier to forest recovery (Holl 2002). In the active restoration treatments, the fast-growing species (*Inga edulis* and *Erythrina poeppigiana*) provided canopy cover and quickly shaded out grasses and other ruderal vegetation (Holl *et al*., in press). Plantations showed higher litter productivity than islands due to higher tree density and canopy cover, consistent with previous studies that demonstrate a strong correlation of litter production with canopy cover and aboveground biomass increase, representing an important measure of net primary productivity (this study, Clark *et al.* 2001). Other factors controlling litterfall in our restoration plots were climate (higher deposition during the dry months) and topography (lower on hillsides).

Litter production in the plantation plots was similar to secondary forests that were 3-5 years older, confirming that planting accelerates productivity (Lugo 1992). Previous studies suggest that stand age is a key factor affecting litterfall but only in the first decade or so after lands are removed from agriculture; after canopy closure there is no clear correlation between litterfall production and stand age (Ewel 1976, Lugo 1992, Zou *et al.* 1995, Ostertag *et al.* 2008). So, treatment differences in terms of productivity will likely decline over time. Although plant species density and diversity were higher in secondary forest plots, they were not correlated with litter productivity, as in previous studies (Lugo 1992, Wardle *et al.* 1997, Scherer-Lorenzen *et al.* 2007).

4.4.2 Litter quality

Higher species diversity in the secondary forest resulted in higher litter quality (greater nutrient concentration and lower C to nutrient ratios) and nutrient input, except for N. This suggests that biochemically, plantation and secondary forest will probably not function in the same way – even if they produce similar amounts of litter. Similarly, Lugo (1992) found that secondary forest litter had higher nutrient concentrations and faster nutrient turnover than plantations, although litter quality in plantations improved over time due to native species enrichment, and some >17-yr old plantations had the same rate of litter turnover as same age secondary forests (Lugo 1992). Scatena *et al.* (1996) reported that N, P, K, Ca and Mg concentration in litterfall increased with successional age. They observed that the nutrient cycling pattern consisted of rapid accumulation of aboveground nutrients during stand closure and rapid turnover and cycling of nutrients through litterfall as the stand matured.

The overwhelming dominance of *Inga* (70% of leaf litterfall), an N-fixing species, strongly influenced nutrient cycling in our plantation plots. Dominance by a single species may not be desirable for restoration, as the dominant litter affects successional dynamics by determining soil conditions, litter accumulation rates and decomposition processes that directly influence the recruitment of native species (Mesquita *et al.* 2001). Although, *Inga* also dominated leaf fall biomass in the island treatment (47%), distribution among species was more equitable as other dicotyledonous species and grasses comprised a larger proportion of litterfall.

Inga edulis has been shown to increase soil nutrient availability and create better conditions for seedling establishment and growth (Nichols *et al.* 2001, Carpenter *et al.* 2004b), however its litter is considered “low-quality” because of the large recalcitrant fraction (Leblanc *et al.* 2006) that can retard decomposition (Palm & Sanchez 1990). In fact, litter accumulation on the forest floor in our plantation plots was much higher compared to secondary forest and islands (Celentano *et al.* 2009), and was superior to the annual litter production, suggesting low decomposition rates (Olson 1963). The litter layer is important in reducing soil erosion and replenishing soil organic matter (Schroth 2003). However, our plantation plots had a very thick litter layer (Celentano *et al.* 2009) which can be problematic for restoration by: (1) functioning as a physical barrier to the emergence of seedlings from small seeds which dominate early-successional seed rain (Cole *et al.* in press); (2) obstructing seeds from direct contact with the soil; and (3) modifying micro-environmental conditions that can promote or inhibit the germination and establishment of plants (Molofsky & Augspurger 1992; Carson & Peterson 1990). Additional studies on seedling establishment are needed to evaluate whether there is a negative effect of litter layer on plant diversity.

4.4.3 Soils

We expected that the higher input of litter and nutrients to the forest floor would improve at least soil C and N content in our restoration plots, as compared to same-age natural regeneration (control). However, no differences in soils parameters were found between treatments even at 0-5 cm depth, suggesting that five years was not enough time for the restoration treatments to affect the evaluated soils properties. Several past studies have shown that the effect of aboveground vegetation on soil nutrient content is not straightforward. Buschbacher *et al.* (1988) found no relationship between soil nutrient content and age, use-intensity, vegetation biomass or species richness in abandoned pastures. Although Salako and Tian (2005) found that trees affected soil properties seven years after planting in agroforestry systems, the intensity of the effects was strongly linked to inherent soil properties.

Considering the high within-site topographic variation in this study, soil nutrients may have been measured at too large a scale (the plot level) to detect small-scale heterogeneity.

The combination of pH, P, and Fe explained 70 percent of the residual variability in litterfall production among our restoration sites. Acidic soils are often associated with nutrient deficiency because soil pH plays a major role in governing nutrient availability to plants (Bhupinderpal-Singh & Rengel 2007). The affinity of soil Fe and Al minerals for P is considered the primary mechanism responsible for P limitation in the tropics (Vitousek 1982, Vitousek & Sanford 1986, Chacón & Dezzeo 2004, Chacon *et al.* 2006), because once P is fixed to oxides of Fe and Al it is no longer available for plant uptake (Schroth *et al.* 2003). Although further studies on nutrient availability and capture are needed to develop a better understanding of this process in our study sites, this result indicates that P availability may control litter production and explain at least part of the high variability of litter production we found among our sites.

4.4.4 Implications for tropical forest restoration

The high variability in litter productivity and nutrient inputs in our sites underscores the importance of site quality in determining whether restoration succeeds, and the danger of extrapolating the outcomes of restoration strategies that have been tested at only one or two sites. Tree planting is the most widespread strategy to restore tropical forests; there is an increasing focus on planting a diversity of native species but many restoration efforts rely on a small number of commercially-available species. Our results show that planting a small number of fast-growing trees to facilitate tropical forest recovery promotes the development of a rapid canopy cover that shades out grasses and provides large amounts of litterfall, similar to more diversified secondary forests. However, the lower plant diversity inherent in large-scale plantings results in poorer litter quality (measured by nutrient concentration and C to nutrient ratios). Accordingly, restoration strategies with more heterogeneous planting designs, such as the islands, may promote a faster increase in plant diversity and litter quality, and accelerate the reestablishment of a less species-specific nutrient cycling system, but seedling recruitment and recovery of leaf litter production may take longer. Another strategy to promote higher species diversity and better litter quality would be to plant a larger number of species at the outset or once the canopy has established and site conditions are appropriate for later-successional species, but this implies higher costs.

4.5 Conclusion

Litter production recovered quickly under the two tropical restorations strategies studied (uniform mixed-tree plantation and tree islands) as compared to areas under natural regeneration with same age. Litter production in the plantation plots was similar to young secondary forest. However, litter quality (measured by nutrient concentration and C to nutrient ratios) is greater in natural systems due to higher plant diversity, and it can influence forest restoration in the future. The dominance of litter from one species is not desirable for restoration practice once it determines nutrient availability and can negatively affect successional pathways. Restoration strategies with more heterogeneous planting design as the islands may promote a faster increase in plant diversity and litter quality, and then accelerate the reestablishment of nutrient cycling. Moreover, our study reveals large differences in litterfall production across sites and it was explained by a set of soils characteristics (pH, P and Fe) that may affect Phosphorus availability for plants. The high variability we found in plant productivity and nutrient inputs in our sites underscore the danger of generalizing or extrapolating the outcomes of restoration strategies for ecological processes such as nutrient cycling. To a better understanding of the nutrient cycle's reestablishment under these tropical forest restoration methods, it will be necessary a long-term monitoring of plant diversity, litter quality, decomposition rate and soils

4.6 Acknowledgments

The experimental infrastructure is financed by the National Scientific Foundation (NSF; DEB 05-15577 for K. D. Holl and R.A. Zahawi) and the Earthwatch Foundation. This research project was supported by the International Tropical Timber Organization (ITTO), the Wildlife Conservation Society (WCS) through the Conservation Leadership Programme (CLP), The Nature Conservancy (TNC) through the Organization for Tropical Studies (OTS) 2008 Las Cruces Restoration Workshop grant, and by the Tropical Agricultural Centre for Research and Higher Education (CATIE). Danielle Celentano is a fellow of the Organization of American States (OAS). We are grateful for the assistance of Juan Abel Rosales and Roman Gomez Meza in the field and Esthefanie Daniela Rodrigues Cerdas in the lab. We are also thankful for the important support received from Darryl Cole and Diego Delgado with logistics, Fernando Casanoves with statistics, Susan G. Letcher with botanical identification, and Gabriela Soto and Guillaume Rousseau with soils. We thank Ima C. Vieira for commenting an early version of the manuscript. We thank all landowners in Coto Brus that allowed us to establish the restoration experiment on their properties.

4.7 Literature Cited

AOAC. Association of Official Agricultural Chemists. 1984. Official methods of analysis. 14th Ed.: U.S.A., Association of Official Agricultural Chemists Inc. 40p.Washington DC, USA.

BHUPINDERPAL-SINGH, AND Z. RENGEL. 2007. The role of crop residues in improving soil fertility. *In* P. Marschner, and Z. Rengel. (Eds.). Nutrient cycling in terrestrial ecosystems, pp 183 – 214. Soil Biology series, Vol. 10. Springer Verlag, Berlin.

BUSCHBACHER, R., C. UHL, AND E. A. S. SERRAO. 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. J. Ecol. 76: 682-699.

CARPENTER, F. L., J. D. NICHOLS, E. SANDI. 2004a. Early growth of native and exotic trees planted on degraded tropical pasture. For. Ecol. Manage. 196: 367-378.

CARPENTER, F. L., J. D. NICHOLS, R. T. PRATT, AND K. C. YOUNG. 2004b. Methods of facilitating reforestation of tropical degraded land with the native timber tree, *Terminalia amazonia*. For. Ecol. Manage. 202: 281-291.

CARSON, W. P., AND C. J. PETERSON. 1990. The role of litter in an old-field community: Impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85: 8-13.

CELENTANO, D., R. ZAHAWI, B. FINEGAN, R. OSTERTAG, R. COLE, AND K. D. HOLL. 2009. Efecto de diferentes estrategias de restauración ecológica de bosques tropicales en la producción, acumulación y descomposición de hojarasca en el sur de Costa Rica. *In* Proceedings of Congreso Iberoamericano y del Caribe sobre Restauración Ecológica pp.59-70. RIACRE, Curitiba, Brazil.

CÉSPEDES, M. V., B. FINEGAN, B. HERRERA, L. D. DELGADO, S. VELÁSQUEZ, AND J. J. CAMPOS. 2008. Diseño de una red ecológica de conservación entre la Reserva de Biosfera La Amistad y las areas protegidas del Área de Conservación Osa, Costa Rica. Recursos Naturales y Ambiente 54: 44-50.

CHACÓN, N., W. L. SILVER, E. A. DUBINSKY, D. F. CUSACK. 2006. Iron reduction and soil phosphorus solubilization in humid tropical forests soils: the roles of labile carbon pools and an electron shuttle compound. Biogeochemistry 78: 67-84.

CHACÓN, N., AND N. DEZZEO. 2004. Phosphorous fractions and sorption processes in soil samples taken in a forest-savanna gradient in the Gran Sabana, South Venezuela. Biology and Fertility of Soils 40: 14-19.

CHAZDON, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Sci. 320: 1458-1460.

CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, J. NI, AND E. A. HOLLAND. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol. Appl. 11: 371-389.

COLE, R. J., K. D. HOLL, AND R. A. ZAHAWI. *In press*. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecol. Appl.

CUEVAS, E., S. BROWN, A. E. LUGO. 1991. Above- and belowground organic matter storage and production in a tropical pineplantation and a paired broadleaf secondary forest. Plant Soil 135: 257-268.

DAILY, G. C., P. R. EHRLICH, AND G. A. SANCHEZ-AZOFEIFA. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecol. Appl. 11: 1–13.

DÍAZ, R., AND A. HUNTER. 1978. Metodología de muestreo de suelos, análisis químico de suelos y tejido vegetal e investigación en invernadero. CATIE, Turrialba, Costa Rica.

EWEL, J. J. 1976. Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. J. Ecol. 64: 293-308.

FAO 2006. Global forest resources assessment 2005: progress towards sustainable forest management. FAO Forestry Paper 147. Food and Agriculture Organization of the United Nations, Rome, Italy. Available on the Internet www.fao.org/forestry/fo/fra/index/jsp.

FINK, R. D., C. A. LINDELL, E. B. MORRISON, R. A. ZAHAWI, AND K. D. HOLL. 2009. Patch size and tree species influence the number and duration of bird visits in forest restoration plots in southern Costa Rica. Restoration Ecol. 17:479-486.

FIELD, C. B., M. J. BEHRENFELD, J. T. RANDERSON, AND P. FALKOWSKI. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. Sci. 281: 237-240.

HOLDRIDGE, L. R., W. G. GRENKE, W. H. HAHEWAY, T. LIANG, AND J. J. A. TOSI. 1975. Forest environments in tropical life zones. Pergamon Press, New York, U.S.A.

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

HOLL, K. D. 2002. Tropical moist forest restoration. *In* A. J. Davy, and Perrow, M. Handbook of Ecological Restoration (vol. II), pp.539-558. Cambridge University Press, Cambridge, UK.

HOLL, K. D., R. ZAHAWI, R. J. COLE, R. OSTERTAG, AND S. CORDELL. In press. Planting seedlings in plantations versus tree islands as a large-scale tropical forest restoration strategy. Restoration Ecol.

INFOSTAT. 2009. InfoStat Versión 2009. Grupo Infostat, FCA, Universidad Nacional de Córdoba, Argentina.

KLINGE, H. 1977. Fine litter production and nutrient return to the soil in three natural forest stands of eastern Amazonia. Geo-Eco-Trop Journal 1: 159-167.

LAMB, D.; AND GILMOUR, D. 2003. Issues in forest conservation. Rehabilitation and restoration of degraded forests. International Union for Conservation of Nature and Natural Resources (IUCN) and The World Wide Fund for Nature (WWF). 122p.

LAMB, D., P. D. ERSKINE, AND J. A. PARROTTA. 2005. Restoration of degraded tropical forest landscapes. Sci. 310: 1628-1632.

LAMBERS, H., J. A. RAVEN, G. R. SHAVER, AND S. E. SMITH. 2007. Plant nutrient-acquisition strategies change with soil age. Trends Ecol. Evol**.** 23: 95- 102.

LEBLANC, H. A., P. NYGREN, AND R. L. MCGRAW. 2006. Green mulch decomposition and nitrogen release from leaves of two *Inga* spp. in an organic alley-cropping practice in the humid tropics. Soil Biol. Biochem. 38: 349-358.

LOSOS, E., AND E. G. LEIGH. 2004. Forest diversity and dynamism: findings from a network of large-scale tropical forest plots. University of Chicago Press, Chicago, U.S.A.

LUGO, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecol. Monogr. 62: 1-41.

MARGALEF, R. 1958. Information theory in ecology. Gen. Systems 3: 36-71.

MEA. Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, DC., U.S.A.

MEENTMEYER, V., E. O. BOX, AND R. THOMPSON. 1982. World patterns and amounts of terrestrial plant litter production. BioScience 32: 125-128.

MESQUITA, R. C. G. , K. ICKES, G. GANADE, AND G. B. WILLIAMSON. 2001. Alternative successional pathways in the Amazon Basin. J. Ecol. 89: 528–537.

MCDONALD, M. A., AND J. R. HEALEY. 2000. Nutrient cycling in secondary forests in the Blue Mountains of Jamaica. For. Ecol. Manage. 139: 257-278.

MILLS, H. A., AND J. B. JONES. 1996. Plant Analysis Handbook II. MicroMacro Publishing, Georgia, U.S.A.

MOLOFSKY, J., AND C. AUGSPURGER. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73: 68-77.

NEPSTAD, D., C. UHL, C. A. PEREIRA, AND J. M. C. DA SILVA. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76: 25-39.

NICHOLS, J. D., AND F. L. CARPENTER. 2006. Interplanting *Inga edulis* with *Terminalia amazonia* yields nitrogen benefits to the timber tree. For. Ecol. Manage. 233: 344-351.

NICHOLS, J. D., M. E. ROSEMEYER, F. L. CARPENTER, AND J. KETTLER. 2001. Intercropping legume trees with native timber trees rapidly restores cover to eroded tropical pasture without fertilization. For. Ecol. Manage. 152: 195-209.

NOBLE, I. R., AND R. DIRZO. 1997. Forests as human-dominated ecosystems. Sci. 277: 522-525.

OELBERMANN, M., AND A. M. GORDON. 2000. Quantity and quality of autumnal litterfall into a rehabilitated agricultural stream. J. Environ. Qual. 29: 603-611.

OLSEN, S.R., AND L. E. SOMMERS. 1982. Phosphorous. *In* A.L. Page (Ed.). Methods of soil analysis(part 2): chemical and microbiological properties. pp. 403-430. American Society of Agronomy, Madison, Wisconsin; U.S.A.

OLSON, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322-331.

OTS. ORGANIZATION FOR TROPICAL STUDIES. 2009. Meteorological data of Las Cruces Biological Station. Avaiable at http://www.ots.ac.cr/.

OSTERTAG, R., E. MARIN-SPIOTTA, W. L. SILVER, AND J. SCHULTEN. 2008. Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. Ecosystems 11: 701-714.

PALM, C. A., AND P. A. SANCHEZ. 1990. Decomposition and nutrient release patterns of the leaves of three tropical legumes. Biotropica 22: 330-338.

R. 2009. R version 2.7.2. The R Foundation for Statistical Computing. Disponible en www.r-project.org/

RICKERT, E. 2005. Environmental effects of the coffee crisis: a case study of land use and avian communities in Agua Buena, Costa Rica. *M.S. thesis*. Evergreen State College, Olympia, Washington, U.S.A.

SALAKO, F. K, AND G. TIAN. 2005. Litter production and soil condition under agroforestry trees in two agroecological zones of southern Nigeria. Journal of Sustainible Agriculture 26: 5-21.

SCATENA, F. N., S. MOYA, C. ESTRADA, AND J. D. CHINEA. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following hurricane Hugo in the Bisley experimental watersheds, Luquillo experimental forest, Puerto Rico. Biotropica 28: 424-440.

SCHERER-LORENZEN, M., J. L. BONILLA, AND C. POTVIN. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116: 2108-2124.

SCHROTH, G. 2003. Decomposition and nutrient supply from biomass. *In* G. Schroth and F.L. Sinclair (Eds.). Trees, crops and soil fertility: concepts and research methods, pp.131-150. CAB International, Wallingford, UK.

SCHROTH, G., J. LEHMANN, AND E. BARRIOS. 2003. Soil nutrient availability and acidity. *In* G. Schroth and F.L. Sinclair (Eds.). Trees, crops and soil fertility: concepts and research methods, pp. 93-130. CAB International, Wallingford, UK.

TOWNSEND, A. R., P. M. VITOUSEK, E. A. HOLLAND.1992. Tropical soils could dominate the short-term carbon-cycle feedbacks to increased global temperatures. Climatic Change 22: 293-303.

UHL, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75: 377-408.

VAN BREUGEL, M., F. BONGERS, AND M. MARTÍNEZ-RAMOS. 2007. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover . Biotropica 39: 610–619.

VITOUSEK, P. M. 1982 Nutrient cycling and nutrient use efficiency. Am. Nat. 119: 53-72.

VITOUSEK, P. M., AND L. R. WALTER. 1989. Biological invention of *Myrica faya* in Hawaii: plant demography, nitrogen fixation and ecosystem effects. Ecol. Monogr. 59: 247-265.

VITOUSEK, P. M., AND R. L. SANFORD. 1986. Nutrient cycling in moist tropical forest. Annu. Rev. Ecol. Syst. 17:137-167.

WARDLE, D. A., AND D. A. PELTZER. 2007. Aboveground-belowground linkages, ecosystem development, and ecosystem restoration. *In* L. R. Walker, J. Walker, and R.J. Hobbs. (Eds.). Linking restoration and ecological succession, pp.45-68. Springer Science, New York, U.S.A.

WARDLE, D. A., K. I. BONNER, AND K. S. NICHOLSON. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness affects ecosystem function. Oikos 79: 247-258.

WALKER, J., AND P. REDDEL. 2007. Retrogressive succession and restoration on old landscapes. *In* L. R. Walker, J. Walker, and R.J. Hobbs. (Eds.). Linking restoration and ecological succession, pp.1-16. Springer Science, New York, U.S.A.

XULUC-TOLOSA, F. J., H. F. M. VESTER, N. RAMIREZ-MARCIAL, J. CASTELLANOS-ALBORES, AND D. LAWRENCE. 2003. Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. For. Ecol. Manage. 174: 401-412.

YARRANTON, G. A., AND R. G. MORRISON. 1974. Spatial dynamics of a primary succession: nucleation. J. Ecol. 62: 417-428.

ZAHAWI, R.A., AND C. K. AUGSPURGER. 2006. Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. Ecol. Appl.16: 464–478.

ZOU, X., C. P. ZUCCA, R. B. WAIDE, AND W. H. MCDOWELL. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico For. Ecol. Manage. 78: 147-157.

4.8 Appendix 1: Species list

List of canopy dicot species in the different restoration plots (Plantation = 6, Islands = 6, Control = 6, and Secondary forest = 3) in Coto Brus, Costa Rica.

Treatment	Species	Family
Secondary forest	*Aster* sp.	Asteraceae
	Allophylus psilospermus Radlk.	Sapindaceae
	Conostegia sp	Melastomataceae
	Cecropia sp	Cecropiaceae
	Cecropia obtusifolia Bertol.	Cecropiaceae
	Cinnamonum sp	Lauraceae
	Conostegia xalapensis (Bonpl.) D.	Melastomataceae
	Critrus sp**	Rutaceae
	*Dipterix Panamensis***	Fabaceae
	Heliocarpus appendiculatus Turcz.	Tiliaceae
	Lauraceae sp	Lauraceae
	Lippia myriocephala Schltdl &	Verbenaceae
	Melastomaceae sp	Melastomataceae
	Ocotea sp	Lauraceae
	Piper crossinervium	Piperaceae
	Piper sp 1	Piperaceae
	Piper sp 2	Piperaceae
	Sapium allenii Huft	Euphorbiacea
	Siparuna tetraceroides Perkins	Monimiaceae
	Solanaceae sp	Solanaceae
	Virola sp **	Myristicaceae
Control	*Citrus* sp **	Rutaceae
	Calea urticifolia (Mill.) DC.	Asteraceae
	Conostegia xalapensis (Bonpl.) D.	Melastomataceae
	Croton draco Schltdl. & Cham.	Euphorbiacea
	Erythrina poeppigiana	Fabaceae
	Heliocarpus appendiculatus Turcz.	Tiliaceae
	Lippia myriocephala Schltdl &	Verbenaceae
	Pteridium sp	Pteridaceae
	Solanum torvum Sw.	Solanaceae
	Verbesina turbacensis Kunth	Asteraceae
	Vernonia patens Kunth	Asteraceae
Islands	*Erythrina poeppigiana**	Fabaceae
	*Inga edulis**	Fabaceae
	Solanum torvum Sw.	Solanaceae
	*Terminalia amazonia**	Combretaceae
	*Vochysia guatemalensis**	Vochysiaceae
	Verbesina turbacensis Kunth	Asteraceae
	Vernonia patens Kunth	Asteraceae
Plantation	*Lippia myriocephala Schltdl &*	Verbenaceae
	*Erythrina poeppigiana**	Fabaceae
	*Inga edulis**	Fabaceae
	*Terminalia amazonia**	Combretaceae
	*Vochysia guatemalensis**	Vochysiaceae

* Species planted for the restoration project.

** Species planted prior to the restoration project.

ARTICLE 2. Restauración ecológica de bosques tropicales en Costa Rica: efecto de diferentes tratamientos en la producción, almacenamiento y descomposición de hojarasca [2]

Resumen: Estrategias de restauración ecológica tienen el potencial de acelerar el restablecimiento del ciclo de nutrientes en áreas degradadas. La producción de hojarasca y la descomposición representan la principal transferencia de materia orgánica y nutrientes de la vegetación al suelo. En este estudio, se evaluó la producción de hojarasca, su acumulación sobre el suelo y la descomposición bajo cuatro tratamientos: Plantación (toda la superficie plantada); islas (árboles sembrados en parches de tres tamaños), testigo (regeneración natural) y bosque secundario joven (7-9 años). Los tratamientos fueron establecidos en parcelas de 50 x 50m en junio de 2004 en seis sitios en el sur de Costa Rica. Las especies introducidas fueron dos nativas maderables (*Terminalia amazonia* y *Vochysia guatemalensis*) intercaladas con dos fijadoras de nitrógeno (*Erythrina poeppigiana* e *Inga edulis*). La hojarasca fue colectada en 12 canastas (0,25 m^2) distribuidas a nivel de las parcelas a cada 15 días entre septiembre de 2008 y agosto de 2009, la hojarasca acumulada sobre el suelo fue colectada en cuatro puntos (0,25m^2) por parcela en febrero y mayo de 2009, y la descomposición evaluada con bolsas de hojarasca llenas de *Inga edulis* entre febrero y junio de 2009. La producción total de hojarasca presentó diferencias significativas entre sitios y tratamientos. Plantación (6,3 Mg ha^{-1}) y bosque secundario (7,3) no difirieron y presentaron una mayor producción que islas (3,5) y el testigo (1,4). Las plantaciones presentaron mayor acumulación de hojarasca (9,4 Mg ha^{-1}). Aunque no hemos encontrado diferencias en las tasas de descomposición entre tratamientos con las bolsas de hojarasca, las plantaciones, islas y testigo presentaron una acumulación de hojarasca mayor que la producción anual indicando basas tasas de descomposición. Los resultados identificaron una gran variabilidad en la producción y acumulación de hojarasca y carbono entre los sitios. Ambas estrategias de restauración activas aceleraron la función de producción de hojarasca y almacenamiento de carbono en comparación con las áreas en regeneración natural. No obstante, eso no implica en la restauración del ciclo de nutrientes bajo eses tratamientos, pues la elevada acumulación de hojarasca sobre el suelo indica una muy baja tasa de descomposición.

Palabras-claves: restauración ecológica, bosques tropicales, hojarasca, carbono, descomposición.

---

[2] Paper in preparation for Revista Recursos Naturales y Ambiente (CATIE) in colaboration with B.Finegan, R.Zahawi, R.Ostertag, R.Cole and K.Holl.

4.9 Introducción

Los bosques tropicales protegen la mayor diversidad biológica del planeta y brindan servicios ecosistémicos vitales. No obstante, la mayor parte de esos bosques se encuentran en suelos de moderada a baja fertilidad (Vitousek y Sanford 1986). Bajo esas condiciones, la biomasa sostiene una importante proporción de los nutrientes que están potencialmente disponibles para la biota, y las plantas han desarrollado mecanismos altamente adaptados para la adquisición y la retención de los nutrientes (Walker y Reddell 2007). Además de alterar la estructura del ecosistema y deteriorar significativamenteel capital natural, la deforestación altera los ciclos de nutrientes y aumenta las pérdidas de nutrientes del ecosistema (Walker y Reddell 2007); ese proceso tiene altos costos ambientales y sociales (MEA 2005). No obstante, la deforestación sigue intensa en la mayoría de los países tropicales, especialmente en América Latina, donde los bosques están siendo talados y rápidamente convertidos para la agricultura (FAO 2006). Estrategias activas de restauración son necesarias en los trópicos considerando la gran escala de degradación (Lamb *et al.* 2005) y la necesidad de mantener procesos ecológicos vitales.

Restauración ecológica se define como el proceso intencional de ayudar al restablecimiento de un ecosistema que ha sido degradado, dañado o destruido (SER 2004). En ese proceso hay secuestro de carbono de la atmósfera en la biomasa, recuperación de hábitat para la biodiversidad y provisión de bienes y servicios ecosistémicos (Chazdon 2008). Además de restablecer la integridad ecológica, la restauración representa una manera de mejorar el bienestar humano en paisajes degradados a través de la recuperación de la productividad de la tierra y del capital natural (ITTO y IUCN 2005, Mansourian *et al.* 2005, Aronson *et al.* 2007). Los principios de la restauración ecológica de ecosistemas terrestres son los mismos que los principios de la sucesión ecológica (Bradshaw 1987). La meta final del proceso no es recuperar integralmente el estado anterior al disturbio, pero si garantizar que las funciones y los procesos ecológicos sean similares al ecosistema original a través del tiempo (SER 2004). Según Lamb y Gilmour (2003), en el futuro talvez sea apropiado buscar la restauración de vegetación natural resiliente y que presente rasgos funcionales para el restablecimiento de algunos servicios ecosistémicos deseados. Diferentes métodos han sido propuestos para acelerar o facilitar, desde el punto de vista ecológico, la restauración en los trópicos (Lamb y Gilmour 2003, Lamb *et al.* 2005). La selección del método más apropiado depende del estado inicial de la degradación, los resultados deseados, y del presupuesto disponible (Chazdon 2008); además del entorno socio-cultural, y marco político.

Desde el punto de vista ecológico, el método más sencillo de restauración es eliminar la fuente de perturbación y permitir al ecosistema recuperarse naturalmente (conocido también como restauración pasiva). Ese método es el más indicado cuando los recursos financieros son escasos y/o el estado de degradación no es excesivo. En este caso, es necesario proteger la zona de cualquier tipo de perturbación externa (incendios, ganado, etc), permitiendo así que los procesos de regeneración ocurran naturalmente (Lamb y Gilmour 2003). Prach *et al.* (2007) sostienen que la sucesión natural es el método que resulta en una mayor diversidad estructural y funcional del ecosistema. No obstante, el abandono no siempre dará lugar al desarrollo sucesional deseado (Schrautzer *et al.* 2007). Muchos factores bióticos y abióticos afectan el restablecimiento del bosque en un área alterada. La ausencia de dispersores de semillas, la falta de nutrientes en los suelos y la competencia de plántulas con gramíneas agresivas son considerados obstáculos importantes (Uhl *et al.* 1988, Nepstad *et al.* 1996, Holl 2002). Manipulaciones del ambiente físico y de la biota pueden reducir el tiempo necesario para la sucesión (Prach *et al.* 2007).

La plantación de árboles en alta densidad es el método más común de restauración activa. Las especies plantadas pueden establecerse rápidamente, suprimir las gramíneas y crear mejores condiciones para el establecimiento de una comunidad más diversa (Reay y Norton 1999). Sin embargo, plantaciones densas presentan altos costos iniciales y mucha inversión en cuanto a mantenimiento (Lamb y Gilmour 2003). Considerando que la mayoría de las iniciativas de restauración tienen presupuesto restringido (Holl y Howarth 2000), técnicas menos costosas pueden ser más atractivas para los agricultores, como por ejemplo la siembra de "islas de árboles", los cuales tienen como objetivo crear una complejidad estructural que imita el proceso de regeneración natural conocido como *nucleación*, donde parches de vegetación succesional crean microhábitat favorable al establecimiento de especies tardías (Yarranton y Morison 1974). Ese método requiere menor cantidad de árboles por hectárea y es más económico que plantaciones tradicionales. Además de la restauración de hábitat para la biodiversidad, los métodos activos tienen el potencial para acelerar el restablecimiento de procesos ecológicos como los ciclos de nutrientes y el secuestro de carbono. Este supuesto puede ser abordado a través del estudio de la dinámica de la hojarasca.

La producción de hojarasca y su descomposición son procesos fundamentales en el ciclo de nutrientes, ya que representan la principal transferencia de materia orgánica y nutrientes desde la vegetación a la superficie del suelo (Vitousek y Sanford 1986). La hojarasca es una medida de producción primaria neta (PPN) del ecosistema y está fuertemente correlacionada con el incremento de la biomasa (Clark *et al.* 2001), la densidad de árboles y la apertura del dosel (Zou *et al.* 1995, Oelbermann y Gordon 2000), siendo afectada por variables ambientales como precipitación, temperatura, elevación y fertilidad de los suelos (Vitousek y Sanford 1986), y la evapotranspiración potencial (Meentmeyer *et al.* 1982). La producción y acumulación de hojarasca incrementa rápidamente en los primeros años de sucesión (Ewel 1976). No obstante, después que el dosel está cerrado, no hay una tendencia clara entre la producción de hojarasca con el aumento en la edad del bosque (Ewel 1976, Lugo 1992, Zou *et al.* 1995, Ostertag *et al.* 2008), así como con la riqueza y diversidad de especies (Wardle *et al.* 1997, Scherer-Lorenzen *et al.* 2007).

La composición de especies determina las características químicas de la hojarasca y afecta el proceso de descomposición (Zou *et al.* 1995, Xuluc-Tolosa *et al.* 2003). El proceso de descomposición de la hojarasca implica una serie de interacciones entre la materia orgánica, los microorganismos del suelo, las comunidades de invertebrados, y las condiciones ambientales. Las comunidades de microorganismos y fauna en el suelo son influenciadas por la cantidad y la calidad de la hojarasca acumulada sobre el suelo y por su distribución espacial (Schroth 2003). Esas interacciones son muy afectadas en áreas degradadas, donde hay bajo aporte y acumulación de materia orgánica y cambios en las características ambientales. Se espera que ese proceso sea restablecido durante el proceso de restauración, con el incremento en el aporte y almacenamiento de materia orgánica.

En ese estudio, se evalúa la hojarasca y el carbono almacenado en el suelo en un proyecto de restauración forestal llevado a cabo en el cantón de Coto Brus, sur de Costa Rica (Holl *et al.* en prensa). El proyecto compara la regeneración natural para dos estrategias de restauración activa (plantación mixta de árboles y plantación de "islas de árboles") que pueden ser un modelo viable para otras regiones tropicales. Ambos sistemas de restauración utilizan dos especies nativas maderables (*Terminalia amazonia* y *Vochysia guatemalensis*), intercaladas con dos fijadoras de nitrógeno (*Erythrina poeppigiana* e *Inga edulis*) que han demostrado aumentar la disponibilidad de nutrientes en el suelo y mejorar las condiciones para el establecimiento de plántulas (Nichols *et al.* 2001, Nichols y Carpenter 2006). El objetivo específico fue evaluar la producción, acumulación y descomposición de la hojarasca en el suelo y el carbono almacenado en la hojarasca y suelo en los dos métodos de restauración activa de cinco años y compararlos con áreas en regeneración natural de la misma edad y bosques secundarios jóvenes (7-9 años). La hipótesis es que después de cinco años: (1) las dos estrategias de restauración activas presentarán más producción y acumulación de hojarasca, mayor contenido de carbono en el suelo y tasas de descomposición más bajas que áreas en regeneración natural debido a una mayor densidad de árboles y menor apertura del dosel; y (2) las plantaciones y los bosques secundarios jóvenes no presentarán diferencias en la producción, acumulación y descomposición de hojarasca y de carbono en el suelo en consecuencia de presentar similar densidad de árboles y apertura del dosel.

4.10 Métodos

4.10.1Área de estudio

El estudio se llevó a cabo en seis sitios ubicados entre la Estación Biológica Las Cruces (8° 47' 7" N, 82° 57' 32" W) y la ciudad de Agua Buena (8° 44' 42”N, 82° 56' 53”W) en Coto Brus, pacífico sur de Costa Rica (Figura 11). El área de estudio es un paisaje agrícola fragmentado localizado en el Corredor Biológico Amistosa - un área prioritaria para la conservación en Costa Rica, ya que tiene por objetivo conectar los mayores remanentes de bosques primarios en el sur del país (Céspedes *et al.* 2008). En los últimos 50 años la mayor parte de la zona de estudio fue deforestada y convertida a uso agrícola, especialmente café. El café fue cambiado a potreros o fue abandonado después de una importante crisis económica (Rickert 2005). Hoy día, menos de 25% del bosque original está conservado en pequeños fragmentos en esta región (Daily *et al.* 2001).

Los sitios de estudio fueron abandonados recientemente y habían sido utilizados para la agricultura (pastizales y/o fincas de café) entre 18 a 50 años antes del inicio del experimento. La mayoría fueron quemados una o dos veces después de la conversión (mayores detalles de los sitios presentados en Holl *et al.* en prensa). Los sitios eran dominados (> 80% de cobertura) por gramíneas (*Pennisetum purpureum* y/o *Urochloa brizantha*) o una mezcla de forraje, gramíneas, plantas herbáceas y *Pteridium arachnoideum*.

Los bosques en la zona se clasifican como Bosque muy húmedo premontanos (Holdridge *et al.* 1975). Los sitios presentan un rango de elevación de 1.000 a 1.300 m y tienen una fuerte pendiente. La temperatura promedio (21 ^{o}C) presenta poca variación durante el año y la zona recibe de 3.500-4.000 mm de precipitación anual, con una marcada estación lluviosa entre mayo y diciembre (Fink *et al*. 2009). Los suelos son Inceptisoles, ácidos (pH ~ 5.5, Al Acidez > 0,5 cmol / kg y la saturación de ácido > 15% a 5-20 cm de profundidad), pobres en fósforo (4,09 mg / kg a 0-5 y 1,95 en 5-10 cm), con niveles bajos a moderados de cationes intercambiables (Ca: 9,74 cmol / kg ± 1,54 SE; Mg: 3,41 ± 0,44; K: 0,47 ± 0,08) y concentraciones muy altas de Fe (142.15 mg / kg ± 11,84). La densidad aparente promedio del suelo es de 0,63 g / cm^3 (± 0,03) y presenta alto contenido de materia orgánica (14% a 0-5 cm y 11% a los 5-20 cm; mayores detalles se presentan en Celentano *et al*. en preparación).

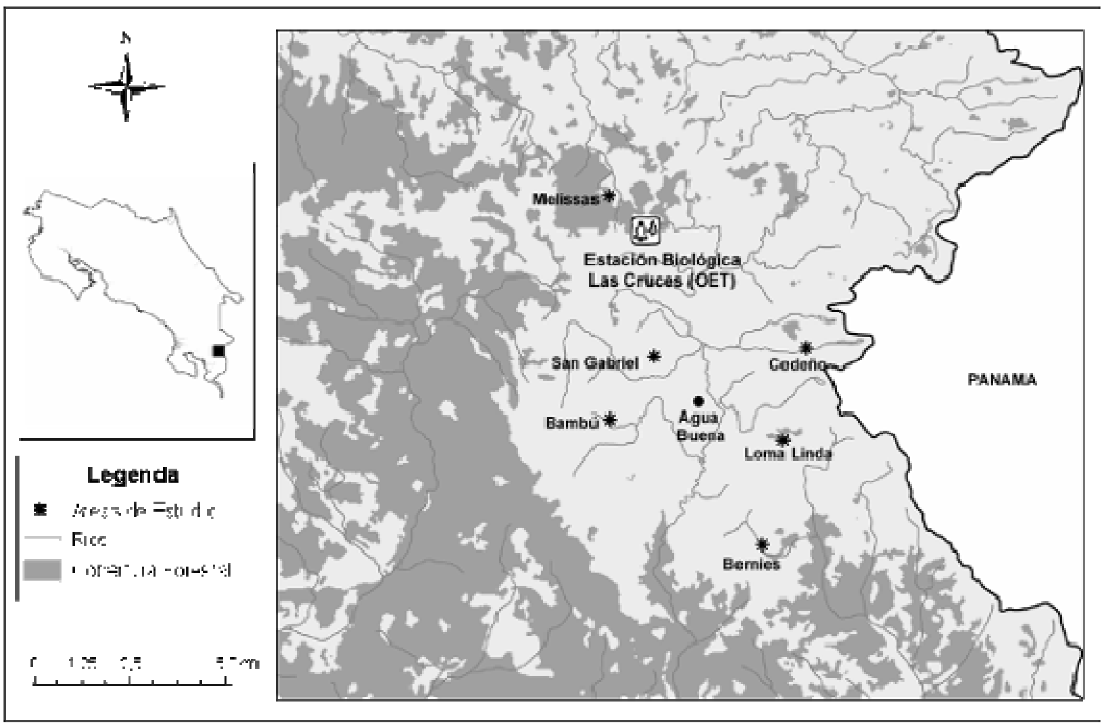

Figura 11. Áreas de estudio en Coto Brus, Costa Rica.

4.10.2 Diseño experimental y tratamientos

En cada sitio (bloques) se establecieron tres tratamientos en junio de 2004 (Figura 12) en parcelas de 50 × 50 m (unidades experimentales). Los tratamientos son: Plantación (P: toda la superficie plantada con una mezcla de especies arbóreas); Islas (I: árboles sembrados en parches de tres tamaños: 4 × 4 m, 8 × 8 m, y 12 × 12 m); y Testigo (T: sin plantación de árboles). Las parcelas fueron plantadas con cuatro especies, siendo dos nativas maderables, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae), *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), y dos especies introducidas de rápido crecimiento y fijadoras de nitrógeno, *Erythrina poeppigiana* (Walp.) O. F. Cook (Fabaceae), e *Inga edulis* Mart. (Fabaceae). Según Holl *et al.* (en prensa), la selección de especies para los tratamientos de restauración estudiados se basó en: (1) alta supervivencia en estudios previos en la región, altas tasas de crecimiento y amplio desarrollo de cubierta de copas en los primeros años, y (2) disponibilidad en los viveros locales. El desarrollo de los árboles sembrados varió mucho entre los sitios (Figura 13). En tres de los seis sitios, una parcela adicional de Bosque Secundario joven (BS: 7-9 años) fue evaluada como un cuarto tratamiento. En total se establecieron 21 parcelas.

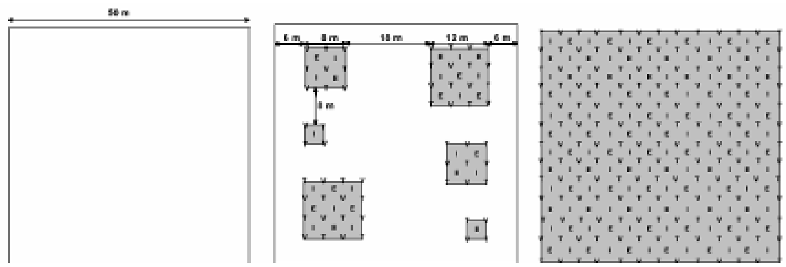

Figura 12. Diseño de los tratamientos: control (izquierda), islas (centro) y plantaciones (derecha). Gris = superficie plantada con árboles. E = Erythrina poeppigiana, I = Inga edulis, T = Terminalia amazonia, V = Vochysia guatemalensis. Blanco = zonas no plantadas.

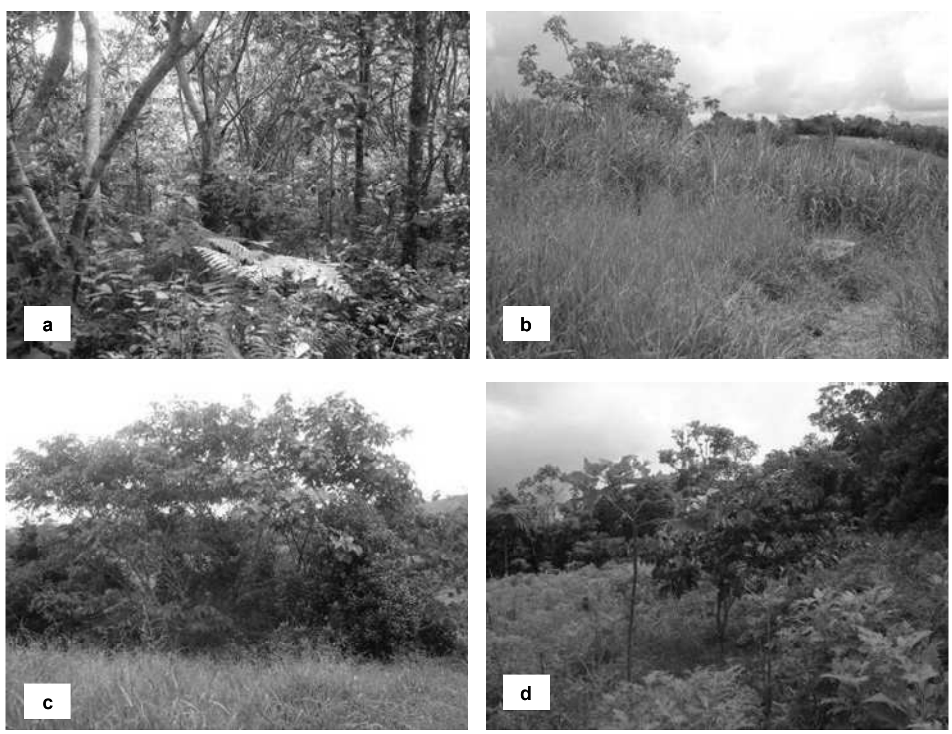

Figura 13. Fotos de los tratamientos con 4 años de edad (a). Plantación en Loma Linda. (b). Control en Cedeño. (c). Una Isla Mediana bien desarrollada en San Gabriel. (d). Una isla grande "mal" desarrollada en Cedeño.

4.10.3 Variables

4.10.3.1 Producción de hojarasca y aporte de Carbono

En cada una de las 21 parcelas fueron ubicadas al azar 12 canastas de 0,25 m^2 de área para la colecta de hojarasca. Las canastas fueron puestas aproximadamente a 0,60 m sobre el nivel del suelo. La hojarasca fue recogida cada 15 días entre los meses de septiembre de 2008 y agosto de 2009. Después de secar en un horno a 65 ^oC por 24-48 hr, la biomasa fue separada en hojas, madera, partes reproductivas (flores, frutos y semillas) y misceláneos (material vegetal indeterminado de pequeña dimensión) para cada muestreo. Una vez al mes, se pesó las hojas separadas por las cuatro especies plantadas (*Terminalia amazonia*, *Vochysia guatemalensis*, *Erythrina poeppigiana* y *Inga edulis*), gramíneas, otras especies dicotiledóneas y material no identificado. Esa identificación no fue llevada a cabo en los Bosques Secundarios (mayores detalles presentados en Celentano *et al. en preparación*).

4.10.3.2 Hojarasca acumulada sobre el suelo

La hojarasca acumulalda sobre el suelo fue cuantificada en febrero y mayo del 2009 y promediada. . Se ubicó un cuadro de 0.25 m^2 con tubos de de PVC en ocho (en las islas) y cuatro (bosque secundario, plantación y testigo) puntos de muestreo definidos al azar en cada parcela de 50 m x 50 m. Toda la materia orgánica vegetal acumulada dentro del cuadro fue recogida y el peso de la biomasa reportado en base seca (mantenida a 65 ^oC por al menos 48 horas) separado en hojas (dicotiledóneas), gramíneas (hojas y tallo), partes reproductivas, madera y otros. Antes de recoger la hojarasca acumulada sobre el suelo, estimamos visualmente su cobertura (%) y medimos con una regla su espesor (cm).

4.10.3.3 Carbono de la hojarasca

La concentración de carbono en las hojas fue determinada para las muestras de hojarasca producida en el laboratorio de Análisis de Suelos, Tejido Vegetal y Aguas del Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) por el método de combustión en equipo auto-analizador (AOAC 1984) para cuatro períodos de análisis: (1) octubre 2008; (2) muestras compuestas de diciembre, enero y febrero; (2) marzo, abril y mayo; y (4) junio, julio y agosto. La concentración de carbono de los otros componentes de la hojarasca (madera, partes reproductivas y misceláneos) fue estimada como la mitad de la biomasa seca (Pearson *et al.* 2005). Con los datos de concentración de carbono y de producción y acumulación, se calculó el aporte y almacenamiento de carbono por hectárea en cada tratamiento.

4.10.3.4 Carbono en el suelo

El suelo fue muestreado en abril de 2009, cuando se recogieron diez muestras al azar en cada parcela a dos profundidades (0-5 y 5-20 cm). Las muestras de cada parcela fueron mezcladas, secadas al aire y tamizadas (2 mm). El análisis químico para determinar la concentración de carbono total se realizó en una única muestra de cuanto volúmen??? compuesta por parcela siguiendo el protocolo estándar del laboratorio de suelos (Díaz y Hunter 1978) del CATIE. Para determinar el contenido de carbono es necesario conocer la densidad aparente del suelo. Para esto, se recogieron cinco muestras para análisis de de densidad aparente (g/cm^3) de cada parcela con un área de 4 cm de rayo por 10 cm de profundidad. Las muestras de densidad aparente se secaron a 105 ^oC durante 48 horas antes de su pesaje.

4.10.3.5 Descomposición

Se estimó la tasa de descomposición anual (k_L) de la hojarasca por el método propuesto por Olson (1963), a través del valor de producción anual de hojarasca (L, en Mg ha^{-1} $año^{-1}$) y del promedio de la hojarasca acumulalda sobre el suelo (Xss, Mg ha^{-1}), donde $k_L = L / Xss$.

Además de eso, el potencial de descomposición entre los diferentes tratamientos fue evaluado en un experimento usando el método "standard leaf-litter species” (Upadhyay *et al* 1985) que utiliza un material vegetal similar para garantizar una calidad de substrato constante. La descomposición fue estimada usando bolsas (*litterbags*) de 25 cm^2 con malla de 2 mm llenas con 10 g de hojas secas homogenizadas de *Inga edulis*. *Inga* fue seleccionada por ser la especie que más aporta hojarasca en los tratamientos de restauración. Las bolsas fueron enterradas superficialmente (~1-2 cm de profundidad) en cada parcela (Bocock y Gilbert 1957). Este estudio fue llevado a cabo en los tres sitios donde hay bosque secundario. El experimento fue instalado en Febrero de 2009 (T_0) y la pérdida de peso de las bolsas fue evaluada en cuatro periodos de incubación ($T_1 = T_0$ + 15 días; $T_2 = T_0$ + 30d; $T_3 = T_0$ + 60d; $T_4 = T_0$ + 135d), cuando cuatro bolsas fueron retiradas de las parcelas, pesadas y promediadas para cada período de incubación. En total fueron instaladas 192 bolsas en el campo (12 parcelas × 4 periodos de incubación × 4 replicas).

4.10.4 Análisis de los datos

El experimento se estableció como un diseño de bloques incompletos (el tratamiento de bosque secundario se replicó solamente en tres de los seis sitios) con el sitio como el factor de bloqueo. Las diferencias en la hojarasca (producción total, acumulación, contenido de carbono y la tasa anual de descomposición) y el carbono del suelo entre las estrategias de restauración fueron analizadas usando modelos mixtos de ANOVA con tratamientos como factores fijos y los sitios como factores aleatorios, y las comparaciones entre tratamiento se llevaron a cabo a través del test LSD de Fisher.

El experimento con las bolsas de descomposición se llevó a cabo según un diseño en bloques completos (solo se usaron los tres sitios donde hay réplicas del bosque secundario) Para evaluar la tasa de descomposición, se calculó y graficó la pérdida de peso de las bolsas de descomposición por tiempo. Después se ajustó la curva de pérdida de peso usando regresiones lineales y exponenciales y se calculó oeficiente *k* de descomposición para cada parcela de acuerdo con el modelo mejor ajustado. Finalmente, se usó una ANOVA para hacer la comparación entre los valores del coeficiente *k* de descomposición entre los tratamientos. Todos los análisis estadísticos y gráficos fueron realizados con InfoStat/ P® (versión 2009, Infostat 2009) y R® (versión 2.7.2; R 2008).

4.11 Resultados

4.11.1 Producción y almacenamiento de hojarasca

La producción anual de hojarasca así como su almacenamiento sobre el suelo difirió entre los sitios y los tratamientos (Figura 14). Hubo gran variabilidad entre los sitios en el promedio de producción (1,1 - 5,7 Mg ha^{-1} yr^{-1}) y acumulación (2,3 - 9,3 Mg ha^{-1}) de hojarasca, y dos sitios tuvieron producción ($F = 31,4$, $p < 0,0001$) y acumulación ($F = 6,26$, $p < 0,0001$) inferior a los demás. El bosque secundario y la plantación presentaron la mayor producción anual de hojarasca, mientras las islas presentaron valores intermedios y el testigo mostró una producción reducida (F = 129,35, $p < 0,0001$). A su vez, la hojarasca almacenada en el suelo fue superior en las plantaciones que en los otros tratamientos (F = 6,51, $p <0,0004$).

El gran almacenamiento de hojarasca en las plantaciones resultó en una cobertura del suelo (97,5%) estadísticamente superior (F = 6,34, $p < 0,0006$) a los otros tratamientos (BS = 83,4%; I = 82,8%; C = 80,6%). De igual manera, las plantaciones presentaron una capa de hojarasca (F = 8,38, $p < 0,0001$) con mayor espesor (3,7 cm), mientras que el bosque secundario (1,8 cm) y el testigo (2,1 cm) presentaron capas más delgadas y las islas tuvieron valores intermedios (2,9 cm). En todos los tratamientos, las hojas fueron el principal componente de la hojarasca producida (P = 87%, I = 88%, C = 89%, BS = 77%) y almacenada (P = 88%, I = 90%, C = 93%, BS = 74%). En los bosques secundarios, la madera representó el 20% de la biomasa seca de la hojarasca acumulada. *Inga edulis* fue la especie que más contribuyó en la producción de hojas en las plantaciones (70%) e Islas (47%). Mayores detalles respecto a la producción de hojarasca están presentados en Celentano *et al.* (en preparación).

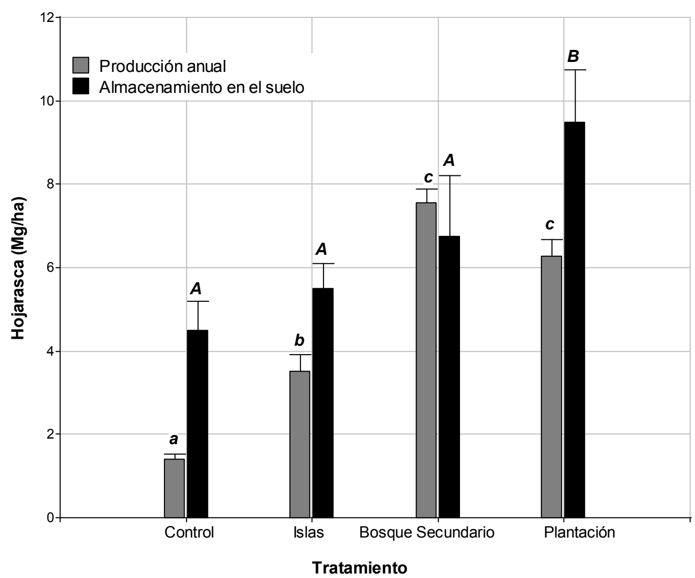

Figura 14. Hojarasca producida(Mg ha^{-1} año^{-1}) y almacenada sobre el suelo (Mg ha^{-1}) en los diferentes tratamientos de restauración (plantación, islas, control y bosque secundario) en Coto Brus, Costa Rica. Letras diferentes indican diferencia estadística ($p < 0,05$) entre tratamientos de acuerdo con la prueba de Tukey.

4.11.2 Concentración, aporte y almacenamiento de Carbono

La concentración de carbono en las hojas varió entre sitios (F = 3,52, p = 0,0343) y tratamientos (F = 9,83, p = 0,0015). El testigo (43%) presentó una concentración de carbono en las hojas estadísticamente inferior a los otros tratamientos (P = 48; BS = 46; I = 46). Como consecuencia de la producción anual de hojarasca, el aporte anual de carbono (Tabla 14) fue superior en el bosque secundario y en las plantaciones, intermedio en las islas e inferior en el testigo. De igual manera, el carbono almacenado en la hojarasca sobre el suelo fue superior en las plantaciones (4,6 Mg C ha^{-1} $año^{-1}$) y en el bosque secundario (2,9). No obstante, el almacenamiento de carbono en hojas fue mayor en la plantación que en todos los otros tratamientos.

Los sitios difieren en cuanto a la concentración de carbono en los suelos (F = 23,02, p = <0,0001). No obstante, no se encontraron diferencias estadísticas entre tratamientos para la concentración de carbono entre 0-5 cm (p = 0,7787) y 5-20 cm de profundidad (p = 0,7806). Tampoco hubo efecto de tratamiento en el contenido de carbono en el suelo (Tabla 1).Se constató que la concentración de carbono a la profundidad de 0-5 cm (8,1% ± 0,7) es estadísticamente superior (t = 12,06; p < 0,0001) que a la profundidad 5-20 cm (6,2% ± 0,5). No fueron encontradas correlaciones entre la concentración de carbono en las hojas y en el suelo.

Table 7. Aporte y almacenamiento de carbono en la hojarasca y suelo por hectárea *(Mg ha^{-1} promedio ± EE) en los diferentes tratamientos de restauración (Plantación, Islas, Control, y Bosque Secundario) en Coto Brus, Costa Rica*

Contenido de carbono (Mg C ha^{-1})	**Control**	**Islas**	**Plantación**	**Bosque secundario**	**F**	***p***
Hojarasca producida ($año^{-1}$)	0.6 ± 0.4^{a}	1.6 ± 0.4^{a}	3.0 ± 0.4^{b}	3.3 ± 0.6^{b}	11.27	0.0008
Hojas	0.5 ± 0.4^{a}	1.4 ± 0.4^{b}	2.6 ± 0.4^{c}	2.5 ± 0.5^{bc}	11.62	0.0007
Otros componentes	0.1 ± 0.1^{a}	0.2 ± 0.1^{ab}	$0. 5\pm0.1^{b}$	0.9 ± 0.1^{c}	8.39	0.0028
Hojarasca almacenada	1.9 ± 0.6^{a}	2.5 ± 0.6^{a}	4.6 ± 0.6^{b}	2.9 ± 0.8^{ab}	6.29	0.0083
Hojas	1.8 ± 0.6^{a}	2.2 ± 0.6^{a}	3.9 ± 0.6^{b}	2.1 ± 0.8^{a}	5.09	0.0168
Otros componentes	0.2 ± 0.1^{a}	0.3 ± 0.1^{ab}	0.6 ± 0.1^{bc}	0.9 ± 0.2^{c}	7.23	0.0050
Suelo total (0 – 20cm)	80.6 ± 8.2	75.8 ± 8.2	75.1 ± 8.2	91.9 ±9.5	-	0.1855
Suelo (0-5cm)	24.4 ± 2.7	23.5 ± 2.7	22.9 ± 2.7	27.9 ± 3.0	-	0.1743
Suelo (5-20cm)	56.2± 5.7	52.4 ± 5.7	52.2 ± 5.7	63.9 ± 6.8	-	0.2238
Total almacenado (hojarasca + suelo)	82.5± 8.3	79.6± 8.3	78.3± 8.3	94.8± 9.5	-	0.1857

Letras diferentes indican diferencia estadística (*p* < 0,05) entre tratamientos de acuerdo con test Tukey.

4.11.3 Descomposición

La pérdida de peso de las hojas de *Inga edulis* en las bolsas de descomposición entre el inicio de febrero y finales de junio de 2009 varió entre 19–23% dependiendo del tratamiento. El modelo de regresión lineal se ajustó mejor a los datos de descomposición (R^2 = 0.92) en comparación con el modelo exponencial (R^2 = 0.90). La curva de pérdida de peso (Figura 15) fue muy similar entre tratamientos y el coeficiente *k* de descomposición (P = 1,01; C = 1,01; BS = 1,0; y I = 0,99) no varió entre tratamientos (p = 0,194) o sitios (p = 0,095). Considerando que la descomposición es fuertemente condicionada por la precipitación, es importante mencionar que el área de estudio sufrió efectos del fenómeno metereólogico *El Niño* y las lluvias fueron inferiores al esperado para ese período (IMN 2009).

A su vez, la tasa de descomposición (k_L) de Olson (1963) estimada para el año fue diferente entre los tratamientos (F = 8,65; p = 0,0025). El bosque secundario presentó un valor estadísticamente superior (1,2) a los otros tratamientos (P = 0,64; I = 0,67; C = 0,4), indicando una tasa de descomposición anual más rápida. El bosque secundario fue el único tratamiento con un valor de producción anual de hojarasca superior al almacenamiento sobre el suelo (k_L > 1; Figura 14).

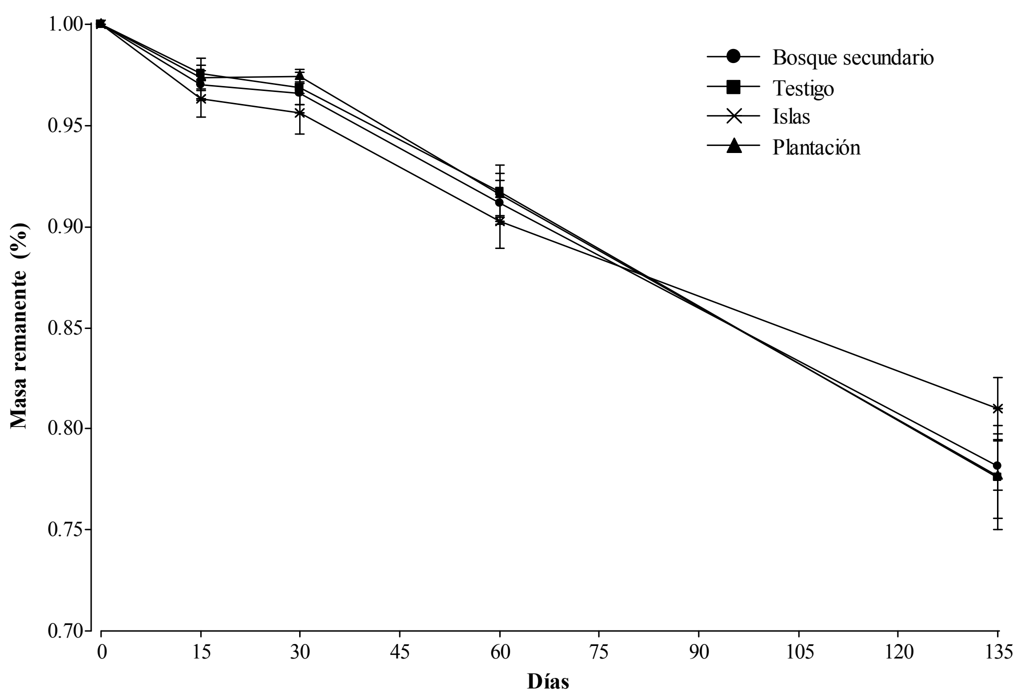

Figura 15. Curva de descomposición (pérdida de peso) en los diferentes tratamientos de restauración (Plantación, Islas, Control y Bosque Secundario) en Coto Brus, Costa Rica.

4.12 Discusión

Entender la dinámica de la producción, acumulación y descomposición de la hojarasca es importante para evaluar el papel de diferentes estrategias de restauración ecológica en el restablecimiento de los ciclos de nutrientes y en el balance de carbono. Las plantaciones presentaron la mayor producción de hojarasca y carbono entre los tratamientos de restauración, siendo similar a los bosques secundarios jóvenes. Las plantaciones de cinco años muestran el potencial para recuperar la función de producción de hojarasca rápidamente en comparación con áreas de regeneración natural y pueden proporcionar algunos de los mismos servicios ecosistémicos que los bosques secundarios más diversos (*i.e.* protección del suelo, almacenamiento de carbono). No obstante, aunque la función de producción pueda ser recuperada rápidamente, es importante destacar que la calidad de la hojarasca en las parcelas, medida por la concentración de nutrientes y proporción entre carbono y nutrientes, es más alta en los bosques secundarios y eso esta correlacionado a una mayor diversidad de especies (Celentano *et al.,* en preparación); resultados similares fueron encontrados por Lugo (1992).

La calidad de la hojarasca influencia fuertemente la tasa de descomposición (Zou *et al.* 1995), afectando la disponibilidad de nutrientes y el proceso de sucesión (Vitousek y Walter 1989). La hojarasca de baja calidad (baja concentración de nutrientes y altos ratios de carbono: nutrientes) retrasa la descomposición y los procesos de mineralización (Wardle y Peltzer 2007) y puede afectar a la restauración. La acumulación de hojarasca sobre el suelo es regulada por la producción y la descomposición. Las plantaciones presentan mayor acumulación de hojarasca que los otros tratamientos. Además, la cantidad acumulada es mayor que la producción anual en todos los tratamientos, con excepción del bosque secundario, indicando una baja tasa de descomposición. La tasa de descomposición en ecosistemas tropicales es generalmente > 2 (Olson 1963); nuestros resultados indican un estado alto de degradación en los sitios y la reducida presencia de las comunidades descomponedoras. Con el tiempo de sucesión, la tasa de descomposición tiende a aumentar y la hojarasca acumulada en el suelo disminuir (Ewel 1976). De acuerdo con el método propuesto por Olson (1963), los bosques secundarios presentan mayores tasas de descomposición.

La velocidad de descomposición es regulada por las condiciones climáticas (temperatura y precipitaciones; Meentemeyer 1977), por la composición de la comunidad descomponedora (Schroth 2003) y por la calidad de la hojarasca (Xuluc-Tolosa *et al.* 2003).

Esos factores pueden justificar por qué no se identificaron diferencias entre los tratamientos en el ensayo con bolsas de descomposición utilizando hojas de *Inga edulis*: (1) el corto tiempo de las bolsas en el campo (135 días); (2) la reducida precipitación en el área de estudio durante el experimento debido al fenómeno climático *El Niño* (IMN 2009); y (3) la calidad de la hojarasca explica más variabilidad en la tasa de descomposición que las variables ambiental. Estudios adicionales de más largo plazo y con diferentes calidades de hojarasca son necesarios para una mejor comprensión de este proceso en los sitios de restauración.

Las especies introducidas en proyectos de restauración activa juegan un papel muy importante en el restablecimiento de los procesos ecológicos. La selección de especies influencia en la tasa y ritmo de crecimiento, la producción de hojarasca y el retorno de nutrientes para el suelo (Cuevas y Lugo 1998), y los subsecuentes procesos de restauración. Entre las especies introducidas en los tratamientos de restauración, *Inga edulis* domina el aporte de hojarasca al suelo (70% en las plantaciones).

Inga crece rápido y promueve la supresión de gramíneas agresivas (Holl *et al. in press*), atrae aves (Fink *et al*. 2009), produce mucha hojarasca que proporciona protección del suelo, aumento de la disponibilidad de nutrientes y beneficia el crecimiento de las especies maderables (Nichols *et al.* 2001, Nichols y Carpenter 2006). Sin embargo, las hojas de *Inga* tienen una elevada fracción recalcitrante y baja tasa relativa de descomposición (Leblanc *et al.* 2006); produciendo un mantillo muy espeso en el suelo (3,7 cm en las plantaciones). Por un lado, eso es bueno porque promueve una protección del suelo deseable en áreas de pendientes, formación de humus estable y potencial secuestro de carbono en el suelo a largo plazo (Leblanc *et al.* 2006). Por otro lado, esas características pueden ser indeseables para la restauración de la biodiversidad. Un mantillo de hojarasca gruesa obstruye el acceso de semillas al suelo, representa una barrera física para la emergencia de especies con semillas pequeñas, modifica las condiciones micro-ambientales promoviendo o inhibiendo la germinación y el establecimiento de plántulas (Molofsky y Augspurger 1992, Carson y Peterson 1990).

Esa hipótesis de *trade-off* entre carbono de la hojarasca y biodiversidad potencial (mayor almacenamiento de carbono de la hojarasca promueve menor biodiversidad) podrá ser comprobada o no para el corto plazo a través de la comparación entre los estudios de lluvia de semillas (Cole *et al. in press*) y establecimiento de plantas nativas que se llevan a cabo en las parcelas de restauración. Será importante verificar si existe el *trade-off* y su temporalidad, quizás a largo plazo el sistema es beneficiado con suelos más fértiles. Eso será importante para establecer recomendaciones y guiar otros proyectos de restauración en los trópicos, especialmente en ese momento donde hay un creciente interes en el carbono forestal para la mitigación del cambio climático.

Áreas en restauración ecológica secuestran carbono de la atmósfera en los diferentes reservorios (biomasa aérea, biomasa subterránea, madera muerta, hojarasca y suelo). Cuantificar el secuestro de carbono en diferentes estrategias de restauración ecológica y compararlas con áreas en regeneración natural (línea base) representa una oportunidad para promover esa actividad frente a los crecientes mercados de carbono. Este estudio permitió verificar que la hojarasca del suelo representa un almacén de carbono que crece rápidamente durante los primeros años del proceso de restauración. No obstante, cinco años no fueron suficientes para detectar efectos de los tratamientos en el contenido de carbono del suelo. Otra constatación importante de ese estudio fue la alta variabilidad entre los sitios en el aporte y el almacenamiento de hojarasca y carbono. Eso evidencia el peligro de generalizar o extrapolar resultados de estrategias de restauración.

4.13 Conclusión

Las estrategias de restauración activas estudiadas (plantación homogénea y en islas) aceleraron la función de producción de hojarasca y almacenamiento de carbono en comparación con las áreas en regeneración natural, siendo las plantaciones similares a los bosques secundarios más diversos. No obstante, eso no implica en el restablecimiento del ciclo de nutrientes bajo esos tratamientos, pues la elevada acumulación de hojarasca sobre el suelo indica baja calidad de la hojarasca, baja tasa de descomposición y el estado de degradación. Además, el grueso mantillo de hojarasca de las plantaciones pode afectar negativamente los procesos subsecuentes de la sucesión. Con el tiempo de sucesión, se espera que la tasa de descomposición aumente y la hojarasca acumulada en el suelo disminuya. Los resultados de ese estudio identifican las condiciones de sitio como un factor importante para determinar la producción y acumulación de hojarasca y carbono.

4.14 Agradecimiento

El proyecto de restauración en Costa Rica es financiado por la Fundación Nacional de Ciencias de los E.E.U.U. (NSF; DEB 05-15577 para K. D. Holl y R. Zahawi) y la Fundación Earthwatch. Este estudio tiene apoyo financiero de ITTO (International Tropical Timber Organization), WCS (Wildlife Conservation Society) a través del Programa de Liderazgo en Conservación (CLP) y TNC (The Nature Conservancy) a través de la Organización para Estudios Tropicales (OET). Danielle Celentano es becaria de la Organización de los Estados Americanos (OEA). Somos muy agradecidos por el apoyo de Juan Abel Rosales y Roman Gomez Meza en el campo y Esthefanie Daniela Rodríguez en el laboratorio. Además, agradecemos el importante soporte de Darryl Cole y Diego Delgado con logística, Fernando Casanoves con estadística, Gabriela Soto y Guillaume Rousseau con suelos, y Adriana Arciniegas con las correcciones del español. Finalmente, agradecemos a los finqueros en Coto Brus que permitieron el proyecto de restauración en sus tierras.

4.15 Literatura consultada

Aronson, J.; Milton, S; and Blignaut, J.N. (Editors). 2007. Restoring Natural Capital: Science, Business, and Practice. Society for Ecological Restoration International and Island Press.

AOAC. Association of Official Agricultural Chemists. 1984. Official methods of analysis. 14th Ed.: USA, Association of Official Agricultural Chemists Inc. 40p.

Bocock; K.L.; y Gilbert; O.J.W. 1957. The disappearance of leaf litter under different woodland conditions. Plant and Soil 9: 197-185.

Bradshaw, A.D. 1987. Restoration: an acid test for ecology. In: Jordan, W.R.; Gilpin, M.E.; and Aber J.E. (Eds.) Restoration ecology. A synthetic approach to ecological research. Cambridge University Press. Cambridge, England.

Carson, W.P.; and Peterson, C. J. 1990. The role of litter in an old-field community: Impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85: 8-13.

Celentano, D.; Zahawi, R.A.; Finegan, B.; Ostertag, R.; Cole, R.; and Holl, K. Litterfall Dynamics and Nutrient Cycling in Different Tropical Forest Restoration Strategies. *En preparación* para Biotropica.

Céspedes, M.V.; Finegan, B.; Herrera, B.; Delgado, L.D.; Velásquez, S.; y Campos, J.J. 2008. Diseño de una red ecológica de conservación entre la Reserva de Biosfera La Amistad y las areas protegidas del Área de Conservación Osa, Costa Rica. Recursos Naturales y Ambiente 54: 44-50.

Chazdon, R.L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320: 1458-1460.

Clark, D.A.; Brown, S.; Kicklighter, D.W.; Chambers, J.Q.; Thomlinson, J.R.; Ni, J.; and Holland, E. A.. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications 11:371-389.

Cole, R. J.; Holl, K. D.; and Zahawi, R. A. In press. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecological Applications.

Cuevas, E.; and A. E. Lugo. 1998. Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. Forest Ecology and Management 112:263-279.

Daily, G.C.; Ehrlich, P.R.; and Sanchez-Azofeifa, G.A. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica Ecological Applications 11: 1–13.

Díaz, R.; and Hunter, A. 1978. Metodología de muestreo de suelos, análisis químico de suelos y tejido vegetal e investigación en invernadero. Turrialba, CATIE.

Ewel, J. J. 1976. Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. J. Ecol. 64: 293-308.

FAO 2006. Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management, FAO Forestry Paper 147. Food and Agriculture Organization of the United Nations, Rome. Available on the Internet www.fao.org/forestry/fo/fra/index/jsp.

Fink, R.D.; Lindell, C.A.; Morrison, E.B.; Zahawi, R.A.; and Holl, K.D. 2009. Patch size and tree species influence the number and duration of bird visits in forest restoration plots in Southern Costa Rica. Restoration Ecology 17: 479-488.

Holdridge, L. R., Grenke, W. G., Haheway, W. H., Liang, T, and Tosi, J. J. A. 1975 Forest environments in tropical life zones. New York, NY: Pergamon Press.

Holl, K. D.; and Howarth, R. B. 2000. Paying for restoration. Restoration Ecology 8: 260-267.

Holl, K. D. 2002. Tropical moist forest restoration. In Perrow, M.R.; and Davy, A.J. (Eds.). Handbook of Ecological Restoration, vol. II. Cambridge University Press: Cambridge. pp.539-558.

Holl, K.D.; Zahawi, R.; Cole, R. J.; Ostertag, R.; and Cordell, S. In press. Planting seedlings in plantations versus tree islands as a large-scale tropical forest restoration strategy. Restoration Ecology.

IMN. 2009. Instituto Meteorológico Nacional de Costa Rica. Sequia Metereologica debido a El Niño. COENOS - Boletín Enos #25 Avaiable at: http://www.imn.ac.cr/publicaciones/enos/B-ENOS252009.pdf

InfoStat. 2009. InfoStat Versión 2009. Grupo Infostat, FCA, Universidad Nacional de Córdoba, Argentina.

ITTO and IUCN. 2005. Restoring forest landscapes: An introduction to the art and science of forest landscape restoration. Technical Series No 23. Yokohama: ITTO.

Lamb, D.; Erskine, P.D.; and Parrotta, J.A. 2005. Restoration of degraded tropical forest landscapes. Science 310:1628-1632.

Lamb, D.; and Gilmour, D. 2003. Issues in forest conservation. Rehabilitation and restoration of degraded forests. International Union for Conservation of Nature and Natural Resources (IUCN) and The World Wide Fund for Nature (WWF). 122p.

Leblanc, H.A.; Nygren, P.; and McGraw, R.L. 2006. Green mulch decomposition and nitrogen release from leaves of two Inga spp. in an organic alley-cropping practice in the humid tropics. Soil Biology & Biochemistry: 349-358.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs 62:1-41.

Mansourian, S.; Vallauri, D.; and Dudley, N. (Eds.). 2005. Forest Restoration in Landscapes: Beyond Planting Trees. Springer, New York, NY. 437

MEA. Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, DC., U.S.A.

Meentemeyer V. 1977. Climatic regulation of decomposition rates of organic matter in terrestrial ecosystems. In: Adriano D.C., Brisbin I.L. (Eds) Environmental chemistry and cycling proces-ses. United States Department of Energy Symposium Series. Washington DC, pp 779-789

Molofsky, J.; and Augspurger, C. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73: 68-77.

Nepstad, D; Uhl, C; Pereira, C.A; and da Silva, J.M.C. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76: 25-39.

Nichols, J. D.; Rosemeyer, M. E.; Carpenter, F. L.; and Kettler, J. 2001. Intercropping legume trees with native timber trees rapidly restores cover to eroded tropical pasture without fertilization. Forest Ecology and Management 152:195-209.

Nichols, J.D.; and Carpenter, F.L. 2006. Interplanting *Inga edulis* with *Terminalia amazonia* yields nitrogen benefits to the timber tree. Forest Ecology and Management 233: 344-351

Oelbermann, M., and A. M. Gordon. 2000. Quantity and quality of autumnal litterfall into a rehabilitated agricultural stream. J. Environ. Qual. 29: 603-611.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322-331.

Ostertag, R., E. Marin-Spiotta, W. L. Silver, and J. Schulten. 2008. Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. Ecosystems 11: 701-714.

Prach, K; Marrs, R; Pysek, P; and van Diggelen, R. 2007. Manipulation of succession. In Walker, L. R.; Walker, J.; Hobbs, R. J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.121-149.

Pearson,T.; Walker, S.; and Brown, S. 2005. Sourcebook for land use, land-use change and forestry projects. Winrock International. 64p.

R. 2009. R version 2.7.2. The R Foundation for Statistical Computing. Disponible en www.r-project.org/

Reay, S.D.; and Norton, D.A. 1999. Assessing the success of restoration plantings in a temperate New Zealand forest. Restoration Ecology 7: 298-308.

Rickert, E. 2005. Environmental effects of the coffee crisis: a case study of land use and avian communities in Agua Buena, Costa Rica. *Msc. thesis*. Evergreen State College, Olympia, Washington, D.C.

Scherer-Lorenzen, M., J. L. Bonilla, and C. Potvin. 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116: 2108-2124.

Schrautzer; J.; Rinker, A.; Jensen, K.; Muller, F.; Schwartze, P.; and DierBen, C. 2007. Succession and restoration of drained fens: perspectives from northwestern Europe. In Walker, L. R.; Walker, J.; Hobbs, R. J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.90-120.

Schroth, G. 2003. Decomposition and nutrient supply from biomass. *In*: Schroth, G.; and Sinclair, F.L. (Eds.). Trees, Crops and Soil Fertility: Concepts and Research Methods. CAB International, Wallingford, UK.

SER. 2004. Society for Ecological Restoration International. 2004. The Primer on ecological restoration. Science and Policy Working Group. Avaiable at www.ser.org

Uhl, C.; Buschbacher, R.; and Serrao, E.A.S. 1988. Abandoned pastures in eastern Amazonia. Patterns of plant succession. Journal of Ecology 75: 663-681.

Upadhyay V.P., Pandey, U., Singh, J.S. 1985 Effect of habitat on decom- position of standard leaf litter species. Biol Fertil Soils 1:201-207

Vitousek, P.M.; and Sanford, R.L. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137-167.

Vitousek, P.M.; and Walter, L.R. 1989. Biological invention of *Myrica faya* in Hawaii: plant demography, nitrogen fixation and ecosystem effects. Ecological Monographs 59: 247-265.

Walker, J.; and Reddel, P. 2007. Retrogressive succession and restoration on old landscapes. In Walker, L. R.; Walker, J.; Hobbs, R. J. (Eds.). Linking Restoration and Ecological Succession. Springer Series on Environmental Management. p.1-16.

Wardle, D. A., K. I. Bonner, and K. S. Nicholson. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness affects ecosystem function. Oikos 79: 247-258.

Wardle, D.A.; and Peltzer, D.A. 2007. Aboveground-belowground linkages, ecosystem development, and ecosystem restoration. In Walker, L. R.; Walker, J.; and Hobbs, R. J. (Eds.). Linking restoration and ecological succession. Springer Series on Environmental Management. pp.45-68.

Xuluc-Tolosa, F. J.; Vester, H. F. M.; Ramirez-Marcial, N.; Castellanos-Albores, J.; and Lawrence, D. 2003. Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. Forest Ecology and Management 174: 401-412

Yarranton, G. A.; and Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. Journal of Ecology 62: 417-428.

Zou, X.; Zucca, C.P.; Waide, R.B.; and McDowell, W.H.. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. Forest Ecology and Management 78: 147-157.