Plant traits and litter decomposition of tree species naturally regenerating in Central America pasturelands

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Plant traits and litter decomposition of tree species naturally regenerating in Central America pasturelands

by

M. JIMENA ESQUIVEL SHEIK

A thesis submitted to the joint program for the degree of Doctor of the Philosophy

Doctoral advisory committee:

PhD. Bryan Finegan
PhD. John Healey
PhD. Fernando Casanoves
PhD. Andreas Nieuwenhuyse

Graduate School, Tropical Agricultural Research and Higher Education Center (CATIE), Turrialba, Costa Rica

School of Environment, Natural Resources and Geography, Bangor University (BU), United Kingdom

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DEDICATION

To my parents; Carlos and Nohemy,

Who are exceptional parents and supported me with their time and love in every new step of life.

To my daughter and husband; Sofia and Raffaele,

Who are both my daily fairy, for them altruistic patience to let mum think in trees for so much time.

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CONTENTS

SUMMARY

This research uses three consecutive approaches to evaluate the links among morphological diversity and ecosystem processes of 65 tree species commonly found in Central American active pasturelands (AP) under conventional management practices. Firstly, we explore tree morphological diversity measuring 17 plant traits (PT) to describe the functional strategies (FS) of tree species in agricultural lands. Secondly, we explore tree responses to anthropogenic disturbances like conventional pasture management testing the relationships of tree morphological diversity with tree abundances and exploring their relative utility to predict tree natural regeneration capacity (CNR) in agricultural lands. Thirdly, we test whether tree species variability in litter quality, decomposition rates and nutrient releases was related with tree morphological diversity and tree abundances to explore the effects of tree characteristics on litter decomposition. This approximation allows exploring for the first time the effects of tree variability on ecosystems processes in anthropogenic environments and the possible effects of actual management over today and future provision of ecosystem services (ES) such as soil fertility replenishment and nutrient cycling offered by trees outside the remnant tropical forests.

Tree functional strategies (TFS) were described as particular combination of PTs strongly related to four main trait dimensions i.e. Leaf Economy Spectrum (LES), stem density, canopy height and reproductive variability spectrums. Measured leaf traits were leaf area, specific leaf area, leaf dry matter content, total carbon, phosphorus and nitrogen leaf content, foliar tensile strength. Whole plant traits included wood density, maximum tree hight and leaf phenology while measured tree reproductive traits were fruit and seed mass, volume, shape and dispersal mode. Tree abundances at three different developmental stages were surveyed once for 76 tree species in nested plots on 46 APs: adult tree (dbh ≥ 10 cm) in one hectare plot, saplings (dbh ≤ 10 but more than 30 cm height) and seedlings (lower than 30 cm height). A decomposition experiment with litterbags under standard environmental conditions (temperature and humidity) was established during four months for litter of 37 tree species to obtain overall (B5), partial (B4) and monthly litter decay rates (b1, b2, b3, b4). Total macronutrients (C, P, N) and C fractions contents (SOL, HEM, CELL and LIG) were measured on fresh and decomposed litter to measure the percentage of nutrient released during litterbags incubation.

Multidimensional relationships among PTs were analyzed using principal components analyses (PCA). Paired relationships among PTs, tree abundances, litter quality, decomposition rates and nutrient releases were analyzed using Spearman Correlation Analyses (CA) for quantitative variables and Logistic Regressions (LoRe) for categorical ones. PT and tree abundances capacity to predict tree natural regeneration was addressed using Multiple Regressions (MR) with Stepwise elimination method.

We found that tree species in APs have wide variability of leaf, reproductive and whole plant traits with leaf variability strongly associated with other plant traits dimensions. LES (conservative vs acquisitive) is strongly correlated with the Stem and Phenology Spectrum (SPS). A novel Reproductive Investment Spectrum (RIS) splitting apart tree species with bigger and heavier fruits and seeds from those with small and lighter ones (expensive vs cheap), was correlated to both LES and SPS. Resulting holistic plant

trait associations were complex showing five main ordination axes explaining between 10 to 20% of tree species variability, without showing any tendency to form tightly-defined "functional groups". Resulted dispersal modes provided good examples of tree strategies that split species' traits variability with particular combinations of whole plant, leaf and reproductive traits.

All PTs are correlated with both tree species abundances and CNR in APs. Some successful PTs at seedlings and saplings stages were different from successful PTs in adult tree cover. Species with denser woods, P rich leaves and expensive seeds have more sapling abundances meanwhile species with C and N rich leaves have more abundant seedlings. Tree species dispersed by cattle were abundant as seedlings and saplings while those dispersed by local fauna were limited in all developmental stages. Adult tree abundances were strongest predictors of tree seedlings and saplings abundances in AP and together with PTs explain a higher proportion of species abundance variability (60 - 67%).

We expand actual knowledge of the afterlife effect of leaf traits to decomposition dynamics, carbon and nutrient cycling stating that tree species with acquisitive leaves decompose faster and release more N, P, C , SOL and HEM than more conservative species. In addition to leaf traits, also stem and reproductive traits are related with differences in litter quality, decomposition rates and macronutrients releases during decomposition, thus linking the afterlife effect of leaf traits directly with tree natural regeneration capacity.

The multidimensional FS observed in APs suggest that loss of any particular tree characteristic could affect different ES offered by actual tree cover remaining in tropical agricultural lands. The significant relationships among PTs and tree abundances show that some PTs favor tree CNR after land use change meanwhile other PTs are associated to species with limited CNR. The significant relationships we found among decomposition rates with PTs and CNR suggest that more abundant trees tend to have faster decomposition rates while less abundant tree species tend to present slow leaf-decomposition rates.

These findings indicate that plant characteristics and tree natural regeneration are linked with ecosystem processes such as litter decomposition which has direct implications for important sustainability factors in agricultural systems such as nutrient and carbon cycling. Actual tree functional diversity and the capacity to provide ES under current management practices in APs will possibly decrease as a consequence of loss of some trees with particular PTs and the limited CNR. Conventional pastures management (i.e. reduction of tree cover) will probably reduce future tree cover diversity by eliminating those species which cannot naturally regenerate in active pastures, slowing tree litter decomposition rates and reducing the rates of nutrient releases, with impacts on actual and future capacity to provide these ecosystem services.

This link between plant characteristics and ecosystem processes is particularly important to improve actual management practices aiming to promote the sustainability of agro ecosystems. This is especially relevant for the management of highly-diverse tropical lands where the effects of forest fragmentation by land use change to agricultural systems on ecosystem services has been understudied.

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Hmax	Adult plant stature
WD	Wood density
PHE	Leaf phenology
SLA	Specific Leaf Area
LA	Leaf size
LDMC	Leaf Dry matter content
LCC	Leaf total carbon content
LNC	Leaf Nitrogen concentration
LPC	Leaf Phosphorus concentration
FTF	Physical strength of leaves
Sha_fru	Fruit shape
Sha_see	Seed shape
Mas_fru	Fruits mass
Mas_see	Seed mass
Vol_fru	Fruits volume
Vol_see	Seed volume
Dis_mod	Dispersal mode
SOL	Soluble carbon
HEM	Hemicellulloce
CEL	Cellullose
LIG	Lignin
BETA 5	Overall decomposition rates
BETA 4	Partial decomposition rates
$\mathbf{b_n}$	Monthly decomposition rates
CA	Correlation analyses
PCA	Principal Component analyses
MRA	Multiple Regression analyses
LoRe	Logistic Regression analyses
r	Correlation coefficient
$\mathbf{r^2}$	Regression coeficients
Dbh	diameter breast height
PAI	Periodic annual increments
RGR	Relative growth rate
AIC	Akaike information criterion
BIC	Bayesian information criterion
DGC	Díaz, Guzman and Cassanoves mean comparison test
PT	Plant traits
AP	Active pasturelands
CNR	Capacity of natural regeneration

CHAPTER 1. GENERAL INTRODUCTION

1.1 Background statement

Pasture degradation is a major problem related to land use in Central America (Szott et al. 2000). Frequently, a gradual decline in forage yield occurs some years after the establishment of pastures usually associated with a decrease in soil fertility. Pasture degradation begins mainly due to poor fertility management in addition to tree cover elimination in previously forested sites, forcing farmers to undertake a costly renewal of pastures, or driving them to abandon pastures and to open new forest areas (Toledo et al. 1982, Fearnside and Barbosa 1998). Non-sustainable livestock management practices reduce the ability of anthropogenic pasturelands ecosystems to provide supporting ecosystem services like the capacity to maintain soil structure and fertility through decomposition of plant litter and animal wastes and also the regulating services of purifying water, as well as the provisioning of food (Milchaunas & Lauenroth 1993, Tilman 1999, Tilman et al. 2002). Extensive livestock production systems including practices like large paddock areas, low grazing rotation, overgrazing, chemical weeding and no fertilization strategies are widely distributed in Neotropical landscapes. Today, it is estimated that 50% of the Central America pastures suffer from some kind of degradation (PD/CATIE-Noruega 2002).

Silvopastoral systems (SPS) have been proposed as sustainable production systems to avoid tropical pasture degradation and increase system productivity. Nitrogen fixation by some leguminous and non-leguminous species could maintain and even improve nitrogen availability through decomposition of shoot litter and roots. Also organic matter input from litter and root turnover from all tree species can play an important role in maintenance of soil physical and chemical properties (Velasco et al. 1999). However, below-ground competition between trees and understory plants for soil moisture and nutrients may reduce the amount of soil nutrients and water available to the herbaceous layer. Competition for light, water and nutrients may affect pasture productivity under and close to trees. In contrast to simpler grass monocultures systems in seasonally dry climates where the productivity strongly decreases during the dry season, the presence of trees in pasturelands can enhance overall pasture productivity during the dry seasons providing nutrition for livestock from tree leaves, fruits and pods in the dry season (Cannell 1996, Rhoades 1997, Cajas-Giron and Sinclair 2001). However research has not so far been able to describe the full set of ecological interactions developed between a diverse tree cover and grass productivity.

Tree cover can reduce pasture degradation and speeds up its recovery through nutrient supply in litter deposition (Young 1989). This hypothesis arises from differences in grass productivity observed between below-crown and open grassland habitats. Such differences has been attributed primarily to a) improved fertility and structure of soils below tree crowns and b) improved water relations of shaded plants (Kellman 1979, Belsky 1992, Belsky 1994, Rhoades et al. 2000). Soils under trees have been observed to have higher level of organic matter, N, Ca, C and K, higher microbial biomass, reduced bulk density and increase water infiltration than open pastureland soils, so called "islands of fertility" below tree crowns (Belsky 1994). In addition, reductions of water loss under tree crowns due to reduction of light intensity reaching the soil layers and its effects on soil and air temperature can sometimes improve below-grown plant relations (Rhoades et al. 1998, Belsky et al. 1989, 1992).

Little is known about the mechanisms responsible for the observed spatial fertility patterns around trees in pasturelands. Higher values of animal manure deposition (wild fauna and cattle), wind deposition of plant material (litter and fruits), soil fauna density, dead root biomass and soil nitrification rates are mechanisms identified as responsible for such contrasting patterns below tree crowns and open pasturelands (Belsky 1994). Patterns of decomposition of the high amount of organic matter deposited around trees however have not been well studied. Litter is the major sink of nutrients and carbon within plants and its decomposition is the mayor source of soil fertility replenishment in diverse soils (Cadisch & Giller 1997). Decomposition patterns are fundamental for understanding C and nutrient fluxes within ecosystems (Blanco et al 2004). Litter quality is determined by its composition and physical characteristics; together with climate, soil nutrient availability, soil biotic communities and other site specific factors it controls the decomposition processes (Berg and McClaugherty 2003). Therefore, in addition to observing the variability of temperature, water, nutrients and SOM concentration around trees, it is necessary to evaluate how plant litter decomposition develops within active pastureland environments to clarify the mechanisms involved in the creation and maintenance of "fertility islands" and their potential benefits to pasture productivity.

There has been a major debate in the ecological literature about the relationship between species diversity and ecosystem function, and therefore whether loss of species diversity threatens productivity and sustainability (Grime 1998, Loreau et al. 2001). Lower leaching losses of inorganic nitrogen (leading to higher soil fertility) and higher biomass have been reported in North American pasture ecosystems with a greater diversity of species (Tilman et al. 1996, Collins et al 2012). Tree species composition in addition could affect nutrient cycling and productivity in active pasturelands. For example, in Central America, under crowns of nitrogen-fixing *Inga* spp. in situ net nitrification rate exceeded that in open-pasture more than six-fold and extractable NO_3--N concentration was 3.6 times higher than in open pasture (6.3 versus 1.7 mg N/g), while beneath non-nitrogen-fixing *Psidium* spp., neither nitrification rates nor the extractable NO_3--N pool were significantly greater than in open pasture (Rhoades 1997). However until today, the effect of a wider variety of tree species usually found in agricultural landscapes, on nutrient cycling and productivity in anthropogenic Neotropical pasturelands remains unknown

Intrinsic litter characteristics significantly influence the decomposition rates (Berg et al. 1999). Trees in active pasturelands have different functional characteristics, e.g. leaf traits, and flowering and foliar phenology, which could make different contributions to nutrient cycling, via litter quality, quantity and timing, or creating diverse microsites for the decomposition process in pastures. Different traits affect the regeneration capacities of trees in grazed or active pasturelands, e.g. those linked to seed dispersal mechanism and germination including seed mass. In managed pastures tree wood density can be important as, along with use value for wood products, fruit, forage or shade, it could affect farmer's decisions to maintain different tree species on these sites. Therefore, identifying both the functional characteristics of tree species in relation to litter quality and nutrient release during litter decomposition, and the regeneration and utility characteristics that determine whether trees are maintained or not in pastures, is vital for understanding how the species composition of tree cover changes and its potential impact on pasture productivity via litter input and decomposition. However, tree species effects on litter input, decomposition, soil fertility and pasture biomass have not previously been researched using either an isolated or pastureland approach to understand their effects on pasturelands productivity. Whether other plant functional traits are associated with those affecting leaf litter quality traits will define current and predicted future overall functional diversity of tree covering agricultural lands and therefore the direction, magnitude and continuity of its effects.

Tree cover diversity in Central American pastures will decrease at least 50% if current management practices are maintained (Esquivel et al 2008). Trees in active pasturelands result from both regeneration of pioneer species and survival of remaining trees from the original forest vegetation. Remnant tree density and diversity could be high in Central America pasturelands (Harvey et al. 2000). However, at least 50% of the tree species in active pasturelands have limited potential for natural regeneration due to limitations to seed dispersal, germination and establishment, or due to pasture management (Esquivel et al 2008). Management practices which do not specifically consider the protection of populations of tree species with limited natural regeneration in pastures are widespread in Central America (Camargo et al. 1999, Barrios 1999, Matinez-Garza & Howe 2003). The expected reduction in tree cover species diversity within these areas could have effects on pastureland productivity and sustainability due to changes in nutrient cycling resulting from loss of tree species with particular functional attributes. However, we still have little knowledge on how tree species affects nutrient cycling in Neotropical anthropogenic pasturelands. Development of silvopastoral systems must therefore take into consideration the different functional characteristics of tree composition and it effects over ecosystem processes like tree regeneration and nutrient cycling in order to propose strategies to recover degraded pasturelands in Central America.

1.2 Aims and context of the research project

This PhD research project was developed with the upport of the project *"Alternatives for the Use of Degraded Pastures in Central America – Degraded Pasturelands" – PD CATIE-NORWAY.* The PhD is focused on tree species functional characteristics and their relationship with ecosystem processes, including productivity and nutrient cycling, in pasture ecosystems in fragmented landscapes of the pilot areas of the project. This PhD focuses on producing high-quality scientific research, but also on providing key scientific support to the technical and participatory development of appropriate options for the use of local tree diversity to recover degraded pastures in areas characterized by chronic rural poverty. The focus of this research was within the broad set of research areas of interest defined by PD CATIE-NORWAY: 1) the characterization of nutrient stocks in different pasture ecosystem components (vegetation, fauna, soil and primary minerals) and the type and magnitude of flows between components; 2) estimation of pasture ecosystem productivity and the factors that limit it and 3) the relationship between the aforementioned ecosystem characteristics and processes and the plant taxonomic and functional diversity of pasture ecosystems, including comparative studies of alternatives to degradation such as grass/legume mixes, protein banks and both naturally and artificially regenerated silvopastoral systems.

The aim of this PhD was to contribute to understanding the role of the tree cover species composition in maintaining or improving soil fertility and pasture productivity in Central America. This study focused on the variability in leaf and litter quality, decomposition rates and nutrient cycling amongst the tree species present in managed pastures. It assessed the role of different leaf traits (physical structure and chemical composition) in determining rates of litter decomposition and nutrient release and how these leaf traits were linked to other whole plant and regeneration-related traits. To reach this general objective, the research encompasses observational, experimental and analytical approaches. First, a wide range of functional traits of tree species, not only those commonly related with litter quality, were used to identify tree species characteristics linked to their function within continually anthropogenic-disturbed pasturelands. Second, the relationship between these observed functional traits of the tree species and their population abundances (linked natural regeneration capacity) in active pasturelands, was evaluated to understand current and possible future changes of tree functional diversity in pasturelands, as well as which plant variables best predict such changes. Third, the effects of the aforementioned tree species composition of active pasturelands, was evaluated by quantifying the differences between species in decomposability and in nutrient release rates of their leaf litter (in an experiment with 37 tree species) and how this was correlated with their leaf traits, traits related to natural regeneration and their population structure. The species tested in this experiment included those with a wide range of functional traits.

Tree litter is an important resource in active pasturelands, and its study in the context of the functional characteristics and natural regeneration of the species that provide it may provide clues about the actual and future role of tree cover in nutrient cycling and its potential to recover degraded pasturelands. Assessing these processes and dynamics will hopefully allow the development of more sustainable pasture production systems under the changing scenarios of climate and land use in the tropics. Specifically it will provide powerful evidence with which to assess the functional impacts of the tree species diversity of managed pasture lands.

1.3 Study site

The study was conducted in the Río Grande de Matagalpa watershed in Central Nicaragua (12°31‟-13°20“N; 84°45‟-86°15“W). The area is located in the municipality of Muy Muy, at sites within an altitudinal range of 280 to 380 m. The predominant land-use is livestock farming with relatively homogeneous livestock management. Livestock production is generally extensive, with an average-stocking rate of 1 livestock unit ha^{-1} and pasture management consisting of rotational grazing, fence maintenance and weeding, either manually by chopping down weeds or recently by the use of herbicides. During the dry season, grazing frequency is irregular.

The natural vegetation of the region corresponds to a transitional tropical sub-humid forest (Holdridge 2000) with semi-deciduous vegetation, and is referred to as seasonally dry tropical forest (Bullock et al. 1995). The vegetation in the study is an assemblage of native and naturalized species including grasses, herbs and woody plants. The term semi-natural grassland is used herein to refer to a pastureland area covered by spontaneous vegetation that grows naturally after forest clearing or on fallow land and which is maintained by grazing management, including fencing and weed control. Semi-natural grasslands consist mostly of grass species of the genus *Paspalum*. Exotic grasses such as *Brachiaria* spp. and *Cynodon* spp., have been planted to increase pastures productivity.

Both naturalized and exotic pasturelands occur in association with scattered trees. Tree composition in active pasturelands is a mix between species of dry and sub-humid forest communities. Mimosaceae, Fabaceae, Caesalpiniaceae and Bignoniaceae are the most species-rich families (comprising ca. 31% of all species), while Sterculiaceae and Boraginaceae are the most abundant families (ca. 54% of all individuals). The highest importance values (mean of relative density, dominance and frequency) were for pioneer species, typical of disturbed areas, dispersed by cattle, wind and wild animals, and actively promoted by farmers for their use as fruits, timber and/or forage (Esquivel et al. 2008).

Geologically, the area consists of tertiary volcanic tuff, a type of pyroclastic rock. The tuff presents a clear stratification, including softer and harder layers. It is probable that many of the landscape undulations are associated with differences in the hardness of the rocks and their variable resistance to erosion. Furthermore, tectonic movements are likely to have influenced the landscape, especially in the transition to the higher mountainous landscape of the Muy Muy municipality. Tuff in the area seems to be relatively impermeable, which explains the limited infiltration of rainwater observed during the early rainy season, especially in flat areas. Even on slopes, there are extensive areas where drainage is limited during part of the rainy season. In flat and lownland ondulated areas, it is common to find soils with vertic properties: soils present wide cracks during the dry season and have prismatic structures, while on steeper slopes soils are more variable set or vertic and Inceptisoils can be founded (Andreas Nieuwenhuyse, pers. comm. 2007).

The topography of the study area is undulating, with slopes of 5-40%, and the dominant soil type in the study sites is a greyish to black coloured vertisol with high organic matter content in the upper horizons (5-8%), clayey subsoil, with a pH between 5.9 and 6.8 in the topsoil, and relatively poor in phosphorous (2-10 ppm). In most cases, the soil has limited drainage during the rainy season. Where the natural slope favours better drainage, browner colours are observed.

1.4 General Objectives

The general objective of this thesis is to evaluate the functional diversity of the tree species present in active pasturelands in central Nicaragua, to understand its relationships with the abundance of natural regeneration and how these changes could affect decomposition rates and nutrient release (specific objectives 1, 2 and 3).

Afurther general objective of the research project was to understand how the functional diversity and variability of tree cover affects nutrient cycling, grass productivity and grass and soil quality in active pasturelands in the central region of Nicaragua.However this further work is not reported here in the main body of this PhD.

The specific objectives of this thesis research reported here are decribed by chapter as follows:

1. Evaluate the functional diversity of the tree community in active pasturelands using whole plant, leaf and regenerative traits (Chapter 2).

2. Evaluate how the functional diversity of tree cover was related with the capacity of tree species to maintain their populations in active pasturelands through natural regeneration (Chapter 3).

3. Evaluate if the differences in decomposition rates and nutrient releases of tree species were related to their functional traits and their natural regeneration capacity (Chapter 4).

1.5 General Hypothesis

H1: The tree species present in active pasturelands encompasses diverse and linked whole-plant, leaf and reproductive traits, which together comprise a definable functional diversity of the tree community (Chapter 2).

H2: Tree species' capacity to naturally regenerate in active pasturelands is related to whole plant, leaf and reproductive functional traits, as well as to adult tree abundance (Chapter 3).

H3: Tree species present in managed pasture lands have different decomposition rates of leaf litter biomass and nutrients releases rates related with leaf, whole-plant traits and with species capacity to naturally regenerate in active pasturelands (Chapter 4).

The following diagram (**Figure 1.1**) explain the relationships among components of a Sylvopastoral System where grass and woody species are combined for livestock production within the framework of the three research chapters (grey lined squares) of this research. The scheme shows how the tree component of SPS adds new interactions (segmented arrows) to those usually identified by conventional livestock management systems (dark black arrows) among the grass component, and the cattle one affecting the soil resource extraction-replenishment loop which negatively affects forest and tree cover in agricultural lands. The thesis research chapters provide insights to understood some links of this system, more specifically: chapter 1) Understanding the wide variability of leaves, wood and fruits/seeds of the tree species in pastures; chapter 2) predicting the different capacities of tree species to naturally regenerate in active pasturelands using this variability together with adult tree abundances resulting from previous management practices; and Chapter 3) Understanding how this capacity can affect other ecological processes like decomposition rates and nutrient releases from tree litter , provides insights on possible functional changes in future tree cover. This is especially relevant if management practices imply the elimination of those tree species with limited natural regeneration and associated plant traits, thus affecting the provision of ecosystem services to livestock managements and to agricultural landscapes.

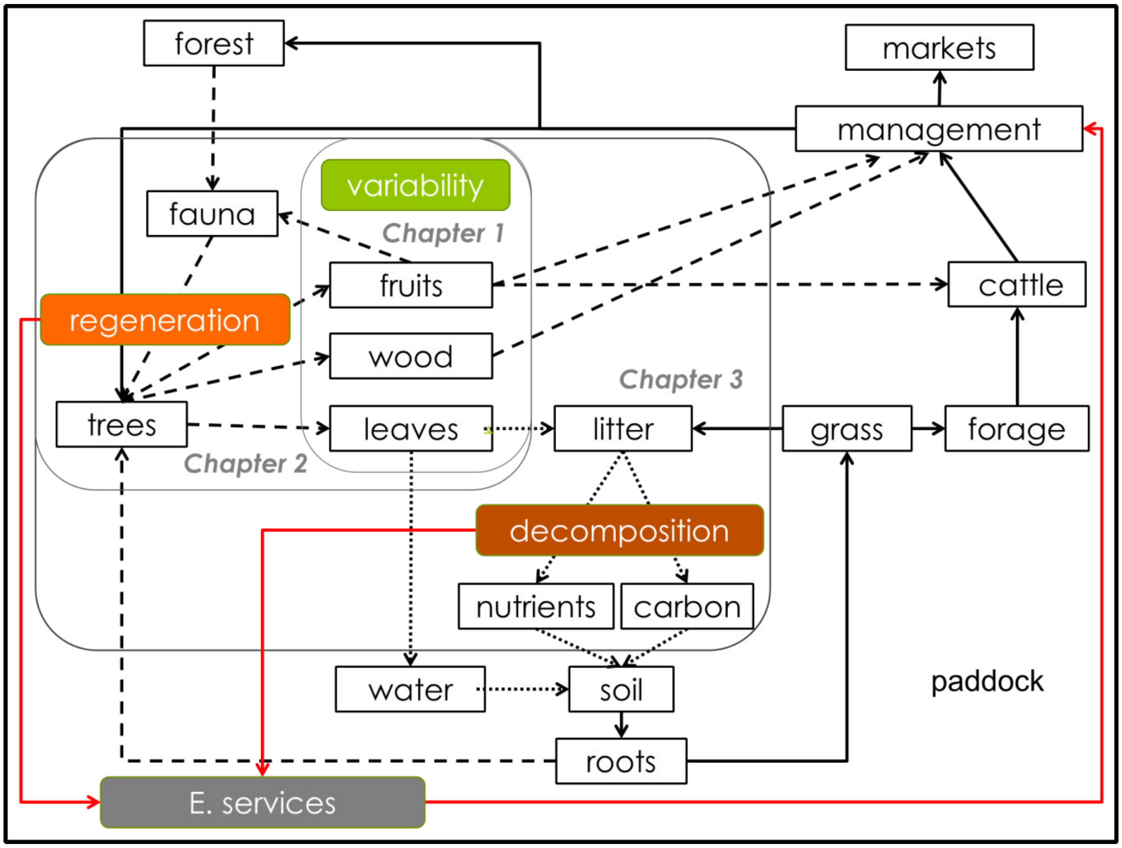

Figure 1.1. Diagram of the relationships among components of a Sylvopastoral System where grass and woody species are combined for livestock production within the framework of the three research chapters (grey lined squares)

CHAPTER 2. VEGETATIVE AND DISPERSAL FUNCTIONAL NICHES OF TREE SPECIES IN SEASONAL TROPICAL PASTURES

2.1 ABSTRACT

The identification of plant strategies outside pristine forest is relevant to improve our understanding of the functional variability of plant responses following deforestation and their effects on ecosystem processes after land use change to agricultural landscapes.

This research described the functional strategies (FS) of 65 tree species commonly found in Central American active pasturelands (AP) under conventional management practices (i.e. reducing tree cover), as particular combination of 17 plant traits strongly related to four main trait dimensions i.e. Leaf Economy Spectrum (LES), stem density, canopy height and reproductive variability spectrums. Measured leaf traits were leaf area, specific leaf area, leaf dry matter content, total carbon, phosphorus and nitrogen leaf content, foliar tensile strength; whole plant traits like wood density, maximum tree high, leaf phenology; and reproductive traits like fruit and seed mass, volume, shape and dispersal mode.

We confirm that LES (conservative vs acquisitive) is strongly correlated with a Stem and Phenology Spectrum (SPS), defining that taller deciduous tree species with softer woods have more fragile and acquisitive leaves than shorter evergreen trees with conservative leaves. A novel Reproductive Investment Spectrum (RIS) splitting apart tree species with bigger and heavier fruits and seeds from those with small and lighter ones (expensive vs cheap), was correlated to both the LES and SPS, showing i) tree species with acquisitive leaves and cheap constructed dispersules (Leaf and reproductive investment spectrum) and ii) taller deciduous trees with cheap dispersules (Stem and reproductive investment spectrum).

Five main ordination axes explain between 10 to 20% of tree species variability for all plant traits interactions, showing the complexity of holistic plant trait associations, without tendency to form tightly-defined “functional groups”. Dispersal modes resulted good examples of tree strategies that split species’ traits variability with particular combinations of whole plant, leaf and reproductive traits.

Tree species in APs have wide variability of leaf, reproductive and whole plant traits with leaf variability strongly associated with the other plant traits dimensions. The multidimensional FS observed in APs suggest that loss of any particular tree characteristic could affect different ecosystem services offered by actual tree cover remaining in tropical agricultural lands.

Key words: functional strategies, tree cover, plant traits, population dynamics, agricultural lands.

2.2 INTRODUCTION

Plant trait measurements have gained increasing attention worldwide during the last decade as an approach to summarize and generalize about plant species' ecology and to understand how ecosystems and their services will change in response to natural and anthropogenic disturbances. Plant functional traits are defined as morphological plant characteristics that are relatively easy and quick to quantify (soft traits) and strongly related to plant functions (hard traits) responsible for plant responses or effects at the ecosystem or biomes scale (Cornelissen 2003). Clearly expressed by Wright et al. (2007) the functional ecology approach analyzes the interspecific correlations (cross-species correlations) among plant traits which are expected to reflect 1) physical, physiological or developmental 'constraints' that limit the independent variation and evolution of the focal traits; and 2) the 'adaptive' outcome of natural selection favoring particular combinations of traits over others forming dimensions of ecological 'strategies'). Cross-species correlations are especially relevant for providing insights into life-history trade-offs that operate within and between environments, and thus also into phenomena such as niche differentiation and species coexistence (Westoby and Wright 2004).

A huge amount of morphological and physiological data coming from around the world has made it possible to increase our knowledge about at least the first three of four main axes describing ecological strategies of tree species: i) the leaf economic spectrum (LES) (Wright et al. 2004), ii) the wood economic spectrum (Chave et al. 2009, Baraloto et al. 2010), iii) seed and fruit size variability (Moles and Westoby 2006) and iv) adult stature as an independent axis of variation (Poorter et al. 2006). The LES shows a continuum of species varying among cheaply constructed leaf area but short-duration return on investment, to species with high leaf mass per area (LMA) or low specific leaf area (SLA) and long leaf lifespan, with higher nitrogen and phosphorus contents and faster gas exchange rates (Wright et al. 2004). Species variability in the 'wood economics spectrum' has been related to plant hydraulics: higher wood density appears to be correlated with smaller leaf and twig sizes, lower conductivity per unit cross-section of sapwood, smaller leaf area per unit of sapwood cross section, and lower vulnerability to embolism (Westoby and Wright 2004). In the seed and fruit size spectrum, species with larger seeds have lower seed number output per area of canopy but higher survival during seedling stages (Westoby et al. 2002). Finally, the maximum-height spectrum describes species trade-offs among mature height, growth rates and shade tolerance: taller trees are proposed to grow faster, have lower mortality rates and have low tolerance of shade (Poorter et al. 2003), however subsequent studies have found more complex relationships amongst these attributes (e.g. Easdale et al. 2007). These four strategy axes summarize a high proportion of ecological variability among forest tree species

A small proportion of studies have addressed how the four observed main axes of species variability interact amongst each other (Westoby 1998, Wright and Westoby 2004, Wright et al. 2007, Baraloto et al. 2010), in contrast to the huge proportion of traits-related studies exploring individual axes of variability as cited previously. Unfortunately, the structure of the interactions between the strategic dimensions of species variability have been explored using only one representative trait or "focal trait" (Westoby 1998) for each strategic component, usually wood density (WD), specific leaf area (SLA) and seed size (mass or volume) together with maximum tree height (Hmax) as an axis in itself. Initially, studies including only some "representative" traits proposed a leaf-height-seed (LHS) plant ecology strategy using SLA, Hmax and seed mass as main axes of species variability where the strategy of a species would be described by its position in the volume formed by the three axes (Westoby 1998). Research on interactions among ecological dimensions based on focal traits of tropical tree species suggested that the dimensions represented by SLA, seed/fruit size and leaf size were essentially independent of each other and thus conveyed largely independent information about plant strategies (Wright et al. 2007). Although the advantages of defining a plant ecology strategy through a single readily-measured variable are obvious, single plant traits are very unlikely to capture as much species variation as multi-trait axes (Westoby 1998).

The functional niche as described by Rosenfeld (2002) is a useful conceptual tool for condensing the multivariate assemblage of species' responses to environmental factors to the space occupied by a species in an n-dimensional functional space. Clark (1954) distinguished two separate meanings for the term niche, the "functional niche" and the "place niche." Clark noted that different species of animals and plants fulfill different functions in the ecological complex, and that the same functional niche may be filled by quite different species in different geographical regions. Other concepts of niche like the Eltonian niche (sometimes called functional or trophic-niche) only focus on the impact of species in the environment rather than on its response to particular resources (Elton 1927). Equally, Hutchinson's (1957) concept of the ecological niche considers all biotic and abiotic resources interacting with species and was defined as a hyper-volume in the multidimensional space of ecological variables, within which a species can maintain a viable population. The functional conception of the ecological niche has recently received new theoretical and methodological attention following the growing interest in functional traits in community and applied ecology (McGill et al. 2006; Ackerly and Cornwell 2007). Is the functional niche extended in an n-dimensional functional space and measured as the species position along axes embodying functional attributes, rather than those concepts including resource variables, the best approach to visualize the multiple variation of species in response to environmental variation (Rosenfeld 2002; Mouillot, Mason and Wilson 2007)?

The evaluation of species distribution and functioning in disturbed areas is also required to test if the plant functional traits approach helps us to predict actual and future plant abundances and distributions in a changing environment. Recent studies of tree natural history trade-offs have focused on the species responses to natural disturbances inside the forest such as to tree falls. Most of the work is implicitly or explicitly about strategies linked to horizontal and vertical light gradients, though some of the trait variation is definitely linked to gradients in factors such as soil and elevation. Land use changes imply massive and abrupt habitat transformations outside pristine forest borders resulting in extended areas of landscapes undergoing strong forest fragmentation. To our knowledge no previous studies have focused on the evaluation of how plant traits are actually expressed and interact in tree communities outside the forest, where tree taxonomic and functional diversity is affected by multiple global change drivers including land use change as well as atmospheric CO_2 concentration, nitrogen deposition, climate, and biotic exchange (Sala and Austin al. 2000). It is at this frontier of functional ecology that we should ask: does our current knowledge about forest tree functional niches predict the general characteristics of tree species and functional diversity that is able to survive outside the forest?

Cattle production has already led to widespread deforestation of tropical dry and moits forests in the Central American region and less than 1.7% of intact forest remains (Calvo-Alvarado et al., 2009). In Central American pastures, the systems studied in the present paper, trees outside forest have an important role in ecosystem processes at the landscape scale, such as increasing habitat diversity, food availability for wild fauna, pollen interchange and dispersal patterns (Harvey et al. 2011). Unfortunately, intensified management practices are reducing this tree cover diversity in tropical landscapes (Esquivel et al. 2008, Fischer et al. 2009). Conventional intensive management practices widespread in the region like the sowing of improved grass monocultures, weed control (using agro-chemicals, fire or manual cutting) and overgrazing do not consider the protection of tree-species' populations with limited natural regeneration in active pastures (Simon et al. 1997; Camargo et al. 1999; Barrios 1999; Martinez-Garza and Howe 2005). Consequently, natural regeneration of at least 50% of the tree species in active pasturelands of seasonal lowlands is constrained due to limitation in dispersal, germination and establishment, or due to pasture management (Esquivel et al. 2008). If current intensive management practices continues these species can be expected to disappear from pastures.

The implications of tree diversity reduction outside forest for ecosystem processes such as nutrient cycling at local (pasture) or landscape scales are unknown. Species' life histories are linked to community functional properties and therefore to ecosystem processes and services (Díaz et al. 2011). Land-use management is often focused on few species and local processes, but in dynamic, agricultural landscapes, only a diversity of "insurance species" may guarantee resilience (the capacity to reorganize after disturbance) (Tscharntke et al. 2005). Land-use intensification using few species may disrupt processes such as crop pollination (Kremen et al. 2004), grassland productivity (Loreau and Hector 2001) and decomposition (Altieri 1999; Schläpfer et al. 1999; Tilman et al. 2002), suggesting how important ecosystem services can be affected via the loss of biodiversity outside forest.

The measurement of functional traits of tree species and the functional characteristics of tree assemblages, combined with determinations of tree species' abundance and biomass, are necessary for understanding tree species' responses to habitat fragmentation and the effects of tree biodiversity loss on ecosystem processes on active pasturelands. Basic questions about the functional characteristics of the actual taxonomical diversity of tree cover in active pasturelands - one of the most abundant land cover types in the neotropics - have not yet been addressed. In other words, we don't know, beyond taxonomical diversity, which are the functional attributes of tree cover that persist after land use change from forest to pasturelands. More importantly, we do not know how these tree functional characteristics directly affect key ecosystem processes supporting natural and anthropogenic ecosystem productivity in active pasturelands.

The differences in tree dispersal characteristics, for example, appear to be a major mechanism through which tree species respond to human intervention and therefore, partially, lead to biodiversity loss and consequent effects on ecosystem services, given that effectively-dispersed species become more abundant in disturbed landscapes (Tscharntke et al. 2005). In these environments, the species' capacity to naturally regenerate in pasturelands could be directly related to their dispersion traits (Janzen and Martin 1982, Powers et al. 2009). If dispersal ability is correlated with leaf and stem traits, then dispersal traits might be linked to ecosystem processes like nutrient cycling and productivity in different vegetation stands. In this respect, Wright et al. (2010) conclude that a successful traits-based ecology of tropical forests requires consideration of a wider range of traits than reported by existing studies. Along the same line, Baraloto et al. (2010) argue for the integrated analysis of traits at the whole-plant scale. Only using a larger set of measured traits can allow us to analyze whether strategies linked to gradients inside forests can predict tree community dynamics outside forests. In general terms, few studies of tropical forests, especially in disturbed systems like that studied here, have achieved these goals.

Traits-based understanding of species' responses to intensive human disturbance is also vitally important for understanding the impact of current and future changes in diversity on ecosystem services in agro-ecosystems, the world´s largest category of land cover (Wassenaar et al. 2007). The interactions of site-specific conditions (e.g. soil, precipitation, temperature and solar radiation) with plant traits and community structure (species' abundances) determine ecosystems properties. Modeling of these linkages is relevant to improving understanding of the fundamental basis of both natural and agricultural productivity such as through nutrient cycling (Perez-Harguindeguy et al., 2000). Therefore, the understanding of how such interactions take place in human-disturbed environments is as important as in the case of how they help predict the resilience of natural ecosystems to environmental changes.

In order to contribute to this knowledge, for 75 tree species found in actively-managed anthropogenic pastures at the study site in Muy muy, Nicaragua, we compiled data of 16 traits classified between each of the four trait categories defined above (whole plant, stem, leaf and dispersal). The two measured whole plant traits were maximum tree height (H-max) and leaf phenology (PHE) and the single stem trait was wood density (WD). The seven measured leaf traits were specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), total leaf carbon (LCC), nitrogen (LNC) and phosphorus (LPC) contents and leaf tensile strength (FTF). The six measured dispersal traits were seed and fruit masses (Mass_see/fru), volume (Vol_fru/mass) and shape (Sha_fru/mass); in addition information was collected about the categorical character dispersal mode. To our knowledge no published study of tropical tree species has evaluated such a high number of key traits across these four trait categories. Dispersal traits are of particular interest to our study given their importance for tree species persistence in managed pastures (Esquivel et al. 2008) and their under-representation in studies that quantify its relationships with other key plant traits. The larger number of studied traits than previous studies allows us to improve the characterization of tree species' functional characteristics linked to their persistence in expanding agro-ecosystems outside the forest environment.

Tree communities outside forest interact with the effects of past and present anthropogenic management in addition to the interaction amongst the species, including competition for resources, which is important for their coexistence. Species traits are important in mediating the outcome of these interactions. The low vertical and horizontal structural diversity of silvopasture vegetation, in addition to the dominance of grass, increases light levels down to seedling heights. There is significant grass-tree competition for soil water which, combined with the high rates of evapo-transpiration due to the lack of canopy cover, can severely limit tree seedling establishment thus shaping tree community composition in silvopastures (Esquivel et al. 2008). Herbivore pressure, mainly due to cattle browsing, in addition to the physical damage generated by cattle (due to trampling, resting and scratching) exert additional pressures shaping tree communities in pastures. These external factors may dominate tree community assembly in pasture environments and overwhelm some of the complex interactions amongst tree species within long-established forest communities. However, the dominance of high light, low moisture and high herbivore pressure may reinforce some interactions and create some new ones.

We expect also to find strong correlations between whole plant, stem, leaf and dispersal traits beyond the commonly used focal traits (Hmax, WD, SLA and seed mass). Some authors suggest that the leaf economics spectrum (LES) is decoupled from the wood economics spectrum (WES) (Baraloto et al. 2010). Others suggest in contrast that WD is negatively correlated with SLA reflecting the continuum from fast-growing pioneer species with low WD to slow- growing shade-tolerant species with high WD (Wright et al. 2006). In addition, H max and LA has frequently been reported to be orthogonal to LES and even to WES (Baraloto et al. 2010). The majority of previous studies predict that we should find WD to be negatively correlated with SLA, and H max and LA to be orthogonal to LES- and WES-related traits. Therefore, the axes of these trait categories in general are likely to be orthogonal, but we expect correlations within them like the LES and WES.

We expect to find strong correlations between whole-plant and leaf traits reflecting integrated trait combinations that enable trees to overcome seasonal drought stress within the studied silvopasture habitats with a low vertical structure in dry-/subhumid forest areas. We thus expect that leaf phenology (measured as the number of months per year a tree has a canopy cover under 50%) will be strongly correlated with Hmax and also with WD. Deciduous tree species are predicted to have low-investment leaves with traits associated with high rates of resource aquisition, while evergreen species tend to have more expensive and resource-conservative leaves with lower water loss rates during dry season. Although taller tree species probably have more water stress (Barnard and Ryan 2003) no previous correlations has found in relation with leaf traits related with tolerance to drought.

As predicted by the LES we expect leaf N and P contents to be positively correlated with SLA, and all to be positively correlated with PHE (treated as a quantitative trait in this study): short-lived leaves should have traits linked to high resource-acquisition in drought-avoiders deciduous species, in contrast to long-lived leaves with resource-conservation traits in drought-tolerant evergreen species. LDMC would thus be expected to be positively correlated with FTF but negatively with PHE, LNC, LPC and SLA. LCC is expected to be positively correlated with LDMC and FTF but negatively correlated with LPC, SLA, LPC, LNC and PHE. LPC has been found also to decrease significantly with increasing rain fall (Marharjan et al. 2011) expecting to be also positively correlate to hydraulic related traits like PHE. SLA has been found to be positively correlated with LNC but not strongly with other leaf traits (Kazakou et al. 2006). Easdale et al. (2007a, 2009) also found that LA is positively correlated with SLA, N and P but negatively correlated with LDMC. LA has been found to be correlated with H max, WD, LPC, LNC, SLA, LDMC and LCC but empirical results frequently contrast with theoretical expectations (Niinemets 2006, Niinemets et al 2007), and therefore we had no particular expectations with respect to LA.

Many of the published trends for dispersal traits are related to latitudinal gradients (Moles et al. 2007) and there is much less understanding of relationships of seed and fruit traits with other traits for tree species within the tropics. In previous studies, “diaspore” (the unit that is dispersed, it can range from a whole fruit, to a group of seeds or individual seed) have been mostly represented by seed mass or volume (Moles et al. 2005), while fruit mass or volume or diaspore shapes have received less attention, although they are relevant for dispersal and post dispersal stages. Diaspores mass, volume and shape are linked to dispersal mode, and affect dispersal distances, seed spatial distributions, incorporation into soil seed banks, vulnerability to predation, germination mode/rate and seedling establishment success. Small seeds tend to disperse further away from the mother plant (Muller-Landau 2008), while stored resources in large seeds tend to help young seedling to survive and establish in the face of environmental hazards (deep shade, drought, herbivory). Smaller seeds can be produced in larger numbers with the same invested resources. Smaller seeds with low shape values (relatively spherical) tend to be buried deeper in the soil, and live longer in the seed bank with a lower risk of predation (Cornelissen et al. 2003). The dispersal mode of “dispersules” (equivalent to disaspores or “propagules”, i.e. the unit of seed, fruit or spore that is dispersed) has consequences for the distances it can cover, the routes it can travel, the places it is dispersed to and also the pre-germination processes that a seed is subject to before reaching the soil surface (Cornelissen et al. 2003, Muller-Landau 2008).

In agreement with previous studies about dispersal traits, we expect that seed mass will be correlated with dispersal syndrome (Muller-Landau et al. 2008, Thompson et al. 2011). Vertebrate dispersal agents (responsible for mamalochory and zoochory) have been associated with higher seed masses whereas abiotic agents (e.g. responsible for anemochory) will favor lighter seeds. Positive relationships between fruit and seed volume are expected overall according to mechanical constraints (Wright et al. 2007), but previous studies have not documented any further relationships between fruit masses or shapes. We expect that tree species develop coordinated investments of resources to dispersal structures, and that therefore bigger and heavier fruits carry the biggest and heaviest seeds not only due to mechanical constraints but also to functional constraints and tradeoffs.

Tree communities outside forest are composed of tree species varying in their regeneration capacity (Esquivel et al. 2008). Some trees in silvopasture are forest remnants, established in these areas before forest cutting and with limited or no capacity to establish new individuals outside forest cover. These species can be considered old-growth forests species and may tend to be characterized byparticular adult traits, i.e. tall species, with high wood density, zoochory and slow growth rates. In contrast, those trees colonizing pasture environments could be considered pioneer species, also with particular adult characteristics, i.e. wind, bird or bat dispersed, with fast growth, low WD and low survival rates. Dispersal has been identified as one of the strongest limitations to tree colonization of open areas (Holl 1999). Therefore we expect that dispersal mode will probably affect the relationships of dispersal with whole plant and with leaf traits.

We expect to find that the strongest relationships of dispersal traits with whole-plant and leaf traits will occur within dispersal mode, due to trees allocating resources to pre-, and post-dispersal stages reflected by leaf and whole plants traits. Although we expect a LHS structure of trait associations within this tree community, a stronger relationship with the L and H axes could be observed for dispersal mode, a trait largely neglected in previous studies. Bigger investments in seeds and fruits probably require a dispersal mode that increases the probability of dipsersules reaching safe sites, for example through endozoochory (Muller-Landau 2008). In contrast, a reduced investment in tree dispersules (mainly with biotic dispersers), higher seed mortality rates with a less directional dispersion mode (like wind) and probably occurring in species with short-lived leaves and greater maximum heights is expected. Taller tree species could probably have also bigger seeds (volume) but not necessarily heaviest seeds (mass).

2.3 METHODS

Study site

The study site was located in the central region of Nicaragua, in the Rio Grande watershed, Department of Matagalpa, Municipality of Muy Muy (12°31’ - 13° 20’ N, 84° 45’ - 86° 15’ W). Annual temperature is 24.5 ºC and means annual precipitation is 1576 mm. A warm rainy season begins in May and ends in October, while a dry cool season takes place between December and April. Heavy droughts are observed in April, but rains quickly create flooding on lowlands between July and August (pers. obs.), while May and November are transitional months with highly variable conditions between years. The Muy Muy landscape consists of plains and undulating areas between 100 and 450 m asl and soils consist mainly of Vertisols, Inceptisols and Alfisols (Nieuwenhuyse, unpublished report). The study sites were located in lowland areas, characterized by hilly, undulating landscape with emerging small hills. Vertisols or Inceptisols with vertic properties are the commonest soils; they are developed on tuff which itself is rather impermeable. On steeper slopes thin Inceptisols can be found. Water drainage is restricted in low-lying areas during the rainy season, while higher positions in the landscape are well drained. Soil texture is clay in low-lying areas and loamy clay on the hill slopes. Soil pH is 6.5-7.5; Soil Organic Matter content in the top 20 cm is about 5-10%, with medium to high Ca, Mg and K contents and low P contents (Nieuwenhuyse, unpublished report).

The natural vegetation in the study area is semi-deciduous tropical dry forest (transition to sub-humid) (Henríquez et al 1995, Meyrat 2000, Holdridge 1984). The dominant land use is cattle production, with some basic grains and coffee cultivation in the highlands. Approximately 53% of the land area is covered by self–sown pasture grasses such as *Paspalum* spp., 22 % is pasture of planted improved exotic grasses such as *Brachiaria* spp. and *Cynodon* spp., 10% is early secondary successional vegetation (‘tacotales’) and only 5% is forest. A high tree cover resulting from natural regeneration is found on the actively-managed pasturelands. In 0.5 ha of active pasturelands an average of 5446 seedlings belonging to 56 species, 177 saplings (22 species) and 20 adults (5 species) were found by Esquivel et al. (2008). However, only 37 % of a total 85 tree species in the study area were found to be regenerating actively under the current management conditions. Regeneration of the remaining 48 species appeared to be limited by seed dispersal, germination, seedling establishment or growth, and was unlikely to maintain their populations (Esquivel et al. 2008). Tree composition in active pasturelands is a mix between species of dry and sub-humid forest communities. Mimosaceae, Fabaceae, Caesalpiniaceae and Bignoniaceae are the most species-rich families (comprising ca. 31% of all species), while Sterculiaceae and Boraginaceae are the most abundant families (ca. 54% of all individuals). The highest importance values (mean of relative density, dominance and frequency) were for pioneer species, typical of disturbed areas, dispersed by cattle, wind and wild animals, and actively promoted by farmers for their use as fruits, timber and/or forage (Esquivel et al. 2008).

Trait measurements

Plant traits were measured on adult trees located in open environments with canopies completely exposed to sunlight. A minimum distance of 50 m was maintained between sampled con-specifics. The plant trait measurements followed Cornelissen et al. (2003). For leaf traits relatively young but fully expanded and hardened leaves without obvious symptoms of pathogen or herbivore attack and without substantial cover of epiphylls were sampled. As far as possible, leaves were sampled at least 2-3 h after sunrise and 3-4 h before sunset. Mature fruits were collected from trees or from soil when fresh fruits and seed recently released and were found. Leaf, fruit and seed samples were stored in a cool box or fridge until processing in the laboratory. Dry (or only slightly moist) samples were taken to avoid rot damage, and rehydratation was used for 6-12 h in a dark room when necessary before measurements. However, where possible, measurements were made within 48 h of sample collection. In general, 3 to 5 leaves or fruits were collected from each of 3 to 10 sampled trees per species (**Table 2.1**).

Table 2.1. Whole plant, leaf and dispersal traits units and sample sizes measured for tree species in neo-tropical and active pasturelands in Central America

Traits groups	Traits Abr.	Plant Traits selected	Measurement unit	Type of variable	Sample size
Whole plant	H max	Adult plant stature	m	continuous	3 – 5 trees
	WD	Wood density	g cm$^{3-1}$	continuous	literature
	PHE	Leaf phenology	month	continuous	3 – 10 trees
Leaf traits	SLA	Specific Leaf Area	mm^2 mg^{-1}	continuous	5 – 10 leaves (3 – 5 trees)
	LA	Leaf size	mm^2	continuous	5 – 10 leaves (3 – 5 trees)
	LDMC	Leaf Dry matter content	mg g^{-1}	continuous	5 – 10 leaves (3 – 5 trees)
	LCC	Leaf total carbon content	%	continuous	5 – 10 leaves (3 – 5 trees)
	LNC	Leaf Nitrogen concentration	%	continuous	5 – 10 leaves (3 – 5 trees)
	LPC	Leaf Phosphorus concentration	%	continuous	5 – 10 leaves (3 – 5 trees)
	FTF	Physical strength of leaves	N (N mm^{-1})	continuous	5 – 10 leaves (3 – 5 trees)
Dispersal traits	Sha_fru	Fruit shape	unitless	continuous	3 - 5 fruits (3 – 5 trees)
	Sha_see	Seed shape	unitless	continuous	3 – 5 seeds (3 - 5 fruits, 3 – 5 trees)
	Mas_fru	Fruits mass	g	continuous	3 - 5 fruits (3 – 5 trees)
	Mas_see	Seed mass	g	continuous	3 – 5 seeds (3 - 5 fruits, 3 – 5 trees)
	Vol_fru	Fruits volume	cm^3	continuous	3 - 5 fruits (3 – 5 trees)
	Vol_see	Seed volume	cm^3	continuous	3 – 5 seeds (3 - 5 fruits, 3 – 5 trees)
	Dis_mod	Dispersal mode	unitless	categorical	-

For whole-plant traits, the maximum plant height (H max, in m) was measured using clinometers on flat sites, vertical measurements or visual estimations in more sloping sites. The biggest trees were selected within the 46 active pasture areas in the study site sampled for tree community composition data in a previous study (Esquivel et al. 2008). Plant phenology (PHE) was measured using visual estimation of the percentage of tree canopy covered by leaves every two weeks over a whole year for adult reproductive trees, taking as a 100% reference the tree canopy density at the end of the previous rainy season. PHE was measured as the number of months the canopy density was < 50%.

For leaf traits, the specific leaf area (SLA) was measured on mature and fully hydrated leaves scanned using Leaf Area Measurements software (LAM V 1.3, University of Sheffield, A.P. Askew, 2003). After area measurement each leaf sample was oven dried at 60 ºC for 72 h, and then weighed. An average of 20 leaves per species were measured, sampling 2-4 leaves per individual. Here we measured just the leaf lamina without petioles or rachis. When collected, the samples (twigs with leaves attached) were wrapped in moist paper and put into sealed plastic bags, so they remain water-saturated. These samples were stored in a cool box or fridge until processing in the laboratory. When necessary, rehydratation was done before measurements for 6-12 h in a dark room, but measurements were mostly done within 48 h of sample collection (Cornelissen et al. 2003). Leaf dry matter content (LMDC) was measured following oven drying leaf samples (at 60 ºC) for 72 h. The same leaves used for SLA were used for LMDC. A pooled sample of oven-dried leaves was used to determine leaf carbon content (LCC), leaf nitrogen content (LNC) and leaf phosphorus content (LPC) for each species (Cornelissen et al. 2003) in the CATIE Soil Labs. Total C and N were measured by combustion analysis with an auto-analyzer. Phosphorus was estimated by humid digestion with a mix of nitro-perclorated acids 5:1 and colorimetry (Henríquez *et al.* 1995). Leaf Tensile Strength or physical strength of leaves (FTF) was measured using a "tearing apparatus" (DIVERSUS project). A leaf fragment from the central section of the leaf (but away from the central vein) following the longitudinal axis (direction of the main vein), or the whole leaf was used. The width of the leaf or the leaf fragment sample (1-10 mm) was measured. The total force used (1 kg = 10 N) was divided by the width of the leaf fragment to obtain the leaf tensile strength.

Mass, volume and shape of both fruits and seeds were measured to obtain complete description about the dispersules (dispersal structure or propagule) as it reaches the soil surface (Cornelissen 2003). At least 3 seeds obtained from 1 to 3 fruits were sampled from 1 to 5 different tree individuals per species. Complete fruits were oven dried for at least 72 h or until they reached a stable weight to obtain fruit and seed masses (Mas_fru, Mas_see). Dispersule shapes (Sha_fru, Shas_see) describe quantitatively the shape or form of the mature and live fruit or seeds. Shape was defined as the variance of the three main dimensions (length, width and thickness (breadth)) of the seed or fruits, after each of these values have been divided by the largest of the values. These shape values lie between 0 and 1 and are unitless. Shape was measured from different seeds and fruits sampled for seed mass. Volume (Vol_fru, Vol_see) was described as the tri-dimensional or cubic space occupied by the fruits and seeds. Fruit and seed volumes were calculated by spherical or ellipsoid geometrical formulas according to their form described by length, width and thickness (breadth). Fleshy fruits were stored in plastic bags and kept in a cool box on fridge until measurements. Naturally dry fruits were air dried prior to storing.

Tree dispersal mode describes the routes traveled by the dispersule units or the vector assisting or moving the dispersule before reaching the soil surface (Cornelissen 2003). The categories defined by Cornelissen (2003) were used and adjusted when necessary for the local community (**Table 2.2**). We were aware that several dispersal modes can assist a dispersule's movements (dispersion) away from a parental tree to reach the ultimate germination place (Fischer et al. 1996). We only use here the dispersal vector involved within the first stage of dispersule release from parental tree within the whole possible range of dispersion movements (main vector) to categorize tree species dispersal mode. Four dispersal modes were identified: Autochory, Anemochory, Zoochory and Mammalochory.

Table 2.2. Dispersule characteristics used to categorize the dispersal mode traits adapted from Cornelissen et al. (2003)

Dispersal modes	Vectors	Dispersal mechanisms / Dispersule characteristics
Autochory (including Ballistochory)	Unassisted dispersal, bristle contraction or seed launching	The seed or fruit has no obvious aids for longer distance transport, falling passively from the plant or dispersule with Hygroscopic bristles on the dispersule that promote movement with varying humidity. Restrained seeds are launched away from the plant by "explosion" as soon as the seed capsule opens
Anemochory	Wind dispersal	Minute dust-like seeds Seed with pappus or other hair, balloons or comas Flattened fruits or seeds with large wings Tumbleweeds , where the whole plant or in-frutescence with ripe seeds is rolled over the ground by wind
Endo-zoochory (Zoochory and Mammalochory)	Internal animal transport	Fleshy often brightly coloured berries, arillate seeds, drupes and big fruits that are evidently eaten by vertebrates (birds, mammals, bats) and pass through the gut before seeds enter the soil elsewhere. Those mainly consumed by wild animals where categorized as Zoochory, instead those eaten exclusively by big mammals like cattle were categorized as Mammalochory.

Wood density (WD) was the only plant trait exclusively obtained by literature review. All the WD data come from standard published papers and from available metadata reviews like those of Chave et al. (2006) and the Global Wood Density Databases of Zanne et al. (2009). Dispersal trait data were also obtained by literature review in order to fill 80 gaps for the Y species for which no samples could be obtained from the field. For these 10 species, fruit and seed masses and dimensions, were obtained from standard published papers and databases (i) that of Moles et al. (2004) for 4 species, (ii) specimen information from Regional floras available on-line, i.e. TROPICOS (Tropicos.org, Missouri Botanical Garden, 2012), Species of Costa Rica (inbio.ac.cr, National Biodiversity Institute, Costa Rica, 2007), Flore Scientific Databases (biogeodb.stri.si.edu/bioinformatics, Smithsonian Tropical Research Institute, 2012) and Agroforestree Database (worldagroforestrycentre.org, World Agroforestry Centre, 2012) for 6 species.

Data analysis

The relationships between plant traits were evaluated using paired Spearman Rank Correlation analyses due to the lack of normality of the measured variables even after application of the common transformations used in ecology. An unbalance data set of 65 species X 17 traits was created due to some of the traits not being measured for all tree species due to lack of available field samples and time limitations for year-round field surveys and lack of any previously published data. Species correlations used all the species with measurements of any given pair of traits. The number of tree species used for paired correlation analyses or “cross-species correlation” of plant traits varied between 25 and 64 species. The sample number of species (n), significance value (p value) and Spearman rank correlation coefficient (r) were reported for each of the 120 cross-species correlation analyses performed (see Table 4 for the resulting integrated correlation analyses).

Principal components analysis (PCA) was used to understand how the patterns of correlations or trait co-variation might be driving species community assemblage. The variability of tree species distribution in a multivariate space explained by plant traits was analyzed using standardized data. A total of seven different PCAs were carried out to evaluate the variability explained by traits for a higher number of species using multivariate analyses (highest traits/specie ratio) and maximizing the use of the unbalanced database of 76 species X 16 traits obtained with the combination of field measurements and literature data, taking into account that the PCAs used only the 25 species with a complete data set of whole plant, leaf and dispersal traits (**Table 2.3**). The extracted axes were considered interpretable using the "Kaiser-Guttman criterion" when they showed eigenvalues (i.e. the variance on the new component that was successively extracted) higher than 1, i.e. eigenvalues higer then the mean of eigenvalues obtained for the specific case of the standardized data (Legendre and Legendre 1998). The significance of the correlations between the ordination axes extracted by the PCAs with plant traits was evaluated using Spearman's Rank Correlation analyses.

Table 2.3. Number of species sampled by plant trait (n) included in the cross-species correlations Spearman analyses (r), for the Principal Components analyses (PCA) done independently for each plant trait dimension: whole plant (W), leaf (L) and dispersal (D) and for their interactions (WL, DW, DL, WLD) and the species/traits ratio by matrix size (n x traits)

Plant dimensions	traits	n	n (r)	n (PCA)	n x traits	traits /species
Whole plant (W)	H_max , WD, PHE	69, 54, 49	39 - 52	39	39 x 3	13
Leaf (L)	SLA, LA, LDMC, LCC, LPC, LNC, FTF	44, 45, 47, 58, 58, 58, 42	40 - 58	37	37 x 7	5,3
Dispersal (D)	Sha_Fru, Mass_fru, Vol_fru, Sha_see, Mass_See, Vol_see	42, 39, 36, 32, 32, 32	29 - 37	29	29 x 6	4,8
Whole plant and leaf (WL)	H_max , WD, PHE SLA, LA, LDMC, LCC, LPC, LNC, FTF	-	33 - 58	27	27 x 10	2,7
Dispersal and whole plant (DW)	H_max , WD, PHE Sha_Fru, Mass_fru, Vol_fru Sha_see, Mass_See, Vol_see	-	24 - 52	18	18 x 9	2,0
Dispersal and leaf (DL)	SLA, LA, LDMC, LCC, LPC, LNC, FTF Sha_Fru, Mass_fru, Vol_fru Sha_see, Mass_See, Vol_see	-	27 - 58	20	20 x 13	1,5
Whole plant, leaf and dispersal (WLD)	H_max , WD, PHE SLA, LA, LDMC, LCC, LPC, LNC, FTF Sha_Fru, Mass_fru, Vol_fru Sha_see, Mass_See, Vol_see	-	41 - 69	25	25 x 16	1,6

The first set of three PCAs were performed independently within each set of traits that have been reported to correlate with main trait axes for tropical trees in previous literature, i.e. respectively whole plant, leaf, and dispersal traits. 1) The first PCA was done using only the three measured whole-plant traits, i.e. Hmax, WD and PHE. 2) The second PCA was done only including the seven measured leaf traits, i.e. SLA, LA, LDMC, LCC, LPC, LNC and FTF. 3) The third PCA was done using only the quantitatively-measured dispersal traits, i.e. fruit and seed shape, mass and volume. The second set of three additional PCAs each combined two of the three sets of traits: 4) whole plant and leaf traits; 5) whole plant and dispersal traits; 6) leaf and dispersal traits. A final integrating PCA was done combining all three sets of traits together; this was carried out in a complete balanced species X trait data matrix for 25 tree species and 16 traits. Finally, logistic regression analyses were run to test the significance and direction of the associations between the observed categorical dispersal modes (zoochory, mammalochory, anemochory and autochory) and the quantitative whole plant, leaf and dispersal traits. All the data analyses were carried out using Infostat Professional software (Infostat 2011).

2.4 RESULTS

Whole plant traits

The Spearman's rank correlation analyses showed that PHE was strongly and negatively correlated ($p = 0.01$) with WD and positively but more weakly correlated ($p = 0.084$) with H max (**Table 2.4**). The evidence was weaker still for an association between WD and H max ($p = 0.11$). Using PCA, a total of 80% of species variability was explained by the first two components in the whole-plant traits' space. The first axis (CP1W) explained 56% of variability (having an eigenvalue higher than 1) for a total of 39 species. Spearman's rank correlation coefficients between traits and this axis showed that CP1W was signficantly correlated ($p \leq 0.05$) positively with WD (0.79) and negatively with PHE (-0.78). In contrast H_max was significantly positively correlated with the second axis, CP2W (0.71), which explained 24.5% of species distribution variability. These correlations indicate that evergreen species tend to have denser wood and lower maximum height than deciduous species, which are less closely related to H-max.

Leaf traits

The Spearman' rank correlation analyses showed that LDMC was strongly ($p \leq 0.01$) positively correlated with SLA, LCC and FTF, but negatively with LPC (and more weakly ($p = 0.053$) with LNC) (**Table 2.4**). SLA was, in addition, very negatively correlated with FTF ($p = 0.0001$), but positively with LNC ($p = 0.001$) (and more weakly ($p = 0.07$) with LPC). LPC was also strongly ($p < 0.01$) negatively correlated with FTF and positively with LNC. LNC was strongly ($p < 0.01$) negatively correlated with FTF and with LA. LCC was also strongly ($p < 0.01$) negatively correlated with LPC. These results show that species with high LDMC tend to have high LCC and high FTF, but low SLA, LPC and LNC. Also, species with high LNC tend to have a high SLA and LPC but a low LA, LDMC and FTF.

The first two principal components for leaf traits (CP1L and CP2L) explained 57% of variance among species within the all-leaf-traits' space (having Eigen values higher than 1) for a total of 37 species. CP1L significantly separates ($p \leq 0{,}05$) species along a spectrum from those with a high LDMC (r for association with axis 0.82), LCC (0.58) and FTF (0.55) from those with high SLA (-0.69) and LPC (-0.68), explaining 35% of species' variability. In contrast axis CP2L distinguishes species with high LA (0.78) from species with high LNC (-0.66), explaining 22% of variability in species' variability.

Whole plant and leaf traits

PHE was negatively correlated ($p \leq 0.05$) with FTF and positively with LPC (**Table 2.4**). H_max was strongly negatively correlated with SLA $p = 0.005$) but weakly with FTF ($p = 0.09$), and positively correlated with LDMC ($p = 0.04$) and very weakly with LCC ($p = 0.13$). WD was only positively correlated with LDMC ($p = 0.007$). These results showed that tree species with dense wood tended to have high leaf dry matter contents, even though leaf dry matter content was not closely related with leaf phenology. In contrast taller species tended to have a low specific leaf area linked to a high leaf dry matter content and strength. The only leaf traits linked to a deciduous leaf phenology were higher concentrations of phosphorous and lower strength.

The most important axis observed in the PCA corresponded to that of leaf economics (indicated by SLA and LPC versus LDMC, LCC and FTF1), which was also strongly correlated with phenology ($p = 0.006$): deciduous species tended to invest less resource per leaf (**Table 2.5**). H max ($p < 0.0001$) and deciduous phenology (PHE, $p = 0.001$) were strongly loaded onto a separate axis from that of the leaf economics spectrum, with opposite loading being shown only by LA ($p = 0.02$). Forty-nine per cent of species variability (amongst 26 species) was explained by these first two components of the PCA combining all leaf and vegetative traits (CP1WL and CP2WL) (**Figure 2.1**). The correlations of Hmax with leaf traits suggest that taller species are more resource conservative. However, this is not reflected at all in the whole plant-leaf traits PCA.

Table 2.4. Spearman correlation coefficients (r) between whole plant (H_max, WD, PHE) , leaf (SLA, LA, LDMC, LCC, LPC, LNC, FTF) and dispersal traits (Sha_Fru, Sha_see, Mass_fru, Mas_see, Vol_Fru, Vol_see) for tree species commonly found in neotropical active pasturelands

	H_max	WD	PHE	SLA	LA	LDMC	LCC	LPC	LNC	FTF1	Sha_Fru	Mas_Fru	Sha_See	Mas_See	Vol_Fru
WD	-0,21 (0,1112) 60	-													
PHE	**0,25** **(0,0836)** **49**	**-0,39** **(0,0131)** **39**	-												
SLA	**-0,43** **(0,0045)** **43**	-0,1 (0,5369) 39	-0,06 (0,6867) 43	-											
LA	-0,13 (0,3979) 44	-0,03 (0,8307) 40	-0,13 (0,3832) 44	-0,09 (0,538) 45	-										
LDMC	**0,3** **(0,0449)** **46**	**0,41** **(0,0074)** **42**	-0,16 (0,2847) 46	**-0,56** **(0,0001)** **44**	0,1 (0,5235) 45	-									
LCC	0,2 (0,1304) 57	-0,04 (0,7584) 52	-0,11 (0,4392) 50	-0,2 (0,2174) 41	-0,2 (0,1978) 42	**0,43** **(0,0042)** **42**	-								
LPC	-0,14 (0,3004) 58	-0,18 (0,2027) 53	**0,32** **(0,0225)** **51**	**0,28** **(0,0731)** **41**	-0,02 (0,9064) 42	**-0,43** **(0,004)** **42**	**-0,37** **(0,0025)** **63**	-							
LNC	-0,06 (0,6729) 61	0,05 (0,6902) 56	0,04 (0,7576) 53	**0,47** **(0,0013)** **43**	**-0,38** **(0,01) 44**	**-0,29** **(0,0528)** **44**	0,003 (0,9816) 63	**0,32** **(0,0098)** **64**	-						
FTF	**0,26** **(0,087)** **45**	0,13 (0,4042) 41	**-0,29** **(0,0661)** **40**	**-0,61** **(<0,0001** **) 40**	0,11 (0,4986) 41	**0,39** **(0,0094)** **43**	0,01 (0,937) 41	**-0,41** **(0,0075)** **41**	**-0,4** **(0,0084)** **43**	-					
Sha_Fru	0,16 (0,2164) 64	0,14 (0,3037) 60	0,14 (0,2881) 56	0,14 (0,3722) 44	**-0,31** **(0,0364)** **45**	0,13 (0,403) 45	**0,28** **(0,0367)** **55**	**-0,22** **(0,1048)** **56**	**0,39** **(0,0021)** **59**	-0,07 (0,6762) 43	-				
Mas_Fru	**0,24** **(0,0841)** **54**	0,07 (0,6137) 51	0,05 (0,7362) 50	**-0,42** **(0,0065)** **41**	-0,11 (0,4692) 42	**0,35** **(0,0237)** **42**	**0,33** **(0,0179)** **51**	**-0,34** **(0,015)** **51**	-0,11 (0,4126) 53	**0,36** **(0,0221)** **41**	**0,23** **(0,091)** **55**	-			
Sha_See	0,04 (0,7615) 59	0,2 (0,1309) 57	-0,11 (0,443) 51	0,08 (0,6163) 42	0,03 (0,8372) 43	0,04 (0,7877) 43	**0,25** **(0,0769)** **53**	-0,17 (0,2105) 54	**0,28** **(0,0338)** **56**	0,08 (0,6306) 41	**0,47** **(0,0001)** **62**	**0,41** **(0,0032) 51**	-		
Mas_See	0,14 (0,3141) 57	0,03 (0,847) 56	-0,07 (0,6261) 53	-0,2 (0,2185) 41	**-0,54** **(0,0002)** **42**	0,23 (0,1391) 43	0,13 (0,3473) 51	**-0,27** **(0,051)** **51**	0,18 (0,2077) 53	0,21 (0,1922) 42	0,06 (0,6399) 58	**0,39** **(0,0043) 52**	-0,2 (0,1451) 55	-	
Vol_Fru	0,18 (0,2053) 53	-0,16 (0,2576) 50	**0,24** **(0,1084)** **46**	0,07 (0,6755) 36	**-0,35** **(0,0339)** **37**	0,19 (0,2629) 37	**0,43** **(0,0032)** **45**	-0,12 (0,4111) 46	0,08 (0,5628) 49	-0,01 (0,935) 35	**0,21** **(0,1099)** **58**	0,13 (0,3952) 44	**0,29** **(0,0402)** **52**	0,14 (0,3259) 49	-
Vol_See	**0,22** **(0,0911)** **58**	-0,12 (0,3707) 55	0,22 (0,1271) 49	-0,03 (0,8457) 41	**-0,43** **(0,0043)** **42**	0,09 (0,5877) 42	0,04 (0,7976) 51	0,01 (0,9508) 52	0,19 (0,1689) 54	0,19 (0,2464) 40	0,07 (0,5666) 61	-0,15 (0,3182) 49	-0,05 (0,6813) 60	**0,46** **(0,0005)** **53**	**0,8** **(<0,0001)** **53**

Showed data include the regression coefficient for logistic models ß, the significance of the regression (p value) and finally include the number of species by each regression n. Bold values were significant at p ≤0,10; bold and underlined values were significant at p ≤0,05 and bold but double underlined were significant at p ≤0,0001.

Table 2.5. Spearman correlation coefficients r between whole plant (H_max, WD, PHE), leaf (SLA, LA, LDMC, LCC, LPC, LNC, FTF) and dispersal traits (Sha_Fru, Sha_see, Mass_fru, Mas_see, Vol_Fru, Vol_see) with the principal components resulting from the PCA analyses resulted from paired trait dimensions interactions (WL, WD, LD) and for all the traits together (WLD)

CP (n)	H_max	WD	PHE	SLA	LA	LDMC	LCC	LPC	LNC	FTF1	Sha_fru	Mas_fru	Sha_see	Mas_se	Vol_fru	Vol_see
CP1 WL (27)	-0,02 (0,9296)	0,26 (0,1852)	**-0,52** **(0,0062)**	**-0,61** **(0,0009)**	0,08 (0,6729)	**0,78** **(0,0001)**	**0,54** **(0,0072)**	**-0,78** **(<0,0001)**	**-0,34** **(0,0897)**	**0,69** **(0,0001)**						
CP2 WL (27)	**0,90** **(<0,0001)**	**-0,39** **(0,0487)**	**0,60** **(0,0012)**	-0,29 (0,153)	**-0,48** **(0,0159)**	0,08 (0,6804)	0,09 (0,6679)	-0,03 (0,8727)	0,14 (0,4946)	0,28 (0,1726)						
CP3 WL (27)	-0,16 (0,4422)	**0,76** **(0,0002)**	-0,31 (0,1254)	0,04 (0,8485)	**-0,35** **(0,0798)**	0,09 (0,6407)	-0,19 (0,3428)	0,32 (0,1146)	**0,67** **(0,0002)**	-0,05 (0,8072)						
CP4 WL (27)	-0,02 (0,9057)	-0,18 (0,3787)	0,08 (0,707)	**0,51** **(0,0081)**	**-0,46** **(0,0223)**	0,11 (0,5903)	**0,62** **(0,0021)**	-0,22 (0,2803)	**0,38** **(0,059)**	**-0,49** **(0,0102)**						
CP1 WD (18)	0,18 (0,4655)	**0,5** **(0,0353)**	**-0,4** **(0,101)**								0,19 (0,4551)	**0,97** **(<0,0001)**	0,03 (0,9196)	**0,97** **(<0,0001)**	**0,95** **(<0,0001)**	**0,73** **(0,0006)**
CP2 WD (18)	**0,42** **(0,0815)**	-0,28 (0,2531)	**0,39** **(0,112)**								**0,79** **(0,0001)**	0,07 (0,7726)	**0,82** **(<0,0001)**	-0,07 (0,7683)	0,17 (0,5011)	-0,15 (0,5542)
CP3 WD (18)	**-0,55** **(0,0177)**	**0,63** **(0,0047)**	**-0,42** **(0,0841)**								0,26 (0,2942)	0,01 (0,975)	0,35 (0,1551)	-0,19 (0,4622)	0,04 (0,8807)	**-0,42** **(0,086)**
CP1 LD (20)				-0,28 (0,3205)	-0,26 (0,3525)	**0,71** **(0,0028)**	**0,62** **(0,0098)**	-0,37 (0,1613)	-0,26 (0,3222)	**0,47** **(0,0652)**	0,21 (0,3977)	**0,93** **(<0,0001)**	0,02 (0,9503)	**0,95** **(<0,0001)**	**0,92** **(<0,0001)**	**0,76** **(0,0002)**
CP2 LD (20)				0,05 (0,8692)	0,1 (0,7149)	0,07 (0,7919)	0,4 (0,1249)	-0,04 (0,8725)	-0,02 (0,9314)	0,15 (0,5879)	**0,6** **(0,008)**	0,05 (0,8291)	**0,85** **(<0,0001)**	-0,09 (0,7144)	0,18 (0,4785)	-0,15 (0,5641)
CP3 LD (20)				0,34 (0,2107)	0,33 (0,2229)	0,08 (0,7893)	-0,05 (0,854)	-0,2 (0,4472)	-0,14 (0,5967)	-0,2 (0,4496)	0,21 (0,4071)	0,07 (0,7876)	0,33 (0,1814)	-0,09 (0,7351)	0,08 (0,754)	-0,33 (0,1797)
CP4 LD (20)				-0,33 (0,2275)	-0,28 (0,321)	0,29 (0,3024)	0,38 (0,1441)	**-0,48** **(0,0611)**	0,38 (0,1435)	0,15 (0,5907)	**0,59** **(0,0093)**	-0,17 (0,5021)	0,1 (0,7039)	-0,15 (0,5619)	-0,16 (0,5307)	-0,01 (0,9734)
CP1 WLD (25)	0,29 (0,153)	0,2 (0,3357)	-0,09 (0,6592)	**-0,54** **(0,0056)**	-0,08 (0,6785)	**0,74** **(0,0003)**	**0,63** **(0,0019)**	**-0,74** **(<0,0001)**	-0,26 (0,2085)	**0,55** **(0,0048)**	**0,39** **(0,0563)**	**0,65** **(0,0015)**	0,29 (0,1672)	0,31 (0,1317)	0,33 (0,1092)	0,28 (0,1739)
CP2 WLD (25)	-0,18 (0,3883)	0,23 (0,262)	**-0,42** **(0,035)**	**0,54** **(0,0052)**	-0,04 (0,8329)	0,1 (0,6215)	**0,5** **(0,0149)**	-0,07 (0,726)	**0,70** **(0,0001)**	-0,24 (0,2413)	**0,56** **(0,0034)**	-0,03 (0,8772)	**0,59** **(0,0018)**	-0,19 (0,3442)	**0,39** **(0,0575)**	0,05 (0,8053)
CP3 WLD (25)	**0,77** **(<0,0001)**	-0,27 (0,189)	0,24 (0,2517)	**-0,62** **(0,0009)**	0,35 (0,0844)	**0,48** **(0,0185)**	0,24 (0,2489)	-0,24 (0,245)	-0,23 (0,2768)	**0,56** **(0,0034)**	**0,4** **(0,0501)**	0,26 (0,1975)	0,25 (0,2288)	-0,28 (0,1761)	-0,07 (0,7373)	-0,17 (0,4262)
CP4 WLD (25)	0,31 (0,1326)	**-0,64** **(0,0006)**	**0,67** **(0,0003)**	0,09 (0,6525)	**-0,42** **(0,0411)**	-0,22 (0,2811)	0,17 (0,4071)	-0,16 (0,4496)	-0,09 (0,67)	-0,23 (0,2767)	**0,39** **(0,0536)**	0,15 (0,4693)	0,07 (0,7395)	0,03 (0,8891)	**0,45** **(0,0278)**	0,28 (0,1782)
CP5 WLD (25)	0,05 (0,8255)	0,22 (0,281)	0,31 (0,1267)	-0,03 (0,8694)	**0,70** **(0,0006)**	0,06 (0,7803)	-0,16 (0,4309)	0,17 (0,406)	-0,18 (0,3974)	-0,08 (0,7169)	-0,27 (0,1891)	0,02 (0,91)	**0,48** **(0,0141)**	**-0,61** **(0,0027)**	-0,08 (0,6979)	-0,31 (0,1265)
CP6 WLD (25)	0,35 (0,0872)	0,23 (0,2636)	0,12 (0,5676)	-0,02 (0,9069)	-0,11 (0,6057)	0,27 (0,1834)	0,16 (0,4443)	**0,52** **(0,0072)**	-0,01 (0,9811)	-0,24 (0,2491)	-0,25 (0,2347)	-0,03 (0,8832)	-0,18 (0,3789)	0,04 (0,827)	-0,04 (0,8358)	-0,08 (0,7065)

Showed data include the Spearman correlation coefficient n and the significance of the regression (p value). The number of species by each regression n is inside parenthesis in each row label. Bold values were significant at p ≤0,10; bold and underlined values were significant at p ≤0,05 and bold but double underlined were significant at p ≤0,0001.

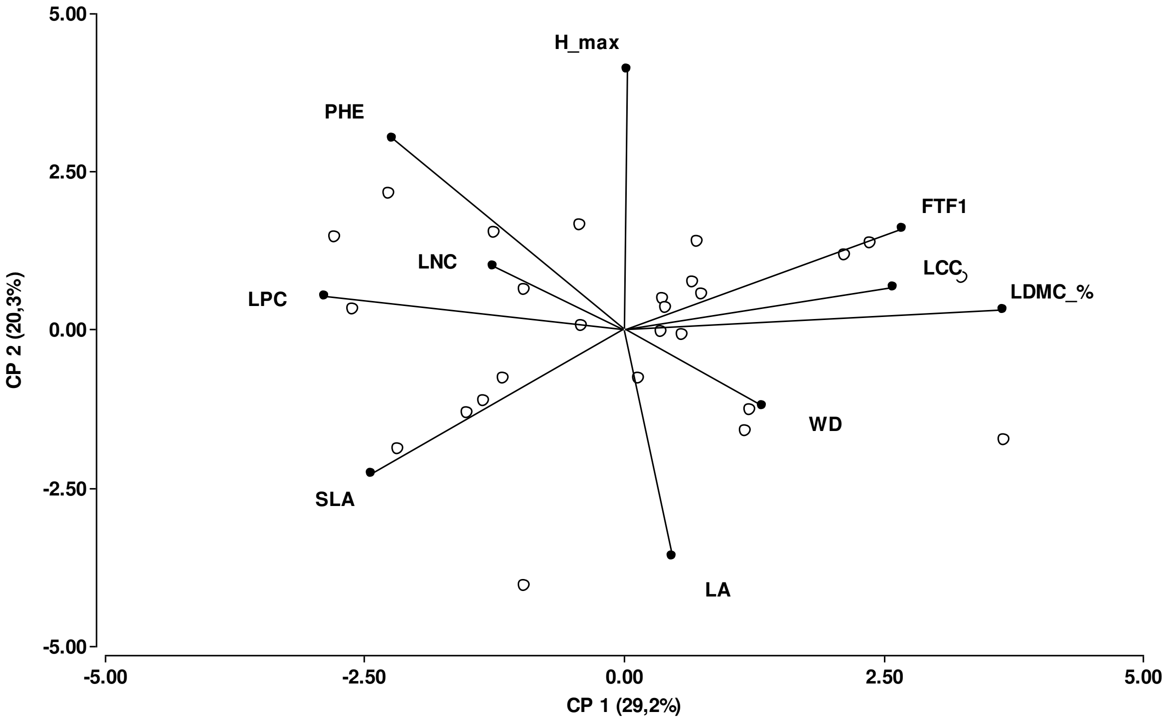

Figure 2.1. PCA biplot for whole plant traits: maximum tree height (H_max), wood density (WD) and leaf phenology (PHE); and leaf traits: specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), total leaf carbon, phosphorus and nitrogen contents (LCC, LPC, LNC) and leaf tensile strength (FTF1), measured for 26 tree species commonly found in actively-managed anthropogenic Neotropical pasturelands.

The correlation of WD with LDMC, which indicates a conservative strategy, is also only very weakly evident in the PCA. In contrast the PCA shows much more clearly the correlation of PHE with leaf traits associated with the leaf economics spectrum: deciduous species tend to have resource acquisitive leaves likely to maximize photosynthetic production during their short lives, while evergreen species tend to have resource conservative leaves, which may be important intolerance of the dry season.

The Spearman's rank correlations analyses between whole plant traits and leaf traits suggest that i) taller species tend to be more resource conservative; ii) tree species with denser wood may also be more resource conservative, however the only leaf trait clearly correlated with WD was LDMC; meanwhile iii) more deciduous species tend to invest less in their leaves (as indicated by low LPC and FTF). The most important axis observed in the PCA corresponded with the leaf economics spectrum, which was also correlated with phenology. H max was loaded on the second independent axis providing some evidence that it was more independent of the leaf economics spectrum, though this is less clear from the individual trait correlations. Meanwhile, WD was primarily displaced to a third axis (together with LNC) though it was also correlated with the second axis.

Dispersal traits

For the 29 tested species, seed mass was strongly positively correlated ($p < 0.01$) with fruit mass and seed volume (**Table 2.4**). Fruit mass was also strongly positively correlated ($p = 0.003$) with seed shape and weakly ($p = 0.09$) with fruit shape. Fruit shape and seed shape were strongly positively correlated ($p = 0.0001$). Fruit volume was correlated with seed shape ($p = 0.04$) and weakly with fruit shape ($p = 0.11$). These results show that tree species with bigger, heavier and longer fruits tended also to have bigger, heavier and longer seeds. However, individual relationships amongst these traits were variable and tended to be stronger for seeds than for fruits, i.e. species with bigger fruits were not necessarily heaviest or carrying heavier seeds, though they were very likely to be carrying bigger seeds. There was a clear trend for species with bigger seeds to have heavier seeds. Fruit and seed shapes were consistently correlated with fruit mass and volume but not with seed mass or volume: longer, heavier and bigger fruit tended to have longer seeds but did not necessarily have heavier or bigger seeds. However, and indirect correlation between dipersule shapes with seed morphology was always present due the strong correlations between fruit shape with fruit morphology and among dispersule shapes. i.e the more voluminous fruits were also the longest fruits, and contain voluminous and longest seeds which were not necessarily the heaviest dispersules. Instead, voluminous seeds were indeed the heaviest ones and were found in the biggest fruits but not necessarily in the heaviest fruits.

The PCA result reflects the strong correlations between the measured fruit and seed traits. The two principal axes explain together a total of 63% of the variation amongst species in trait values of fruit and seed mass, volume and shape (**Figure 2.2**). The first axis explains 33%, the second axis 30% and a third axis an additional 18% of species variability (having eigenvalues higher than 1). Spearman’s rank correlation coefficients between dispersal traits and the first two axes (CP1D and CP2D) showed that Axis 1 reflects a spectrum of seed and fruit mass ($r = 0.95$ and 0.81 respectively) and volume (0.72 and 0.62 respecively), and axis 2 was defined by increasing elongation of seed and fruit shape (0.85 and 0.89) respectively, which were strongly orthogonal to axis 1.

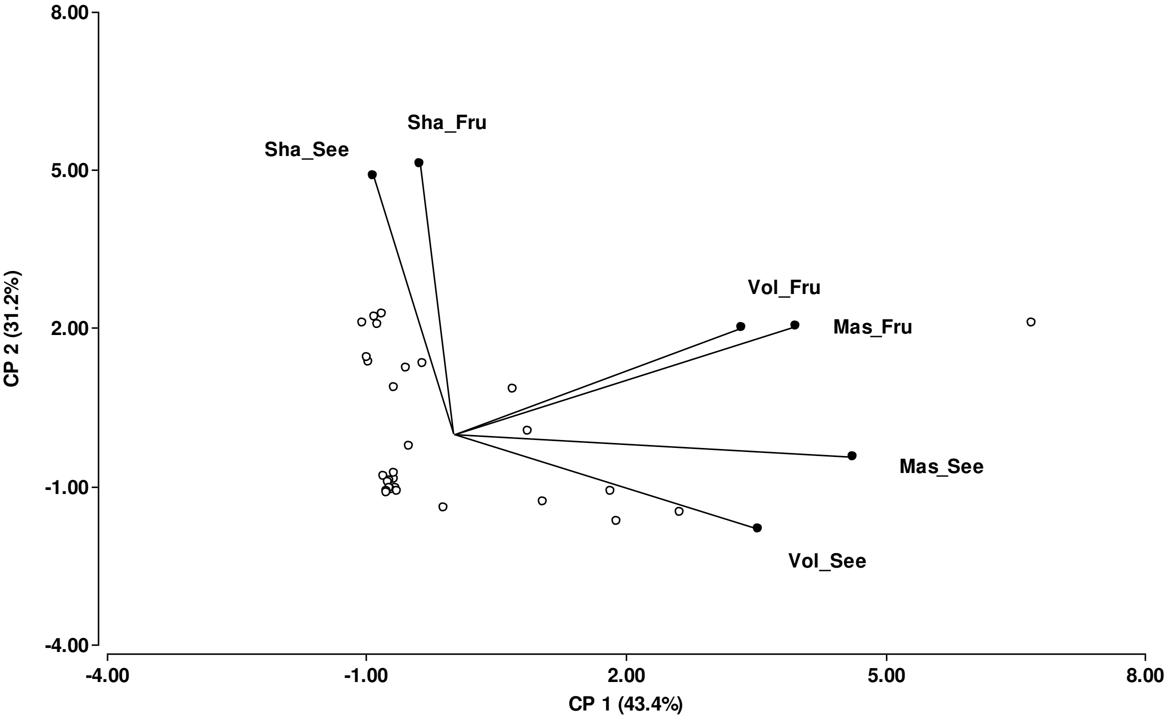

Figure 2.2. PCA biplot for dispersal traits: fruit and seed mass (Mas_Fru, Mas_See), volume (Vol_Fru, Vol_See) and shape (Sha_Fru, Sha_See) measured for 29 trees species commonly found in actively managed anthropogenic Neotropical pasturelands

Dispersal mode

The majority of the tree species (64%) were mainly dispersed by animals (zoochory) (**Table 2.6**). Within this set, almost half of the total number of species (49%) were dispersed mainly by native fauna like frugivorous birds, bats or small rodents, which eat the entire fleshy fruits (drupes or berries) or the fleshy endocarps (arils) ingesting at the same time the small and spherical seeds and subsequently releasing them away the parental trees after digestion of the fruit (endozoochory). A lower proportion of the total species (15%) have a different form of zoochory with indehiscent well-protected fruits (with a wood-like exocarp) enclosing succulent endocarps or, when dry, containing a sweet to sour oleaginous substances (like honey) and are particularly attractive for consumption by cattle which eat these fruits during the dry season together with their enclosed bigger seeds that are dispersed in the cattle dungs. These tree species are considered to be originally dispersed by big mammals (mammalochory) like native horses, gomphotheres, ground sloths, and other megafauna, which are already extinct from South-America (Pleistocene) and have been replaced today by cattle (seed dispersal anachronism) reducing the extinction risk of these species (Janzen and Martin 1982).

Table 2.6. Dispersal modes of tree species commonly found in active pasturelands categorized according with fruit and seed characteristics (Cornelissen et al. 2003)

	Anemochory		Autochory		Mammalochory		Zoochory		
1	Ced odor	15	Alb guac	28	Aca penn	39	Acr mexi	57	Cur amer
2	Cei aesc	16	Bra inti	29	Alb sama	40	Ann cher	58	Dyo Sali
3	Cei pent	17	Cass elli	30	Cas sylv	41	Ann reti	59	Ery berte
4	Coc viti	18	Cro drac	31	Cres alat	42	Bix orel	60	Fic isop
5	Cor alli	19	Del reg	32	Ent cycl	43	Bur sima	61	Fic maxi
6	God aesc	20	Glir sepi	33	Gua ulmi	44	Cal cand	62	Gen amer
7	Lon parv	21	Leu shan	34	Hym coub	45	Cap fron	63	Mac tinc
8	Lue cand	22	Lon macr	35	Ing vera	46	Cas cory	64	Mut cala
9	Lue sema	23	Lon mini	36	Psi guaj	47	Cas gran	65	Myr flor
10	Pach quin	24	Lys auri	37	Spo momb	48	Cas peru	66	Phi lanc
11	Pla parv	25	Pte offi	38	Spon purp	49	Cec pelt	67	Pit dulc
12	Rob lind	26	Sap sapo			50	Cin trip	68	Ran arma
13	Tab ochr	27	Zant elep			51	Cop arom	69	Sap macr
14	Tab rose					52	Cor coll	70	Sci exce
						53	Cor dent	71	Tri amer
						54	Cor pana	72	Tri hava
						55	Cor pyra	73	Vit gaum
						56	Cup guat	74	Xyl flexu
								75	Zue guid

The second most frequent dispersal mode (19%) was wind (anemochory), as indicated by species having dry and woody fruits (capsules or legumes) which open during the dry season (dehiscent) to expose dry endocarps containing small and light seeds some with papus-like anatomical structures (wings). The third most frequent dispersal mode (17%) was characterized mainly by seeds without any particular additional structure (fleshy or dry), that are located inside dry fruits with woody exocarp having mainly explosive or passive dehiscence during the dry season (ballisticory), with no evidence for the role of a primary biotic or a-biotic vector (autochory).

The logistic regression analyses showed strong correlations between these dispersal modes and the measured fruit and seed traits. Anemochory was positively correlated with Sha_fru and Sha_see, and negatively with Mass_see, and weakly ($p \leq 0,10$) with Sha_see and Vol_fru Mammalochory was correlated positively to

Mass_fru, and Vol_fru Mass_see. In contrast, Zoochory was negatively correlated to Sha_fru, Mass_fru, Sha_see and Vol_fru. Autochory was positively correlated with Sha_fru. Just Vol_see was also not correlated to any particular dispersal mode (**Table 2.7**).

Table 2.7. Regression coefficient for logistic models (ß) between whole plant (H_max, WD, PHE) , leaf (SLA, LA, LDMC, LCC, LPC, LNC, FTF), dispersal traits (Sha_Fru, Sha_see, Mass_fru, Mas_see, Vol_Fru, Vol_see) with the main dispersal modes tree species commonly found in neotropical active pasturelands

	Anemochory	Autochory	Mamalochory	Zoochory
H_max	**0,04(0,0185) 69**	-0,01(0,6121) 69	0,02(0,1951) 69	**-0,03(0,0117) 69**
WD	-0,02(0,2129) 64	**0,04(0,079) 64**	0,01(0,5233) 64	-0,01(0,4126) 64
PHE	**0,05(0,0261) 59**	-0,04 (0,8843) 49	-0,03(0,2572) 59	-0,02(0,3282) 59
SLA	0,01(0,6532) 44	0,04(0,314) 44	**-0,06(0,0803) 44**	0,01(0,6941) 44
LA	-0,02(0,4207) 45	-0,02(0,4928) 45	-0,02(0,4791) 45	**0,05 (0,035) 45**
LDMC	0,0014(0,9581) 47	-0,0027(0,9278) 47	**0,07(0,0294) 47**	**-0,05 (0,0307) 47**
LCC	0,0025(0,8896) 58	0,03(0,1669) 58	**0,07 (0,0193) 58**	**-0,04(0,00287) 58**
LPC	**0,03 (0,1089) 58**	-0,0042(0,832) 59	**-0,05(0,0373) 59**	0,01(0,6362) 59
LNC	-0,0034(0,8432) 62	**0,07(0,0069) 62**	-0,05 (0,0673) 58	-0,02(0,1391) 62
FTF1	-0,01(0,7156) 46	**-0,08(0,0655) 46**	0,06(0,083) 46	0,01(0,8226) 46
Sha_Fru	**0,04(0,0407) 69**	**0,04(0,0299) 69**	0,02(0,2991) 69	**-0,06(0,0002) 69**
Mass_Fru	0,01(0,6294) 56	-0,02(0,4257) 56	**0,08(0,0062) 56**	**-0,04(0,0266) 56**
Sha_See	**0,11 (0,1017) 32**	0,02(0,4068) 62	0,02(0,3117) 62	**-0,04(0,0142) 62**
Mass_See	**-0,11 (0,0569) 36**	-0,0006(0,9761) 60	**0,07 (0,1036) 36**	0,0041(0,7823) 60
Vol_Fru	**0,04(0,1057) 58**	-0,01(0,7719) 58	**0,06(0,028) 58**	**-0,05(0,0108) 58**
Vol_See	-0,01(0,7759) 61	0,0013(0,9509) 61	0,03(0,1133) 61	-0,02(0,3002) 61

Showed data include the regression coefficient for logistic models ß, followed inside parenthesis by the significance of the regression (p value) and finally include the number of species by each regression n. Bold values were significant at p ≤0,10; bold and underlined values were significant at p ≤0,05 and bold but double underlined were significant at p ≤0,0001.

These correlations between seed and fruit traits and dispersal modes show that dispersal by wind was characterized mainly by bigger and longer fruits with longer and lighter seeds. Those species dispersed by cattle have bigger and heavier fruits with heavier seeds. In contrast, tree species dispersed by native wild animals were characterized by smaller, more spherical and lighter fruits with and lighter seeds. Finally, autochorous species were mainly characterized by longer fruits, but not by particular fruit and seed volume or mass or seed shapes.

Dispersal and whole plant traits

H-max, WD and PHE were significant ($P < 0.05$) correlated with dispersal modes (**Table 2.7**)), whereas whole plant traits correlation with dispersal fruit and seed traits were quicker (**Table 2.4**). The closest to this significance level were the positive correlations between H_max and Mas_fru ($p = 0.08$) and Vol_see ($p = 0.09$). There was weak evidence for a correlation between PHE and Vol_fru ($p = 0.11$). A total of 62% of the variability amongst the 22 tested species variability was explained by the two main axes of the PCA combining the three whole plant and six quantitative fruit and seed traits. A third axis increased the explained variability to 76%. These three axes had eigenvalues higher than 1 (**Figure 2.3**).

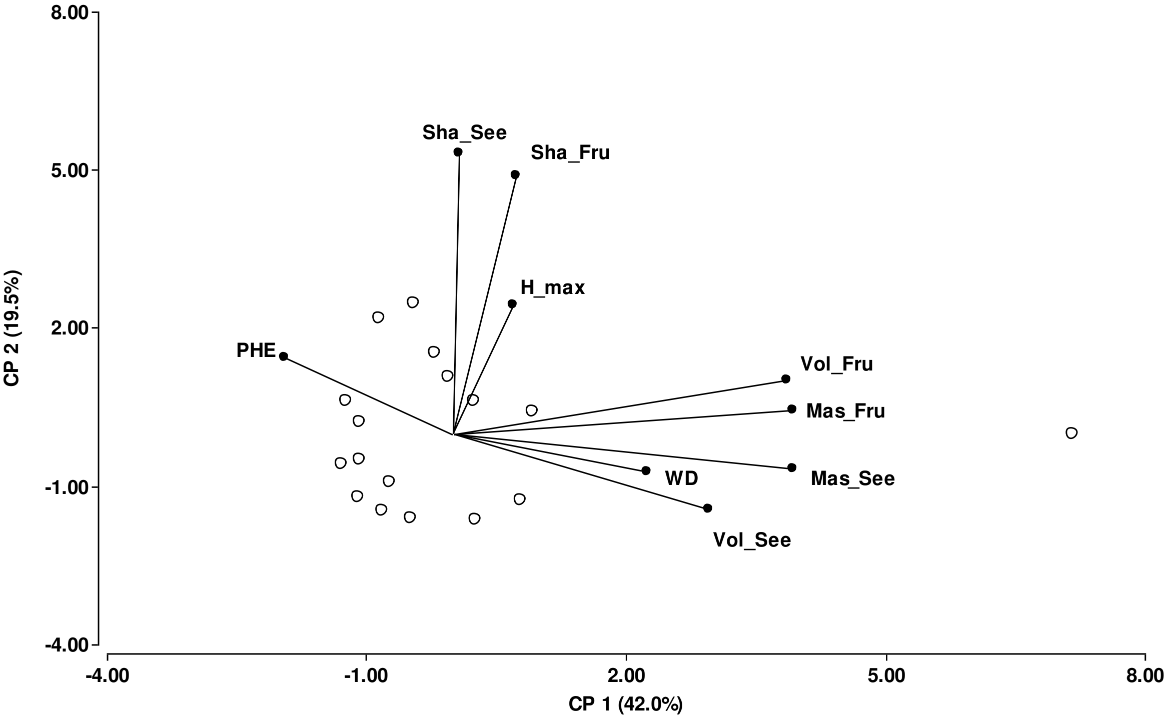

Figure 2.3. PCA Biplot showing species distribution by whole plant traits: maximum tree height (H_max), wood density (WD) and leaf phenology (PHE); and dispersals traits: fruit and seed masses (Mass_Fru and Mass_See), volume (Vol_Fru, Vol_See) and shape (Sha_Fru, Sha_See), measured for 18 tree species commonly found in actively-managed anthropogenic Neotropical pasturelands

Fruit and seed mass and volume were very strongly positively correlated with CP1 ($p < 0.0001$); fruit and seed shape were most strongly correlated with the second axis (CP_2) ($p \leq 0.0001$). However, the three whole plant traits, H_max, WD and PHE, were mainly correlated with the third axis (CP_3), with only WD showing a significant correlation ($p = 0.04$) with CP 1 (**Table 2.5**). Therefore, the first axis distinguishes tree species on the basis of dispersule size and weight, with denser wood being associated with bigger and heavier dispersules. The second main axis separate species on the basis of dipersule shape, and the third axis is largely unrelated to seed and fruit traits.

The PCA results emphasized the independence of the dispersule and whole-plant traits that is obvious in the correlations. Probably CP1 was determined by the very strong inter-correlation of the seed and fruit dimensions, and the whole traits has been pushed down because they are not correlated with dispersules and are less strongly correlated with each other. The logistic regression analyses between whole plant and dispersal traits highlights the association of H_max and PHE with anemochory (species reaching a greater stature and deciduous tend to be wind dispersed) and the negative association of H_max with zoochory (**Table 2.7**). WD was not strongly correlated with any dispersal mode.

These results mean that deciduous species and/or species belonging to the higher canopy stratum tend to be dispersed by wind and those tree species belonging to the lower canopy stratums in contrast tend to be dispersed by animals. In contrast, dispersule dimensions and dispersal mode are independent of wood density and its implications for species strategies. These results suggest also that taller tree species tend to have heaviest fruits and biggest seeds, meanwhile more deciduous tree species tend to have bigger fruits.

Dispersal and leaf traits

At least one of the fruit and seed traits was significantly ($p < 0.05$) correlated with each of the measured leaf traits (**Table 2.4**). Amongst the leaf traits largest number of significant correlations occurred for LA (negatively with four), LCC (positively with three), and LNC (positively with two). Amongst the fruit and seed traits the largest number of significant correlations occurred for Mas Fru (three positive and two negative); Sha Fru (two positive and one negative); and Vol Fru (one positive and one negative). In general heavier fruits tended to occur in species with higher LCC, LDMC, stronger leaves and lower LPC and SLA. The first two main axes for the PCA combining dispersule and leaf traits explained 54% of the variability for the 20 tested species (**Figure 2.4**). The first axis (CP1) was strongly significantly ($p < 0.01$) and positively correlated with all four dispersule mass and volume traits and two leaf traits (LDMC and LCC) (**Table 2.5**). The second axis (CP2) was significantly correlated ($p < 0.01$) with only fruit and seed shape. The explained species variability was increased to 67% and to 78% with the third and four main axes respectively (having also Eigen values higher than 1); their only significant trait correlation was between Sha fru and axis 4. Species' investments of biomass, carbon and nutrients in tree leaves were strongly correlated with the biomass, size and shape of tree dispersules. CP1 separated species with physically stronger leaves with high leaf dry matter and carbon which had large and heavy dispersules from species with the opposite attributes.

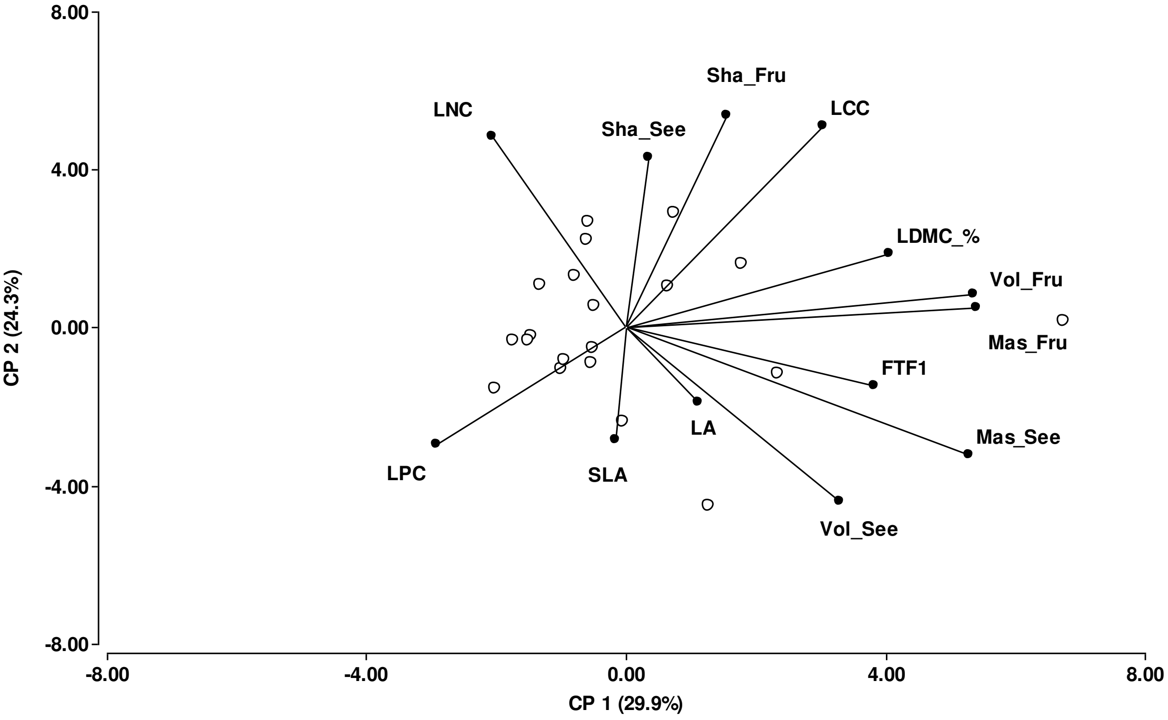

Figure 2.4. PCA biplot showing species distribution by dispersal traits: fruit and seed masses (Mass_Fru and Mass_See), volume (Vol_Fru, Vol_See) and shape (Sha_Fru, Sha_See); and leaf traits: specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), total leaf carbon, phosphorus and nitrogen contents (LCC, LPC, LNC) and leaf tensile strength (FTF), measured for 20 tree species commonly found in actively-managed anthropogenic Neotropical pasturelands

The logistic regressions results showed evidence that all the measured leaf traits were correlated with dispersal mode, most notably mamalochory (dispersal largely by cattle) (**Table 2.7**): mamalochory was significantly ($p < 0.05$) correlated with high LDMC and LCC and low LPC and SLA. In contrast zoochory (dispersal by native wild animals) was significantly correlated with low LDMC and LCC and high LA. Autochory was significantly positively correlated with LNC and weakly negatively with FTF ($p \leq 0.1$) . Anemochory was not significantly correlated with any leaf traits.

These results allow us to describe clearly LES associations with all dispersal components. Tree species dispersed mainly by local animals had big leaves with a reduced biomass and total carbon contents. In contrast tree species dispersed mainly by big mammals i.e. cattle, had physically strongest leaves with higher dry matter and carbon contents but with low N and P contents and a reduced specific leaf area. Tree species with parental seed dispersion showed mainly higher amounts of N with a reduced foliar strength. Finally, species with seed dispersed by wind tend to have leaves with a higher phosphorus contents.

Whole plant, leaf and dispersal traits

The final PCA including all measured/literature-derived whole plant, leaf and dispersule traits together was carried out for 25 tree species. The first two main axes explain together just 36% of tree species variability (20% and 16% respectively), and the third main axis (explaining 15%) increased the total to 51% and fourth, fifth and sixth main axes explained a further 11%, 10% and 6% respectively. Therefore, the six principal axes (having Eigen values higher than 1) together explain 78% of tree species variability in the complete multivariate traits distribution.

Axis 1 was significantly ($p < 0.01$) correlated with five leaf and one dispersule trait (**Figure 2.5**). It corresponds well with the LES being positively correlated with LDMC, LCC and FTF and negatively with LPC and SLA, while also being positively correlated with Mas fru. The second axis was more related to dispersule shape (significantly positive with longer seeds and fruits) as well as LNC and evergreen phenology. The third axis was very significantly ($P < 0.001$) positively correlated with H_max and negatively with SLA; it was also significantly ($P < 0.05$) positively correlated with LDMC and weakly ($p = 0.05$) positively correlated with long fruit. Axis four was significantly ($p < 0.05$) correlated with deciduousness and large fruit but negatively with WD. Axis five was positively correlated with LA and negatively with seed mass. LPC was the only trait significantly correlated with axis 6.

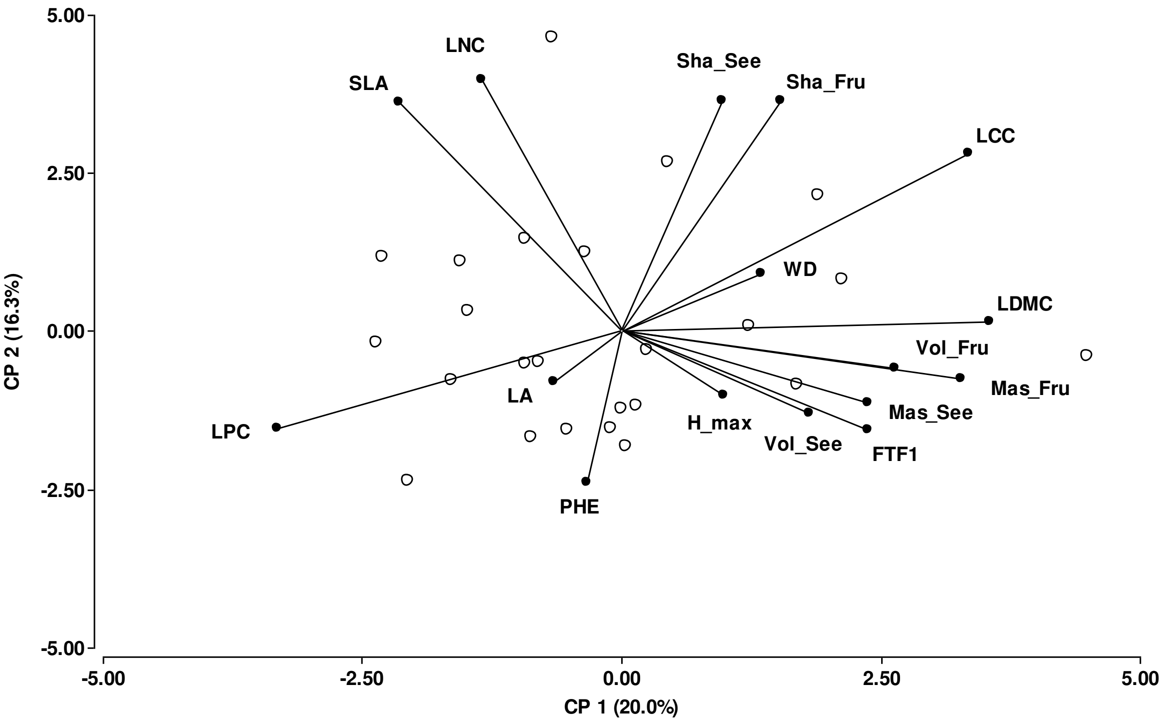

Figure 2.5. PCA biplot showing species distribution by whole plant (H_max, WD, PHE), leaf (SLA, LA, LDMC, LCC, LPC, LNC, FTF) and dispersal (Sha_Fru, Sha_See, Mas_Fru, Mas_See, Vol_Fru, Vol_See) traits measured for 25 tree species commonly found in actively-managed anthropogenic Neotropical pasturelands.

The first main axis corresponds well with the LES separating tree species with high leaf dry mass, carbon and strength from species with high leaf phosphorus content and SLA. Furthermore it demonstrates the association of this spectrum with fruit mass (high values associated with leaf resource conservation traits). The second main axis differentiates tree species according to dispersule shape and shows how longer shapes are associated with high leaf nitrogen content and evergreen phenology. The third main axis separates tree species reaching a high maximum height and tending to have physically stronger leaves with high dry matter content from those with a high specific leaf area. More deciduous tree species with lower wood density are shown to be associated with larger fruit by the fourth main axis. The fifth main axis shows an association between larger leaves and lighter seeds.

These results showed that whole plant, leaf and dispersal traits of tree species were not correlated with each other. No single axis explained more than 20% of the variation amongst species when all of these traits were analysed together, with five independent axes each explaining between 20% and 10% of the variation illustrating the complexity of the pattern of trait associations, and the high dispersion of species and trait vectors within this multivariate space with no tendency for them to form tightly-defined “functional groups”.

2.5 DISCUSSION

Whole plant traits

As expected *WD was not related to H max. PHE was positively correlated to H max and negatively to WD.*

We didn’t find any relationship between H max and WD meaning that taller and shorter species can develop similar wood densities. Taller tree species in this community (H max > 32m) like *Cedrela odorata, Ceiba pentandra* have indeed low wood densities (WD<0,46 g/cm^3) and species belonging to the lower canopy stratum (H max < 19 m) like *Pithecelloboum dulce* and *Lonchocarpus parviflorum* have some of the highest WD (WD > 0,69), but there were also other considerable number of other low stratum species like *Coclospermum vitifolium* and *Erythrina berteroana* which also share the low wood densities observed in the taller species. As suggested by Poorter and Bongers (2006) for all Hmax values, a range of strategies across the acquisitive-conservative spectrum are viable.

Our results show also that phenology, measured as the number of months tree canopy has a leaf cover under 50%, was negatively correlated with WD. This means that deciduous species, like *Ceiba pentandra* and *Pachira quinata* which can be considered drought avoiders (Marharjan et al. 2011), were taller and have softer woods than the evergreen species, instead those species reducing the canopy cover under 50% by less than one month, which can be then consider drougth-tolerants, like *Casearia sylvestris* and *Mutingia calabura*, were mainly characterized by low heights and hard woods.

Such correlations between PHE - WD and PHE - H max have been explained by previous studies according to tradeoffs between investments in water balance, in light requirements and in growth rates. The lack of significance between WD and H max can be related to the presence of diverse phenological status. Poorter (2008) hypothesized that wood fraction (in relation to gas and water fractions in tree stems) decreases with higher light requirements and adult stature of tree species, although he found such tendency for shaded tolerant species (significant negative) but not for pioneer species (relation that tend to be positive) due to the replacements of short lived species with low wood densities to quickly reach their maturity height to complete their life cycle , by taller, less light demanding but longer lived pioneers with higher WD to persist more long time. We found a significant negative correlation between WD and H max when just the more deciduous species were included in the analyses. Instead, a non-significant correlation was found again between WD – H max for "quick" deciduous (species with no more than 2 months with a reduced tree canopy) and evergreen species (species performing a complete leaf renewal in less than one month or performing continuous leaf renewals through the year). This implies that deciduousness and a low wood density are in fact an strategy for overcoming the higher drought stress and the higher cavitation risk faced by tall trees, probably in addition to wood density association with hydraulic traits (Poorter et al. 2010 Maharjan et al. 2011). In contrast, evergreen species have high wood densities and lower adults' stature, but these do not present linear relationship inside the observed range of heights and wood densities for evergreen species. Therefore, evergreen species might have developed additional morphological and physiological strategies to overcome water stress which do not necessarily compromise adult stature either and wood density tradeoffs.

Associations between WD – PHE – H max in open pasture sites seem be reflecting also differences in growth rates, although no formal analyses has been performed here to test this hypotheses. The taller species with low WD for example were extremely-deciduous species (between 4 and 6 months with a reduce leaf canopy cover) with relatively faster growth rates (*Cedrela odorata* increase 0,13 cm in dbh periodic annual increments - PAI) and can be considered long lived pioneers and drought-avoiders. The lower species with high WD like L. *parviflorum* and P. *guajava* were evergreen to moderate deciduous species (with no more than one month with a reduce leaf canopy cover) with lower growth rates (DAP increases in 0,06 and 0,07 PAI) and could be considered then shade and drought tolerants. The lower species but with low WD like C. vitifolium and E. berteroana were highly variable in phenology (between extremely deciduous to evergreen species) with a high light requirements but reach maturity faster with higher growing rates (dap increase 1,66 and 0,95 cm PAI respectively) (short-lived pioneers).

Temporal, vertical or horizontal variation in light levels does not strongly affect tree growth in dry forests (Fowler 1989; Nath et al. 2006). No previous studies have evaluated the correlations between these vegetative traits for tree species outside forests-stand conditions. Probably light requirement is not the most important factor to model relationships between WD and H max in dry seasonal sites. Variability in water availability, which may vary strongly among years (Bullock 1997) and have important consequences for tree growth (Brienen et al. 2010) could be a more influential factor in a strong-light environment. This could be observed in the resulting axes from PCA. The drought resistance by tolerance or avoidance seems to be driving the expressions of WD and H max and its relationships in tree communities under water stress conditions. Outside the forest cover, in open pasture conditions the ability to survive in water-stress conditions could determine survival and maintenance of viable populations. Therefore, we should not expect to find a strong negative relation between H max and wood densities in tree community, mainly because tree forest species surviving here will be those well adapted to tolerate water stress thanks to several different strategies beyond the tree height – wood density tradeoffs.

Leaf traits

***PHE was positively correlated to LPC, negatively to FTF and LDMC but not related to SLA. SLA was positively correlated to LNC but not to LPC. SLA was also negatively correlated to FTF and LDMC. It was hypothetized that LPC will be positively correlated to PHE; LPC and LNC positively correlated to PHE and negative to SLA*.**

Phenology was positively correlated to LPC as found by Marharjan (2011) but we didn't find any relationship between phenology and SLA, contrary to Leaf Economy Spectrum expectations. PHE was in addition negatively correlated to LTS, although no correlation was found either with LA, LCC or LDMC. Therefore deciduous species were characterized by high leaf phosphorus contents and a reduction of leaf tensile strength. This result suggests that deciduous species could be effectively reducing water loss via stomata due to the higher P content, which affect CO_2 concentrations and reduce water loss (Wright et al. 2001) but without implying an expected higher efficiency in light use reflected in high rates of photosynthesis and respiration expressed by a low SLA and high LNC. This observation could imply that deciduous species must have alternative morphological or physiological strategies to overcome the expected higher photosynthetic efficiency. The reduced WD could allow deciduous and the higher P content in leaves, could be an adequate strategy to overcome the water-economy tradeoff, without compromising a higher range in SLA values. Deciduous species probably have a higher vessel density and to store high amounts of water in wood tissues and the high P levels in leaf tissues increase the CO_2 gradients reducing stomata water loss during the wet season. Leaf abscission in dry season must be reducing risks in water economy due to the higher range of SLA observed for these species.

Evergreen species in contrast tend to have a small P content in leaf and a high LTS consistent with a conservative strategy. However, the lack of significance between PHE and SLA remains unclear for evergreen species which have no clear adaptation to water stress in wood tissues. Could the lack of correlations between LPN and PHE to SLA be reflecting the high variability of SLA values found for the whole species community with different PHE status? When correlation between LPC and SLA was partitioned by PHE status, a significant positive correlation between SLA – LPC was observed just for the more evergreen species (those with up to 3 months in reduced canopy cover) and no significant correlation was found for the more deciduous species (between 4 and 6 months with a reduce canopy cover). Therefore, evergreen species will have low LPC with respect to deciduous species, but the SLA will decrease with LPC inside this reduced range of phosphorus content for evergreens. This positive correlation between nutrients and SLA has been explained by a larger fraction of support structures in thicker and denser leaves that possess a lower SLA, and the reduced requirement for mineral nutrients for construction of foliage with low SLA (Niinemets and Kull 1998; Niinemets 1999). This observation goes in line with previous studies expecting that nutrient contents traits as major contributors to the acquisitive-conservative leaf traits spectrum (Díaz et al. 2004) increased with a reduce leaf carbon resources allocations, expressed here in a negatively correlation to LTS, and have a more efficient light capture per unit leaf mass because of their high SLA (Marharjan 2011), except that this strategy in outside tree communities apply just to more evergreen species.

LNC was not correlated to LPC. LPC and LNC were negatively correlated to LDMC. LPC is positively correlated to PHE but negatively to LCC and FTF. LNC is positively correlated to SLA and FTF but negatively to LA. We expect that LPC and LNC were negatively or positively correlated to SLA but negative to LDMC, LCC and FTF.

In comparison to LES (Wright et al. 2004) our results showed that leaf phosphorus and nitrogen content do not co-vary equally with changes in leaf dry matter investment by area unit or either positively to leaf span related traits like phenology.

LNC was positively correlated to SLA and no association was found with PHE. Instead as expected, LPC was positively correlated PHE, but not correlated to SLA. In addition to LES Wright (2004) defined mostly by nutrients concentrations and SLA, our results showed also that LPC, LNC and SLA were correlated independently to other leaf traits like LDMC, LCC, LA and FTF. LNC was negatively correlated to LA in addition to its positive correlation to SLA. Instead LPC was negatively correlated to LCC in addition to its positive relation to PHE. Both nutrient contents in addition to SLA were also inversely correlated to FTF: LNC were positivity instead LPC and SLA were negatively correlated to FTF.

This result means that, species with a high investment of dry matter in the construction of a functional leaf unit (independently of the area) will in fact produce leaves with low content of phosphorus and nitrogen as expected, but both nutrients must be related to different physiological mechanisms reflecting in their independent variability to other leaf traits. Leaf nitrogen content is low in big leaves and in leaf with a higher investment in dry matter content, but increase together with specific leaf area implying a low efficiency in leaf construction, i.e. a higher dry matter required to construct a determinates leaf area. The positive correlation between nutrients and SLA has been explained by a larger fraction of support structures in thicker and denser leaves that possess a lower SLA, and the reduced requirement for mineral nutrients for construction of foliage with low SLA (Niinemets and Kull 1998; Niinemets 1999). Additionally, higher N content is positively correlated to A_{mass} (net maximum photosynthetic rate per unit mass). LNC increases with FTF, implying that plant resources investment in defense structures against physical damage increase when nitrogen content in leaves also increase, an important feature in systems with a high herbivore rate like active pasturelands. Leguminous species, those expected to have the higher levels on nitrogen in leaves will consequently be expected to have strongest leaves reflected in a reduced herbivory rates which could be reflecting also a reduced decomposition rates.

The phosphorus contents in contrast, increases with PHE, do not vary linearly with specific leaf area but decrease with higher overall leaf dry matter content and higher structural carbon inversions for leaf construction. This means that higher phosphorus content are found in deciduous species with a reduced carbon invested in structural and overall leaf construction and in leaf defense structures. This result goes in line with previous observations where LPC has been found also to decrease significantly to increasing rain fall (Marharjan 2011) and positively correlated to hydraulic related traits like PHE and negatively with LDMC, LCC and FTF as LPC is a major contributor to the acquisitive-conservative leaf traits spectrum (Díaz et al. 2004). A higher LPC content in deciduous species and associated traits goes also in line with previous observations of a positive relation with litter decomposition rate (Prajjwal et al. 2011).

LA was negatively correlated to LCC and LNC. We expected that LA was positive/negative correlated to H max, WD, LPC, LNC, SLA, LDMC and LCC.

LA relationships with leaf and stem economics spectra are not so clear. Some authors have observed strong correlations between LA and SLA that could be positive or negative (Niinemets 1998, Shipley 1995) instead was not included into leaf spectrum reviews (Wright et al. 2004). It has been hypothesized that dense woods could support bigger leaves due to a greater biomechanical strength (Niklas 1995) and increased cavitation resistance (Hacke and Sperry 2001). However, Baraloto et al. (2010) highlighted in addition that the higher construction costs associated to denser woods could also favour smaller leaves presence (Hacke and Sperry 2001; Pickup et al. 2005; Wright et al. 2007).

Our results cannot deny or support hypotheses about direct relationships between WD and LA, or between WD and SLA but instead we found indirect relationships between WD, LDMC, LCC, SLA and LA. WD was positively correlated to LDMC, and SLA and LA were negatively correlated to LDMC and LCC respectively. Therefore in this system, species with more resources inversion in wood construction invest also more on overall leaf construction, including structural and functional leaf components. This species with costly overall leaf constructions (high LDMC) mainly reduce the overall resources invested by leaf area (low SLA) to produce cheapest leaves no matter what leaf area produced. Instead, increases in leaf area were directly reflecting reduction in structural leaf construction (low LCC) but not necessarily in overall construction costs (LDMC), no matter these last two carbon leaf measurements also positively co-varied. Unless, we can indirectly relate increases in construction costs of wood tissue to reduced LA, our results underlined two additional relations: i) LA and SLA could be decoupled from STS (at least were not directly correlated to WD) but not from LES, being correlated to LCC and LDMC respectively, and therefore ii) the importance of a fine partitioning in the measurements of construction components is required, like LDMC and LCC, to understand in detail the acquisitive and conservative leaf or wood spectrums. Our results about coordinated tissue investments in leaves and wood support the hypothesis that allocation strategies of cheap or expensive tissues occurring to a whole plant level result in synchronized construction costs of leaf and stem tissues (Grime et al., 1997 in Bartolo, 2010).

We should emphasize here that WD is independent from LA and SLA. Therefore a high or low dry matter inversion in wood (WD) did not imply a determinate direction in LA or SLA variability. These traits were definitely linked closely to C resources inversions and construction costs in both important plant organs, but many different structural or physiological strategies could be available to avoid water or light stress in leaves, and even tissue damage or lost by herbivores, independently on mature leaf area expression or the dry matter ratio inversion in leaf and woods.

In contrast to Bartolo et al. (2010) we observed that LA was associated to LES but decoupled from SES maybe responding to his suggested prediction of a higher association between LA to LES in sites with a lower rainfall. But a decoupling of LA from FTF was also observed in this tree community no matter the higher risk of tissue damage by herbivores in the studied system, contrary to his second prediction of a reduce advantages of a tougher tissue with an increasing laminar size. In contrast to Bartolo et al. (2010), we found that larger slight and cheap leaves related to soft woods are also a plausible life vegetative strategy.

Relationships between leaf and vegetative traits of Neotropical tree species

Our results evidence an interesting story about the structure of interactions between two important plant species variability dimensions like those expressed by whole plant and leaf traits. Deciduous species are predicted to have acquisitive leaves to maximize photosynthetic production during their short lives, while evergreen species should have conservative leaves, partly in order to tolerate the dry season.

Contrary to the decoupled wood density hypothesis about WD being orthogonal to all the leaf traits, WD was correlated to other leaf and vegetative traits. WD was negatively correlated to PHE and positively to LDMC and FTF, but not correlated to SLA as expected for some authors (Wrigth et al. 2006). Therefore, species with dense woods are evergreen species with high amounts of dry matter content for overall leaf construction represented also in strong tensile force. Instead, deciduous species with low densities will have a low dry matter content invested in overall leaf construction and reflected also a low capacity to resist physical damage. WD has been correlated to water economy and resistance to damage and could be the driving factor for the observed tendencies in open pasture sites, where deciduous species escape to drought stress reducing water loss through leaves and probably storing water in wood. In contrast, the evergreen species will have to invest higher amounts of dry matter resources in their leaves to avoid water loss and resist herbivore damage to leaves when no water is being probably stored in wood at the same time that a hard wood could make them resist the higher herbivores visits during dry seasons.

In contrast we found that not single trait was unrelated indicating orthogonality of the ecological strategy dimensions represented i.e leaf, vegetative and dispersion. All leaf traits measured were correlated to other traits belonging to the same leaf dimension but also to traits belonging to one or two of the additional dimensions represented by vegetative and/or dispersal traits. LA and LNC were correlated to dispersal traits like Fru Sha, instead LCC was correlated also to SeeSha and FruMass. LDMC was the only leaf trait correlated to a vegetative trait i.e. WD in addition its correlations to other leaf traits but without being also correlated to any trait in the dispersal dimension. In contrast, SLA, LPC and FTF were leaf traits correlated to vegetative and at the same time to dispersal dimensions' traits. SLA was correlated to H max and to Mass_fru; LPC was correlated to PHE and to Sha_fru, Sha_see and Mass_see; finally FTF was correlated to WD and PHE in addition to Mass_fru and Mass_see.

Dispersal traits

Biggest, heaviest and large fruits do not have small, lighter or spherical seeds

All measured dispersal traits (fruit and seed mass, volume and shapes) were correlated between each other indicating mainly the absence of a triangular relationship between fruit and seed traits. Fruit volume, mass and shape were strongly correlated to seed traits implying that biggest, heaviest and longest fruits carry the biggest, heaviest and longest seeds. Our results do not support the expectation of a 'triangular' relationship between seed and fruit size due to physical constraint which determine that seeds cannot be bigger than fruits and imply that large-fruited species could have a wide range of seed sizes whereas small-fruited species should have small seeds only (Wright et al. 2007). The positive correlation found between fruit volume and seed volume indicates that biggest fruit with smallest seeds was not a successful strategy within this tree community. In addition to Wright et al. (2007) observations about the tight correlations between fruit and seed volume, we observed also that fruit and seed masses plus fruit and seed shapes were also strongly correlated (r values were 0,80, 0,39 and

0,47 respectively). Therefore, biggest, heaviest and longest fruits have biggest, heaviest and longest fruits seeds although biggest, heaviest and longest fruit could anatomically carry smallest, lighter and more spherical seeds. These results implied that strong functional relations in addition to mechanical constraints determine together fruits and seed morphology, supporting the idea that coordination of life-history traits together with the mechanical constraints define better the relationships between fruit and seed size as suggested by Moles et al. (2005).

Biggest fruits and heaviest fruits have bigger and heaviest seeds with the higher biomass investments.

The strong positive correlations between fruit and seed volume and masses implied also a coordinated plant investment on dispersal structures with big and heaviest fruits carrying also biggest and heaviest seeds. These correlations mean also that trees make similar inversions i.e. highest or lowest, on both dispersal structures and on parental provisioning granted for offspring establishment. In fact, we observed in addition to the very obvious finding that volume and mass were also tightly correlated, also the less obvious findings that i) fruit and seed masses were correlated and that ii) fruit volume was tightly correlated with the whole seed morphology (mass, volume and shape). Fruit volume association with seed morphology and fruit and seed mass correlations suggests that trees develop a coordinated strategy to allocate more or less resources to the whole dispersal structures and not just to seed volume. Large-seeded tree species have higher survival through early seedling establishment than small-seeded species (Moles and Westoby 2004). According with the highest investments on seed, more expensive investment on fruits structures should also represent an inherent benefit in the dispersal process. Bigger and heaviest fruit and seeds probably follow a particular dispersal mode that increases probabilities to reach a higher number of safe places for the specie, where once arrived bigger no matter their lowest production, bigger seeds will have an increased survivorship in contrast to the higher production of smallest seeds.

Tree investments on dispersal traits are coordinated with dispersal mode

Previous studies have mentioned correlations between seed mass with dispersal modes (Westoby et al. 1996) but a complete characterization of fruits and seeds traits by dispersal mode are uncommon. Fruits and seeds of tropical tree species vary widely in their size and morphology and are dispersed by a broad array of dispersal agents (Levey et al. 1994; Muller-Landau and Hardesty 2005). Seed dispersal patterns depend on the interaction between the local frugivore communities with the plant attributes that influence attractiveness to dispersers, or with plant attributes which affect the final deposition of seeds in the case non animal assisted dispersion. The majority of studies have been focused on relationships between seed mass or seed production with dispersed distances from parental trees or with height of parental tree (Moles et al. 2004, 2008), the relationships between seed mass with other dispersal traits and with different dispersal modes has paradoxically receive less attention. The magnitude and spatial distribution of seed rain clumping and in any bias in where the seed arrives in a determinate habitat is at least as important as the maternal resources (Muller-Landau and Hardesty 2005) and are necessary in order to understand if the different paths that tree species follows in a community achieve or not a more successful regeneration.

We have found that in addition to seed mass other seed and fruits traits have a stronger functional correlation with dispersal modes. Fruit and seed volume, mass and shape were correlated with the main dispersal modes of tree species commonly found in active pasturelands. In fact not one dispersal trait was correlated to all the main dispersal traits within this community, rather different fruit and seed traits were more strongly correlated to one dispersal mode than to another, explaining impossibility to predict dispersal modes based in a unique dispersal trait like seed mass. The strongest and more abundant relationships were found between fruit and seed shapes, fruit volume and masses with zoochory and mammalochory followed by fruit shape and seed masses with anemochory and with autochory, reflect the higher proportion of species dispersed by biotic agents in tropical lands. Tree species dispersed by local fauna showed the more rounded, smallest and lighter fruits carrying also the most rounded seeds. In contrast, tree species dispersed by big non-volant mammals' i.e cattle, have the biggest and heaviest fruits carrying the heaviest seeds. Tree species dispersed by wind have the lighter seeds and the longest fruits. Those trees with unassisted dispersion tend to have longest fruits, but were not correlated to fruits or seed masses.

The facts that fruit volume was related with all seed morphology and that seed mass together with other seed and fruit traits were correlated with particular dispersal modes imply that tree species balance the highest investments on dispersal structures and maternal resources to offspring's during dispersal process, even previous to germination or early growing stages. Therefore, biggest fruits have the highest probabilities to be heaviest and longest ones and also the highest probabilities to have the longest, heaviest and bigger seeds (independently of the number of seeds by fruit) and to be dispersed by big mammals which determine seed spatial distribution increasing or reducing their inherent probabilities to survive. Similar observations about selective consumption driving big and heaviest fruit and seed has been found in tree species dispersed by large mammals in Africa and South America (Janzen and Martin 1982). Smallest fruits had the higher probabilities to be spherical and lighter carrying also spherical fruits and being dispersed by local fauna like birds and bats. The consumption of fleshy fruits by frugivorous animals has been reported to affect the maximum mean fruit size for some plants, particularly the relationship between fruit size and gape width determines whether or not the fruit can be swallowed by some bird species (Jordano 1987). Endo-zoochorous dispersing birds can be expected to optimize their energy intake through fruit selection and hence exert a positive selection even with fruit content as their reward, translating this selection to seed morphology, that is to say, favoring big enough fruits with small enough and easy swallowed seeds (Sobral et al. 2010). The time seeds remain passing through dispersers´ systems and therefore the dispersal distances vary according to animal and seed size. Instead, rather longest fruits tend to have lighter seeds dispersed by wind or by the same parental tree. The different dispersal vectors caring big or small seeds define the distribution of seed rain for both seed sizes (Muller-Landau and Hardesty 2005).

Tree species with more expensive fruits and seeds correlate with dispersal modes with a more dispersal effectiveness i.e a higher probability to colonize a safety place to establish successfully new offsprings. There is wide variation in patterns of primary seed rain among tropical tree species (Gentry 1982). Seed dispersal mode did explain significant variation in seed rain clumping: animal-dispersed species showed higher clumping of seed deposition that wind or autochorus dispersed species unless did not explain significant variation in seed dispersal distances due mainly to the high variability within species with the same dispersal mode (Muller-Landau et al. 2008). Substantial proportions of interspecific variation in seed production, seed dispersal distances, and clumping of seed deposition has been found to be explained by relatively easily measured plant traits, especially dispersal mode, seed mass, and tree height (Muller-Landau et al. 2008). In consequence, dispersal modes with a higher clumping distribution of biggest seeds away enough the parental trees but directed to specific favorable habitats, like has been observed commonly for endozoochoruous dispersion by nonvolant mammals, could increase seed survival and dispersion fitness to compensate the costly fruit and seed and their low production. In contrast, tree species with lighter seeds and/or fruits having a relatively lower construction cost expressed mainly by lighter seeds and not so heavy fruits, were correlated with dispersal modes with a less specific seed dispersal distributions commonly exhibited by abiotic vectors like wind or by the non-assisted dispersion like ballistically or explosive fruits, reducing the probabilities to reach safe places for survival increasing seed mortality but compensated by an abundant seed production.

The fact that seed mass and fruit mass were related to each other supports the idea about a coordinated investment of resources for dispersal structures compensate by a more effective dispersal mode. However not only fruit and mass shape were correlated with dispersal modes, rather a specific combination of dispersule volume, mass and shape were correlated to the main dispersal modes identify for this tree community, according with the stated dispersal syndromes idea. As a whole, more expensive dispersule constructions have more focal dispersal modes, meanwhile lower cost dispersule constructions have more dispersal modes with a resulting wider scope, confirming again the initial idea about tree investment on dispersal traits coordinated with other stages of tree life history. In this tree community fruit volume can be considered a relatively easy measurable and good indicator of tree investment on dipersule structures due to its strong correlations with other fruit characteristics and with the whole seed morphology (volume, mass and shape).

Fruit and seed volume and mass were orthogonal with fruit and seed shape

Fruit and seed shape co-varied independently from fruit and seed volume and masses suggesting that changes in fruit and seed shape could be responding to different selective forces than those operating for dispersal masses and volume. Although fruit and seed shape were strongly correlated between each other, neither fruit or seed shape were correlated with seed volume or mass, meanwhile seed shape was indeed correlated with fruit morphology. This lack of association between seed shape and seed volume and mass, and its strong correlation with fruit shape imply that seed shape could be an independent dimension of tree natural history nevertheless their correlation with fruit and seed masses and with dispersal modes. In fact, the multivariate analyses confirm these observations from the cross species correlations, showing that fruit and seed volume and mass were correlated with the main principal component and instead fruit and seed shape were mainly correlated to the second and orthogonal axes.

Seed shape could be responding to additional selective forces related with tree reproductive stages further to dispersule production and dispersion, like seed dispersal and seed incorporation to soil seed banks. Fruit shape was correlated with fruit volume and mass and strongly correlated with seed shape, meanwhile seed shape was not correlated either with seed mass nor volume. The first PCA separates two orthogonal axes the first for mass and volume and the second for shape. This implies that dispersal shape was not subjected to the same co-variability observed for seed and fruit masses and volume. Seed size and shape predict seed persistence in the soil for British and Argentinian herbaceous plant species (Thompson et al. 1993, 1994, Funes et al. 1999). Those species with small, rounded seeds tend to have persistent seeds while those with larger, more elongate or flattened seeds usually lack persistence. Ease of burial, as small, rounded seeds are incorporated into the soil more easily than large, elongated or flattened seeds and are therefore less likely to be eaten by seed predators determining seed longevity. However, species with large and/or elongate or flattened persistent seeds were relatively common as well as small and rounded persistent seeds in New Zealand and in Australia (Leishman and Westoby 1998, Moles et al. 2000). Moles et al. (2000) suggest that species with small, rounded seeds cannot help but be incorporated into the soil, and are only ecologically viable if they have the ability to persist until such time as a disturbance event brings them back to the surface. A possible relationship between seed size, shape and immediate germination was proposed by Moles et al. (2000) as a functional relation underlaying the size and shape variability and persistence.

Seed mass has been found positively correlated with time to seedling emergence, and negative with time between emergence and production of the first true leaf, but not with seedling establishment probably due to many stochastic factors affecting seedling establishment during any given recruitment episode at any given site. Seed mass was not related with cause of death, but 57% were killed by herbivory and 21% % were killed by drought (Moles and Westoby 2004). Rapid germination can be advantageous in environments where favourable conditions for seedling establishment are short-lived. Early leaf production might also be important in determining the outcome of competitive interactions between large and small seedlings, through their effects on the size of seedlings at encounter. Small-seeded species have an initial advantage over large-seeded species, as the number of seeds a plant can produce for a given amount of reproductive effort is negatively related to seed size. But biggest seeds will compensate by seedling establishment due to more resources but also for a higher probability to reach safety places according with dispersal mode.

The biggest investments does in seeds and fruits for a dispersal mode that maximizes the probability to find safety places for germination probably to pay off by a higher seedling establishment due to the highest resources invested in dispersal. Correlations between fruit and seed masses with dispersal modes could probably evidence a plant strategy to assure a successful colonization and natural regeneration through new open areas like open pasturelands. This reproductive investment in dispersion strategies can be related also with tradeoffs among biomass resources allocation to other plant structures like leaf or whole plant traits related with further growing and survival within the colonized environment.

Lighter but not small seed species have abiotic dispersal vectors

Our results also support previous observations related with the higher abundance of vertebrate seed dispersal agents in tropical ecosystems that might have allowed tropical species to radiate into larger seed masses than was possible for species growing in the temperate zone, where the predominantly abiotic dispersal agents might favor small seeds (Lord et al. 1997). Half of the tree species (49%) were mainly dispersed by local animals (zoochory) which in addition to those tree species particularly attractive for cattle consumption (15%), due to woody fruits but filled with oleaginous substances (mammalochory), make of endozoochorous the most common dispersion mode. Just 19% was observed for those tree species using wind as dispersal vector (anemochory) while the resting 17% have unassisted dispersion mode (autochory). In contrast to wind dispersed seeds, the three species dispersed by cattle were also correlated with seed mass, having the biggest seeds.

In contrast with previous empirical data (Leishman et al., 1995) our results confirm that species with wind dispersal have lighter but not smaller seeds than species with animal dispersal. The statement that small seed species have abiotic dispersal vectors has been widely accepted without making a clear differentiation among seed mass and seed volume. Accordingly to this perception we found that seed volume and seed mass were positively correlated, but in contrast to the previous statement we also found that seed mass was correlated to dispersal modes like anemochory and zoochory, meanwhile seed volume was the only seed trait not associated with any dispersal mode. These results imply that dispersal mode cannot be predicted only by seed size probably due to a huge range in seed size amongst wind dispersed species, as indeed there is too amongst animal dispersed species. More detail should be take into account to distinguish seeds that are consumed within fruit and pass through animals guts (which limits their size) versus those seeds dispersed by wind which could have a bigger volume but must be lighter or even can be heavier than some of the endo-zoochorous dispersed by local fauna but have aerodynamic adaptations i.e. wings.

Tree investments on dispersal traits are coordinated with other stages of tree life history

Dispersal traits and modes were correlated with whole plant traits

Whole plant traits and dispersal traits were strongly correlated with dispersal modes meanwhile tree maximum height and leaf phenology were marginally correlated with fruit mass and seed and fruits volume. These results showed that tree investments in dispersal structures were also correlated with tree investments in other stages of tree life history like growth rate, defense against physical damages and tolerance to drought, expressed by the variability of H_max, WD and PHE. The strongest associations between whole plant traits and dispersal traits change for each dispersal mode, indicating that the tradeoff between plant resources allocated to dispersal or to other plant structures were not independent from tree strategy assumed during dispersion. Maximum tree height was correlated with anemochory and zoochory but not with autochory or mammalochory. Wood density was only correlated with autochory and leaf phenology was only correlated with anemochory. Instead, fruit shape was correlated with anemochory, autochory and zoochory but not with mamalochory. Fruits mass and volume were mainly correlated with mammalochory and zoochory, instead seed mass and shape were only correlated with anemochory and zoochory. Independently of tree dispersal mode, taller tree species just tend to have heaviest fruits and biggest seeds, instead more deciduous tree species tend to have biggest fruits. These results indicate that in order to understand the implication of whole plant and dispersal traits correlations the dispersal mode is a relevant condition that has been manly neglected by so many cross species relationships studies.

The observed associations between whole plant traits with dispersal modes and fruit and seed traits indicate that tree maximum height, leaf phenology and wood density were components not isolated from reproductive fitness, rather were articulated by dispersal modes with strongest associations with fruits and seed morphology. Ours results show up for example that relationships between plant height and fruit and seed morphology co-varied at different levels within each dispersal modes to define tree life strategies. Seed mass and tree height do not co-vary in similar strength by each dispersal mode. Seed mass and tree height were correlated with tree species dispersal by wind; meanwhile only seed size, but not tree maximum height were correlated with tree species dispersed by big non-volant mammals. In contrast, tree height but not seed mass, was correlated with dispersion by local fauna; meanwhile either tree height or seed mass were correlated with non-assisted dispersion. These differences of correlations between tree height and seed size by dispersal show up the variability that tree species have in life styles to deal with dispersal success integrating other stages of tree life history with fruits and seed characteristics. Similarly in a large-scale, cross-species quantification about correlations between dispersal distance and both seed mass and plant height, Thompson et al. (2011) showed that seed mass was positively related to mean dispersal distance, that plant height had substantially stronger explanatory power than did seed mass but also that the relationship between seed mass with dispersal distance was not significant within dispersal modes. As suggested by Thompson (2011) this lack of relationships between seed mass and dispersal distance could be because species adjust their investment in energetic rewards for dispersers or dispersal structures (primary or secondary) to increase dispersal distances, depending not only in seed mass. In addition, as observed in our results, plant resources investments in dispersal structures and the resulted tradeoffs between dispersal and whole plant traits changed according with each dispersion strategy.

In fact, four clear tree species morphological and functional strategies come out from these whole plant and dispersal traits associations. 1) Taller and more deciduous trees species have wind dispersed seeds, having biggest, longest and heaviest fruits with biggest, longest but lighter seeds. 2) Smallest tree species were dispersed by local fauna, having smallest, lighter and more spherical fruits caring more smallest and rounded seeds. 3) Tree species with non-assisted or parental seed dispersion have longest fruits, dense woods (direct correlations), more evergreen canopies and heaviest seeds (indirect correlations). Finally, 4) tree species dispersed by non-volant mammals were not directly correlated by whole plant traits, being characterized more by their biggest and heaviest fruits carrying also heaviest seeds.

Tree species dispersed by local fauna have smallest and lighter fruits and have shorter tree sizes probably according to fauna vertical stratification. Birds and bats mainly forage the low medium strata in dry – humid forest were a highly availability of rather small fruits are founded. Instead tree species dispersed by non volant mammals have the biggest and heaviest fruits and the heaviest seeds but have not any particular height. Dispersion of these tree species do not require of a particular height to expose fruits and increase dispersal success. Other authors observed that endozoochorous species that were protected, large and coloured by orange, yellow, brown or green were classify as mammal-dispersed (nonvolant mammals including rodents, ruminants and elephants), in contrast to unprotecteck (no husk) relatively small (less than 1,4 cm diameter) and red, white, black, blue, purple or multicoloured (Janson 1983, Gautier-Hion et al. 1985, Gentry 1982, Willson et al. 1989) which contrast inside the green canopy. Gentry (1982) observe also that tree species dispersed by bird and baths were shorter than those dispersed by mammals. In rain forest the non volant mammals account for the higher consumption of fruits and seed biomass. The big and heaviest ripe fruits of these species are released to the ground, beneath or near the canopy edge, were foraging mammals found them and eat them (Guimarães et al. 2008) attracted mainly by the smell sense due to the in general strong sweet-sour smell of like honey substances surrounded seeds, and therefore probably without have a particular dispersal advantages with a higher or reduced height for dispersal success.

In contrast, the dispersal distances of the longest and lighter seeds from did clearly increase in taller tree. Previous studies have identified that taller species have larger seeds and take longer to reach maturity. Plant height is another important trait for species' life-history strategies, affecting species' abilities to capture light (Falster and Westoby 2005). Tall species within all life forms tend to have higher annual seed production, larger seeds, greater longevity and greater reproductive lifespans than do short species (Moles and Leishman 2008). We do confirm this cross species correlation between tree height and seed volume but at marginal levels. In addition, we find a less reported correlation between tree height and dispersal mode, indicating that taller tree species were wind dispersed species, having heaviest and longest fruits but lighter and longest seeds. Taller anemochorous species have heaviest fruits probably due the woody and dehiscent fruit epicarp which open when ripe responding to drought stress, exposing the lighter seeds to be transported by wind. The longest fruits have a longitudinal distribution of seeds which probably increase the contact surface of winds passing though the fruit to disperse seeds. We found also that the anemochorus species were the more deciduous ones, which having a low tree canopy cover during the longer time by year and during the driest months when also fruits ripen, favor also probably the wind passage trough tree canopy, reducing the nearest physical obstacles to increase dispersal distances of the lighter seeds. Tree species with a non- assisted dispersion in contrast seems to have a widely variarety of strategies to release their seeds with therefore a wide variarety of heights and seed masses to assure successful dispersal events, resulting in no correlations between tree height, dispersal traits and this parental dispersal mode.

Therefore, we found that seed size and fruit size were tightly related and that plant height was weakly correlated with fruit and seed mass similar to Wrigth et al. (2007). However we found in addition that whole plant traits and dispersal traits were correlated with dispersal modes together or alternatively, possibly affecting this weak correlation between tree height and seed mass, supporting the idea about a tree coordinate strategy with dispersal structures to model correlations between dispersal and whole plant traits and trees life history

Dispersal traits modes were also correlated with leaf traits

The leaf traits strongly correlated with the leaf economic spectrum (Wright 2004) like SLA, LCC, LDMC, LNC, LPC and FTF were all correlated with fruit and seed volume mass and shape. Dispersal traits and dispersal modes were also strongly correlated with leaf traits implying also that leaf economic spectrum were strongly articulated with tree dispersal strategies. SLA was negatively correlated with fruit mass; LA was negatively correlated with fruit shape, volume and seed mass and volume; LDMC was positively correlated with fruit mass meanwhile LCC was also positively correlated with all fruits traits (shape, mass, volume) and seed shape. LPC was also negatively correlated with fruit and seed mass and fruit shape; LNC was correlated with fruit and seed shapes; and finally FTF was correlated with fruit and seed masses and seed volume. Anemochory was correlated with LPC; autochory was correlated with LNC and FTF; mammalochory was correlated with SLA, LDMC, LPC and FTF; and finally Zoochory was correlated with LA, LDMC and LCC.

A relative higher number of correlations were found between leaf traits and fruit sizes implying the direct correlation of leaf morphology with dispersal syndromes (57%), but also a relevant proportion include seed sizes (48%) implying that also the further paths in tree development were compromised within these correlations. Mainly fruit mass, but also fruit volume and shape, co varied with SLA, LDMC, LCC, LPC and FTF showing that tree investments in leaf construction reflect those on dispersal structures. Tree species with more expensive leaves i.e physically strong leaves having high contents of total biomass and carbon but reduced phosphorus contents and a reduced area produced by leaf dry matter content (those species located in the positive extreme of the leaf economy spectrum), have also heaviest, biggest and longest fruits. Tree species with heaviest seed were also allocated associated with expensive leaves but mainly due they direct association of seed mass with more fragile leaves having a reduced phosphorus content, meanwhile longest seeds have also direct correlation with highest total carbon and nitrogen leaf investments and biggest seed with LNC and FTF. In contrast, in general those tree species with cheapest leaf construction located in the opposite side of the LES showed more spherical, smaller and lighter fruits and seeds.

Leaf morphology was strongly correlated also with dispersal modes implying that co-variation in tree leaf, fruits and seeds constructions costs were also coordinated within the different tree strategies to disperse seeds and assure future populations. Tree species dispersed by wind tend to have higher phosphorus content in more deciduous leaves at the same time that have lighter seeds in longest and heaviest fruits and grow up to the higher canopy stratums. In addition, tree species dispersed small local fauna have bigger leaves with lowest leaf dry matter and carbon contents, in completely opposition with those species dispersed by big mammals like the cattle, which have stronger leaves with a higher dry matter contents but a reduced phosphorus content and area produced with it biomass unit, at the same that have biggest and heaviest fruits with relatively heaviest seeds. Even tree species with non-assisted seed dispersion were correlated with leaf morphology, having also physically fragile leaves with highest nitrogen contents, and longest fruits.

The strong correlations between leaf, dispersal traits and dispersal modes evidence that other ecological process like herbivore defense, water balance and nutrient cycling, commonly related with leaf morphology, were also compromised with dispersion modes and with plant resources investment on dispersule construction. Leaf traits like FTF, SLA, LDMC and LCC have been related with defense against herbivore or with leaf vulnerability to herbivory and physical hazards (Wright and Westoby 2002, Coley 1983, Perez-Harguindeguy et al. 2003). Leaves with a reduce specific leaf area also has been related with shade-tolerance (Kitajima, 1994; Walters and Reich, 1999) and water balance (Poorter 2008). As cited by Markesteijn et al. (2011) tough, well-protected leaves with low SLA, shade-tolerant species reduce leaf herbivory, and enhance leaf longevity and hence lifetime carbon gain and plant survival in the shaded understory. We found in addition than these tree species do invest also in expensive fruits (heavy and bigger) which allow a relatively more directed dispersion of biggest seeds. Tree species dispersed by big non volant mammals probably benefit from physically stronger leaves with a reduce palatability resulted from higher amounts of total biomass and carbon to reduce the physical damage on foliage due to leaves direct or occasional consuming by mammals browsing their fruits, like is actually observed with cattle. Well-protected leaves with low SLA has been also correlated with drought-tolerater strategies to balance water contents increasing the root length to maximize the access to water or reduce water releases by a reduced transpiration (Markesteijn et al. 2011). However the lack of correlation between leaf phenology and mammalochory implies that wider transitional stages between extreme deciduosness (4 to 6 months with a reduced leaf canopy) and complete evergreens canopies (full leaf canopy year round) were compatible with mammals dispersed species, unless the negative sense of their correlations imply that more probably this well-protected leaves were more associated with a moderate deciduodness (between 1 to 3 month with a reduced leaf canopy cover).

The endozoochorus strategy performed by the small frugivoruous local fauna (i.e. birds and bats) have a completely opposite leaf characterization to those species dispersed by big mammals. Mainly biggest leaves with a reduced total leaf dry matter contents and carbon were found within these zoochorous tree species, having also smaller, lighter and more spherical fruits carrying spherical seeds in rather shorter trees. The maximum height and leaf traits did correlate positively with dispersal traits as expected for these tree species, but not tree height and leaf.

Tree species dispersed by wind tend to have higher phosphorus content on more deciduous leaves at the same time that have lighter seeds in longest and heaviest fruits and grow up to the higher canopy stratums.

The more expensive leaves were now also associated with mammalochory and probably will be associated with slow growing rates, accordingly with better defense against hervibory, having probably longer lifespan and lower rates of nutrient cycling.

LA was negatively correlated with dispersal traits in contrasts to previous observation by Wright et al. (2007). LA was strongly correlated with seed size (volume and mass), fruit mass and shape. Therefore, tree species with bigger leaves have small fruits and seeds with lighter seeds in rather spherical fruits, meanwhile tree species with small leaves have longest and heaviest fruits with rather big and heaviest seeds. It has been long recognized that twig size is positively correlated with the size of attached appendages. Known as Corner's rule (Corner, 1949), this correlation has been widely demonstrated both for interspecific and intraspecific comparisons (see Yang 2009) but mainly in relation with leave size meanwhile few in addressed directly the twig size - fruit sizes relationship (Chen et al. 2009). We found also that LA tend to be positively correlated with zoochorus trees, indicating that tree species dispersed by birds and bats have the biggest leaves and accordingly with previous stated correlations between dispersal modes and fruits traits, have also the smallest and lighter fruits. These significant relationships could probably response more to the dispersal mode interaction which indirectly relates tree species with zoochory dispersion with the smallest tree species which having more competition for light within the original forests, will require higher leaf areas. We have not measured of twig size to contrast our correlations between leaf area and fruits size with possible differences in the tradeoff between leaf - twig – fruits size axe.

These results imply that these two trait-based strategy dimensions were not disarticulated and have ecological importance for tropical tree species communities.

Has not being clearly tested why big species could have bigger fruits beyond the physical constraints that a small plant cannot support big diapores (Leishman et al. 2000, Wrigth et al. 2007). Easily, bigger trees can have an increased dispersal distances for those anemochorus or autochorus species (Leishman et al. 2000) meanwhile the higher survivorship required at juvenile stages for taller trees higher could be benefit from bigger seeds (Moles et al. 2004). This last possible explanation needs to be tested carefully quantifiying the relationship between seed mass and survival from seed production to reproductive maturity.

Both leaf and dispersal traits were correlated to the main two and three PC axes. LDMC, FTF, dispersule masses, Vol_Fru and LPC were respectively positive and negatively correlated to the first main axe CP_1 when the 20 species with a complete leaf and dispersal trait data set were included in a PCA for dispersal and leaf traits. LCC, LNC together with dispersule shapes and Vol_see were also respectively positive and negatively correlated to the second main axe CP_2. In contrast, SLA and LA were positively correlated to the third and four main axes CP_3 CP_4.

Dispersal modes were correlated to all leaf traits. All leaf trait correlates to at least one or two dispersal modes, instead three of the four main dispersal modes identified were correlated to at least two, three or even to five leaf traits at time. Just one dispersal mode, Anemochory was not correlated to any leaf trait. Autochory was positively correlated to LNC and tend to be negatively correlated to FTF. Zoochory was positively to LA and negatively correlated to LCC and LDMC. Mammalochory was positively correlated to LDMC and LCC but negatively correlated to SLA, LPC and LNC.

Integrated trees strategies in active pasturelands:

Wind dispersed tree species were taller and more deciduous, have higher phosphorus contents on leaves and longest dispersules (fruits and seeds) with lighter seeds. Self dispersed tree species have denser woods, more fragile leaves with higher nitrogen contents and longest fruits. Tree species dispersed by local fauna were smaller, have biggest leaves with lower biomass and total carbon investments, have small and lighter fruits and more spherical dispersules (fruits and seeds). Tree species dispersed by big mammals (i.e. cattle within this anthropogenic environment) were not correlated with whole plant traits but with leave and dispersal traits. Tree species dispersed by big mammals have stronger leaves with higher biomass and total carbon contents but a low specific leaf area and phosphorus contents, together with a big and heaviest fruits and heaviest seeds.

These results reflect the variability plant coordinated strategies mixing particular combinations of the 3 main axes of trait covariability identified nowadays i.e. i) leaf economic spectrum, ii) seed size – seed output- seedling survive and iii) tree height-early growing rates-shade tolerance, within these tree community. In addition, these results help to understand how tree species' traits were related to dispersal mode, which is related with dispersal distance, seedling establishment, and therefore is crucial for understanding the ecology of plant dispersal colonization to new environments.

In this chapter, we do not use 'phylogenetic' analyses to test for the effect of evolutionary divergences in trait-pairs over the correlation patterns observed within the cross-species analysis as suggested by Felsenstein (1985). We are aware that the taxonomic biases in the dataset could contribute substantially to cross-species results. However, our main objective in this paper is to describe present-day traits species values in a particular environment and tree community. Phylogenetic' analyses to confirm the absence of the evolutionary divergences effect will be relevant at further research stages to address different questions about how the range of trait values has arisen phylogenetically through evolutionary history (Westoby and Wright 2004) and when additional tree communities within pasturelands will be compiled at higher regional or word-wide scales. The majority of previous studies on 'cross-species' correlations have found strong similarities with those using phylogenetic correlations (i.e. Zanne et al. 2005). This is possibly due to the fact that closely related species retain similar ecological characteristics (phylogenetic conservatism of traits or niche conservatism) (Blomerg et al. 2003, Ackerly 2009).

2.6 CONCLUSIONS

Tree species in active pasturelands have wide variability of plant traits, more specifically:

We confirm the presence of a leaf variability spectrum (equivalent to the Leaf Economy Spectrum (LES)) which split apart conservative leaf species with high LDMC, LCC, FTF but low SLA and LPC from those with more acquisitive leaves having the opposite characteristics (acquisitive – conservative).

Tree species also vary also in the stem and phenology variability spectrum (SPS) confirming that taller deciduous trees have softer woods than shorter evergreens (deciduous softer – denser evergreens).

We found that tree species vary also in a fruit and seed investment spectrum, splitting apart tree species with bigger and heavier fruits from those with small and lighter fruits and seeds (cheap – expensive).

Moreover we found that leaf, reproductive and whole plant traits are strongly associated i.e. leaf characteristics are linked with other plant variability, more specifically:

A leaf and reproductive investment spectrum showed than acquisitive leaves have cheap fruits and seeds in contrast to conservative tree species which have expensive fruits and seeds construction (acquisitive and cheap).

A stem, phenological and reproductive spectrum split apart deciduous tree species with small and lighter seeds from evergreen species with more expensive fruits and seeds (deciduous and cheap).

A leaf, stem and phenological spectrum outline that deciduous tree species (with a short leaf life span) have more fragile acquisitive leaves and softer woods (low LCC but high LPC) than evergreen species which

> have more conservative leaves and denser woods (deciduous, acquisitive and softer woods).

Plant traits interact in several spectrums of variability defining different plant strategies where investments in fruits and seeds construction are related with leaf and stem economies.

The complexity of the pattern of plant trait associations showed no tendency to form tightly-defined "functional groups" with holistic associations occurring in several diverse axes of traits variability.

Dispersal types are good examples of tree strategies that display species' traits variability which display different arrangements of leaf, whole plant and reproductive traits, more specifically:

> Tree species dispersed by wind were taller, deciduous, having rich phosphorus leaves, bigger and longest fruits and carrying lighter seeds. Tree species dispersed by local fauna were shorter with big but cheap constructed leaves (low LCC) carrying small, lighter and spherical fruits with spherical seeds. In contrast, tree species dispersed by big mammals like cattle showed strong and expensive leaves (high LDMC and LCC) poor in nutrients (low LPC and LNC) carrying big and heavy fruits with heavy seeds. Tree species with parental dispersion have dense woods but fragile nutrient rich leaves (high LNC) having the longest fruits.

The multidimensional tree functional strategies observed in APs suggest that loss of any particular tree characteristic could affect different ecosystem services offered by actual tree cover remaining in tropical agricultural lands.

CHAPTER 3. ADULT TREE ABUNDANCES AND PLANT TRAITS PREDICT TREE SPECIES NATURAL REGENERATION IN ACTIVE NEOTROPICAL PASTURELANDS

3.1 ABSTRACT

Species different capacity to naturally regenerate (CNR) is an ecological property of plant communities key to conserve the decreasing fraction of local diversity remaining in agricultural lands and related ecosystem processes.

A reduction of tree cover diversity can produce negative impacts on actual and future provision of ecosystem services if some plant traits (PT) favor tree CNR after land use change meanwhile others are associated to species with limited CNR.

We evaluate the relationships between PT and adult tree cover with tree seedlings and saplings abundances and their contribution to the CNR of tree cover diversity under disturbances generated by active pastureland (AP).

Tree abundances (adult, saplings and seedlings) and 17 PT related to four main trait dimensions (leaf, stem density, canopy height and reproductive variability spectrums) were measured on 76 tree species in 46 APs. Measured leaf traits were leaf area, specific leaf area, leaf dry matter content, total carbon, phosphorus and nitrogen leaf content, foliar tensile strength; whole plant traits were wood density, maximum tree high, leaf phenology; and reproductive traits were fruit and seed mass, volume, shape and dispersal mode.

All PT are correlated with both tree species abundances and CNR in APs. More abundant adult trees were taller deciduous species with softer woods, small and conservative leaves, with expensive and longest fruits carrying big and longest seeds, dispersed by wind and cattle.

Some successful PT at seedlings and saplings stages differ with adult tree cover: species with denser woods, P rich leaves and expensive seeds have more sapling abundances meanwhile species with C and N rich leaves have more abundant seedlings. Tree species dispersed by cattle were abundant as seedlings and saplings but those dispersed by local fauna were limited in all developmental stages. Adult tree abundances were strongest predictors of tree seedlings and saplings abundances in AP and together with PL explain a higher proportion of species abundance variability (60 - 67%).

Actual tree functional diversity and the capacity to provide ecosystem services under current management practices in APs will possibly decrease as a consequence of the limited CNR of some trees with particular PT.

Key words: responses to disturbances, seedlings, saplings, tree cover, population dynamics, agricultural lands.

3.2 INTRODUCTION

The capacity of tree species to regenerate after disturbances is a key ecological property of plant communities potentially determining today and future ecosystems services. The selective pressures from environmental conditions, disturbances and biotic interactions act distinctively over individuals at different developmental stages i.e. seedlings, saplings, adults and diasporas (Boege and Marquis 2005). Each developmental stage has differences in physiological and morphological attributes and constraints, generating different responses to the selective pressures exerted over tree ontological development and shaping species populations (Elger et al. 2009). At community level, the relative abundance of species and their population structure, reflect the differential species´ ability to reproduce under the prevailing environmental conditions in response to natural and anthropogenic disturbances like herbivores, droughts and deforestation (Kitajima and Fenner 2000, Esquivel et al. 2008). In addition, the relationships between species abundance by developmental stage with species physio-morphological traits potentially reflect the successful functional “responses” to overcome such selective pressures. At the same time, the relationships among functional traits and demography could evidence the main “constraints” tree species should face to complete their life cycle in a specific habitat, adding functional information to the tree communities’ structure. Therefore, if some plant traits are more successfully promoting high tree abundances than others, they probably will affect ongoing ecosystem processes like litter decomposition. In consequence, a reduction of tree cover diversity can produce negative impacts in future ecosystem services provided by tree species communities (i.e. nutrient cycling) if some plant traits (PT) favor tree provision of ecosystem services if some plant traits (PT) favor tree capacity to naturally natural regeneration capacity (CNR) after land use change meanwhile others are associated to species with limited CNR.

However the direct relationships between tree species abundances with different functional traits in a tree community have been explored by a small number of studies. During the last few decades community ecology has searched for general rules associating species characteristics with biotic factor and environmental conditions (Keddy 1992). In this process the links between species demographic structures and ecosystems processes has deal with contrasting interpretations. Some authors have suggested that disturbance responses involve demographic rather than physiological traits, therefore highliting the independence of traits relevant to disturbance response from those involved in ecosystem effects and processes (Díaz and Garnier 2002). In contrast, others argue that presence and abundance of species in a habitat could be predicted from a particular subset of ecophysiologycal traits, with others being filtered out due to the environmental and biotic interactions (Keddy 1992). Therefore, the number, relative abundance, and functional identity of plant species potentially influence ecosystem processes (Chapin et al. 2002). As postulated by Grime (1998) in the ''biomass ratio hypothesis'' which states ''the extent to which the traits of a species affect ecosystem properties is likely to be strongly related to the contributions of the species [. . .]'' taking explicitly into account the number, relative abundance functional identity of the species present in determinate habitat (Garnier et al. 2004).

The species' capacity to successfully complete their life cycles in a specific habitat and its effects on the functional structure of tree communities has been exclusively studied inside pristine forest or native grasslands. However, tree species natural regeneration has a key role also in the community structure in the agricultural lands adjacent to forest frontiers. Increasing our knowledge about natural regeneration in agricultural lands is especially relevant in areas where pristine forests are under high deforestation pressures like seasonal dry tropical forests, both for ecological and practical reasons. Tropical dry forest originally represented 42% of the tropical vegetation worldwide (Murphy and Lugo 1995) but is one of the most threatened tropical terrestrial ecosystems, precisely due to the conversion of these areas into agricultural lands (Sanchez-Azofeifa et al. 2005). The damaging consequences of this land use change include the loss of ecological services (such as biodiversity and watershed protection), the loss of many goods (such as timber and non-timber forest products), and the loss of means of existence for forest dwelling people (Lamb et al. 2005).

Agricultural lands conserve an important fraction of local diversity (Pimentel et al. 1992, Harvey et al. 2006). In the neotropics, tree cover in agricultural landscapes typically occurs in the form of riparian forests, forest fallows, live fences and dispersed trees (Harvey et al. 2006). This tree cover does not have common origins, in contrast is a mixed community including remnant individuals which survive the cutting of the original forest, together with new colonizers coming from conserved forest fragments and introduced individuals deliberately sown by farmers. These tree resources are often actively managed by farmers to provide products such as firewood, timber, fruits and fodder for cattle, and services such as watershed functions and shade for cattle (Harvey et al. 2004, Gordon et al. 2010). Although trees are principally retained by farmers for productive purposes, they may also provide habitats, resources, and landscape connectivity for animals (Estrada et al. 2000, Harvey et al. 2004). Some literature has also compared animal diversity on agricultural land vs. forest in the neotropics (Estrada et al. 2000) indicating for example that tree components outside offers resources for 54% of terrestrial native mammals foraging inside and outside the forest (Daily et al 2003), an impressive amount for biodiversity conservations issues.

Paradoxically the ecology of tree components in agricultural lands has not received attention beyond the taxonomical diversity, despite the several functional attributes which have been pointed out implicitly with the conservation values of trees outside the forest for biodiversity. For example, diverse whole plant, leaf and fruits characteristics should be found in tree cover to be able to offer diverse food and habitat sources for diverse animal taxa (Harvey et al. 2004). In addition, key ecological processes like tree natural regeneration just have been started to be addressed beyond the forest edges (Esquivel et al 2008), no matter it huge relevance for the maintenance of plant communities and ecosystem processes and services as cited previously. Tree natural regeneration is an ecological process especially relevant in anthropogenic disturbed ecosystems like pasturelands, were tree cover is continually depleted following conventional management to increase grass and livestock productivity (Nepstad et al. 1999). Seed dispersal from forest fragments for example is an important process to colonize new open areas particularly outside forest (Aide 2000). However we don’t know which morphological or physiological characteristics are associated with the observed different natural regeneration capacity of tree species to colonize and maintain viable populations in these areas (Esquivel et al. 2008).

Conversely we have started to be aware that even the diversity of tree cover in agricultural landscapes is also threatened to decline under the continuity of conventional management strategies i.e intensive over-grazing and pesticide use (Esquivel et al. 2008, Gibbons et al. 2008, Fischer et al. 2009). In one of the few studies of the ecology of the trees in active tropical pastures, it was found that tree species have different capacities to maintain viable populations within these habitats (Esquivel et al. 2008). In this study in a seasonal central American environment, half of tree species in active pastures had abundant seedlings, saplings and adult populations, meanwhile seedlings or saplings were absent for the other half of species indicating their incapacity to renew this populations within this continually disturbed habitat (Esquivel et al. 2008). The natural regeneration capacity of tree species as responses to disturbances typical of anthropogenic habitats like pasturelands, involved: they inherited (genetic) development of physiological and morphological characteristics, and their interactions with external ecological factors like preexisted vegetation (i.e. exotic grasses), animals (i.e.cattle) and environmental conditions (i.e. soil soil fertility) (Price et al. 2001). Despite the last decades of massive efforts to evaluate the functional characterization of diversity worldwide (Wright et al. 2004, Díaz et al. 2007, Chave et al. 2009, Moles et al. 2007), we know little about the functional characteristics of the tree cover in the agricultural lands.

Neither the natural regeneration patterns or the functional characteristic of tree components in agricultural lands can be predicted from the actual knowledge coming from pristine forest areas mainly due to the high variability between models resulting from different forest types i.e dry and humid forests and differences in nature and intensity of the disturbances inside and outside the forest (Viera and Scariot 2006). The different patterns of natural regeneration observed in dry forest areas in comparison with moist forest for which a higher amount of ecological natural regeneration studies have been based were carefully described by Viera and Scariot (2006). Different environmental conditions inherent to these forest types (rainy seasonality and temperatures), disturbance regimens (i.e. fires and slides) and the differences on the morphological and physiological responses of tree species to overcome such site conditions (like phenology, seed dispersal, seed germination seedlings establishment, fire resistance and resprouting capacity) has been identified as responsible for such differences between in regeneration patterns between dry and moist forest reflected finally on the inherent tree communities structure and richness of such contrasting forest types (Viera and Scariot 2006). Reponses to tree fall gaps for example has been widely considered to be focal regeneration sites in moister tropical forests, but can decrease the seedling survival dry forest due the extremely high soil temperatures and low humidity (Gerhardt 1999; Mclaren and McDonald 2003a, 2003b).

Most knowledge about natural tree regeneration after anthropogenic disturbances outside the forest has come from the observation of forest succession in abandoned pasturelands (Holl 1999). The models of natural regeneration in abandoned pastures identify that seed dispersal, safety microenvironments for seed germination and the competition with pre-established grasses are the main limiting factors (Zimmerman et al. 2000). The number of seeds dispersed by animals in abandoned pasture for example, decreased dramatically to more than 5 m from forest edge (Holl 1999) mainly due to the few forest birds and bats able to move into open areas outside the forest (Cardoso da Silva et al. 1996, Howe and Smallwood 1982). Tree species dispersed by wind were also dependent on distances to forest edges and surrounding vegetation unless were able to have higher seed densities at higher distances from seed sources in the forest or in the preexisting vegetations in the pastures (Holl 1999). Abandoned pastures with a reduced vertical and horizontal plant stratification and species diversity remain therefore dominated by grasses which cover profusely the soil reducing the early establishment of trees and shrubs (Uhl et al. 1988). These bottlenecks for woody regeneration in abandoned pastures stand can be hold by for long periods stopping succession advances due to the higher growth and increased dominance of grasses cover (Uhl et al. 1988). Once pioneers trees and shrubs set out in these conditions, the structural complexity of the landscape increase, forming patches of woody vegetation in the matrix of herbaceous cover. Now, local birds and bats visit frequently this woody “islands” increasing the density of seeds dispersed by birds under this vegetation and surrounding areas (McDonnell and Stiles 1983, Holl 1998) increasing pastures diversity and speeding up succession advance (Lugo and Helmer 2004).

In contrast, few studies have identified the pathways of woody vegetation in anthropogenic pasturelands under actively grazing pressures (Arnaiz et al. 1999, Esquivel and Calle 2001, Esquivel 2008). These studies confirmed the relevance of previous existed woody vegetation to act as foci for tree species colonization within the pasturelands. For example, abundance and richness of tree and shrub seedlings were studied under 57 isolated trees of four different tree species and in adjacent (5m) pasture plots without the influence of prestablished woody vegetation in pastures under active livestock production in the Andean moist pre-montane tropical lands (Esquivel and Calle, 2001). With the exception of *Montanoa quadrangularis* (a wind dispersed pioneer), regeneration of woody species below isolated trees was richer and more abundant than in open pasture, suggesting that these trees with fruit dispersed seeds enhance the seed rain and provide favourable microsites for the germination of those of secondary species that are unable to reach, germinate or established in open pasture sites (Holl 1998, McClanahan and Wolfe 1993, Guariguata et al. 1995, Robinson and Handel 1993, Toh et al. 1999). A higher proportion of bird dispersed species are able to reach pasturelands under trees remnants of forest (Guevara et al. 1986). Meanwhile other tree species colonize grasslands from forest edges, reaching open areas by wind or cattle dispersion. Some species domain tree communities meanwhile other can be rare but successful species.

In areas under continuous disturbance such as active pastures, additional anthropogenic factors influence the process of seed dispersal and its dynamics in addition to those observed inside tree forest and in abandoned agricultural lands. Livestock (horses and cattle) for example, scatter the seeds of leguminous trees as *Enterolobium cyclocarpum* (Janzen 1981, 1982) and fruits such as *Psidium guajava* (Somarriba 1995). These animals can consume a high amount of fruits and disperse seeds of high densities of these species in their dung. The different characteristics of mobility and habitat preferences of these dispersers over wildlife, influence the dynamics of natural regeneration of trees in active pasture regarding abandoned degraded areas (Radford et al. 2001). For example, three years after the experimental application of cattle dung in Mediterranean abandoned pastures, its vegetation showed a significant increase in tree species richness of species found only in active grazing areas (Traba et al 2003). Animals capable of dispersing seeds in anthropogenic disturbed areas can expand plants populations, colonizing habitats that would not achieve successfully without their interaction (Chambers and MacMahon 1994). Thus, the effects of domestic animals become more important in the dynamics of dispersion of the natural regeneration of degraded areas and active pastures. Despite its influence, variability of results has not been widely explored. Specific fruits and seed characteristics of tree species related with different mechanisms to colonize these areas will probably related with the abundances of tree seedlings and saplings, shaping tree community structures and processes.

Seedling establishment and seed dispersal are considered the most important stages in the natural regeneration of trees. The study of both processes has been more addressed inside than ouside the forests, despite them crucial effects to determine the tree colonization patterns in deforested areas. Different dispersion strategies determine patterns of distribution of seeds and consequently define the conditions under which seedlings and saplings will live or die. Thus the demography of seedlings reflects plants responses to the selection pressures on seeds and seedlings in the dispersed sites (Howe 1990). Density dependent mortality, microclimate conditions, nutrient availability, competition with existing vegetation and herbivory are the main factors determining seedling establishment and development in natural and anthropogenic factors. Newly germinated seedlings may experience higher mortality near adult individuals where usually high densities of seeds occur, due to intraspecific competition or further attacks by pathogens or herbivores (Gilbert et al. 2001). In contrast, the least likely survival of seedlings over long distances are related to new habitats at greater distances from parent trees and probably lower proportion of microsites suitable for germination, survival and establishment of the species (Auspurguer and Kitajima 1992).

The availability of nutrients in different soil microsites also determines the growth and survival of seedlings in natural and disturbed areas. The survival and growth of tropical tree species in areas of pasture are lower than in other land uses including forests (Somarriba and Beer 1987). The biomass of leaves, stems and roots of several tree species seedlings growing in pastures do not differ to those observed in forest although the nutrient levels are lower in forest than in grassland areas (Holl 1999). The low survival of seedlings in grasslands possibly due to severe competition from grasses, which can cover completely and prevent seedling growth and development as has been reported for other species evaluated in abandoned pastures (Gonzalez and Fisher 1994). The dispersal mode which influences seed rain characteristics (distance and density) and the capacity to be establish and growth under limited resources must be all important characteristics to overcome seedling and sapling stages of tree regeneration in active pasturelands.

Additionally, cattle grazing can increase or decrease the likelihood of recruitment of woody plants in various ways (Archer 1995). By grazing and browsing the domestic herbivores interact with seed banks and tree seedlings and saplings causing direct and indirect changes in the vegetation of natural regeneration in these areas. Direct effect on mortality resulted from the consumption of plant tissue with the consequent loss of CO_2, water and nutrient uptake associated with the biomass reduction of leaves and roots (Archer 1995). Indirect effects from cattle trampling were changes in ground cover, microclimate, soil properties, nutrient cycling and changes in competitive interactions for these limited resources. The indirect effects of cattle activities may become more important than the direct effects due to its ability to shaping the dynamics and properties of an ecosystem (Archer 1995). In contrast, cattle may favor the establishment of seedlings dispersed in their dung. The dung reduces competition with grass roots and avoids trampling (Somarriba 1995), reducing the high pressures of selection by herbivores or physical damage imposed by grazing. However, few studies have evaluated the effect of actively grazing managements on tree regeneration in pastures (Esquivel et al 2008). Palatability and tolerance to defoliation in addition to dispersal mode must be characteristics of tree species affecting saplings abundances of tree species surviving in active pasturelands.

Management practices of active pastures exert a strong selection pressure on the early stages of plant development tree. A high tree cover in pastures is no guarantee that the natural regeneration will not decrease in future years (Harvey and Haber 1999). Periodical cuttings, intentional fires or the use of herbicides are common to reduce woody colonization over pastures, but also through these farmers practices can reduce the establishment of some species of seedlings, can in contrast favor the establishment of others, influencing composition, distribution and population densities of tree species naturally regenerating in active pastures (Esquivel et al. 2008). The maintenance of woody components in the landscape scale, may favor a higher number of microsites and recruitment centers for the establishment of tree species in agricultural landscapes. However, few studies have evaluated how the proximity of propagules sources in the landscape i.e forests or isolated trees, and their botanical composition of these sources, influence colonization of degraded areas to these areas by native vegetation. For example, higher densities of seedlings, greater species richness and largest number of forest species were found under windbreaks connected to forests and under trees forest remnants isolated in pasturelands (Harvey 2000). Therefore the presence, abundance, composition and distribution of isolated trees in the landscape could increase the diversity and abundance of seedlings in degraded landscapes (Esquivel et al. 2008).

In consequence, dispersal, leaf and whole plant traits of tree species must be strongly related with the abundances of the early stages of tree natural regeneration i.e. saplings and seedlings, reflecting the trade off to successfully maintain tree populations in active pasturelands which give shape to tree community structures and affect ecosystem processes. Dispersal traits like fruit and seed sizes together with dispersal mode will probably be strongly correlated with tree regeneration abundances due to importance of seed dispersal for the colonization of these open sites outside the forest. Bigger dispersules (seeds and fruits) probably increase the colonization and establishment chances for tree species due their highest investments on directed dispersal (zoochory) to reach safe microsites and with the higher parental resources to survive under low resources sites like the active pastures soils. Those tree species dispersed by cattle and wind will probably have a dispersal advantages over those dispersed by local animals like bird or bats due to their higher independence from the pre-established woody vegetation, resulting in higher seedlings and saplings densities. The correlation of small dispersules with tree regeneration abundances will probably depend on dispersal mode, because bird and bats will probably have lower abundances than those dispersed by wind. Therefore biggest (mass, volume) and cattle dispersed seed could be probably enhancing the tree regeneration capacity in active pasturelands.

Leaf plant traits (SLA, LA, LDMC, LCC, LNC, LPC and FTF) may be correlated with natural regeneration abundances in active pasturelands due their strong relationships with water control, resources use and herbivores defence. Those more conservative tree species with higher LDMC, LCC and FTF will be probably positively correlated with tree regeneration abundances because these characteristics confer more physical resistance to leaf damage caused during cattle grazing and browsing. However, those more acquisitive tree species with a high SLA, LNC and LPS but with low carbon related measures could be also positively correlated with higher abundances of tree regeneration due to the stronger capacity to grow faster in conditions of limited availability of resources like the active pasturelands. No clear expectations were hypothetized around LA relationships with tree natural regeneration. Leaf traits correlation could be stronger for saplings than for seedlings due to the strong dependence of saplings stages on environmental conditions than seedlings when parental resources has still effects of and enhanced tree regeneration capacity in active pasturelands.

Whole plant traits like H_max, PHE and WD are probably correlated with natural regeneration abundances in active pasturelands due their strong relationships with growth, water control and resistance to physical damages. Taller tree species could be positively related with seedling and saplings abundances because higher growing rates associated to taller tree species allowing seedlings and saplings rapidly escape from the strong environmental constrains during these early developmental stages. A higher wood density could also give stronger capacity to tolerate physical damages at early developmental stages increasing the abundances of tree natural regeneration under constant grazing and browsing pressures. Finally, we can not propose a priori a pattern for the association between phenology and tree regeneration abundances because deciduous species and evergreen species have successful mechanisms to avoid water stress, and both could have variable correlations with the abundances of early tree developmental stages.

The abundance of adult tree cover inside the agricultural lands is an important factor correlated with the abundances of tree natural regenerations (Esquivel et al. 2008) but is not clear yet if they relative importance to predict natural regeneration abundances is higher or lower than the prediction strength of plant traits. Today adult tree components in active pasturelands have been resulted from a complex interaction between historic natural and anthropogenic disturbances shaping the actual tree cover functional composition. Previous natural disturbances when the forest cover still domain, ages since forest cutting, management intensity, land users decisions making regard the tree cover components in managed areas (windbreaks, isolated trees, riparian forests) and their neighbourhoods (forest remnants) shape actual tree cover in active pasturelands. The functional characterization of these adult tree cover in active pasturelands has not been studied previously, but encompasses huge relevance because the natural and historic anthropogenic disturbances has been mainly widely spread within the tropical lands and because the direct influence that these woody components could have on the future functional scenarios in the agricultural lands. Therefore, if tree adults abundances were strongest predictors than functional traits anyway the functional characterization of those tree cover reinforce their importance, because those tree species able to proliferate or dominate within this areas will be those with the higher probability to maintain their populations.

However, there are not previous studies predicting the abundances of tree natural regeneration from functional plant traits in agricultural lands. The most similar approaches have been not attempted in tropical systems, only in abandoned vineyards in France (Shipley et al 2006), herbaceous ecosystems in temperate North America (Sudding et al. 2005) and in unproductive limestone grassland in UK (Thompson et al. 2001) including only herbaceous vegetation and not tree species. A total of 94% of the variance of relative abundances were explained by Shipley et al (2006) using eight functional traits (proportion perennial, seed number, seed maturation date, SLA, aboveground vegetative mass, stem mass, leaf mass and heigh) for 30 herbaceous species without including population dynamics. Under controlled conditions of fertility and disturbance Thompson et al. (2001) found that regenerative traits like seed mass and germination characteristics were the best predictors of invasibility success after 2 years in a experimental grass community of 54 native species, but that after 5 years no single trait was a good predictor of invasiveness. Also in experimental conditions for more than 900 herbaceous species, Suding et al. (2005) found that the risk of species loss due to fertilization ranged from >60% for the rarest species to 10% for the most abundant species, meanwhile some of the functional traits groups studied (photosynthetic pathway, N-fixing symbiont, life span, height, vegetative spread, origin) like perennials and species with N-fixing symbionts experienced increased risk of local extinction after fertilization, regardless of their initial abundance. Therefore, both plant traits and tree cover abundances will be relevant for predicting for the first time the tree natural regeneration abundances using in tropical anthopogenic environments where the functional role of those tree species with limited regeneration capacity will be susceptible to extinction and will be essential to maintain biodiversity. Whereas abundance was consistently important across all the studied that included it, functional mechanisms were often system-dependent within these grassland environments.

As a novel approach, we evaluate the relationships between plant functional traits and adult tree cover with tree seedlings and saplings abundances and their relative role to predict the capacity of today tree cover diversity in agricultural landscapes to regenerate naturally under the ongoing disturbances generated by livestock production. We addresed a more fundamental question like what determine the relative abundance of each species in a determinate environment?. We aim to provide information to answer this question for tree species regenerating in actively managed environments. Are functional traits good predictors of such early development abundances? I.e can tree species natural regeneration abundances in active pasturelands be predicted from whole plant, leaf and dispersal traits? Or the tree cover inside the same areas could be a better predictor? Due to the complex and historical effects of the natural and anthropogenic disturbances influencing the actual composition of the adults tree cover, we have no questions related to correlations between traits and the abundance of adults. However we addressed for the first time also, a widely functional description of the adult tree cover commonly found in the agricultural lands of dry to humid –transition forest areas in the Central America region.

In order to reach these objectives, we assembled functional trait data for 76 tree species commonly found in active pasturelands (anthropogenic grasslands sowed with exotic and native grasses after the removal of native forest) and their abundances measured on 46 different pastures under common management's options in the study area region. A wide spectrum of 17 plant traits, the highest reported for tropical tree species to date, were measured aiming to obtain a relevant characterization of tree life history with leaf, reproductive and whole plant traits related with growing development and regeneration processes. Dispersal traits include: fruit and seed masses (Mass_see, Mass_fru), volume (Vol_fru, Vol_see), shapes (Sha_fru, Sha_see) and dispersal mode; leaf traits included: specific leaf area (SLA), leaf area (LA), leaf dry matter contents (LDMC) total carbon, nitrogen and phosphorus content), foliar tensile strength (FTF); and whole plant traits measured were: maximum tree heigh (H_max), leaf phenology (PHE) and woody density (WD).

3.3 METHODS

Trait measurements

A total of 17 plant traits were measured on adult trees (dbh ≥ 10 cm) for a total of 76 tree species growing in active pasturelands located on Matagalpa, Nicaragua, Central America (12°31' - 13° 20' N, 84° 45' - 86° 15' W). Maximum tree height (Hmax), wood density (WD) and leaf phenology (PHE) were measured as whole plant traits. Leaf traits measured were specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), total leaf carbon, nitrogen and phosphorus contents (LCC, LNC LPC) and physical strength of leaves (FTF). Measured dispersal traits include fruit and seed masses (Mass_fru, Mass_see), volume (Vol_fru, Vol_see) and shape (Sha_fru, Sha_see).

Plant traits were measured on adult trees located in open site environments with canopies completely exposed to sunlight and following the general considerations made by Cornelisen et al. (2003). A minimum distance between conspecifics of 50 m was maintained for sampling. For leaf traits relatively young but fully expanded and hardened leaves without obvious symptoms of pathogen or herbivore attack and without susbtancial cover of epiphytes were sampled. As far as possible, leaves were sampled at least 2 – 3 h after sunrise and 3 – 4 h before sunset. Mature fruits were collected from trees or from soil when fresh fruits and seed recently released and were found. Leaf, fruits and seeds samples were stored in a cool box or fridge until processing in the laboratory. Dry and moist samples taken to avoid rot damage of the samples, and re-hidratation was used for 6 to 12 h in a dark room when necessary, but will be desirable measure within the following 48 h of collecting sampled. In general, sample sizes by traits were 3 to 5 leaves or fruits collected from of 3 to 5 trees by species to obtain a mean value of each trait for specie (**Table 3.1**).

The maximum plant height (H max) was measured using clinometers on flat areas (m), vertical measurements or visual estimations in the more slope areas. The biggest trees were selected within 46 active pastures (paddocks) where tree community composition was sampled in a previous study (Esquivel et al. 2008). Plant phenology (PHE) was measured using visual estimation of the percentage of tree canopy cover by leaves (%) every two weeks over a year round for adult and reproductive trees, taking as 100 % reference the tree canopy density at the end of the previous rainy season. PHE was measured as the number of months the canopy density was < 50%.

The specific leaf area (SLA) was measured on mature and full hydrated leaves scanned Leaf Area Measurements software (LAM V 1.3, University of Sheffield, A.P. Askew, 2003). After area measurement each leaf sample was oven dried at 60ºC for 72 h, and then weighed. An average of 20 leaves by species was measured, sampling 2 – 4 leaves by individual. Here we measured just the leaf lamina without petioles or rachis. When collected, the samples (twigs with leaves attached) were wrapped in moist paper and put them in sealed plastic bags, so they remain water- saturated. These samples were stored in a cool box or fridge until processing in the laboratory. Re-hidratation was done previous measurements for 6 to 12 h in a dark room when necessary, but measurements were mostly done within the following 48 h of collecting sampled (Cornelissen et al. 2003).

Leaf dry matter content (LMDC) was measured by oven drying leaf samples (60 – 70ºC) for 72 hours to determine dry mass content. The same leaves used for SLA were used for LMDC. A pooled sample of oven dried leaves was used to determine LNC, LCC and LPC contents for each species (Cornelissen et al. 2003) in CATIE Soil Labs. Total N and C were estimated by combustion analysis made with FlashEA 1112 CN auto-analyzer. P was estimated by humid digestion with a mix of nitro-perclorated acids 5:1 and colorimetry (Henríquez *et al.* 1995).The Leaf Tensile Strength or physical strength of leaves (FTF) was measured using a “tearing apparatus” (DIVERSUS project). A leaf fragment from the central section of the leaf (but away from the central vain) following the longitudinal axis (direction of the main veins), or the whole leaf was used. The width of the leaf or the leaf fragment sample (1 – 10 mm) was measure. The total force registered (1 Kg = 10 N) was divided by the width of the leaf fragment to obtain the leaf tensile strength.

Table 3.1. Plant traits (continuous) units and sample sizes measured on adult trees (dbh ≥ 10 cm) and abundances of tree species naturally regenerating on neo-tropical and active pasturelands in Central America

Traits groups	Traits Abr.	Plant Traits	Units	Sample size (individuals by specie)
Whole plant	H max	Adult plant stature	m	3 – 5
	WD	Wood density	g cm$^{3-1}$	literature
	PHE	Leaf phenology	month	3 - 10
Leaf traits	SLA	Specific Leaf Area	mm^2 mg^{-1}	5 - 10
	LA	Leaf size	mm^2	5 - 10
	LDMC	Leaf Dry matter content	mg g^{-1}	5 – 10
	LCC	Leaf total carbon content	%	5 – 10
	LNC	Leaf total nitrogen content	%	5 – 10
	LPC	Leaf total phosphorus content	%	5 – 10
	FTF	Physical strength of leaves	N	5 – 10
Dispersal traits	Sha_fru	Fruit shape	unitless	3 - 5 fruits (3 – 5 trees)
	Sha_see	Seed shape	unitless	3 – 5 seeds (3 - 5 fruits, 3 – 5 trees)
	Mas_fru	Fruits mass	g	3 - 5 fruits (3 – 5 trees)
	Mas_see	Seed mass	g	3 – 5 seeds (3 - 5 fruits, 3 – 5 trees)
	Vol_fru	Fruits volume	cm^3	3 - 5 fruits (3 – 5 trees)
	Vol_see	Seed volume	cm^3	3 – 5 seeds (3 - 5 fruits, 3 – 5 trees)
	Dis_mod	Dispersal mode	unitless	-
Abundances	Seedlings	Seedlings abundances (0.1 m ≥ heigth ≤ 0.3 m.)	indivifuals	7 m2 /paddock (46 paddocks) 126 m2
	Saplings	Sapling abundances (0.3 > height + d.b.h. ≤10 cm.)	individuals	400 m2/paddock (46 paddocks) 0,5 has
	Adults	Adults abundances (d.b.h.≤ 10 cm)	Individuals	1 ha/paddock (46 paddocks) 46 has

Fruits and seed mass, volume and shape were measured to obtain complete description about the entire reproductive dispersules (dispersal structure or propagule) as it enters to the soils (Cornelissen 2003). At least 3 seeds coming from 1 to 3 fruits were sampled from 1 to 5 different tree individuals by specie. Complete fruits were over dried at least 72 hours or until reach a stable weight to obtain fruit and seed masses (Mas_fru, Mas_see). Dispersule shapes (Sha_fru, Shas_see) describe quantitatively the shape or form of the mature and alive fruit or seeds. Dispersule shape is the variance of seed or fruits three main dimensions, i.e. the length, the width and the thickness (breadth), after each of these values has been divided by the largest of the values. Shape values or variance lie between 0 and 1 and are unitless. Dispersule shape was measured from different seeds and fruits sampled for seed mass. Dispersule volume (Vol_fru, Vol_see) describe the tri-dimensional or cubic space or volume occupied by tree fruits and seeds. Fruits and seed volume were calculated by spherical or ellipsoid geometrical formulas according to dispersule form described by length, width and thickness (breadth). Fleshy fruits were stored in plastic bags and keep in a cool box on fridge until measurements. For naturally dry fruits, air dried will be use previous to storing.

Tree dispersal mode describes the routes traveled by the dispersule units (fruits or seed) or the vector assisting or moving the dispersule previous reaching the soil surface Cornelissen (2003). The categories by Cornelissen (2003) were used and adjusted when necessary to the local community (**Table 3.2**). We were aware that several dispersal modes may be assisting dispersule unit's movements (dispersion) away from a parental tree to reach the ultimate germination place (Fischer et al. 1996). We only use here the dispersal vector involved within the first stage of dispersule release from parental tree within the whole possible range of dispersion movements (main vector) to categorize tree species dispersion mode. Four dispersion modes were identified: Autochory, Anemochory, Zoochory and Mammalochory.

Table 3.2. Dispersule characteristics used to categorize the dispersal mode traits adapted from Cornelissen et al (2003)

Dispersal modes	Vectors	Dispersal mechanisms / Dispersule characteristics
Autochory (including Ballistochory)	Unasisted dispersal, bristle contraction or seed launching	The seed or fruit has no obvious aids for longer distance transport, falling passively from the plant or dispersule with Hygroscopic bristles on the dispersule that promote movement with varying humidity. Restrained seeds are launched away from the plant by "explosion" as soon as the seed capsule opens
Anemochory	Wind dispersal	Minute dust-like seeds Seed with pappus or other hair, balloons or comas Flattened fruits or seeds with large wings Tumbleweeds , where the whole plant or in-frutescence with ripe seeds is rolled over the ground by wind
Endo-zoochory (Zoochory and Mammalochory)	Internal animal transport	Fleshy often brightly coloured berries, arillate seeds, drupes and big fruits that are evidently eaten by vertebrates (birds, mammals, bats) and pass through the gut before seeds enter the soil elsewhere. Those mainly consumed by wild animals where categorized as Zoochory, instead those eaten exclusively by big mammals like cattle were categorized as Mammalochory.

Wood density (WD) was the only plant trait exclusively obtained from literature review. All the WD data come from standard published papers and from available metadata reviews like those from Chave et al. (2006) and the Global wood density databases from Zanne et al. (2009). Complementary dispersal traits data were obtained also from literature reviews in order to increase the number of species obtained from the field. Dispersule masses and dimensions, i.e. the length, the width and the thickness (breadth) were obtained from standard published papers and data bases like Moles et a.l (2004), specimens information from Regional floras available the on line i.e. TROPICOS (Tropicos.org, Missouri Botanical Garden, 2012), Species of Costa Rica (inbio.ac.cr, National Biodiversity Institute, Costa Rica, 2007), Flora Scientific Databases (biogeodb.stri.si.edu/bioinformatics, Smithsonian Tropical Research Institute, 2012) and Agroforestree Database (worldagroforestrycentre.org, World Agroforestry Centre, 2012).

Abundance of adult tree cover and tree natural regeneration

Study plots were established in 46 actively used pastures on 17 cattle farms. These plots were selected to ensure a non-grouped spatial arrangement that covered the different conditions of pastures present in the region. The pastures were selected on the basis of grass composition and were representative of pastures in the region. The selected pastures were dominated (i.e. cover = 70%) by one of three grass types: (i) *Urochloa* spp. [*Urochloa brizantha* (Hochst. ex A. Rich.) Stapf and *Urochloa decumbens* Stapf] previously named *Brizantha* spp. (B, n = 15); (ii) mixtures of *Cynodon nlemfuensis* Vanderyst and *Cynodon dactylon* (L.) Pers. (C, n = 13); or (iii) naturalized grasses (i.e. not planted or seeded) such as Paspalum spp. (N, n = 18) (Esquivel et al. 2008). Abundance of seedlings, saplings and adult trees were sampled in the 46 pastures in the rainy season from May to late July (Esquivel et al. 2008). Species, height, diameter at breast height (d.b.h.) and crown sizes (two diameters along perpendicular axes) were identified and measure for each tree individual. Seedlings were defined as woody plants with a height between 10 and 30 cm, saplings as woody plants with heights > 30 cm and d.b.h. ≤ 10 cm, and adult trees as plants with d.b.h. > 10 cm. (Esquivel et al. 2008).

Adult trees were sampling in 1 ha plot by pasture (10000 m^2), saplings were sampled in a mean of 10 quadrat plots per pasture (4000 m^2), while seedlings were sampled in a mean of 18 circular plots (126 m^2) per pasture. The total area of each pasture varied from 1 to 22 ha (mean 5·82 ± 1·34 ha). Further details about sampling scheme, design, pasture management conditions and characteristics of the natural regeneration of these tree species can be found in Esquivel et al. (2008).

Statistical analyses

Three types of analyses were performed to provide different approximations to plant traits relationships with tree regeneration abundances: correlation, logistic regressions and a multiple regression. First, the partial Spearman correlations analyses were used to evaluate interspecific relationships (cross-species analysis, Poorter et al. 2008) between regeneration abundances with functional traits, while controlling for pasture type. Cross-specific correlation analysis identifies statistically significant linear abundance-trait relationship, their direction and strength (r). Second, logistic regression analyses were used to identify also the significance of tree species abundances in the different developmental stages with dispersal strategies or syndromes as categorical variables. Finally, multiple regressions analyses (MRA) were performed to evaluate how much of the variability in tree species abundances was explained by plant traits at each early developmental stage: seedling and saplings. All the analyses were done using an unbalanced species x traits data base build using the mean abundances by plot (density) per specie and developmental stage founded in the three different types of grass together with the mean values of the 17 plant traits observed by species.

The relationships between tree abundances by developmental stage and pasture type with whole plant, leaf and dispersal traits were tested using Partial Correlation Analyses (CA). These partial correlations analyses remove the grass type effect from the regeneration abundances sampling model in three different pastures types avoiding therefore any confounding effect of pasture management over the correlations between abundance of tree natural regeneration with plant traits. In order to do this, the residual values resulted from the ANOVA to test effects of pasture Grass type (B, E, N) on regeneration abundances (with abundances previously rank-transformed to to overcome lack of Normality) were correlated with the RANG values of whole plant, leaf and dispersal traits using Pearson coefficients. The partial Spearman Correlation analyses were able to test the relationships between abundances of tree natural regeneration with plant traits without interferences of grass effects. The Partial Spearman Correlations were compared with additional Spearman coefficients done using the original values of tree regeneration abundances and 16 traits (a non-partial Spearman correlations) to confirm for difference in Spearman coefficients due to a confounding effect due to pasture Grass type

According to the categorical nature of dispersal mode variables and the continuous nature of the abundance counting, the strength of the relationships between the abundances of tree natural regeneration by each developmental stages (seedling, saplings and adults trees) with dispersal modes were evaluated using logistic regression.

Multiple linear regression analysis (MRA) were used to evaluate which plant traits predict a higher proportion of the variability observed for tree regeneration abundances in active pasturelands. Individual models were calculated for seedlings and saplings abundances as dependent variables and using the plant traits significatively correlated each early developmental stage as regressors. Models were calculated also for seedlings and saplings abundances including adult tree abundances and plant traits as independent variables to test if the variability explained with the adult tree cover was greater than those observed only with plant traits to predict tree natural regeneration capacity. The Grass type (B, E, N) was also included as class variable (by including dummy variables) within both regression models developed by tree regeneration stage (seedlings and saplings) to evaluated and correct for possible effect of Grass type over the multiple regression between stage of tree abundances and plant traits. The pasture type from which the tree abundances were obtained did not affect the multiple regression relationships for any developmental stage and therefore the resulted models were shown without including the pasture factor (data not shown).

Our main objective with multiple regression was to describe the directions and relative magnitudes of the plant traits explaining tree regeneration abundances but not to explain the most variance. In order to select the best model for our main objectives we did the following steps: 1) All the original values of measured plant traits were included in MRA without any transformation or elimination method. 2) The partial residuals of the model were inspected to detect outliers and lack of fit of the different regressors. 3) Polynomic terms, mostly of quadratic and cubic order, were included to the MRA when the partial residuals suggest them to adjust linearity. This procedure continues until the inspection of the partial residues of the model showed absence of any pattern. Centered regressors were used for all the polynomial orders when polynomic functions were necessary to avoid multicoliniarity between polynomic terms of the same regressors; 4) Stepwise elimination method, a method for adding and removing terms systematically from a multilinear model (Legendre and Legendre, 1998) was used to retain the plant traits associated ($p < 0,05$) with seedlings and saplings trees abundances. 5) Outliers' presence and Normality assumption (a Q-Q plot with $r^2 \geq 0.94$) were tested. Adjusted - r^2 (higher is better), AIC (Akaike Information Criteria) and BIC (Bayesian Information Criteria) criterion (smaller is better) were used to select the best fit model. 6) The Variance Inflation Factor (VIF) was used to avoid multicolianiarity, excluding the factors having a $VIF \geq 5$ from the model. 7) Finally, original variables were transformed when normality assumption was not reached following these steps. The normality assumption was held for the error term of all these this models (Q-Q plot, r2>0.94), as well as linearity (simple linear patterns in the graphic between partial residuals and each trait) and heteroscedasticity (no function pattern in the residuals against predicted scatter plot).

A total of 76 tree species were surveyed for tree abundances by developmental stage and plant traits generating an un-balanced data set of 76 species × 16 traits because not all the plant traits were measured for all the species (missing values). The abundances were obtained from three different pasture types (B, E, N) resulting in increased data matrix of 228 data coming from 76 species x 3 grass types x 16 mean traits values. A total of 25 tree species have a complete record for each trait generating a balanced sub-database of 75 data coming from the species abundances of 25 tree species in the three grass types. The partial Spearman correlations analysis (CA) between plant traits and the abundances of tree regeneration stages were calculated using between 32 and 76 species by paired correlation analyses, varying depending on the traits considered. In contrast MAR were calculated using the 31 and 26 species respectively for seedling and saplings stages having the complete data set of plant traits measured for the specific combination of traits entered as potential regresors generating dataset of 95 and 83 values taking into account the abundances variability by grass types. Therefore, the CA paired correlations between the abundance of tree regeneration stages were tested with more power than MAR. The results from these approaches (CA and MRA) were complementary and not necessary equal, first because the incomplete data set, and second because MRA consider in addition the co-variance structure among all the regressors.

3.4 RESULTS

Relationships of plant traits with abundance of tree natural regeneration

Whole plant, leaf and dispersal traits were significatively correlated with the abundances of the tree populations within disturbed environments (**Table 3.3**) suggesting that plant traits can predict tree natural regeneration capacity in active pasturelands, although the variances explained were quite low.

However, the relationships between adult abundances and abundances of the early developmental stages showed higher correlation coefficients than the relationships between plant traits and tree abundances. The positive relationship between saplings and seedlings abundances showed the highest correlations coefficients followed by their respective positive correlations with adult's tree abundances (**Table 3.3**, **Figure 3.1**) the abundance of adult trees has a higher effect than trait values on tree regeneration capacity in active pasturelands and that could be a stronger predictor of plant responses to disturbance than functional traits. Therefore, more abundant populations of tree seedlings and saplings in active pasturelands were found for those tree species having higher abundances of adult trees within the pastures (**Figure 3.1**) but the tree species with a more abundant natural regeneration in disturbed areas showed also a particular functional characterization (**Figure 3.2**).

Table 3.3. Partial Spearman correlations coefficients (r) between the abundances of natural tree regeneration in active pasturelands (residuals) with whole plant, green and dispersal traits including additional dispersal (r is followed by p-value inside parenthesis followed by the number of species sampled (n), highlited significance levels are: **p<0.001,** **p< 0.05**, **p<0.10**)

Traits groups	Traits	Seedlings	Saplings	Adults
Whole plant	H_max	**0,25 (0,0003) 69**	**0,15 (0,0366) 69**	**0,38 (<0,0001) 69**
	WD	0,05 (0,5278) 64	**0,21 (0,0031) 64**	-0,13 (0,0797) 64
	PHE	0,09 (0,2377) 58	0,02 (0,7644) 58	**0,35 (<0,0001) 58**
Leaf	SLA	**-0,14 (0,1011) 44**	**-0,19 (0,026) 44**	**-0,23(0,0091) 44**
	LA	**-0,18 (0,0357) 45**	**-0,19 (0,026) 45**	**-0,30 (0,0004) 45**
	LDMC	**0,15 (0,07) 47**	**0,23 (0,0063) 47**	0,10 (0,2496) 47
	LCC	**0,13 (0,0767) 58**	0,08 (0,2848) 58	**0,15 (0,0534) 58**
	LPC	-0,08 (0,2847) 59	**-0,12 (0,0995) 59**	-0,06 (0,3932) 59
	LNC	**0,13 (0,0732) 62**	0,10 (0,1583) 62	0,10 (0,1841) 62
	FTF	-0,05 (0,5221) 46	-0,01 (0,9198) 46	-0,03(0,7328) 46
Dispersal	Sha_Fru	**0,19 (0,0068) 68**	**0,15 (0,0329) 68**	**0,19 (0,0064) 68**
	Mas_Fru	**0,23 (0,0124) 39**	**0,19 (0,0404) 39**	**0,16 (0,0821) 39**
	Sha_See	**0,22 (0,0022) 62**	**0,21 (0,0038) 62**	**0,16 (0,0246) 62**
	Mas_See	0,10 (0,1975) 59	**0,12 (0,1065) 59**	-0,03 (0,6638) 59
	Vol_Fru	**0,36 (<0,0001) 57**	**0,31 (<0,0001) 57**	**0,48 (<0,0001) 57**
	Vol_See	**0,29 (0,0001) 61**	**0,23 (0,0019) 61**	**0,40 (<0,0001) 61**
Abundances	Seedlings		**0,77 (<0,0001) 76**	**0,55 (<0,0001) 76**
	Saplings			**0,51 (<0,0001) 76**
	Adults			

Eight plant traits: Hmax, SLA, LA, Sha_fru, Sha_see, Mass_fru, Vol_fru and Vol_see were correlated with all three developmental stages, indicating they key relationship with a successful tree natural regeneration in active pasturelands and with tree species responses to disturbances. H_max together with Sha_fru, Sha_see, Mass_fru, Vol_fru and Vol_see were positively correlated with seedlings, saplings and adult's abundances, meanwhile SLA and LA were negatively correlated (**Table 3.3**). The correlations coefficients of these eight traits were higher for the relationships with adult tree populations than with seedlings or saplings populations. The strongly positively correlations of H_max, Sha_fru, Sha_see, Mass_fru, Vol_fru, Vol_see and the negative correlations of SLA, LA with adults abundances reflect the strong functional responses of the actual adult tree cover outside the forest resulted from the complex interactions between natural and anthropogenic selection forces.

The relationships between seedlings abundances with these whole plant and dispersal traits followed in strength, having the relationships between saplings abundances with leaf traits the lower correlation coefficients. The slightly more stronger positive correlations between whole plant traits (H_max) and dispersal traits (Sha_fru, Sha_see, Mass_fru, Vol_fru, Vol_see) with seedlings than with saplings abundances, probably suggest also that this characteristics help to overcome mainly the limitations in seed dispersal and seedling initial establishment. The slightly more stronger negative correlation between leaf traits (SLA and LA) with saplings than with seedlings abundances suggest that these traits are probably more relevant to with saplingsurvival and adult growth up to maturity.

Other plant traits were correlated only with abundances of early developmental stages but not with adult abundances indicating that this trait is a morphological characteristic that definitely enhances natural regeneration in active pasturelands independently of adult abundances. One plant trait, LDMC was correlated only with both early stages of tree development, having positive and strong relationships with saplings and more weakly with seedlings abundances. A higher LDMC in saplings and seedlings probably enhance tree early developmental stages sapling survival via reducing leaf damages and consumption by hervivories and/or reducing drought mortality.

In contrast, some plant traits were correlated only with adult abundances but not with seedlings and saplings abundances, like PHE, which has a strong and positively relationship with adult abundances.

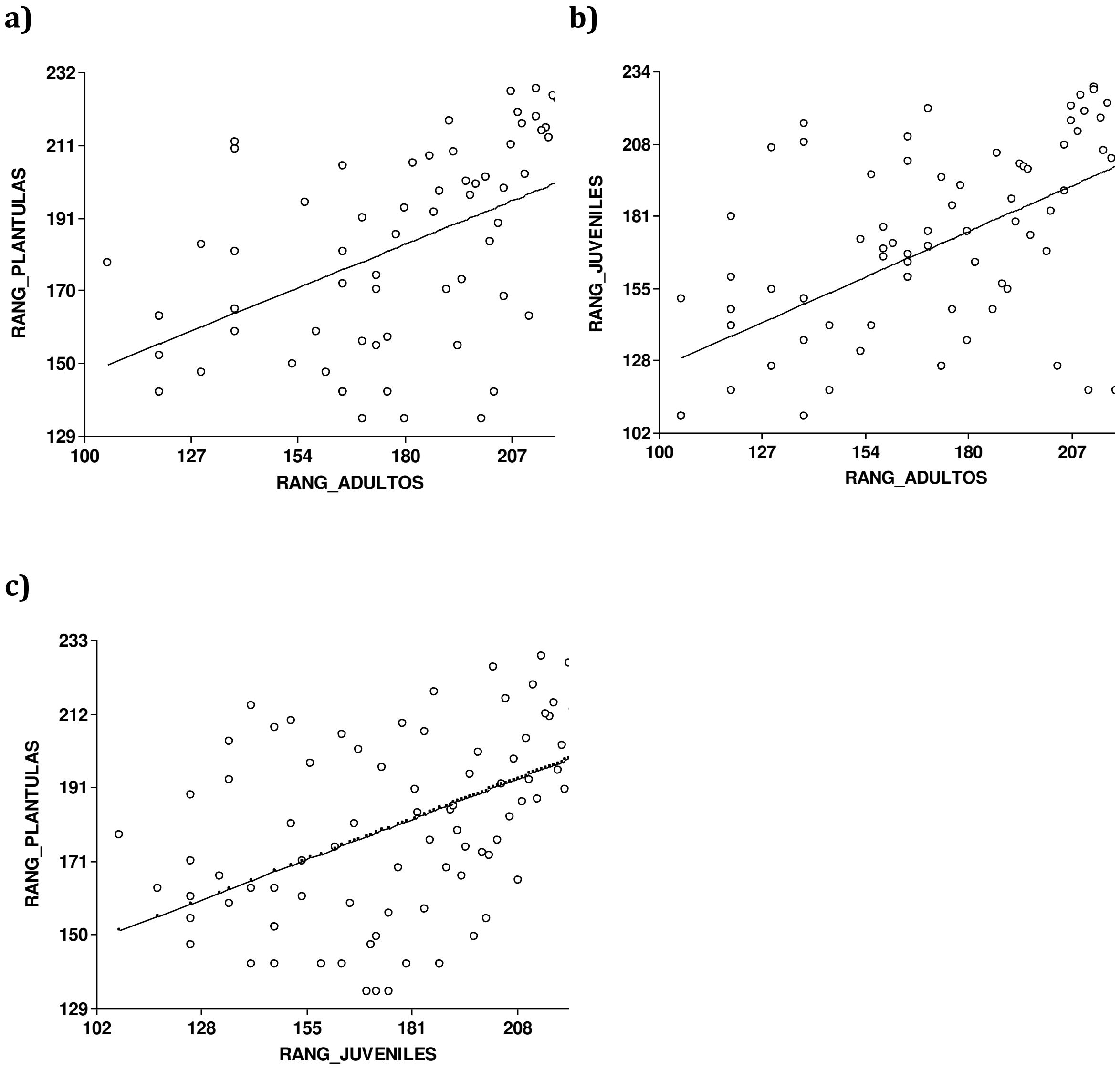

Figure 3.1. Relationships between adults, saplings and seedlings abundances of tree species in neo-tropical and active pasturelands in Central America (r and p values in table 3.3)

Finally, other leaf and whole plant traits were correlated with adult abundances and with one of the two of the early stages of tree natural regeneration. For example, LCC was positively correlated with adults and seedlings abundances but not correlated with saplings abundances; meanwhile WD was positively correlated with tree saplings abundances but negatively correlated with adult abundances.

The number of plant traits correlated with the abundances of early tree natural regeneration and the strength of these relationships varies among developmental stages and sets of measured plant traits. In general, dispersal, leaf and whole plant traits were correlated with both early developmental stages, but more plant traits were strongly ($p \leq 0.05$) correlated with saplings stages (10) than for seedlings stages (7). H_max, LA, Vol_fru, Vol_see, Sha_fru, Sha_see and Mass_fru were correlated with seedlings abundances and in addition, WD, LDMC and SLA were correlated with saplings abundances. Vol_fru was the plant trait more strongly correlated with the abundances of both developmental stages. In general, the positive relationships between abundances of tree early developmental stages with dispersal traits showed highest correlation coefficients, being even quite higher for seedlings than for saplings abundances, but keeping the same decreasing order at both stages: Vol_fru, Vol_see, Sha_fru, Sha_see and Mass_fru.

In contrast, the strength of the positive relationships between the abundances of early natural regeneration with leaf and whole plant traits, which followed in strength of the correlations to dispersal traits, did vary following different patterns for both developmental stages. In general, whole plant traits showed highest correlations coefficients for seedling abundance meanwhile leaf traits showed highest correlations coefficients for leaf traits higliting their different relative influence for each of the early tree developmental stages. For example, the observed correlation coefficients with whole plant traits like H_max were higher for seedlings (0,25) than for saplings (0,15) at the same time that also WD was positively correlated with saplings abundances. In addition, the correlation coefficients for the relationships between abundances and leaf traits were stronger with saplings than with seedlings abundances. In this case, although the correlation coefficient of LA was just slightly higher for saplings (0,19) than for seedlings (0,18), two more leaf traits i.e. LDMC and SLA were also highly correlated with saplings but not with seedlings abundances (**Figure 3.2**) Other leaf traits like LDMC, SLA, LCC and LNC were only weakly correlated with seedlings abundances; meanwhile LPC and other dispersal trait like Mass_see were only weakly correlated with saplings abundances.

These results showed that plant traits are directly correlated with the abundances of tree natural regeneration after disturbances like active livestock management. Taller tree species regenerate successfully having more abundant saplings and seedling populations in active pasturelands. Tree species with dense woods have more abundant populations of saplings unless tree species with softer woods were more abundant at adult's stages. Deciduous tree species were also the more abundant trees in active pasturelands, but were nor related at all with tree early stages. Tree species more conservative leaf strategies (lower SLA, LA and LPC together with high LDMC and LCC) were the more abundant species at all tree developmental stages. Finally, tree species with bigger and heaviest fruits and longest dispersules were more abundant at all developmental stages in active pasturelands.

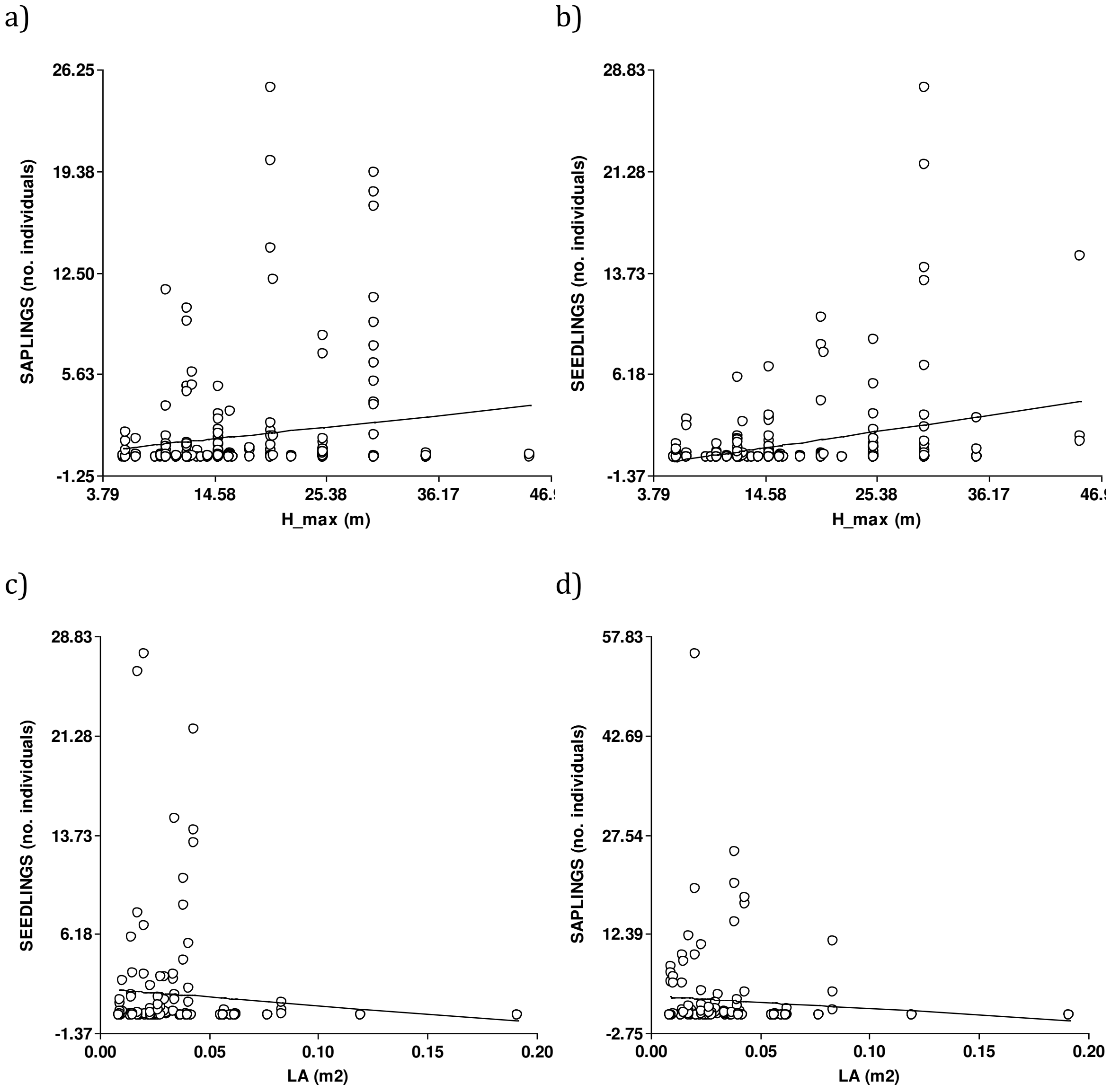

Figure 3.2. Relationships between adults, saplings and seedlings abundances with some plant traits of tree species in neo-tropical and active pasturelands in Central America.

Functional characterization of adult's tree community in active pasturelands

A functional description of the adult tree component in agricultural lands as well as of their reationships with tree adult abundances in active pasturelands is equally relevant to our main chapter objective focused to explain correlations between plant functional traits with the abundances of tree early delopmental stages. In addition, the observed differences in the significant correlations between traits and abundances between developmental stages give insights over the possible changes in the functional characterization of tree cover within these disturbed areas due the different regeneration capacities of these tree species with particular functional niches.

The abundance of adult trees was correlated with whole plant, leaf and dispersal traits no matter the strongly variable factors influencing adult's trees composition and abundances in active pasturelands (**Table 3.3**). Adult tree abundances were strongly and positively correlated with Vol_fru, Vol_see, H_max, PHE, Sha_fru, Sha_see, Mass_fru and LCC, and were negatively correlated with LA, SLA and WD. Therefore, the tallest and more deciduous tree species with lighter woods have the more abundant adult populations. In addition smallest leaves with highest total carbon contents and therefore a low specific leaf area were common leaf characteristics of the more abundant adult tree species in these habitats. The biggest and longest diaspores with heaviest fruits characterized also the tree species with the highest adult's populations. These results imply that the actual assemblage of adult's trees in active pasturelands has a direct association with functional species characteristics besides the complex convergence of natural and anthropogenic selection exerted over this tree component in active pasturelands.

The functional characterization of adult populations was similar to the functional description found for the early developmental stages of tree species naturally regenerating in active pasturelands. The more abundant seedlings and saplings populations were found for taller tree species, with more conservative leaf in the use of resources i.e. small leaves with high carbon and leaf dry matter content and with a low specific leaf area, also with bigger and longest dispersules and heaviest fruits. However, other plant traits were exclusive correlated with the abundances of early developmental stages and not with the abundances of adult tree populations. Tree species with higher total carbon and nitrogen for example were more abundant at saplings stages, meanwhile also those with highest phosphorus in leaves and heaviest seeds were more abundant as saplings, but none of these characteristics was correlated to more abundant tree species at adult's stages. Conversely, a higher abundance of tree saplings was observed also for species with dense woods, meanwhile the more abundant adult tree species have mainly softer woods.

Relationships of dispersal mode with abundance of tree natural regeneration

Dispersal mode was correlated with tree abundances at the three different developmental stages (**Table 3.4**). Mammalochory was positively correlated with seedlings, saplings and adults abundances. In contrast, Zoochory was negatively correlated with abundances of the three all tree developmental stages, but strongest with adults abundances, followed by seedlings and tending to be correlated with saplings abundances. Anemochory was also positively correlated with tree abundances but just at adult tree stages. Finally, Autochory was not correlated tree abundances at any developmental stages.

Table 3.4. Partial Spearman correlations coefficients between the abundances of natural tree regeneration in active pasturelands (residuals) with whole plant, green and dispersal traits including additional dispersal

Abundances	Seedlings		Saplings		Adults	
Dispersal types	Est.	p-value	Est.	p-value	Est.	p-value
Mamalochory	**0,01**	**0,0108**	**0,01**	**0,0047**	**0,01**	**0,0001**
Zoochory	**-4,70E-03**	**0,0396**	**-3,70E-03**	**0,0908**	**-0,01**	**<0,0001**
Anemochory	4,10E-03	0,1519	3,20E-04	0,9101	**0,01**	**0,0026**
Autochory	-3,70E-03	0,2372	-1,70E-03	0,5555	-1,30E-03	0,6443

These results showed that dispersal mode can predict abundances of tree natural regeneration in active pasturelands. Those tree species dispersed by cattle were the species having the most abundant tree regeneration in active pasturelands at all developmental stages. Tree species dispersed by wind were also the most abundant adult’s tree species, but were not so successfully at earlier developmental stages. Tree species dispersed by wild animals like birds and bats were in contrast to the species with the lowest abundances through the whole tree developmental stages. Tree species dispersed by the same parental tree in contrast, didn’t have any particular association with a more abundant or restricted tree natural regeneration in active pasturelands.

Multivariate relationship of plant traits with abundance of tree natural regeneration

The multiple regression models showed that dispersal, leaf as well as whole plant traits were also explaining more than half of the total interespecific variance observed in tree natural regeneration abundances in active pasturelands. As observed in the pair-wise plant traits and tree abundances relationships, some plant traits explained a relevant proportion of inter-specific variability in the multivariate models for both early tree developmental stages. Dispersal traits like Sha_fru and Sha_see, together with whole plant traits like H_max and leaf traits like LDMC were predicting seedling and also sapling abundances taking into account the interspecific and multivate variability, underlying the key role of these traits in the successful of tree natural regeneration in these areas (**Table 3.5**). In contrast, other plant traits have a multivariate predictive value (p=0.05) within the fitted models only for one of the two developmental stages. Leaf traits like LNC, LCC, LA and dispersal traits like Vol_Fru were predicting seedlings abundances but not saplings abundances, indicating the more relevant role of these leaf and dispersal traits to develop a successful seedling population in active pastures.

A total of 55% of species variability in sapling abundance was explained together by whole plant, leaf and dispersal traits (R^2=0.55 and the adjusted R2 was 0.52), indicating that plant traits predict tree sapling abundances. The partial determination coefficients (r^2) were higher for dispersal traits like Sha_fru and for whole plant traits like H_max, than for leaf traits and other dispersal traits like LDMC and Sha_see. Therefore, dispersal and whole plant traits make the higher contributions to explain the interspecific variability observed in saplings abundances.

A higher proportion of variability in saplings abundances, 67%, was explained when adult tree abundances were also included within the multiple regression analyses (R^2=0.60, adjusted R^2=0.51). Now, tree adult abundances together with plant like Sha_fru and LDMC explained together the abundances of tree saplings. Sha_fru had the higest r^2 values within this adult dependent model, followed by sapling abundances together with LDMC.

In addition, 56% of species variability in seedling abundances was predicted by whole plant, leaf and dispersal traits (R^2=0.56; R^2 Aj=0.51). The variability observed in seedling abundances was mainly predicted by dispersal traits like Sha_fru followed by H_max, Sha_see, LNC, LA, Vol_fru and finally LDMC (ranked by decreasing order in partial determination coefficients r^2). These results imply that unless dispersal and whole plant traits make the highest contributions to explain seedlings abundances leaf traits play also and important roles at this first stage. A higher proportion of variability in saplings abundances, 67% was explained when adult tree abundances were also included within the multiple regression analyses (R^2=0.67, R^2 Aj=0.66). Abundance of adult trees was the main predictor of tree sapling abundances now followed by Sha_see and finally by LCC.

Table 3.5. The total, adjusted and partial determination coefficients (r^2, r^2Ad) for the multiple regression models and estimated parameters obtained for plant traits and adult abundances as predictors of tree natural regeneration abundances (seedlings and saplings) in active pasturelands

Abundances	Traits/abundances included	MRA model terms	Est.	p-value	r^2 (r^2 ad)
Saplings without adults	H_max, WD	const	-2.39	**0.0003**	0.55 (0.51)
	SLA, LA, LDMC, LPC	Sha_Fru_Car^2	65.72	**<0.0001**	0.8464
	Sha_fru, Sha_see	Sha_Fru_Car	-17.06	**<0.0001**	0.8836
	Vol_fru, Vol_fru	H_max	0.19	**0.0005**	0.8836
	Mas_se	H_max^2	-3.30E-03	**0.0023**	0.8281
		Sha_See_Car	3.7	**0.0217**	0.0484
		LDMC_%	0.03	**0.038**	0.0676
Saplings with adults	H_max, WD	const	-0.72	**0.0566**	0.60(0.58)
	SLA, LA, LDMC, LPC	radultos	0.76	**<0.0001**	0.3721
	Sha_fru, Sha_see	Sha_Fru_Car^2	38.38	**0.0001**	0.7056
	Vol_fru, Vol_fru	Sha_Fru_Car	-8.76	**0.0017**	0.7396
	Mas_se, Adults	LDMC_%	0.03	**0.0158**	0.0784
Seedlings without adults	H_max, LNC	const	1.07	0.1382	0.56 (0.52)
	SLA, LA, LDMC, LCC	Sha_Fru_Car^2	83.47	**<0.0001**	0.8649
	Sha_fru, Sha_see	Sha_Fru_Car	-24.03	**<0.0001**	0.9216
	Vol_fru, Vol_fru	H_max	0.04	**0.0001**	0.2601
		Sha_See_Car	5.97	**0.0001**	0.2916
		LNC_Car	-0.68	**0.0007**	0.1936
		LA^2	-188.43	**0.007**	0.0961
		Vol_Fru_Car	-9.20E-05	**0.008**	0.1156
		LDMC_%	0.03	**0.023**	0.0784
Seedlings with adults	H_max, LNC	const	1.86	**0.0927**	0.67 (0.66)
	SLA, LA, LDMC, LCC	radultos	1.05	**<0.0001**	0.6241
	Sha_fru, Sha_see	Sha_See_Car	3.26	**0.0005**	0.1444
	Vol_fru, Vol_fru	LCC_Car	-0.05	**0.0379**	0.0576
	Adultos				

These results reinforce the strong correlations between plant traits and adult tree abundances with tree early regeneration abundances observed in the paired correlations. In addition, the MRA results imply that adult trees together with plant traits explained a higher proportion of tree natural regeneration after disturbances like those continually exerted over tree populations in active pasturelands. Interestingly these results suggest also that the strength of the relative contribution of adult's trees or plant traits to the abundances of tree natural regeneration depend on the developmental stage: adult's tree abundances have a stronger contribution to established seedlings than to established saplings populations. Finally, these results imply also that the success on the establishment of early stages of tree natural regeneration can be predicted strongly by dispersal traits, but that also by whole plant and also leaf traits explain such success and that their additional relevance also varies with tree ontogenic development.

3.5 DISCUSSION

Dispersal, leaf and whole plant traits were correlated with the abundance of tree natural regeneration in active pasturelands

As predicted, whole plant, leaf and dispersal traits were correlated with the abundances of tree regeneration in active pasturelands. H_max, SLA, LA, Sha_fru, Sha_see, Mass_fru, Vol_fru and Vol_see were correlated to all three developmental stages indicating that they have a key relationship with successful natural regeneration in active pasturelands and with tree species responses to disturbances. I.e. these whole plant and dispersal traits were positively correlated with adult, saplings and seedling abundances, meanwhile these leaf traits were negatively correlated with abundances. The strong positive correlations between these traits with adult abundances reflect the functional characterization of the actual adult tree cover surviving outside the forest which resulted from the complex interactions between natural and anthropogenic selection forces. The strong correlations between these key whole plant, leaf and dispersal traits with the tree early developmental stages suggest these are successful strategies to overcome disturbances. Therefore, taller tree species having longest and biggest diaspores with heaviest fruits and also having small leaves with low specific leaf area are those with the more abundant populations naturally regenerating in active pasturelands. These morphological characteristics may enhance tree species' capacity to successfully overcome limitations in seed dispersal, seedling establishment, saplingsurvival and adult growth up to maturity, some of the main "bottle necks" of natural regeneration to maintain a viable population within active pasturelands, a highly and permanent disturbed habitat.

Maximum tree height was positively correlated with the abundance of tree natural regeneration. In previous studies H_max has been positively correlated with growth rates and negatively with mortality rates in several neotropical forests (Poorter et al. 2008). In forest environments the correlation between maximum tree high and faster growth rates has been explained as an adaptive advantage to maximize light capture, a vital resource but highly variable inside forest sites (see also Westoby 1998, Poorter et al. 2005). Light availability in open pasture sites, however, is probably not a limiting factor from the sapling stage on and tree species with high light requirements and faster growth rates therefore can proliferate within these environment once, of course, they have been able to successfully overcome the first stages of seed dispersal, seedling establishment and survival of herbivore attacks within these highly grazed and browsed areas. The commonly named "gap colonizers", those species capable of quickly colonizing sporadically open areas inside the forest (i.e. caused mainly by fallen trees) could be also those species able to colonize open areas beyond the forest border into the adjacent pasture matrix. Two of the most abundant tree species founded in the active pastures of our study area have been classified as early successional, *Cedrela odorata* L. (Menalled and Kel 2001) and *Cordia alliodora* (Ruiz and Pavón) Oken) (Coll et al. 2008) and have also higher maximum tree height within these habitats. Their faster growth rates during the early developmental stages could be advantageous for tree species colonizing pasturelands because tree seedlings can quickly escape from light competition with grasses increasing their chances for a successful establishment in active pasturelands (per. obs).

Fruit and seed volume and shape were positively correlated with the abundance of tree natural regeneration. Tree species having longest and biggest dispersules and heaviest fruits were also the species abundant in all the developmental stages in active pasturelands. These results suggest that these both fruit and seed characteristics have a key influence for tree regeneration capacities in active pasturelands. Longest and biggest dispersules with heaviest fruits were probably facilitating seed dispersal and seedling establishment stages of natural regeneration in active pasturelands. Seed size (measured as mass or volume) has strong influences in dispersal distances (Jansen et al. 2004), germination, establishment and growth rates of seedlings (Mazer 1990, Paz et al. 2005), key factors to succeed in open pasture sites (Zimmerman et al. 2000). Large seeds carry on more reserves to ensure seedlings establishment in low-resources conditions and to produce larger seedlings with a higher probability of escaping from size-dependent mortality and from hervibore damage (Kitajima 2002, Harms and Dalling 1997). In open areas outside the forest like in active pasturelands, tree species with biggest seeds probably also benefit with a higher content of reserves to produce big seedlings that can establish in low-resources conditions, to quickly overcome the dense grass cover and survive herbivorous damage.

Bigger seeds were positively correlated to tree abundances in all developmental stages, indicating that tree species with bigger seeds have more abundant tree natural regeneration in active pasturelands. Bigger seeds have been correlated with an increased capacity to grow with low resource availability (Westoby et al. 2002), lower seed production (Henery and Westoby, 2001) and a reduced probability of reaching safe sites (Wright et al. 2006). In contrast, our results indicate that tree species with bigger seeds (volume) are predictors of a more abundant seedling bank in active pasturelands. As stated by Westoby et al. (2002) probably the higher resources allocation within the biggest seeds (measured as seed mass or volume) increases the probability of successful seedling establishment in the face of environmental hazards that in active grasslands could be determinated by low water and nutrients availability and high grass competition (Zimmerman et al. 2000).

The longest dispersules with bigger and heaviest fruits were related with particular seed dispersal strategies that probably increase seeds probabilities to reach safety places increasing also further seedling establishment rates. As stated in our previous chapter 2, dispersule shapes, masses and volume have been found correlated with dispersal modes: small and spherical seed and fruits have been found to be dispersed by local fauna, meanwhile longest fruits with longest and lighter seeds have been mainly dispersed by wind, and biggest and heaviest fruits with heaviest seeds have been found to be dispersed mainly by cattle. In addition, we observed that tree regeneration abundances were also significatively correlated with tree species main dispersal mode. Tree species dispersed by cattle (a particular kind of mammalochory) were the more abundant tree species in all developmental stages. Fruits dispersed by cattle tend to have the biggest and heaviest fruits with heaviest seeds. Once consumed, cattle dung provides an enhanced microhabitat for seed germination and seedling establishments through a substrate that reduce grass competition and cattle damage through grazing and browsing (Malo and Suarez 1995, Cosyns et al. 2005).

In contrast, those tree species with seed mainly dispersed by wild fauna had lower abundances in all tree developmental stages. These tree species in fact have more spherical, small and lighter dispersules. The highly fragmented tree habitat component of active pasturelands probably restricts wild fauna mobilization reducing the seed rain to under tree canopies reducing therefore their relative abundances within these ecosystems. In addition, tree species having morphological adaptations for wind dispersed seed were also abundant in adult stages, but such high abundance of mature trees with anemochorous dispersion was not reflected in higher abundances of early developmental stages. In the previous chapter 2, we observed that wind dispersed trees were correlated with lower seed masses. A low seed size has been found in species with a high density of seeds by dispersule unit, being considered also better colonizers of ephemeral sites in space and time (Dalling et al. 1998, Moles et al. 2004). Wind was probably a more successful seed dispersion vector to reach the open pasturelands matrix, but their successful seedling and sapling establishment will depend on reaching a successful microsite and growing quickly enough to avoid grass competition for light and water. Unless faster growth rates could be can be observed for tree wind dispersed species like *Cordia alliodora*, it is probabe that their further success in seedling and sapling establishment probably depends on additional characteristics like defense against herbivorous attacks. Therefore unless wind dispersed seeds could easily reached open pasture areas, this condition does not imply higher abundances of tree natural regeneration in disturbed areas.

Appropriated strategies to survive the herbivore attacks are also required for tree species to proliferate their populations in active pasturelands together with an advantageous seed dispersal mode and high establishment rates. We found that SLA and LA were negatively correlated with adult, saplins and seedling abundances. The more abundant tree species have small but expensive leaves having a higher investment in carbon for their construction. Low SLA leaves tend to be thicker and dense and physically robust and less attractive to herbivores than leaves with a high SLA (Coley 1985, Wright and Westoby 2002). Low SLA leaves tend to be longer lived and may lead to longer plant life spans (Sterck et al. 2006). Kitajima (1994) found that SLA was a good predictor of seedlings growth and survival and Poorter and Bongers (2006) founded that SLA was good predictor of sapling height growth. Our results suggest however that SLA has a key role in the survivorship of trees at all developmental stages in active pasturelands, when tree species abundances of early developmental stages increases consistently when SLA decreases. Tree leaves with a higher investment of biomass in producing leaf area are probably a good defense against herbivore attack and damages due to cattle grazing and browsing.

Other plant traits were correlated exclusively with early stages of development suggesting that maybe different morphological characteristics during the development of trees can increase tree species survival during the natural regeneration in active pasturelands. LDMC was positively correlated with seedling and sapling abundance but not with adult abundance, indicating a stronger relationship with early tree establishment stages and therefore a key role enhancing seedling and sapling establishment. Higher amounts of biomass invested in leaves probably enhance seedling and sapling defense against herbivores due to increase in physical strength of leaves or due to reduced leaf palatability for consumers (Elger and Willby 2003). We didn't find a significant correlation between tree species abundance and FTF to support that LDMC can also increase the physical resistance to damage due to cattle grazing or browsing. However, FTF measures leaf resistance to tearing, while higher LDMC in leaves probably implie an increase of more recalcitrant C fractions like lignin, celluloses and memicelluloses or other secondary metabolites which reduce leaf digestibility or palatability mainly for cattle, so that both traits may affect grazing palatability (Coley et al. 1985, Hanley and Lamont 2002).

LCC and LNC were positively correlated with seedling abundance, and therefore tree species with higher carbon and nitrogen content in leaves have more abundant individuals at early developmental stages. LCC was positively correlated also with adult abundances and therefore the higher abundance of seedlings of those tree species with higher LCC could be though to reflect only the higher dispersule sources (more dispersible potential sources then more seeds dispersed and more seedlings abundances). However, LCC has been also positively correlated with defense against herbivores consumption and negatively with palatability as measured by the amount of structural carbon invested to construct one functional leaf and with leaf C/N-ratio (Schädler et al. 2003). Therefore, these species probably experienced lower mortality rates due to herbivore attacks allowing them to develop more abundant seedling populations. Unpalatable leaves have low LNC and high leaf tensile strength, which depends on LDMC (Pérez-Harguindeguy et al. 2000, Wardle et al. 2002), these traits determining also carbon-rich structural compounds and high recalcitrant C fractions like lignin, which strengthen leaves significantly (Choong et al. 1992, Wright and Illius

1995) and determine leaf digestibility and litter decomposition (Swift et al. 1979, Melillo et al. 1982, Schädler et al. 2003).

Conversely to the low palatability hypothesis, LNC was also positively correlated with seedling abundance, indicating that other additional mechanisms are also feasible to develop a successful population or seedlings in active pastures. In contrast to LCC, LNC was not correlated with adult abundance, indicating that those tree species with higher nitrogen content on leaves have must a more successful seed dispersal, germination and/or seedlings establishment rates, independently of adult abundances and to the higher risk of mortality due to higher palatability associated to higher LNC. Therefore, the strategy of tree species to have higher abundances of saplings in active pasturelands, probably rely not only on the reduction of herbivore damage risk, but also in another mechanism evidenced by the correlations with other traits. In fact, as stated previously, the higher abundances of seedlings were also positively correlated with H_max and dispersal traits, even more than with saplings abundances, probably due to higher photosynthetic rates required for tree species with higher growth rates allow them to quickly escape from competitions and herbivores within the preexisting vegetation. In addition, tree species with higher LNC as well as those with higher early regeneration abundances, were positively correlated with specific dispersal strategies like mammalochory, which provide additional advantages to this species via cattle dung, serving as an enriched environment and as a physical defense against herbivores and competition.

In addition, a good defence against herbivores has been also related with high quality leaves, like those with higher nitrogen contents. Tree species with high quality leafs but well defended against herbivores will have clear advantages to succeed their populations in active pasturelands. Leaves with higher nitrogen contents have been related with higher photosynthetic rates in full sun exposures. In contrast, long-term shading of isolated plants generally results in leaves that have a lower photosynthetic capacity and leaf nitrogen content per unit area, and a larger investment of total available nitrogen in chlorophyll and light-harvesting compounds (Evans, 1996; Hikosaka and Terashima, 1996; Evans and Poorter, 2001). Apart from the decrease in leaf thickness, shading also causes a decrease in leaf density, the net result being a higher amount of leaf area formed per unit of biomass invested in leaves (Poorter et al. 2005). Therefore, in open pastureland the high availability of sun exposure is a favourable environment for tree species with high photosynthesis requirements and low palatability, which can develop here successful populations ones of course they have been able to successfully overcome seed dispersal and germination.

LPC and Mass_see were plant traits also marginally correlated but only with sapling abundances, indicating that tree species with low leaf phosphorus contents and with heaviest seeds could have higher saplings abundances. Biggest seeds (according to volume or mass) have been related with more parental resources to grow quickly escaping from the high mortality rates at early developmental stages. The positive tendency in the relationship between Mass_See with seedlings abundances could support this idea but the lack of significance indicates that other more relevant mechanisms and morphological traits could be implicated on assuring higher abundances at seedling stages like an inherent faster growth (reflected by the positive correlations of H_max with seedling abundances) and more conservative leaves with low palatability and desiccation risks (reflected by the negative correlations of LA, SLA and LPC but positive with LDMC). A reduced content of phosphorus in leaves reflected only in saplings stages probably reflects the strong influence that the plant strategy to obtain nutrients have on the saplings stages when all the mineral nutrients for growing comes from the environment and not from the maternal resources which favoring seedlings growth or neither by massive internal redistributions of nutrient as can happen in adult trees (Pallardi 2008). Therefore, although a tendency for those tree species with more conservative leaves to have more abundant seedlings populations; the relationships with other traits make possible the identification of further successful strategies to overcome limitations in active pasture site colonization.

Functional characterization of adult tree cover in active pasturelands

Natural interactions, historic disturbances and farmers’ decisions shape adult tree cover in agricultural lands (Harvey at al 2006). Management strategies affect tree regeneration richness and composition shaping biodiversity of future tree cover outside forest (Esquivel et al. 2008). We do not attempt to explain the ultimate causes of the observed correlations between plant traits with adult abundances due to the complex interactions between natural and anthropogenic historical management. However, our results showed the first functional description of the actual tree cover in agricultural lands. This functional description has special relevance as agricultural landscapes cover a higher proportion of land and have been consider an important source of biodiversity within the highly fragmented tropical landscapes (Harvey et al. 2006). In addition to the previous described correlations between plant traits and tree abundances (H_max, SLA, LA, Sha_fru, Sha_see, Mass_fru, Vol_fru and Vol_see) found for adult tree abundances as well as for early developmental stages, other plant traits were exclusively correlated with adult tree abundances, reflecting all those complex interaction out of the scope of the present study.

Leaf phenology and LCC for example, were positively correlated with adult abundances; meanwhile wood density was negatively correlated, indicating a direct relationship of these traits with tree species maintenance within these agricultural lands located on dry transition to humid regions. Therefore, the most abundant adult tree cover in active pasturelands is characterized by taller and deciduous tree species, with soft woods, small leaves with higher total carbon content and low specific leaf area, longest and biggest dispersules and heavy fruits. Whether these species are able to naturally regenerate or not will probably affect future tree cover characterization. Other plant traits were correlated only to adult abundances but not with seedling and sapling abundances, like PHE, implying that leaf life spans per se is not a mopho-physiological condition relevant to assure an abundant natural regeneration capacity of tree species in active pasturelands.

WD was negatively correlated with adult tree abundances but positively correlated with sapling abundance in active pasturelands. This result mean that tree species with lighter woods were the most abundant tree species as adults but not as sapling stages were tree species with dense woods are those able to develop abundant sapling populations. WD has been found to be closely related with shade tolerance and with some vital plant functions like defense, stability water relationships, carbon gain and growth (Santiago et al. 2004). WD has been found negatively correlated with growth and mortality rates in several neo-tropical forests (Poorter et al. 2008). Therefore, tree species with lighter woods (low WD) grow faster but died more frequently, have lower tensile strength at rupture and less elasticity, have a higher capacity to store water but a lower capacity to store C than do species with dense woods (high WD). Tree species with lighter woods has been successfully established as individual adult in active pasturelands.

More abundant saplings populations of tree species with dense wood in active pasturelands could be explained by an increase in resistance to herbivores damages. The early stages of dense wood tree species probably have relatively more resistance to physical damage by cattle due to higher WD of saplings stems which confer a higher physical strength and flexibility increasing their capacity to successfully survive at sapling stages. In addition, WD is generally correlated with a low SLA meaning that in addition to stronger sapling stems to resist cattle physical damages when grazing, a low SLA probably reduces herbivore consumption increasing again their chances to have an abundant sapling population in active pasturelands. This is a parallel condition to the observation inside forests, where a high wood fraction is advantageous for species that mainly regenerate in the shade, because it is protected from falling debris, an important mortality agent for understory tree species (Poorter et al. 2008) even seedlings and saplings (Kitajima 1994, Muller-Landau 2004).

Adult abundance was strongly and positively correlated with sapling and seedling tree abundance.

The strongest correlations with tree regeneration abundances in active pasturelands were found for adults abundances, suggesting that the abundance of adult trees has a relevant effect on tree regeneration capacity in active pasturelands and that it could be a stronger predictor of plant responses to disturbance than functional traits. These strong correlations between trees abundances were followed in strength the relationships between tree regeneration abundances with dispersal, leaf and whole plant traits respectively. These results confirm some observations made for other systems such as by Sudding et al. (2005) in herbaceous ecosystems in temperate North America, who find a negative relationship between abundance and extinction probability. These results reinforce the importance of retaining and maintaining an abundant and diverse adult tree cover within pastures and agricultural lands to encourage natural tree regeneration (Mayfield and Dayly 2005, Esquivel et al. 2008). Several previous studies have suggested that many tree species are unable to reproduce successfully and maintain populations in pastures over the long term (Janzen 1986, Esquivel et al. 2008). The limited seed rain (Radford et al. 2001) and the unfavorable microsites and microclimatic conditions in open pasture (Nepstad et al. 1996, Holl et all 199) are known to reduce tree colonization. Results like these suggest that environmental filtering during pasture colonization should select for tree species with certain combinations of traits that contribute to overcoming barriers to colonization of pastures, and that species lacking these trait combinations will be slow to colonize. Our study supports this to an extent, as already discussed. However, our results strongly indicate a simple positive relationship between seed availability – determined by adult abundance – and regeneration abundance suggesting that colonization of these pasture is effectively trait-neutral or trait-random (see Suding et al. 2005)

A higher abundance of adults also has been positively related with a higher genetic diversity implying that more but also better seeds will be dispersed from a more abundant mature population, increasing the probabilities for a successful germination and establishment. Grass competition (Schaller et al. 2003), cattle grazing (Archer 1995) and pasture management (Teague and Dowhover 2003) also limit tree regeneration in active pasturelands. The strong positive correlations between seedlings and sapling abundances we observed imply in addition that a higher number of seedlings increase the probability by chance to successfully survive and growth to the next developmental stage due the higher mortality rates that prevailed in these continually disturbed environment.

The fact that most but not all the observed correlations among plant traits with tree abundances were observed for adults trees and also for early developmental stages, indicates that together with adult tree abundances the functional composition of such tree cover are relevant because is going to be maintain through the future population. However the fact that some relationships between plant traits and abundances were found only in the early developmental stages, let open the gap in which the functional traits have a relevant role also in the prediction of tree natural regeneration after disturbances.

Plant traits predict the abundances of tree natural regeneration in active pasturelands, but adult abundance is the strongest predictor.

Whole plant, leaf and dispersal traits predict tree regeneration abundances in active pasturelands. A total of 55% and 56% of species variability in sapling and seedling abundances were explained together by whole plant, leaf and dispersal traits indicating that plant traits predict an important percentage of tree natural regeneration abundances. The fact that dispersal together with leaf and whole plant traits were found in both models indicates also that only and integrative assessment of plant functional traits make it possible to predict a relevant proportion of inter-specific variability in responses after disturbances. Tree sapling abundance was predicted by Sha_fru, H_max, LDMC and Sha_see; meanwhile tree seedling abundance was predicted by H_max, Sha_see, LNC, LA, Vol_fru and finally LDMC.

Dispersal traits like Sha_fru and Sha_see, together with whole plant traits like H_max and leaf traits like LDMC were predicting seedling and also sapling abundances underlying they key role in the successful of tree natural regeneration in these areas. These results agree with our previous expectations about a relevant role of dispersion traits over the population composition and structure of trees outside the forest. Sha_fru and Sha_see have been found correlated with different dispersal modes (see Chapter 1 results): longest fruits has been correlated with anemochorus and autochorus tree species while more spherical fruits and seeds were related with zoochorus tree species dispersed mainly by local fauna. More abundant tree species as seedlings and sapling were mainly dispersed by big mammals like cattle, meanwhile the less abundant tree species were those dispersed by zoochorus tree species. Therefore longest fruits and seeds were dispersed by more successful vectors to reach wide open pasture sites. In addition, the potentially higher growth rates associated with tree species with higher maximum tree heights and strongest leaf to avoid herbivorous damages, define optimal strategies to successfully overcome the limited dispersal, early establishment and growth of tree species in after disturbances in active pasture sites.

Leaf traits like LNC, LCC, LA and dispersal traits like Vol_Fru were predicting seedling abundance but not saplings abundances, indicating the more relevant role of these leaf and dispersal traits to predict the successful establishment on the post-germination earlier tree ontogenic populations.

As expected, higher percentages of variability can be explained with the inclusion of adult abundances. A total of 67% of tree species variability was predicted by tree adult abundances and plant traits. These reinforce the strong correlations between plant traits and adult tree abundances with tree early regeneration abundances observed in the paired correlations. In addition, the MRA results imply that adult trees together with plant traits explained a higher proportion of tree natural regeneration after disturbances like those continually exerted over tree populations in active pasturelands. Sha_fru and LDMC together with tree adult abundances predicted saplings abundances; instead tree adult abundances together with Sha_see and LCC predicted saplings abundances. Interestingly these results suggest also that the strength of the relative contribution of adult trees or plant traits to the abundances of tree natural regeneration depend on the developmental stage: adult tree abundances have a stronger contribution to established seedlings than to established saplings populations. Finally, these results imply also that the success on the establishment of early stages of tree natural regeneration can be predicted strongly by dispersal traits, but that also by whole plant and also leaf traits explain such success and that their additional relevance also varies with tree ontogenic development. However, unless plant traits do predict the abundances of tree natural regeneration in active pasturelands, adult abundance is the strongest predictor.

3.6 CONCLUSIONS

Tree species' capacity to naturally regenerate in active pasturelands is related with different plant traits which are characterized by four main plant traits dimensions, namely: leaf, stem density, canopy height and reproductive variability spectrums.

Adult tree cover was dominated by taller deciduous tree species, with expensive investments in dispersules (fruits and seed) and wind or cattle dispersion, dominating also further tree cohorts, more specifically:

> Taller deciduous tree species with softer woods, small and more conservative leaves (low SLA, high LCC) with expensive (big, heavy) and longer fruits carrying big and longest seeds dispersed by wind and cattle represented the most abundant adult tree cover. Taller tree species with conservative leaves (high LDMC) and expensive fruits dispersed by cattle were also more abundant at both early developmental stages.

However, some successful plant traits at seedlings and saplings tree stages were different from those successful in adult tree cover. In response to the presence of cattle and other factors associated with active pastures, tree species with denser woods, low P, high N and more expensive seeds dispersed by cattle, have more abundant early development stages. More specifically:

> Tree species with denser woods, P rich leaves and expensive seeds (heaviest) have more sapling abundances, meanwhile those tree species with C and N rich leaves have more abundant seedlings.

Tree species dispersed by cattle have abundant seedlings and saplings banks in active pasturelands, while tree species dispersed by local fauna were limited in all developmental stages.

Adult tree abundances were strongest predictor of tree seedlings and saplings abundances in active pastures but a higher proportion (i.e. between 60 and 67%) of species abundance variability was explained by both adult tree abundances and plant traits.

Present tree cover is dominated by particular tree characteristics with higher capacity to naturally regenerate. However actual pasturelands managements are favoring different plant traits at sapling and seedlings stages, probably dominating future tree cover under current management practices.

As a consequence, actual tree functional diversity in active pasturelands will decrease due to the limited capacity of some trees (with particular leaf, reproductive and whole plant traits) to naturally regenerate under actual pastureland management possibly affecting future ecosystems process in agricultural landscapes.

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CHAPTER 4. LITTER QUALITY AND DECOMPOSABILITY OF NEOTROPICAL TREE SPECIES WITH DIFFERENT CAPACITY TO NATURALLY REGENERATE IN ACTIVE PASTURELANDS

4.1 ABSTRACT

The link between plant characteristics and ecosystem processes is important for the sustainability of the agro ecosystems and has received too limited attention especially regarding the high diversity tropical lands continually threatened by land use changes from forest to agricultural systems. This research explores for the first time the relation between plant functional traits, decomposition rates and nutrient releases for 37 Nicaraguan tree species with different capacities to naturally regenerate in agricultural lands such as anthropogenic pastures. A total of 17 plant traits related to four main trait variability dimensions like i) leaf, ii) stem ii) height and iv) reproductive spectrums were measured on adult trees (dbh $\geq$ 10 cm). A decomposition experiment under controlled conditions was established for monthly litterbags collection during four months and seven chemical traits were measured on leaves, fresh and decomposed litter. Finally, the abundance of saplings and seedlings of such species was surveyed in managed pastures. We expand actual knowledge of the afterlife effect of leaf traits directly to decomposition dynamics, carbon and nutrient cycling including a higher number of tropical tree species than previous studies. We found that tree species with high P, N, C in green leaves have also high P, N, C in fresh litter and that tree species with acquisitive leaves decompose faster, release more N, P and C than more conservative species. However, our results extend even further this afterlife effects linking also particular C fractions contents of green leaves to different decomposition dynamics. Another novel result was to observe that in addition to leaf traits, also stem and reproductive traits are related with differences in litter quality, decomposition rates and macronutrients releases during decomposition, thus linking the afterlife effect of leaf traits directly with tree natural regeneration capacity. These significant relationships outline that more abundant trees tend to have faster decomposition rates while less abundant tree species tend to present slow leaf-decomposition rates.

Our findings indicate that plant characteristics are linked with ecosystem processes such as litter decomposition and tree natural regeneration with implications for important sustainability factors in agricultural systems such as nutrient and carbon cycling.

Key words: ecosystem effects, leaf nutrients, carbon releases, C fractions, leaf traits, reproductive traits, dispersal mode

4.2 INTRODUCTION

The decomposition of litter has important ecosystem-level implications through regulating build up of soil organic matter, releasing nutrients that are available for plant growth, and influencing the flux of CO_2 from the soil (Wardle 2003). Resulting soil properties, in turn, have strong impacts on plant community composition, diversity and productivity (Wardle 2004). The diversity of plant tissues and decomposer microorganisms can be considered the local biotic drivers of these soil and plant feedbacks (Parton et al. 2007). Diverse plant tissues and their linked litter qualities generate heterogenic substrates with contrasting quality affecting the activity of microorganisms and, indirectly, plant growth (Dehlin et al 2006).

It is well accepted that variation between species in the properties of important photosynthetic plant tissues like leaves can usefully be represented in terms of a major axis of plant evolutionary trade-offs, which distinguish nutrient-acquisitive species with high nutrient but low carbon contents, from nutrient-conservative species with the opposite composition (Wright *et al.* 2004). More recent ecological research has focused on the relationships between such plant functional traits and ecosystem processes such as litter decomposition rates, to elucidate if the outcomes of plant evolutionary trade-offs have clear consequences for soil-plant feedbacks (Thompson 2011). However, these first approaches have come mainly from studies in temperate regions (e.g. Vaieretti et al. 2005, Freschet et al. 2012) or focused on herbaceous species with only a low proportion of woody species (Cornwell et al. 2008, Beaker et al. 2011).

How species loss in an ecosystem could affect ecosystem functioning has also been a major question in ecology during recent decades (Lawton 1994) incorporating various hypotheses of how ecosystem functioning would respond to biodiversity loss and even to its restoration (Lake et al 2007). Such hypotheses include those of ‘rivet-popping’ (Ehrlich & Ehrlich 1981), redundancy or “passengers and drivers” theory (Walker 1992) and the diosyncratic ecosystem responses to species loss (Naeem 1998). All of these theories place particular ecosystem responses to biodiversity within a theoretical gradient of species’ effects from one extreme, where species have strong similarities in their effects on system functioning (rivets), through the case where individual species have very distinct effects (as a “driver”) as opposed to those species that function as “passengers” to the other end of the gradient where individual species have multiple effects which can change ecosystem functioning in unpredictable directions (idiosyncratic). Some empirical results have continually support one or these theories or another (Tilman et al. 1996).

As well as research focusing on the differences in litter effects between individual species (the effect of “species identity”) others have focused on the effects of the species richness of litter. Typically, Wardle (1997) found there to be no relationship between species richness of litter and overall litter decomposition rate (Wardle 1997). Hard et al. (2001) suggested that the three theories listed above describe aspects of the same generalized theory but that the exact nature of the relationship between biodiversity and ecosystem function depends on the scale of biodiversity and the ecosystem evaluated (Hard et al 2001). It is widely recognized that better characterization of the range of (bidirectional) relationships between biodiversity and ecosystem functioning for different ecosystems is required to predict the impacts of biodiversity loss, e.g. on delivery of ecosystem services. However, study of the effects of biodiversity on ecosystem properties has mainly focused on net primary productivity (Wardle 1997).

It is particulary important to research biodiversity-ecosystem function relationships for tropical tree communities because of their high diversity (and continued interest in evolutionary and ecological mechanisms creating and maintaining this diversity) and because of their importance for global ecosystem function. However, the practical challenges posed by this high diversity and the long-life spans of most trees compared with most herbaceous species has limited research into the effects of loss of tropical tree biodiversity. There is a lack of even basic descriptive information about the variability of litter quality and decomposition rates amongst tree species within tropical tree communities.

Nutrient cycling (and the role in this of litter decomposition) have special relevance in tropical ecosystems because nutrient availability is a major limiting factor to agricultural productivity on many old and depleted tropical soils after conversion from forest (Turner et al. 2007). Many of these soils are deficient in N, P or both and cannot support sustainable crop production without external inputs (Sanchez & Logan 1992). Inputs of organic matter from the leaf litter of trees has been found to play a major positive role in the fertility of soils in tropical agroforestry systems through their contribution to the maintenance and increase of soil organic matter, linked to the recycling of nutrients (Young 1997). Some trees species can further enhance soil fertility by adding N through N_2-fixation (Mafongoya et al. 1998). However, the rate at which nutrients are recycled via tree leaf litter depends on its rate of mass input, nutrient concentration and decomposition rates, which in turn depends on litter quality, physico-chemical environment and soil decomposer community (Teklay and Malmer 2004). Some African tree species which produce leaf litter with a high concentrations of tannins, which would be considered to make them of 'poor quality' in terms of rate of decomposition, have been found to provide an improvement of soil organic matter stocks with benefits for soil fertility and agricultural productivity (Teklay and Malmer 2004). The maintenance and improvement of soil fertility in tropical agroecosystems is of critical importance to underpin food provisioning. It is a high priority to determine how it is influenced by the identity and diversity of tree species retained within these ecosystems.

The remaining, sometimes high, tree diversity in agricultural lands is endangered worldwide (Esquivel et al. 2008, Gibbons et al. 2008, Fisc

her et al. 2009). The different capacities of tree species to reproduce and maintain viable populations within these areas even when agricultural management is intensified was predicted to lead to a reduction by half of the tree diversity in Central America pasturelands by Esquivel et al. (2008). This will result in major changes in tree community composition which is likely to have a major impact on ecosystem function mediated, e.g., by leaf litter impacts on soil as described above (Vitousek et al. 1997, Chapin et al. 2000, Díaz and Cabido 2001, Lavorel and Garnier 2002). However, the high taxonomic diversity of tree cover recently reported in Central American pasturelands (Harvey et al. 2006) has not been evaluated in terms of such aspects of functional diversity. We do not know to what extent this taxonomic diversity is linked to inter-specific differences in leaf litter qualities, neither if these inter-specific differences in leaf litter quality will affect ecosystem process like decomposition and nutrient cycling.

Few studies, however, have included a sufficiently wide range of tree species in decomposition experiments to be able to extrapolate the effects of diversity in litter quality on decomposition and nutrient cycling rates up to a whole diverse tropical tree community. The most common approach has been to select no more than five contrasting tree species to make a detailed description of their litter qualities and comparisons of the litter decay curves in field conditions (Teklay and Malmer 2004). Such studies have tended to select tree species belonging to different functional types defined by categorical classifications like leaf phenology (deciduous and evergreen) and N-fixation capacity, with the implicit assumption that other tree species with these same characteristics also share the same chemical (e.g. C fraction, polyphenols and condensed tannin concentrations) and physical (e.g. SLA, LA and FTF) litter quality properties, or that the differences amongst them do not have significant effects on the observed decomposition or nutrient cycling rates (Wedderburn and Carter 1999).

An increasing number of litter decomposition experiments in standard conditions (e.g. “microcosms”) have been carried out during the past 20 years to evaluate litter decomposability. However, in virtually all cases they include less than 20 species (usually representing only a subset of the composition of a given plant community). Most studies are focused on the evaluation of litter-by-substrate interactions rather than comparisons between different plant tissues (Sariyildiz and Anderson 2003). Only recently has the scope of laboratory and field decomposition experiments been expanded using meta-analyses to make comparisons amongst many different studies including large numbers of species worldwide (Cornwell et al. 2008). However, I have found no published study of the decomposition rates of litter from > 20 tropical tree species that are commonly present in tree communities on agricultural lands outside the forest, such as anthropogenic pastureland. Extension of knowledge about the impact of tree species on ecosystem function from natural systems to lands used for agricultural food production is especially important because low and unsustainable productivity of these lands threatens both human welfare and increased deforestation of remaining forests worldwide (Gibbs et al. 2009).

The observed differences between species in leaf elemental content (especially N, P and C) have been used to evaluate the effect that changes in species composition of litter mixtures have on nutrient cycling and even ecosystem Net Primary Productivity (NPP). Wedderburn and Carter (1999) suggested that a mixture of litter types could be used to manipulate the timing of nutrient release to benefit pasture growth. They stated that initial lignin and the lignin-to-N ratio content in leaf litter controls the rate of decay thus predicting the relative abilities of the different tree species to release nutrients to the pasture systems. They suggested that seasonal effects on leaf litter quantity and quality were not as important as the over-riding chemical differences between tree species. However, they only evaluated two common tree species with contrasting leaf phenology (deciduous and evegreen) and N-fixing capacity. There have been many studies on litter decomposition and nutrient release of tree species in tropical Africa (Teklay and Malmer 2004), but few with a wide range of indigenous and tropical tree species for the neotropics.

Leaf litter decomposition rates are regulated by physical (Cornelissen et al. 1999; Pèrez-Harguindeguy et al. 2000), chemical (Wardle 2002) and biotic factors interacting between each other in their influence on the metabolism of fungi and bacteria as the main agents of litter decomposition (Heal et al. 1997). There has been much research on the effect on the rate of decomposition of the chemical litter quality which is itself determined by the amount of water soluble C, including polyphenols (Mafongoya et al. 1998, Hättenschwiler and Vitousek 2000), N and low lignin (Melillo et al. 1982). Tree species with higher concentrations of nutrients (especially N) like total P and the more labile C components (like polyphenols and tannins) tend to have faster decomposition rates. In contrast, the concentration of more recalcitrant carbhoydrates like lignin, celluloses and hemicelluloses tends to be associated with lower decomposition rates. Physical characteristics have only tended to be included in litter quality descriptions in recent studies; the two main characteristics used are specific leaf area (Kazakou et al. 2006) and foliar strength (Pèrez-Harguindeguy et al. 2000, Dominy et al. 2008). However, the intrinsic rates at which different leaf quality components decompose through the process of leaf senescence and litter decomposition remain largely unknown (especially for tropical tree species). Some studies about the role of cellulose and lignin as regulating factors of litter decomposition rate have been reported from temperate and boreal coniferous and deciduous forests and Mediterranean ecosystems (Berg et al. 1996, Couteaux et al. 1998, Di Nardo et al. 2001, De Marco et al 2012) but such information about tropical trees is scarce. The extent to which the components of chemical leaf quality and its inter-specific variability in tropical trees changes during leaf development (including senescence) and its correlation with other leaf traits will be important in understanding the functional basis by which tree species composition and diversity contributes to ecosystem nutrient cycling and inputs of soil organic matter.

A number of leaf traits (especially specific leaf area, leaf nitrogen content and leaf dry matter content) that are part of the ‘economics spectrum’ described by Wright et al. (2004) at the leaf level, and tightly related to potential relative growth rate (RGR) (Kazakou et al. 2006), are also considered to be related to leaf litter decomposition rate. Leaf toughness, or resistance to fracture, may protect leaves from physical hazards such as falling debris and trampling (Read and Stokes 2006), reduce mortality subsequent to physical damage (Alvarez-Clare and Kitajima 2007) and enhance leaf life-span and whole-plant survival, especially in shade conditions (Kitajima and Poorter 2010). This leaf toughness has been found to be correlated with cell wall fiber content, which is also known to reduce the digestibility of leaves (Sanson 2006). Kitajima and Poorter (2010) found that some material properties of leaves (e.g. fracture toughness and tissue density) but not others (e.g. lamina thickness) were negatively correlated with palatability to a generalist herbivore and positively correlated with leaf life span, sapling survival, and shade tolerance in 19 woody species from the Bolivian Amazon. Likewise, Alvarez-Clare and Kitajima (2007) found that material toughness and tissue density (but not structural toughness of leaves and stems) were positively correlated with seedling survival of eight neotropical tree species. The specific relationship between leaf litter decomposability and whole plant traits remains unexplored except as part of the wider body of evidence in support of the “economics spectrum” model and the tendancy for a trade-off between plant traits conferring rapid resource acquisition and those conferring resource conservation (Fresquet et al 2012). No published studies have evaluated the relationships between species’ leaf litter decomposition rates and both leaf traits and whole plant traits (like wood density, maximum tree height and leaf phenology) as well as seed dispersal traits (like fruit and seed masses, volume and shape, in order to give a holistic overview of the contribution of species composition and diversity to ecosystem function which encompasses both the potential of species to persist in disturbed, managed agroecosystems as well as their role in nutrient cycling.

Addressing these knowledge gaps, this chapter evaluates the differences amongst tree species abundant in Central American silvopasture in their decomposition rates and the extent to which these rates are associated with leaf traits, then with other whole-plant traits and finally (via those traits) with capacity for natural regeneration in active pasturelands. A further objective was to assess the extent to which the rate of decomposition of different leaf mass fractions was correlated with the rate of loss of total litter mass (as an indicator of overall decomposition rate). This is important to assess whether the rate of total litter mass loss is a good indicator of the contribution of litter decomposition to nutrient cycling and inputs of soil organic matter. Four consecutive approaches were developed to meet these objectives. In the first, three main questions about the variability of species decomposition rates and their correlation with leaf traits were addressed, namely: i) how much do tree species differ in their rates of leaf litter decomposition, and in their foliar composition of macronutrients and C fractions? ii) are leaf litter decomposition rates of tree species correlated with nutrient and C fraction concentrations in fresh leaves and in fresh litter? and iii) to what extent are tree species' nutrient and C fraction concentrations in fresh leaves correlated with those in fresh litter (or are they heavily altered by variation amongst species in their rates of nutrient reabsorption (or leaching) during foliar senescence)? The rationale for these questions relates to the importance of knowing the extent to which tree species differ not only in green leaf traits, but also in litter quality, decomposition rates, and potential to release macronutrients and C fractions which can bring new insights into the afterlife effects of traits known to be strongly linked to the leaf economics spectrum.

In the second approach, more mechanistic questions were addressed about the relationships between macronutrient and C fraction concentrations measured in green leaves and in fresh litter with their losses during the litter decomposition process. I ask: i) whether the rate of decomposition of each of the different leaf mass fractions is strongly correlated the rate of loss of total litter mass (as an indicator of overall decomposition rate), or whether the rates of decomposition of these fractions varies greatly (if so the resulting question is how much species differ in their relative rates of decomposition amongst these fractions)?; ii) which model best fits the rate of decomposition of the different fractions? and iii) where decomposition rates of the C fractions do differ amongst tree species, which are best predicted by different foliar traits? If tree species differ in their rates of decomposition of different C fractions, and this difference is predicted by some leaf traits, this has consequences for how the "functional diversity" of tree species (as characterized by these traits) contributes to ecosystem function in terms of rates of nutrient cycling and inputs of soil organic matter.

In the third approach, questions were addressed about the relationships of whole plant and dispersal traits with litter quality traits and rates of decomposition and nutrient release. The first question is whether whole-plant traits and traits of non-foliar organs (especially those linked to the plant resource use-conservation economics axis) correlate with foliar litter quality and decomposition rates. For the set of species included in this study I evaluated both the linkage between leaf traits and the "afterlife" litter decomposition rates and between leaf traits and whole plant traits.

The fourth stage addresses the ultimate purpose of this study: to evaluate if there is a functional trait-based relationship between the regeneration capacity of tree species in managed pasturelands and their impact on ecosystem function via leaf litter decomposition and nutrient release rates. The following question was addressed: Do tree species with different capacities to regenerate naturally in managed pasturelands differ in their leaf litter decomposition and nutrient releases rates? If so, a subsidiary question is which functional leaf traits are most strongly associated with this correlation.

Several hypotheses were developed for each of these four stages of the research. For the first stage, I hypothesize that the species comprising diverse tree cover commonly found in active pasturelands in Central America (Esquivel et al. 2008) differ in their litter quality, litter decomposition rates and nutrient release rates. I predict that foliar nutrient and C fraction concentrations are tightly correlated with their concentrations in fresh litter across species and therefore that foliar traits predict leaf litter decomposition rates. In terms of chemical concentrations, I specifically predict that LNC, LPC and SOL are positively correlated with leaf litter decomposition rates, and that LCC, LDMC, LIG, HEM and CEL are negatively correlated with leaf litter decomposition rates. In terms of physical leaf traits, I predict that: SLA is positively correlated with leaf litter decomposition rate, however LA is positively correlated with LNC and LPC, and FTF is positively correlated with LDMC, LIG, HEM and CEL, and therefore both and are negatively correlated with leaf litter decomposition rates.

For the second stage, I hypothesize that macronutrient and C fraction concentrations in green leaves are correlated with their concentrations in fresh litter. For the macronutrients (LNC and LPC) and the soluble carbohydrate (SOL) I predict that their foliar concentrations also predict their rate of loss during leaf litter decomposition. I also predict that the concentration of recalcitrant carbohydrate fractions (LIG, HEM, CEL) in green leaves are correlated with their concentrations in fresh litter but negatively with the rate of leaf litter decomposition. Species with litter that decomposes more quickly are also predicted to have a higher rate of decomposition of the recalcitrant carbohydrate fractions that it contains. In relation to the changes in concentration of nutrients and C fractions I predict that losses of the more labile nutrient and C fractions will be greater during senescence than during decomposition, however the opposite will be true for the recalcitrant fractions (provided that the studied time period of litter decomposition is long enough). I also hypothesize that the rate of loss of total litter mass is strongly correlated with the rate of decomposition of each of the different leaf mass fractions. I predict that the rate of loss of total litter mass is positively correlated with the losses of the labile fractions but negatively correlated with the losses of recalcitrant fractions.

For the third stage, I hypothesize that a range of plant morphological traits (i.e. not only foliar traits but also whole plant and dispersal traits) of tree species found in active pasturelands are correlated with rates of leaf litter decomposition and nutrient release. I specifically predict that the whole plant traits WD, Hmax and PHE and the dispersal-related traits Mass_fru, Mass_see, Vol_fru, Vol_see, Sha_fru and Sha_see are all correlated with rate of litter decomposition and nutrient release. If such correlations occur, I predict that they will be linked to foliar traits associated with the plant resource use-conservation axis. I specifically predict that H_max and PHE are positively correlated with foliar concentration of macronutrients and therefore with rates of leaf litter decomposition and nutrient release. I predict that the correlation with leaf litter decomposition rate will be stronger for PHE than for H_max because PHE will be more strongly negatively correlated with LDMC, LCC, LIG, HEM and CEL. In contrast I predict that WD, Mass_Fru, Vol_Fru, Mass_See and Vol_see are all positively correlated with LDMC, LCC, LIG, HEM and CEL, and therefore negatively correlated with leaf litter decomposition rate. We expect also that Sha_fru and Sha_see are positively correlated with foliar total C, and C fractions total N in fresh litter and decomposition rates.

For the fourth stage, I hypothesize that the abundance of natural regeneration of the trees species found in active pasturelands is correlated with rates of leaf litter decomposition and nutrient release (linked via leaf traits). In this case there are two alternative, competing hypotheses: (i) that species achieve higher abundance of regeneration in active pastureland due to more rapid growth rate linked to higher foliar concentrations of macronutrients and SOL and therefore higher rates of leaf litter decomposition and nutrient release; (ii) that species achieve higher abundance of regeneration in active pastureland due to greater resistance to herbivory linked to higher foliar concentrations of recalcitrant C fractions (especially LIG) and lower concentrations of macronutrients and therefore lower rates of leaf litter decomposition and nutrient release.

To test these hypotheses the rate of loss of total leaf litter mass and of separate mass fractions of 37 neotropical tree species comprising 50% of the tree community in active pastureland in Nicaragua were measured in a decomposition experiment conducted in a controlled greenhouse environment. Litter properties of these 37 species were measured: concentrations of macronutrients (LNC, LPC), total C (LCC) and C fractions (SOL, HEM, CEL and LIG) and the physical traits LA, SLA and FTF. For a subset of 19 of the species measurements were made of the same chemical and physical traits in green leaves. Correlation tests were made between the green leaf and litter traits, and between these traits and decomposition rate variables. In addition, correlation tests were made between all of these, and existing data of whole plant and dispersal-linked morphological traits. To my knowledge no previous studies have evaluated these relationships between leaf traits, litter traits, litter decomposition rate, whole plant traits and population structure. Changes in land and ecosystems and their implications for global environmental change and sustainability are a major research challenge for the ecological and human environmental sciences (Turner et al 2007).

4.3 METHODS

Litter decomposition experiment in standard environmental condition

Species selection

A sub-sample of 37 out of the 76 tree species found as adult trees in the active pasturelands in the central region of Matagalpa in Nicaragua were used to measure decomposability of leaf litter in a litterbags decomposition experiment under standard environmental conditions (temperature and humidity) inside a greenhouse. Plant morphological traits in green leaves and total macronutrients contents and C fractions were measured for all the species used in this experiment. Species were selected mainly by litter availability and include species with contrasting abundance of natural regeneration, leaf phenology, and green leaf and litter quality.

Litter fall collection

Litter from 36 tree species was collected using litter traps and manual collections of litter fallen lifted (fresh litter) under at least five different isolated trees for each species in active pastures, weekly over the whole four month period. Two circular litter traps (1m diameter) were located at five and ten m away tree trunk under canopy tree area. Litter traps with smallest mesh (1 x 1 mm) were used to collect litter from tree species with compound leaves and small leaflets where the individual leaflets litter was then carefully manually collected. Tree litter was manually collected and sorted between species without including leaves contaminated by non-litter material, e.g. animal faeces. Leaves litter was manually separated from branch, flower, fruit or other tree litter. Primary and secondary rachis of compound leaves and petioles from simple leaves were also manually separated from leaflets or leaf lamina litter.

Litter was collected during the January to April 2008 dry season, oven-dried at 65° C for 72 hours to remove moisture and to determine dry weight, and stored in paper and plastic bags until the decomposition experiment was set up. The litter collected for each of these 36 species were thoroughly mix/homogenize before sub-sampling from this mixture was used to fill the litterbags i.e. obtaining a mean sample of tree species litter quality and minimizing the “natural variation” amongst the replicates. Only foliar lamina was used for decomposition experiments and chemical analyses. Rachis and petioles litter was dried in isolation from leaf lamina litter and was used to obtain an independent determination of their biomass and chemical composition (data not shown).

The biomass proportions invested in each leaf structure (petioles or rachis and lamina) by tree species were also obtained by leaf unit (data not shown). Decomposition rates reported here were obtained only for the leaf lamina or leaflets, the main photo-synthetically active tissues in compound or simple leaves.

Litter bags

Plastic mesh bags of 20 x 15 cm and 2 mm mesh sized were filled with 10 g of litter dry mass by species (monotypes) for a standard decomposition experiment. A sample of stored litter was oven-dried before litterbags were filled (to obtain the percentage humidity accumulated due to storage) and was used to correct the initial litter amount that should be weighed to fill each litterbag with exactly 10 g of dry mass by species. Size of leaf litter was highly diverse between species and individuals. Leaf litter size range varied from 2.6 x 5.4 mm in *Enterolobium cyclocarpum* to 26 x 7 cm in *Anona cherimmola* and even to 50 x 45 cm in *Cecropia peltata*. Tree litter of all species was cut into homogeneous fragments of approximately 2 x 2 cm to be able to compare decomposability of leaf litter material between different tree species. Only the leaf litter of *Enterolobium cyclocarpum* was not cut due to it leaf size being lower than the regular litter fragments. To cut the leaf litter removes other physical characteristics that could affect also species litter decomposition rates in the field. The area and form of the whole leaf could influence litter decomposition rates for example influencing the leaf–soil contact surface, the litter and soil humidity retention and the physical microhabitat formation to promote colonization by decomposers (per. obs).

Therefore, decomposition rates obtaining by this experiment were not an accurate estimation of species natural decomposition rates in the field. In contrast, this litter manipulation provides similar litter fragments for more accurate comparisons of decomposition rates between species due specifically to litter tissue qualities. In addition, the use of entire leaves in a previous decomposition experiment during the dry season of 2007 (data not shown) caused a strong clustering of leaves forming a compacted strata of litter inside litter bags, affecting the estimation of decomposition rates due to the creation of a litter clustering condition never observed in the field. In contrast, litter fragments were freely distributed within the litterbags allowing the free movements of water and decomposers (per.obs).

Litter beds in standard conditions

A total of four litter decomposition beds of approximately 3.50 x 1.5 x 0.20 m were constructed to contain the litter bags inside a CATIE greenhouse at Turrialba, Costa Rica. Sun exposure was controlled inside the greenhouse and the medium time between the field capacity and the permanent wilting point of the soil profile was used to regulate the frequency of water additions (app. every three days). Litter beds were constructed with wood and filled to ca. 20 cm depth with homogenized soil obtained from pasture sites next to remnant forest near Turrialba. The soil used in the litter beds was different to that in the Nicaragua field site though it did also include a pasture natural decomposer community. The litterbags were buried at 10 cm depth in the soil profile to reduce microclimatic variability and accelerate the rate of decomposition. A plastic mesh covered all the litter decomposition beds to avoid animal or accidental removals.

Experimental design

Because sun exposure and temperature can vary among litter beds, each litter bed was considered a block. The 37 litter species (first treatment factor) were randomly distributed into each block. The experimental unit for species consist in four litter bags with litter of the same species (sampling units for time) to which each of the four harvesting times (second factor) were randomly distributed. One bag from each of these plots was randomly harvested at each date. The resulting experimental design is a split-plot replicated in blocks. The main plot contains the experimental units for species factor and the split-plot contains the experimental units for time factor (**Figure 4.1**).

Inside each main-plot, the four litterbags filled with litter of the same species were placed one next to another and harvested at different times (t1, t2, t3, t4) avoiding confounding effects of position and species. Each block contain only one main plot by species i.e. the four bags each one for one harvested time by specie, avoiding confounding effects of position and harvested time. Therefore, a total of 4 litterbags were collected by specie by time and 148 litterbags by harvested time, resulting in a grand total of 560 litterbags for this standard decomposition experiment with four replicate bags per combination of 37 species and four harvest times. Similar spatial distributions were used within each litter bed and minimal distance between litterbags within main and split plots was ca. 5 cm, resulting in a litterbags density of 20 per m^2 of litter bed.

Litter decomposition rates

The four litterbags replicates per species were harvested at each of four different collection times (4, 8, 12 and 16 weeks) between August and November 2008. The litter mass remaining in each litterbag was gently washed with running water to eliminate mainly soil residues, using a plastic mesh sieve of 1 mm to control the possible removal of the smallest litter material during this process. The cleaned litter material was then air dried for 12 hours and thereafter manually sorted to eliminate bigger non-litter material mainly invertebrates remains or mineral contaminants like chippings. Remnant litter material bigger than 1 mm was then oven dried at 65 °C for 72 hours (after this time no further mass loss was occurring) and stored in plastic bags. The mass weight (grammes) by litterbag was used to calculated the percentage of remaining litter mass in each litterbag (Rem1, Rem2, Rem3, Rem4), maintaining the independency between replicates per species and obtaining also the mean remaining mass at each harvesting time (t1, t2, t3,t4).

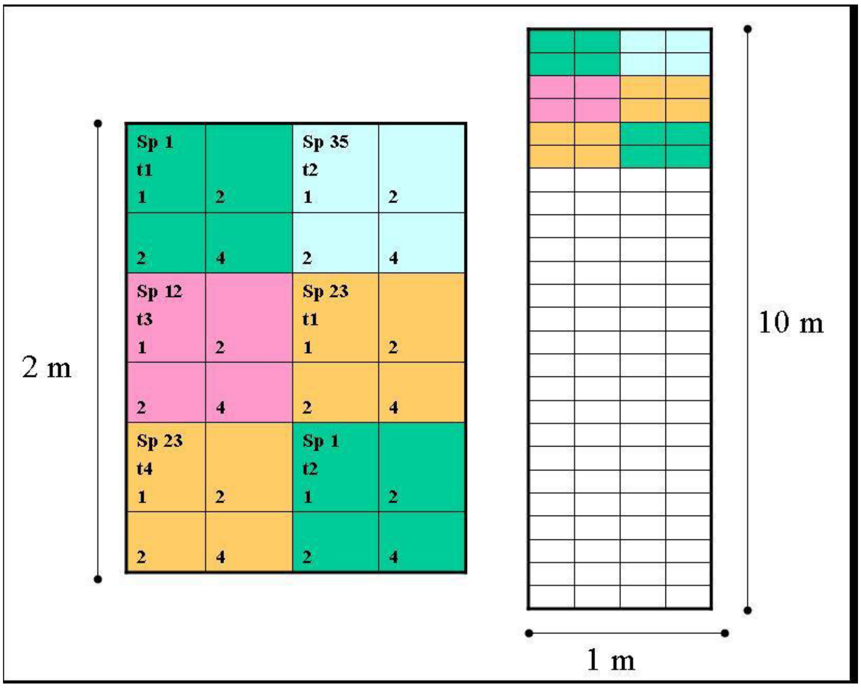


Figure 4.1. Spatial layout of litterbags within 2 m^2 of each of the 4 litter beds located in a glasshouse in CATIE. Six plots with 24 litterbags were located by 2 m^2 of litter bed.

The percentages of remaining mass were used to construct four independent litter decay curves per species during the four months of litter decomposition corresponding to the randomized plot structure designed. Overall and monthly decomposition rates were also calculated using single exponential (1) and quadratic decay models (2) using the following equations (Teklay and Malmer 2004):

$Mr(t) = Mo \exp(-kt)$ (1) [Infostat model was: %Rem=alpha*exp(-beta*Tiempo)]

$Mr(t) = \theta \pm \eta t - \sigma t^2$ (2)

Where Mr(t) is litter mass at time t weeks of incubation, Mo is initial mass, k is the decay coefficient (week -1) (1); θ is a constant (in g or %), η and σ (in g or % units, $week^{-1}$ and w^2 respectively) are parameters (slopes) that estimate a “linearly increasing or decreasing” substrate and an easily decomposable (quadratic) declining substrates, respectively (2). The assumption behind the quadratic model used, is that some components could increase initially due to immobilization (e.g. N) or transformation of some substrates of lower decomposability (Teklay and Malmer 2004).

We decide to calculate three different measurements of decomposition rates: overall decomposition rate (BETA 5), partial decomposition rates (BETA 4) and monthly decomposition rates (b1, b2, b3, b4). Overall decomposition rates (decay coefficients or k values) were calculated with 100% as the initial point (t0, when the whole 10 g of dried matter was placed in the decomposition beds) (BETA 5). Partial k values were also calculated (BETA 4) using the percentages of remaining litter at weeks 4, 8, 12 and 16 fitted in a simple exponential model, without including 100% as the t0 value.

Therefore, the overall decomposition rate, BETA 5, was fitting a linear decay curve including the initial four weeks of litter decomposition. In contrast, the partial decomposition rate, BETA 4, was fitting a linear decay curve, based on mass loss in each period after the initial four weeks. In addition, monthly decomposition rates were calculated to estimate independent changes in mass decay during each of the four four-week periods (beta1, beta2, beta3, beta4). Decomposition rates during the first four weeks of litter incubation (b1) were expected to describe phase I of the theoretical model of liter decomposition; b2, b3 and b4 as well as BETA 4 were expected to describe phase II, and the overall decomposition rate (BETA 5) included both phases. These overall and partial decomposition rates calculations were made separately to provide more precise descriptions of different components of litter decomposition to test correlations with litter qualities and plant traits.

Litter quality

Composite samples for each species of the fresh and remaining litter at the end of the incubation period (week 16) were used to determine the initial and final litter quality based on concentrations of macronutrients (N and P), total C, and C fractions (ash, lignin, cellulose, hemicelluloses and soluble compounds). Concentrations of N, P and C were analyzed in the Soil, Vegetal Material and Water Laboratory of CATIE in Costa Rica, which is subscribed to the International Plant-Analytical Exchange (WEPAL), Wageningen. Total N and C concentrations were measured by combustion at 1800 °C with gasses analysed by a chromatography column connected to a thermic conductivity detector using a Flash EA 1112 NC Analyzer. Total P content was determining by humid digestion with a mix of nitro-perclorated acids 5:1 (HCl) and colorimetry (using ammonium molybdate and stannous chloride) and reading a UV/V espectophotometer at 660nm (Henríquez et al. 1995).

The percentages of C fraction contents in litter were determined using an ANKOM 2000 Fiber Analyzer in the Laboratories of the Environment Centre Wales at Bangor University, UK. Lignin contents were separated from cellulose, hemicelluloses and from non-structural compounds (sugars, starch, proteins and lipids) by consecutive extractions of a plant sample using the filter bags technique, done in the order of NDF (neutral detergent fiber), ADF (acid detergent fiber) and ADL (acid determined lignin) (ANKOM 2000 Fiber Analyzer, Operator's Manual, 2011. http://www.ankom.com/media/documents/A2000series_Manual_RevE_083011.pdf). During the NDF digestion, the fraction that is washed off by the NDF solution (soapy water) contains soluble cell contents like carbohydrates, lipids, pectins, starch, soluble proteins and non-protein nitrogen. The fraction that is left in the bag contains hemicellulose, proteins bound to the cell walls, cellulose, lignin, and recalcitrant materials. During the ADF digestion, hemicelluloses and bound proteins are washed off. The fraction left behind by the ADF solution (a 1.00 Normal sulfuric acid and detergent solution) contains cellulose, lignin, and recalcitrant materials. During the ADL digestion, cellulose is washed off by the ADL solution (72% sulfuric acid) leaving only lignin and recalcitrant materials. The ash or recalcitrant material percentage was estimated by incineration of litter material at 550 °C for 8 hours.

Plant traits

Whole-plant, leaf and dispersal traits were measured for a bigger group of 76 tree species commonly found in active pasturelands in the field site in Nicaragua (**Table 4.1**). The whole plant traits were maximum tree height (Hmax), Leaf phenology (PHE) and wood density (WD). Leaf traits were measured in mature green leaves and included specific leaf area (SLA), leaf size (LA), leaf dry matter content (LDMC), leaf total carbon, nitrogen, phosphorus content (LCC, LNC and LPC) and physical strength of leaves (PSL or FTF). The dispersal traits measured in adult mature trees were fruit and seed masses, volume and shapes (Mass fru, Mass see, Vol fru, Vol see, Sha fru, Sha see respectively). A detailed and complete description of these plant traits can be found in chapter 2.

Natural regeneration of tree species

The abundance of 76 tree species was surveyed in 46 active pasturelands on 17 cattle farms in the central Region of Matagalpa in Nicaragua in 2004 (Esquivel et al. 2008). The relative abundance of individuals in three main size classes was observed: seedlings (germinated plants from 10 to 30 cm height), saplings (individuals with more than 30 cm height and less than 10 cm in DBH) and adults trees (DBH > 10 cm). Adult trees were sampling in 1 ha plot by pasture (10000 m^2), saplings were sampled in a mean of 10 quadratic plots per pasture (4000 m^2), while seedlings were sampled in a mean of 18 circular plots (126 m^2) per pasture (Table 3.1). The total area of each pasture varied from 1 to 22 ha (mean 5·82 ± 1·34 ha). The pastures were selected on the basis of grass composition and selected to ensure a non-grouped spatial arrangement that covered the different conditions of pastures present in the region. The selected pastures were dominated (i.e. cover = 70%) by one of three grass types: (i) Brachiaria spp. [*Urochloa brizantha* (Hochst. ex A. Rich.) Stapf and *Urochloa decumbens* Stapf] previously named *Brachiaria* spp. (B, n = 15); (ii) mixtures of *Cynodon nlemfuensis* Vanderyst and *Cynodon dactylon* (L.) Pers. (C, n = 13); or (iii) naturalized grasses (i.e. not planted or seeded) such as *Paspalum* spp. (N, n = 18) (Esquivel et al. 2008).

Tree species densities by developmental stage and pasture type were used to correlate natural regeneration abundances with decomposition rates and leaf litter quality. Tree species densities by developmental stage and pasture type were obtained as the ratio between the total abundances of seedlings, saplings and adults by the number of pastures surveyed by pasture type (B, E, N). The possible pasture type effect over the natural regeneration abundances was discounted from tree species densities using as variables for the further analyses in this chapter including regeneration abundances, the residual values of the ANOVA testing for differences in abundances of adult, saplings and seedlings by pasture type, named partial or residual abundances, to perform the correlation analyses. These partial correlation analyses take off the grass type effect from the regeneration abundances sampling model, avoiding therefore any confounding effect of pasture management over the correlations between abundance of tree natural regeneration with decomposition rates, litter quality and macronutrient releases. Further details about sampling scheme, design, pasture management conditions and characteristics of the natural regeneration of these tree species can be found in chapter 2 and in Esquivel et al. (2008).

Table 4.1. Number of species and sample sized surveyed to measure tree decomposition rates, litter quality (macronutrients and C fractions in fresh and decomposed litter), plant traits (whole plant, leaf and dispersal) and natural regeneration abundances for tree species commonly found in active pasturelands in Matagalpa, Nicaragua, Central America

Data sets	Variables	Variable description	n species	Units	Sample size
Decomposition	BETA_5	overall decomposition rate	37	g*month-1	4 litterbags / 4 times / 4 months
	BETA_4	partial decomposition rate	37	g*month-1	4 litterbags / 4 times / 4 months
	b1, b2, b3,b 4	monthly decomposition rates	37	g*month-1	4 litterbags / 4 times / 4 months
	Rem1, Rem2, Rem3, Rem4	monthly percentage of remaining mass	37	%	4 litterbags / 4 times / 4 months
Macronutrients	C_t0, N_t0, P_t0	Fresh litter (t0)	43	%	3 – 10 trees, composite sample
(C, P, N)	C_t4, N_t4, P_t4	Remaining litter (t4)	37	%	3 – 10 trees, composite sample
	C_green, N_green, P_green	Green leaves (green)	61	%	3 – 10 trees, composite sample
	C_loss, N_loss, P_loss	Losses (Loss)	36	%	3 – 10 trees, composite sample
C Fractions	Fresh litter (t0)	Fresh litter (t0)	36	%	3 – 10 trees, composite sample
(SOL, HEM, CEL, LIG, Ash)	Remaining litter (t4)	Remaining litter (t4)	33	%	3 – 10 trees, composite sample
	Green leaves (green)	Green leaves (green)	20	%	3 – 10 trees, composite sample
	Losses (Loss)	Losses (Loss)	33	%	3 – 10 trees, composite sample
Whole plant traits	H max	Adult plant stature	69	m	3 – 5 trees
	WD	Wood density	54	g cm-3	literature
	PHE	Leaf phenology	49	month	3 – 10 trees
Leaf traits	SLA	Specific Leaf Area	44	m2 kg-1	5 – 10 leaves (3 – 5 trees)
	LA	Leaf size	45	mm2	5 – 10 leaves (3 – 5 trees)
	LDMC	Leaf Dry matter content	47	mg g-1	5 – 10 leaves (3 – 5 trees)
	LCC	Leaf total carbon content	58	%	5 – 10 leaves (3 – 5 trees)
	LNC	Leaf Nitrogen concentration	58	%	5 – 10 leaves (3 – 5 trees)
	LPC	Leaf Phosphorus concentration	58	%	5 – 10 leaves (3 – 5 trees)
	FTF	Physical strength of leaves	42	N	5 – 10 leaves (3 – 5 trees)
Dispersal traits	Sha_Fru	Fruit shape	42	adimentional	3 - 5 fruits (3–5 trees)
	Mass_Fru	Fruit mass	39	g	3 – 5 seeds (3-5 fruits, 3 – 5 trees)
	Sha_Sem	Seed shape	32	adimentional	3 - 5 fruits (3 – 5 trees)
	Mass_Sem	Seed mass	36	g	3 – 5 seeds (3-5 fruits, 3 – 5 trees)
	Vol_Fru	Fruit volume	32	cm3	3 - 5 fruits (3 – 5 trees)
	Vol_See	Seed volume	32	cm3	3 – 5 seeds (3-5 fruits, 3 – 5 trees)
Regeneration	Seedlings	Seedling abundance	75	individuals	46 pastures, 1 ha/pasture
	Saplings	Sapling abundance	75	individuals	46 pastures, 0,4 has/pasture
	Adults	Adult abundance	75	individuals	46 pastures, 126 m2/pasture

Statistical analyses

An ANOVA model for a split plot design where the main plots are the species, the split-plots are the time levels and the blocks are replications, was used to evaluate the two main factors and its interaction for the percentages of remaining litter mass (Rem). We used the Mix Model frame to take into account autocorrelations in repeated measures in time and the heteroscedasticity of variances among species. Several autocorrelation models were evaluated and the best model was selected by mean of Akaike information criterio (AIC) and Bayesian information criterion (BIC) criterion. Differences in percentages of remaining litter mass (Rem) between species, time and its combinations were evaluated using Di Rienzo, Guzman and Casanoves (DGC) mean comparisons test (Di Rienzo et al. 2002).

In order to compare the decomposition rates among species we followed next steps. First: we performed a non-linear regression model for each species using time as regressor variable. In order to obtain independent BETA estimations, four regressions (one for each replicate) for each species using time as regressor variable, were also obtained.

A simple exponential model was used to obtain $\alpha$and β as parameters describing litter decay curves. Second: The four BETA parameters estimated by species were used to run an ANOVA test for a complete block design, where the main plots were the species, consider a fixed effect and the replicates or blocks were consider a random effect. Third: after rejection of the ANOVA null hypothesis, differences in decomposition rate between species were done using DGC mean comparisons test (Di Rienzo et al. 2002). Finally, the same steps were repeated to estimate and to evaluate differences between species in partial decomposition rates (BETA 4). Monthly decomposition rates (b1, b2, b4, b5) were estimated to perform linear correlations with litter quality components.

A single value for each species was obtained for litter quality measured as total macronutrient contents (N, P and C) and C fractions (SOL, HEM, CEL and LIG) in fresh litter (t0) and remaining litter (t4) after the four months of litter decomposition. Bar or point plots were used to shows the level of variation founded amongst the species for each parameter. The percentages of these nutrients measured in litter samples (%) were used to calculated the their contents in grams (g) within the fresh litter placed in litterbags (10 grams) and within the mean values of remaining mass by specie (variable amounts of litter by specie) at the end of the decomposition incubation. The loss of total macronutrients and C fraction with litter decomposition were calculated as the subtraction between (grams) the initial and final nutrients contents in litter (g) and as the proportion (%) that these lost amounts in grams represent from the initial content of nutrients in fresh litter. The content (%) of total macronutrients and C fractions in green leaves and fresh litter were used to calculate the amounts of total macronutrients and C fractions lost through senescence process, calculated in grams and as the proportion (%) lost from the initial content in green leaves. The contents of total macronutrients or C fraction in percentage (%) express the relative proportion that each component are having in the leaf material; meanwhile the amounts express in grams express the real amounts released by component thought senescence and decomposition. The nutrients loss rates were equivalent to these measurements. Correlations of litter decomposition measures (BETA 4, BETA 5 and b1, b2, b3, b4) with initial macronutrient (N, P and C) and C fractions (SOL, HEM, CEL and LIG) and their proportion loosed during decomposition (%) were evaluated by linear regression and correspondence analyses.

The relationships of tree species overall (BETA 5), partial (BETA 4) and four-weekly (b1, b2, b3, b4) leaf litter decomposition rates, the percentage of remaining litter mass at four week intervals (Rem t1, Rem t2, Rem t3, Rem t4) and the rate of nutrient release with plant morphological traits (whole plant, leaf and dispersal traits) and fresh and remaining litter quality (macronutrients and C fractions) and population abundance in seedling, sapling and adult size classes were analyzed. The test used was Spearman rank correlation due to the lack of normality of some variables, carried out in InfoStat Professional software (2011). Three main groups of correlation analyses were run consecutively in order to analyze the relationships between leaf litter decomposition rates and litter quality, plant traits sets and population abundances by size class. Each data set of plant traits contains information for a different number of species within the community of trees in active pasturelands due to constraints on obtaining appropriate plant samples during the different sampling periods. Therefore, each one of the previous paired analyses or correspondence coefficients had different n values, reported by each table and which varied within a range of 20 to 65 species per correlation pair.

Spearman rank correlation coefficients were calculated to test the relationships of decomposition rates and rates of nutrient release with traits indicating litter quality and other plant traits. This method was used because of the deviation of data distributions from normality. Partial correlation analyses were performed to calculate Spearman rank correlation coefficients between decomposition rates, nutrient release, litter quality and other plant traits/population statistics. In order to do this, the residual values resulting from the ANOVA to test effects of pasture type on species population abundance in each size class were correlated with decomposition rates, nutrient release and litter quality variables once rank transformed using Pearson correlation coefficients. A Rank transformation arrange the original variables values in rank order, then assign the smallest a value of 1, the next smallest a value of 2 etc. A Pearson correlation analyses over two variables rank transformed are equivalent to a Spearman correlation analyses. This non-parametric analysis produces uniform residuals for the rank-transformed variable. Therefore, abundances and decomposition values were previously transformed to RANG to overcome lack of Normality. This partial Spearman Correlation analyses were able to test the relationships between abundances of decomposition rates and nutrient release with litter quality and population abundance in each size class without any interference of grass type effects on the latter. As many multiple correlations were carrying out we cannot simply accept a standard $p < 0.05$ threshold as defining which correlations are real and which are non-existent. On average, one in 20 correlation tests of two variables which are (in fact) not correlated will show as $P < 0.05$ by chance. Similarly many correlations which are real will give P values > 0.05 by chance. Therefore we underlined those correlations having a significance level of $P < 0.1$.

4.4 RESULTS

Leaf litter decomposition rates and leaf quality of trees commonly found in active pasturelands

Differences in decomposition rates between tree species

Tree species commonly found in active pasturelands have a wide variability of tree litter decomposition rates (**Table 4.2**, **Figure 4.2**). ANOVA shows significant differences between the percentages of remaining litter mass (% Rem) between species (n=37, F-value= 87.53, p<0.0001), times (n=4, F-value= 1404.18, p<0.0001) and species*time (n=148, F-value= 4.96, p<0.0001). The mean percentage of remaining litter mass over the four months of litter incubation for all tree species was 53% (**Table 4.2**, **Figure 4.2**). The mean percentages of remaining litter mass dropped from 100% to 67% during the first month (Rem1) of litter decomposition, being the higher losses of litter mass as expected.

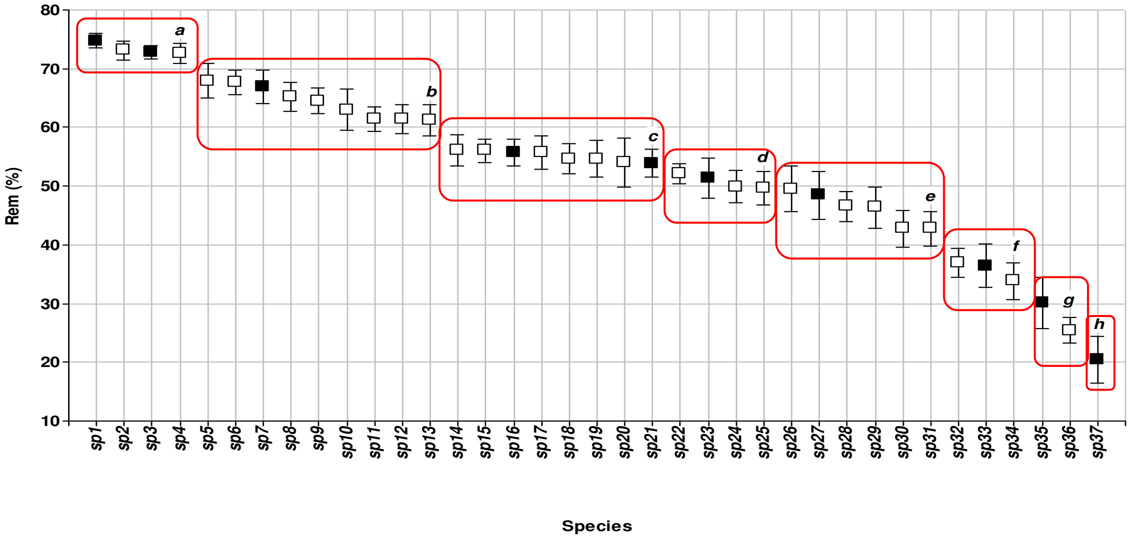


Figure 4.2. Mean percentages of remaining litter mass (Rem) during 4 months of incubation in standard conditions for 37 tree species commonly found in active pasturelands in Central America. Different letters indicate ANOVA significant differences in mean Rem ($p \leq 0.05$). Black points remark the location of some common tree species in the Rem gradient belonging to each significant identified species group.

Consecutive reductions in the mean percentages of litter remaining mass went down to 56% during the second month (Rem2), to 49% during the third month (Rem3) and reached 41% at the end of the fourth month of litter decomposition (**Table 4.2**). The significant interactions between species and time reflect the variability of tree species litter decay curves over the whole length of litter decomposition process (**Figure 4.3**).

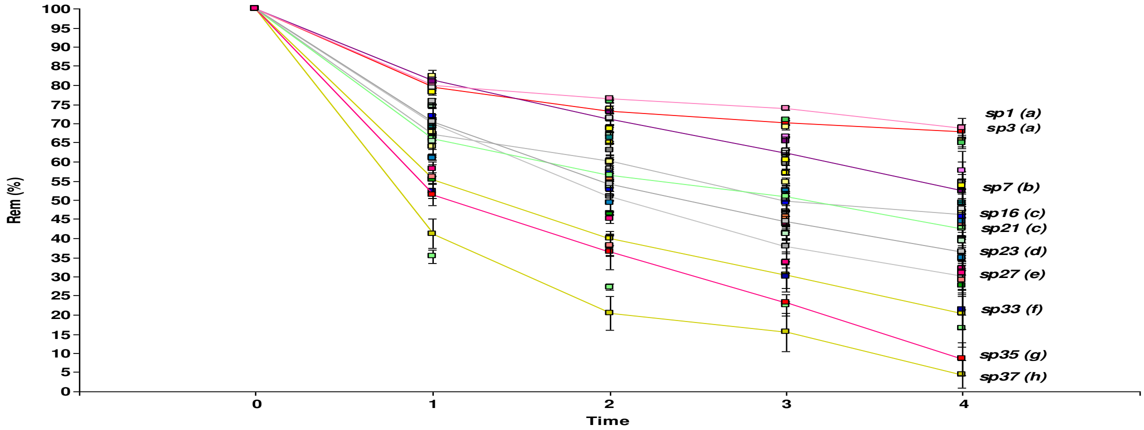


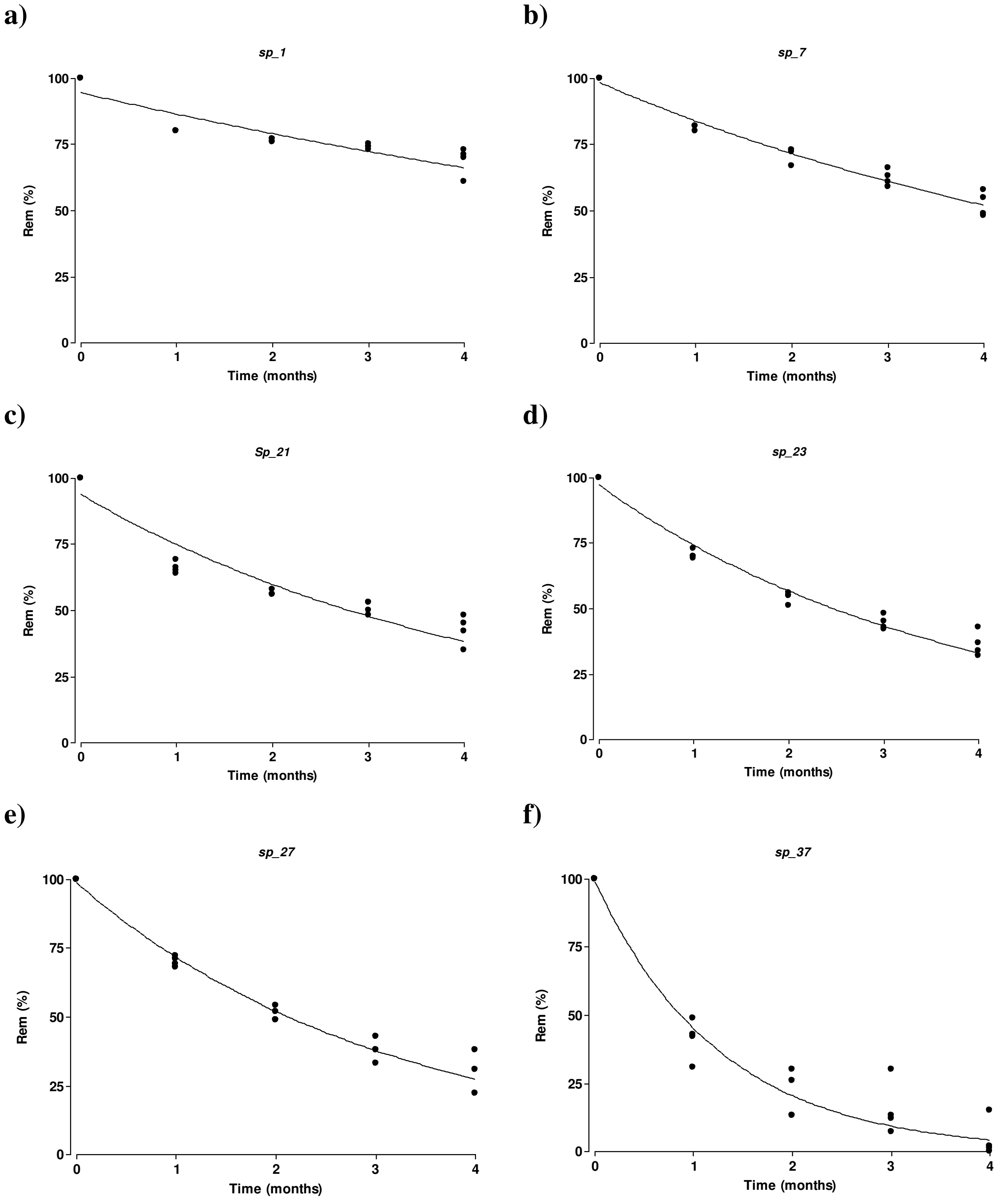
Figure 4.3. Litter decay using the percentage of remaining litter mass (Rem) after each litterbags harvest (every 4 weeks) for 37 tree species commonly found in active pasturelands in Central America during the 4 months of litter incubations under standard conditions. Coloured lines indicate the location of some common tree species and of those located in the extreme of the litter decay gradient according to the mean Rem. Letter indicate ANOVA significant differences ($p \leq 0.05$).

Table 4.2. Mean and range of variavility (Minimum and maximum values) of the percentage of remainig litter mass (Rem), the overall (Beta 5), partial (Beta 4) and monthly decomposition rates (b1, b2, b3, b4) estimated by specie (n=37) and using four regressions (n=148) by each species, using time as regressor variable

Variable	Parameter	n	Mean (S.E)	S.D.	Min	Max
Rem	4 months(ave)	37	53.53	13.44	20.44	74.81
	Rem 1	148	67.61	11.54	31	87
	Rem 2	148	56.48	13.85	13	77
	Rem 3	148	49.37	14.9	7	75
	Rem 4(final)	148	41.54	16.86	0	73
BETA 5	Estimation	37	0.26	0.15	0.09	0.78
	S.E.	37	0.02	0.01	0.01	0.07
	T	37	13.89	4.14	7.9	25.07
	p - value	37	p < 0.0001	-	p < 0.0001	p < 0.0001
	Estimation	148	0.27	0.15	0.08	0.93
	S.E.	148	0.04	0.03	0.01	0.2
	T	148	8.15	7.86	2.96	87.31
	p - value	148	0.01	0.01	1.00E-04	0.06
BETA_4	Estimation	36	0.18	0.12	0.05	0.66
	S.E.	36	0.02	0.02	0.01	0.13
	T	36	9.19	3.95	3.91	22.8
	p - value	36	p < 0,0001	-	p < 0.0001	0.0016
	Estimation	148	0.1900	0.1500	0.0200	1.0700
	S.E.	148	0.0300	0.0300	0.0011	0.2900
	T	148	11.2800	15.8400	2.7900	121.6100
	p - value	148	0.0300	0.0300	0.0001	0.1081
b1	Estimation	37	0.32	0.14	0.14	0.69
b2	Estimation	37	0.27	0.13	0.11	0.75
b3	Estimation	37	0.22	0.15	0.06	0.84
b4	Estimation	37	0.17	0.18	0	0.93

Litter mass decay curves were significantly fitted to simple exponential decay models for all tree species including those with the highest and lowest percentages of remaining mass (**Table 4.2**, **Figure 4.5**). ANOVA for the overall (BETA 5) and partial (BETA 4) decomposition rates also showed significant differences between tree species (p<0.0001, F= 38.9336, gl=36 and p<0.0001, F= 6.36, gl=36 respectively). The mean overall decomposition rate (BETA 5) calculated with four regression by species (n=148) was 0.27 for the total 4 months of litter incubation and the mean partial decomposition rate (BETA 4) was 0.19 for the final 3 months of litter decay. The monthly decomposition rates values (b1, b2, b3, b4) calculated by specie tend to be higher during the first month of litter decay and lower for the final month as expected, but also the values observed for 37 specie showed that their ranges of variability (minimum and maximum values) increased from the first to the final month of litter incubation (**Table 4.2**).

Figure 4.4. Litter decay curves fitted to a simple exponential model regression for the four months of litter decomposition (the estimated BETA 5) in standard conditions for some of the 37 tree species commonly found in active pasturelands in Central America (Beta values vary from 0,09 to 0,78 from a) to f); p≤0,001 for all species)



A total of 8 different groups of species with similar mean percentages of mean litter remaining mass (Rem) and overall decomposition rates (BETA 5) were observed by DGC mean comparisons test (p<0.0001, F= 209.18, gl=140) (**Figure 4.5**).

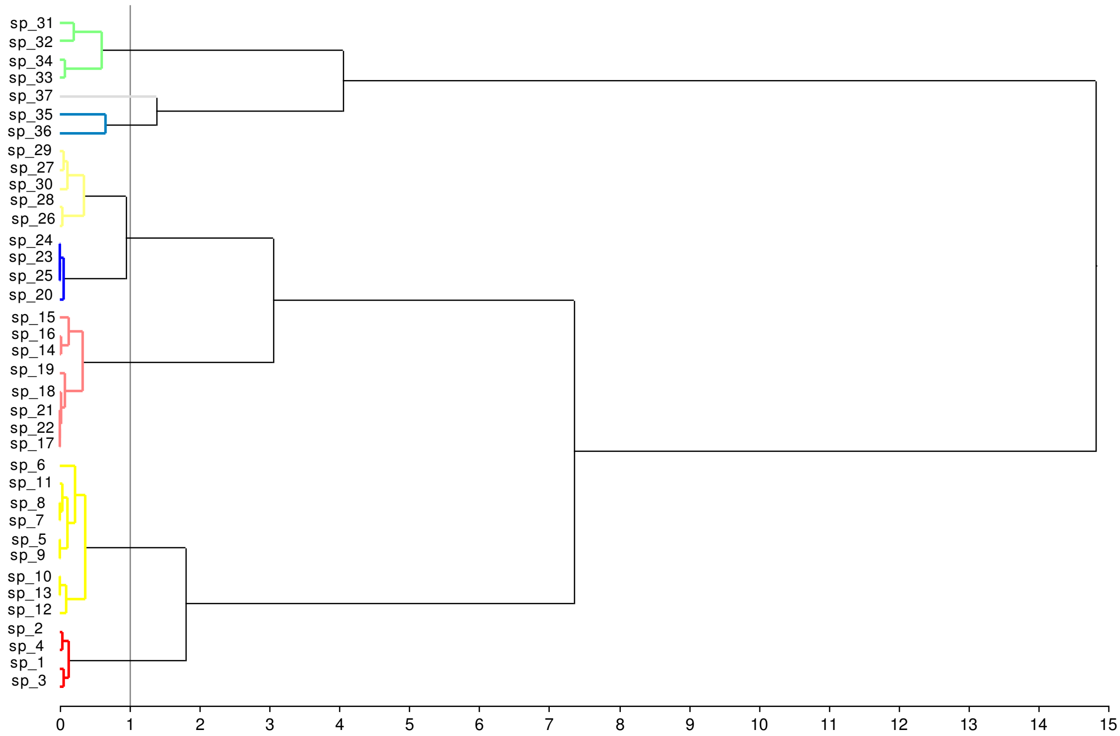


Figure 4.5. Cluster plot showing tree species similarities (Euclidean distance and Ward method) in decomposition rates regressions parameters (BETA 5) estimated by specie in a 4 months litter decomposition experiment under controlled conditions in Central America. The cutting identify groups of species with more similar decomposition rates according to a DGC mean comparison test ($p \leq 0.05$) performed *a-posteriori* to an ANOVA (Wilks F= 209.18; $p < 0.0001$)

A higher number of tree species (21) belong to species groups with a mean decomposition rates below the general mean (BETA 5 = 0.27) reducing their litter mass among 10% to 22% during the 4 months of litter incubation (a=0.10, b=0.16, c=0.22). A reduce number of species (12) showed decomposition rates faster than those tree species (4) with a mean decomposition rate (d=0.27), decomposing between 31% and 77 % of their litter mass during the same time of litter incubation (e=0.31, f=0.41, g=0.60, h=0.77).

Differences in litter quality between tree species

Tree species commonly found in active pasturelands showed a wide variability of total macronutrients (P, N, C) contents (%) in leaves between species and throughout the process of leaves senescence and decomposition (**Table 4.3**, **Figure 4.6**).

Table 4.3. Mean percentages (%) of total macronutrients (Phosphorus - LPC, Nitrogen - LNC and Carbon - LCC) and C fractions (Soluble compounds - SOL, Hemicelluloses - HEM, Cellulose - CEL and Lignin - LIG) contents in green leaves, fresh (t0), remaining litter (t4) and mean percentages of it loses through leaves senescence (from green to litter transition) and during decomposition process (from fresh litter to remaining litter) in tree species commonly found in active pasturelands in Central America

Traits	Green leaves (%)			Fresh litter (t0, %)			Remaining litter (t4, %)			Losses green – t0 (%)			Losses t0 – t4 (%)		
	n	Mean± S.D.	Min-Max	n	Mean± S.D.	Min-Max	n	Mean± S.D.	Min-Max	n	Mean± S.D.	Min-Max	n	Mean± S.D.	Min-Max
LPC	33	0.18± 0.05	0.04-0.33	36	0.1± 0.04	0.04-0.22	36	0.12 ± 0.06	0.05-0.4	31	46.85± 16.27	8.88-68.51	36	46.17± 20.77	2.01-94.63
LNC	33	2.67± 0.59	1.03-3.94	36	1.4 ± 0.47	0.93-2.7	36	1.99 ± 0.43	1.32-2.95	33	45.37± 14.37	0.02-68.37	36	41.29± 21.03	8.24-93.39
LCC	33	46.93± 3.01	41.51-52.67	36	44.48± 4.36	35.46 - 52.14	36	40.75 ± 5.64	28.88 - 49.01	28	7.16± 4.77	0.0002-20.87	36	61.12± 14.86	32.8-96.14
SOL	19	47.1± 10.06	30.54-67.61	40	45.14± 7.86	29.51 - 67.02	35	51.21 ± 9.41	30.72 - 69.29	17	8.75± 13.28	0-46.56	35	53.68± 16.03	27.81-95.25
HEM	19	9.68± 2.83	6.22-18.43	40	8.09± 2.88	2.19-13.82	35	8.59 ± 3.57	2.2-17.27	17	20.36± 23.13	0-71.68	35	52.45± 27.94	0-96.19
CEL	19	22.52± 5.54	11.67-31.52	40	23.2± 5.21	12.91 - 32.78	35	12.65 ± 3.28	5.92-19.81	17	2.84± 7.54	0-31.04	35	76.83± 10.92	49.64-97.9
LIG	19	20.83± 7.35	8.44-39.54	40	21.49± 8.36	6.04-39.26	35	22.59 ± 9.16	6.6-45.06	17	9.18± 14.47	0-48.13	35	54.3± 18.55	19.94-94.43

Almost half of the phosphorus content in green leaves (46%) was lost through senescence and the same amount (46%) was loose from fresh litter through decomposition process. The mean percentage of total phosphorus decrease from 0.18% in green leaves to 0.10% and 0.12% in fresh litter and in remaining litter respectively, after decomposition process. The mean content of nitrogen was 2.67% in fresh litter, decreasing at a mean value of 1.50% during senescence, and to 1.99% after decomposition process. Again, similar proportions of 45% and 41% of N were loosed from green and fresh litter through leaves senescence and decomposition. In contrast, the higher mean total content of carbon in green leaves (46%) decreased only 7% during the senescence process meanwhile it highest losses (61%) were observed through decomposition process (**Table 4.3**, **Figure 4.8**).

LCC inter-specific variability (difference between the maximum and minimum mean content observed) was higher in all leaf stages (11%, 17% and 20% respectively) than the variability in mean contents observed for LNC (2.9%, 1.77%, 1.63% respectively) and lower for LPC (0.29%, 0.18% and 0.35% respectively). However the variability in LPC (59% and 92%) LNC (68% and 85%) lost through senescence and decomposition between tree species were higher than those observed for LCC (21% and 63% respectively).

Tree species commonly found in active pasturelands showed a wide inter specific variability in the range of C fraction content between leaves stages and C fractions (**Figure 4.8**) unless the mean percentages of most C fractions contents in leaves were similar thought leaves senescence and decomposition (**Table 4.3**, **Figure 4.9**). Losses of C fractions were higher during litter decomposition (52 – 76% of initial contents in fresh litter) showing CEL a higher mean percentage of losses and the lower range of variability than the other fractions, which differ mainly by the higher variability in HEM losses through decomposition between tree species. The mean percentage of SOL, LIG and HEM contents in the remaining litter at the end of the four months of litter incubations, were similar to those observed on fresh litter and green leaves, being SOL (51%) higher than LIG (22%) and HEM (9%). Only CEL mean percentage in remaining litter (12%) was reduced to half it content in fresh litter and green leaves (22-23%) (**Table 4.3**). In remaining litter as observed in green leaves and fresh litter, the range of variability between species of SOL and LIG was wider (38%) than for HEM (12%) and CEL (19%).

SOL showed the highest mean percentages in all leaves stages: 47% in green leaves, 45% in fresh litter and 51% in decomposed litter; followed by CEL in green leaves (22%) and fresh litter (23%) but not in decomposed litter (12%) were LIG contents were higher (22%). HEM constitutes the lower proportions in all leaves stages (9%, 8% and 8.5%). SOL and LIG showed the wide variability mean contents between tree species in green leaves (37% and 31%) fresh (37% and 33%) and decomposed litter (38% for both). Lower inter-specific variability was observed for the mean content of CEL and HEM in green leaves (19% and 12%), fresh (19% and 11%) and decomposed litter (13% and 15%).

All C fractions have lower reductions during leaves transition to fresh litter (2 – 20% of initial contents in green leaves) and their contents in fresh litter were similar to those in green leaves, showing HEM the highest percentages of losses and variability, followed by SOL and LIG, and finally by CEL (**Table 4.3**).

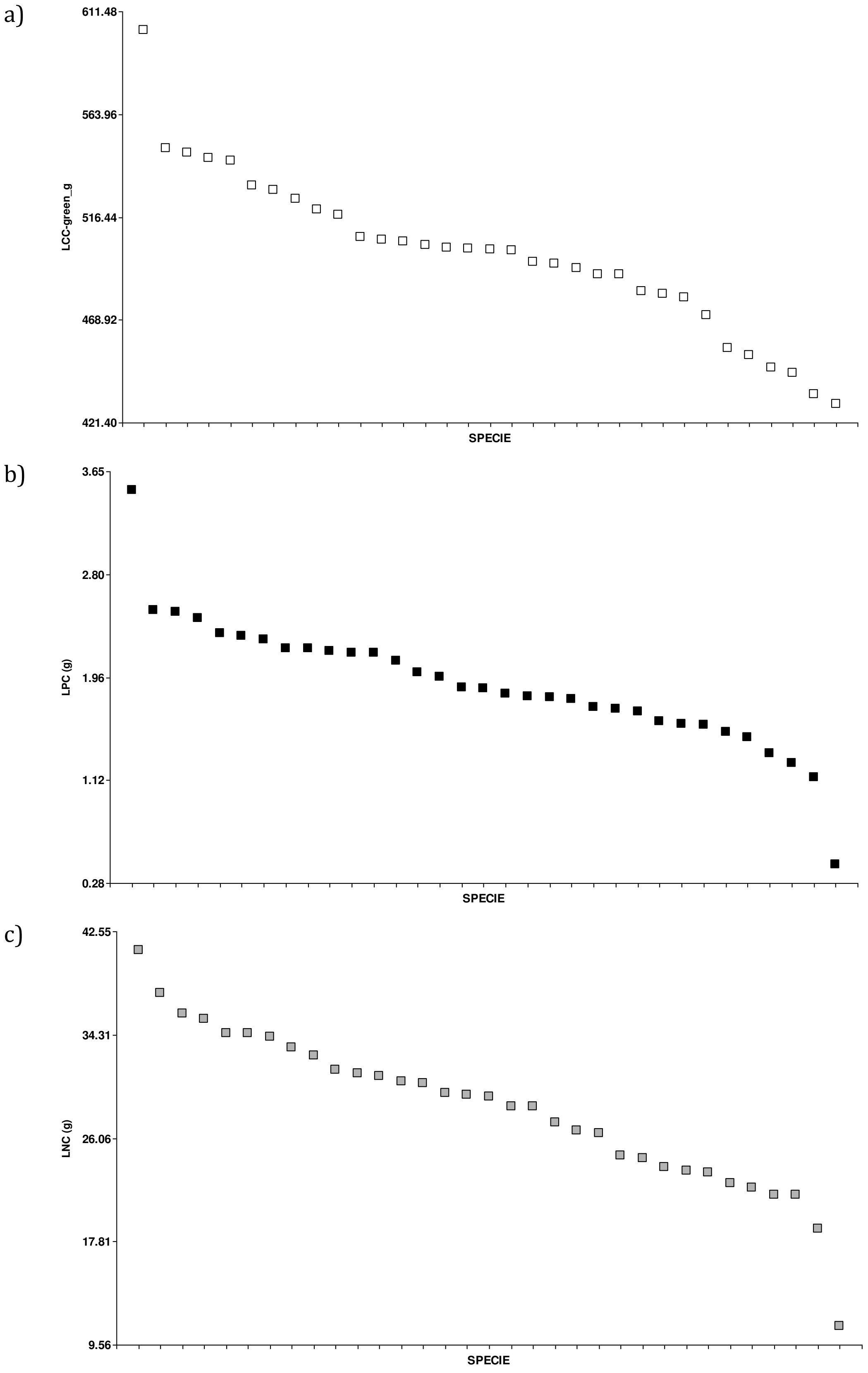


Figure 4.6. Mean total contents of a) Carbon – LCC, b) Phosphorus – LPC and c) Nitrogen - LNC in green (0) leaves of tree species commonly found in active pasturelands in Central America.

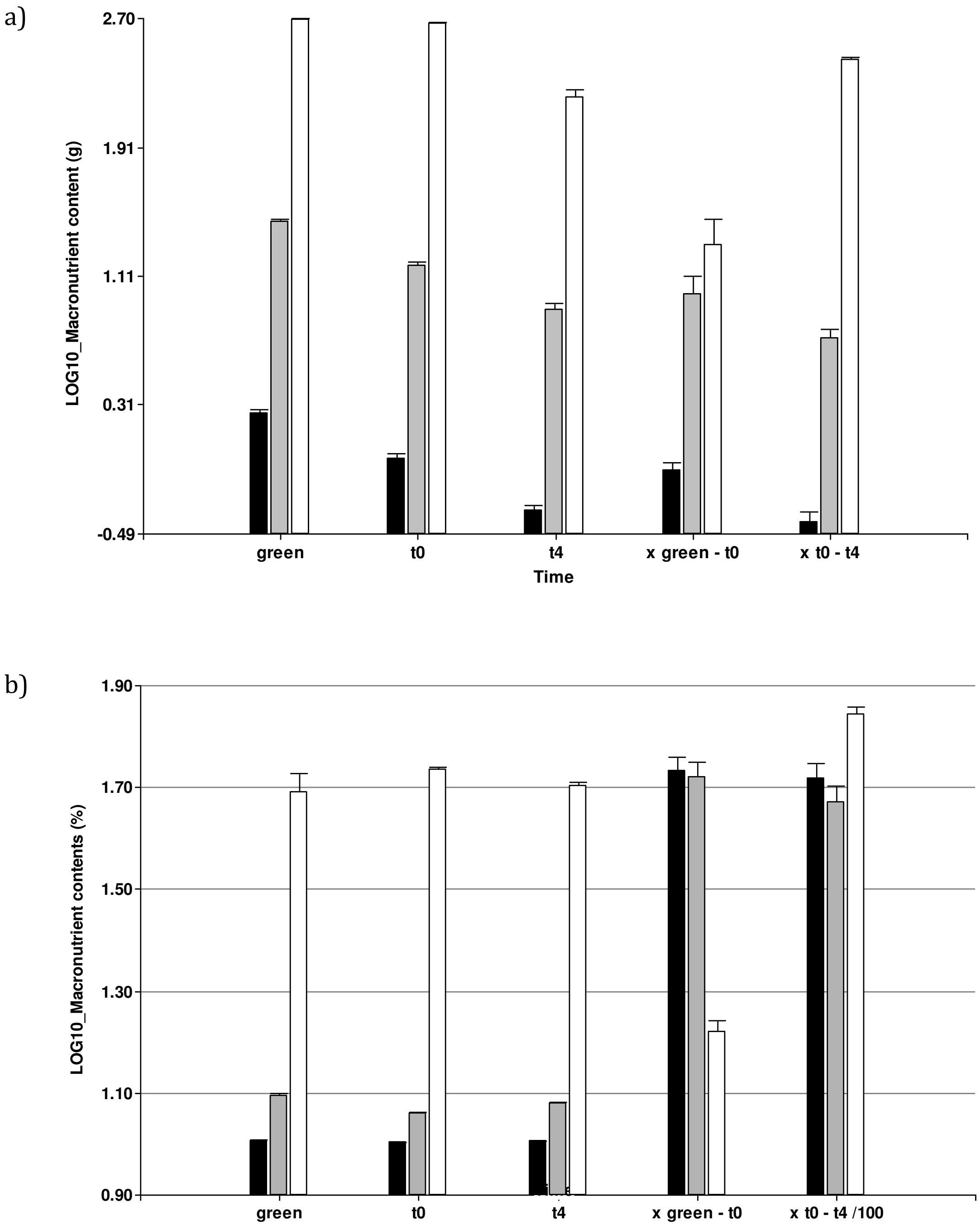


Figure 4.7. Mean total macronutrients contents (Phosphorus - LPC, Nitrogen - LNC and Carbon - LCC) expressed in a) grammes (g) and b) percentages (%) in green leaves (green), fresh litter (t0), remaining litter (t4) after decomposition and their looses after leaves senescence (green –t0) and decomposition (t0 – t4) measured in tree species commonly found in active pasturelands in Central America. Contents in grams (g) should be divided by 100 to obtain the real values. LPC contents in black, LNC in gray, LCC in white.

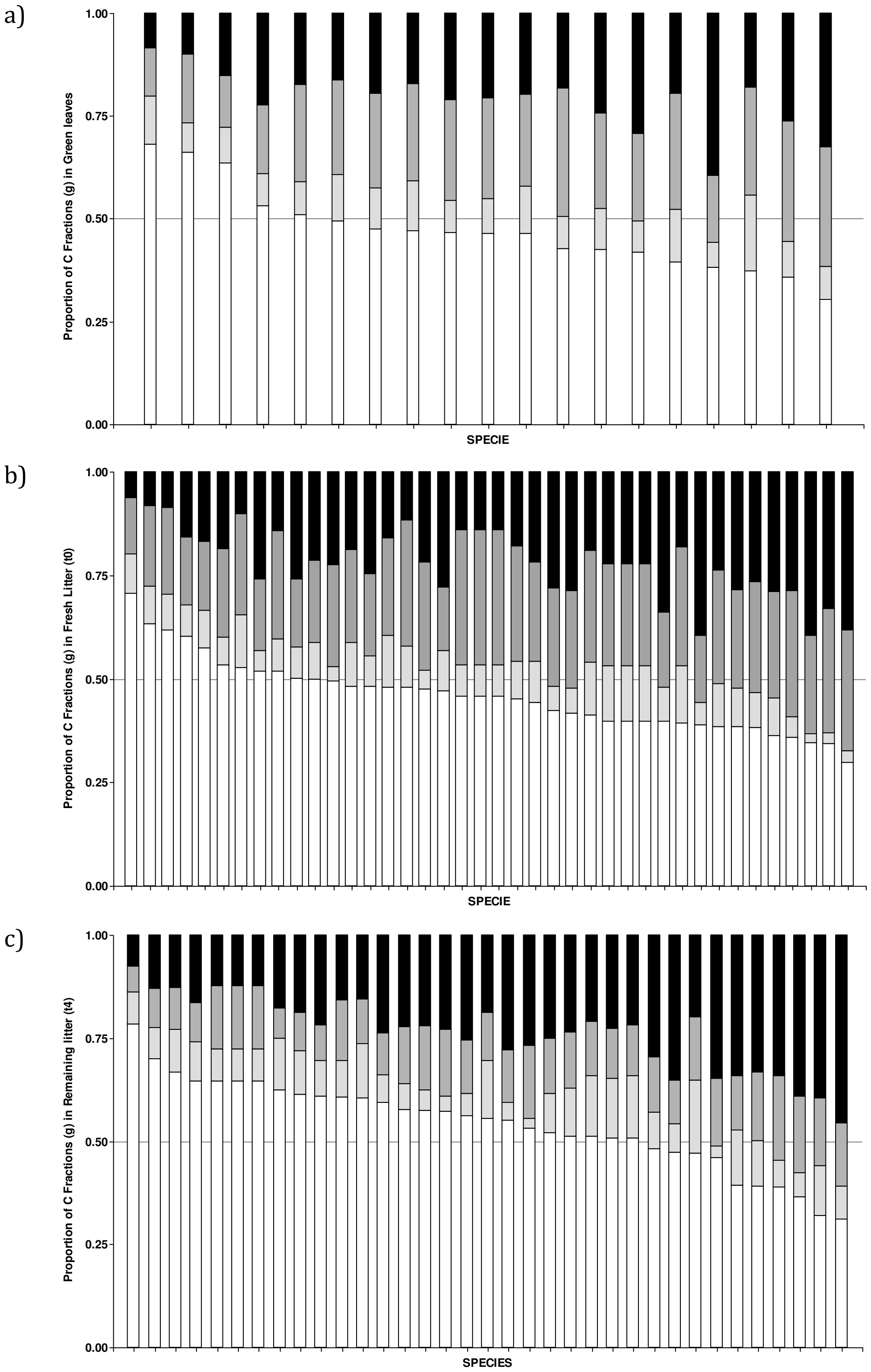
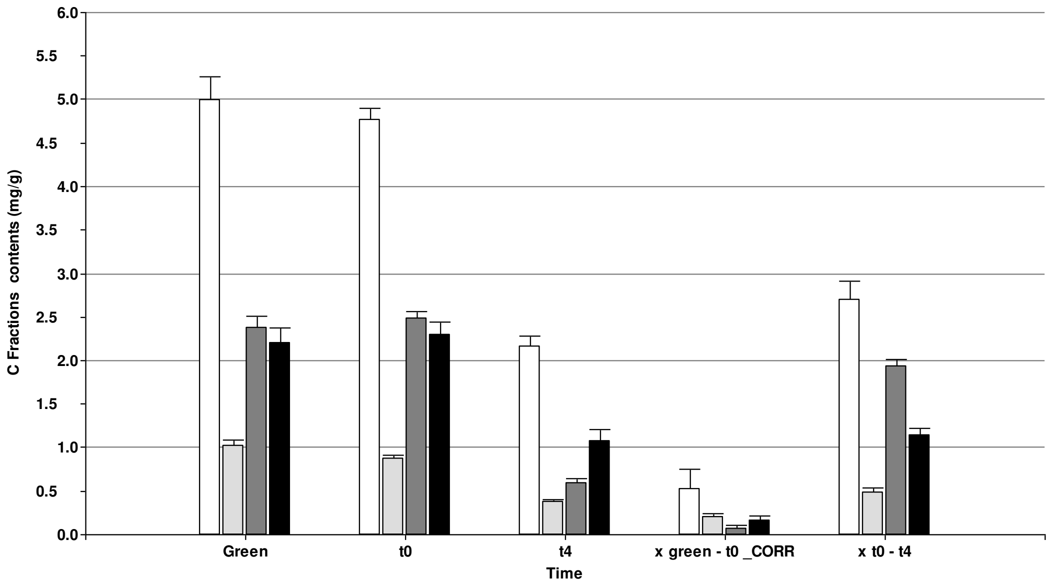


Figure 4.8. Mean contents (g) of C fractions (Soluble compounds - SOL, Hemicelluloses - HEM, Cellulose - CEL and Lignin - LIG) in a) green leaves, b) fresh (t0) and c) remaining litter (t4) in tree species commonly found in active pasturelands in Central America. SOL contents in white, HEM in light gray, CEL in dark grey and LIG in black

a)



b)

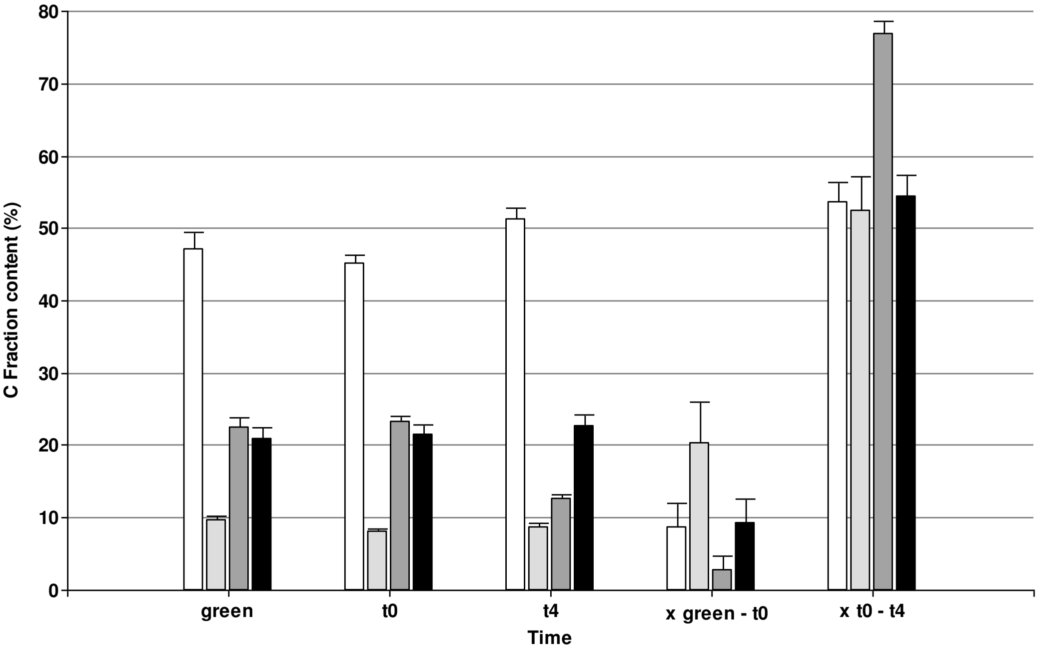


Figure 4.9. Mean contents of C fractions (Soluble compounds - SOL, Hemicelluloses - HEM, Cellulose - CEL and Lignin - LIG) expressed in a) litter (g) and b) percentages (%) in green leaves, fresh litter, remaining litter after decomposition and their looses after leaves senescence (from green to litter transition) and decomposition (from fresh litter to remaining litter) measured in tree species commonly found in active pasturelands in Central America. SOL contents in white, HEM in light gray, CEL in dark grey and LIG in black

In general, a wide variability in the mean percentages of total macronutrients and C fractions contents were found in tree species commonly found in active pasturelands. C fractions contents were more stable through senescence than through litter decomposition and also than macronutrients. The low differences in the percentage of total C contents in from green leaves to fresh litter seem to be related with SOL and HEM looses, meanwhile the higher looses in total C during litter decomposition seem to be more related with CEL reductions than with the reduction of the other C fractions proportions in decomposed litter. Higher inter-specific variability was found in the amounts of LPC and LNC through senescence and decomposition, comparable only with the variability in HEM looses through both process.

Relationship of tree leaf litter decomposition rates with quality in leaves and litter

As expected leaf litter decomposition rates of tree species are correlated with fresh litter quality. Leaf litter decomposition rates of tree species naturally regenerating in active pasturelands were correlated with leaves LDMC, with some but not all the macronutrients i.e. LCC and LPC, and with some C fraction contents like SOL, HEM and LIG in their fresh litter. Overall, partial and monthly decomposition rates were negatively correlated with LDMC, C and LIG content (grames and percentages), positively correlated with P, SOL and HEM contents (grames and percentages), and there was no correlation with N or CEL content in tree fresh litter (**Table 4.4**). Therefore those tree species with lower LDMC, C and LIG content together with the highest P, SOL and HEM content in fresh litter had higher decomposition rates. The strongest correlations with decomposition rates were found with LIG, followed by HEM, P, C, SOL and LDMC.

Tree species' contents of dry matter, C, P and N in green leaves were found to be closely correlated with those in fresh litter (**Table 4.7**). LDMC and LCC in green leaves were positively correlated with C contents in fresh litter. LPC was positively correlated with P in fresh litter. LNC was positively correlated with N contents in fresh litter. Other plant foliar traits measured in green leaves like SLA, LA and FTF were correlated with litter macronutrients and C fractions but were not correlated with any decomposition rate measured (**Table 4.6**). Only SLA tends to be negatively correlated with the partial decomposition rate for the three final months of decomposition. SLA tends to be positively correlated with N content in fresh litter. LA was negatively correlated with N and C (percentages and grams) in fresh litter. FTF was not correlated with any nutrient content measured in litter.

All C fractions measured in green leaves were tightly correlated with the percentages of C fractions in fresh litter (**Table 4.7**). SOL content of green leaves was positively and strongly correlated with SOL, followed by HEM and negatively correlated with LIG and CEL in fresh litter. HEM in green leaves was positively strongly correlated with HEM in fresh litter and tends to be positively correlated with SOL and negatively correlated with LIG in fresh litter. LIG content in green leaves was strongly and positively correlated with LIG and negatively correlated with SOL and HEM contents in fresh litter. Finally, CEL content in green leaves was only positively correlated with CEL contents in fresh litter. The strongest correlation between green leaves and litter was found for CEL contents, followed by LIG, HEM and SOL respectively, being SOL more strongly correlated with LIG in fresh litter than with SOL.

The same correlations observed between decomposition rates and litter quality, were found between decomposition rates and macronutrient and C fraction contents in green leaves (**¡Error! No se encuentra el origen de la referencia.**, **Table 4.7**). LDMC and total nutrient concentrations (LPC, LNC and LCC) of green leaves were also correlated with overall, partial and monthly decomposition rates. LCC and LDMC were negatively correlated with overall and monthly decomposition rates and positively correlated to remaining litter masses. LPC in green leaves was positively correlated with overall and partial decomposition rates and negatively correlated with monthly amounts of remaining litter. LCC and LDMC correlations with monthly decomposition rates were stronger for the first three months than for the last four month of decomposition (b4), similar to LPC which was not correlated at all with b4 or with T1. LNC was not correlated at all with any decomposition rate also in green leaves and was only negatively correlated with the remaining litter at the end of the first month of decomposition (T1). LDMC, LCC and LPC in green leaves and fresh litter were also correlated with decomposition rates. However, the Spearman rank correlation coefficients were relatively less strong for LPC and LNC in green leaves (0,40 for LPC; -0,47 for LCC; -0,38 for LDMC) than in fresh litter (0,55 for LPC, -0,39 for LCC; -0,49 for LDMC).

Table 4.4. Spearman rank correlation coefficients of the relationships of overall and partial decomposition rates with a) the contents (%) and losses (% or g) of dry matter fractions, total macronutrients and b) C fractions in leaves, fresh (t0) and decomposed (t4) litter for 37 tree species regenerating naturally in active neotropical pasturelands

a)	BETA_4	BETA_5	b1	b2	b3	b4	T1_Rem	T2_Rem	T3_Rem	T4_Rem
LDMC	**-0,34** **(0,0531)**	**-0,40** **(0,0228)**	**-0,37** **(0,0367)**	**-0,39** **(0,0237)**	**-0,39** **(0,0237)**	**-0,32** **(0,074)**	**0,39** **(0,0253)**	**0,4** **(0,022)**	**0,38** **(0,0278)**	**0,4** **(0,0198)**
LPC	**0,51** **(0,0026)**	**0,48** **(0,0044)**	**0,43** **(0,0119)**	**0,49** **(0,004)**	**0,48** **(0,0049)**	**0,33** **(0,0596)**	**-0,35** **(0,0453)**	**-0,51** **(0,0026)**	**-0,47** **(0,0057)**	**-0,49** **(0,0036)**
LNC	-0,09 (0,6005)	0,08 (0,6518)	0,19 (0,2887)	0,08 (0,6578)	-0,04 (0,8268)	-0,16 (0,3785)	**-0,33** **(0,0624)**	-0,16 (0,3786)	-0,08 (0,6432)	-0,08 (0,6775)
LCC	**-0,50** **(0,0028)**	**-0,54** **(0,0011)**	**-0,53** **(0,0015)**	**-0,56** **(0,0006)**	**-0,49** **(0,004)**	**-0,35** **(0,0486)**	**0,45** **(0,0079)**	**0,58** **(0,0004)**	**0,57** **(0,0005)**	**0,53** **(0,0014)**
P_t0	**0,55** **(0,0005)**	**0,58** **(0,0002)**	**0,51** **(0,0016)**	**0,57** **(0,0003)**	**0,54** **(0,0007)**	**0,32** **(0,0545)**	**-0,43** **(0,0084)**	**-0,58** **(0,0002)**	**-0,56** **(0,0003)**	**-0,6** **(0,0001)**
N_t0	-0,08 (0,6361)	0,08 (0,6238)	0,12 (0,4834)	0,09 (0,6138)	0,02 (0,8966)	-0,0035 (0,9836)	**-0,31** **(0,067)**	-0,12 (0,4895)	-0,09 (0,6027)	-0,08 (0,6248)
C_t0	**-0,50** **(0,0021)**	**-0,53** **(0,0008)**	**-0,52** **(0,0012)**	**-0,55** **(0,0006)**	**-0,45** **(0,0059)**	**-0,31** **(0,0641)**	**0,42** **(0,0132)**	**0,56** **(0,0003)**	**0,56** **(0,0004)**	**0,50** **(0,0028)**
P_t4	**0,76** **(<0,0001)**	**0,76** **(<0,0001)**	**0,65** **(<0,0001)**	**0,76** **(<0,0001)**	**0,75** **(<0,0001)**	**0,63** **(<0,0001)**	**-0,57** **(0,0002)**	**-0,73** **(<0,0001)**	**-0,75** **(<0,0001)**	**-0,78** **(<0,0001)**
N_t4	0,09 (0,5983)	0,22 (0,1885)	0,25 (0,1299)	0,22 (0,1856)	0,18 (0,2744)	0,15 (0,3783)	**-0,37** **(0,0228)**	-0,22 (0,1878)	-0,23 (0,1639)	-0,22 (0,1863)
C_t4	**-0,60** **(0,0001)**	**-0,62** **(<0,0001)**	**-0,6** **(0,0001)**	**-0,62** **(0,0001)**	**-0,55** **(0,0004)**	**-0,39** **(0,0157)**	**0,49** **(0,003)**	**0,63** **(<0,0001)**	**0,63** **(<0,0001)**	**0,61** **(0,0003)**
P_loss	**0,58** **(0,0002)**	**0,71** **(<0,0001)**	**0,7** **(<0,0001)**	**0,7** **(<0,0001)**	**0,61** **(0,0001)**	**0,34** **(0,0402)**	**-0,74** **(<0,0001)**	**-0,72** **(<0,0001)**	**-0,69** **(<0,0001)**	**-0,7** **(<0,0001)**
N_loss	**0,72** **(<0,0001)**	**0,84(** **<0,0001)**	**0,75** **(<0,0001)**	**0,83** **(<0,0001)**	**0,78** **(<0,0001)**	**0,56** **(0,0004)**	**-0,81** **(<0,0001)**	**-0,83** **(<0,0001)**	**-0,82** **(<0,0001)**	**-0,84** **(<0,0001)**
C_loss	**0,92** **(<0,0001)**	**0,98** **(<0,0001)**	**0,87** **(<0,0001)**	**0,97** **(<0,0001)**	**0,93** **(<0,0001)**	**0,7** **(<0,0001)**	**-0,83** **(<0,0001)**	**-0,94** **(<0,0001)**	**-0,96** **(<0,0001)**	**-0,98** **(<0,0001)**

b)	BETA_4	BETA_5	b1	b2	b3	b4	T1_Rem	T2_Rem	T3_Rem	T4_Rem
Sol_t0	**0,48** **(0,0032)**	**0,53** **(0,0009)**	**0,47** **(0,0041)**	**0,53** **(0,001)**	**0,46** **(0,0044)**	**0,34** **(0,0416)**	**-0,45** **(0,0077)**	**-0,52** **(0,0012)**	**-0,5** **(0,0019)**	**-0,52** **(0,002)**
Hem_t0	**0,45** **(0,0055)**	**0,59** **(0,0001)**	**0,63(<0,0001)**	**0,6** **(0,0001)**	**0,45** **(0,0059)**	0,24 (0,1625)	**-0,62** **(0,0001)**	**-0,62** **(<0,0001)**	**-0,61** **(0,0001)**	**-0,55** **(0,0005)**
Cell_t0	-0,16 (0,3491)	-0,22 (0,2019)	-0,13 (0,4445)	-0,21 (0,21)	-0,2 (0,241)	-0,15 (0,3953)	0,2 (0,2319)	0,2 (0,2366)	0,19 (0,2704)	0,24 (0,1594)
Lig_t0	**-0,61** **(0,0001)**	**-0,67** **(<0,0001)**	**-0,69** **(<0,0001)**	**-0,68** **(<0,0001)**	**-0,53** **(0,0008)**	**-0,31** **(0,0617)**	**0,57** **(0,0008)**	**0,69** **(<0,0001)**	**0,68** **(<0,0001)**	**0,63** **(0,0002)**
Sol_t4	**0,67** **(<0,0001)**	**0,56** **(0,0006)**	**0,45** **(0,0079)**	**0,54** **(0,0011)**	**0,6** **(0,0002)**	**0,46** **(0,0072)**	**-0,33** **(0,0653)**	**-0,48** **(0,0045)**	**-0,54** **(0,0013)**	**-0,59** **(0,0009)**
Hem_t4	0,06 (0,7266)	0,18 (0,3069)	0,26 (0,1462)	0,19 (0,2854)	0,07 (0,6981)	-0,05 (0,7878)	**-0,32** **(0,0721)**	-0,22 (0,2099)	-0,21 (0,2425)	-0,16 (0,3841)
Cell_t4	**-0,62** **(0,0001)**	**-0,68** **(<0,0001)**	**-0,58** **(0,0004)**	**-0,66** **(<0,0001)**	**-0,63** **(0,0001)**	**-0,44** **(0,0111)**	**0,62** **(0,0005)**	**0,65** **(<0,0001)**	**0,65** **(<0,0001)**	**0,69** **(0,0001)**
Lig_t4	**-0,67** **(<0,0001)**	**-0,64** **(0,0001)**	**-0,61** **(0,0002)**	**-0,63** **(0,0001)**	**-0,58** **(0,0004)**	**-0,35** **(0,0464)**	**0,46** **(0,0096)**	**0,6** **(0,0002)**	**0,64** **(0,0001)**	**0,63** **(0,0004)**
Sol_loss	**0,75** **(<0,0001)**	**0,85** **(<0,0001)**	**0,76** **(<0,0001)**	**0,85** **(<0,0001)**	**0,77** **(<0,0001)**	**0,55** **(0,0009)**	**-0,8** **(<0,0001)**	**-0,83** **(<0,0001)**	**-0,83** **(<0,0001)**	**-0,84** **(<0,0001)**
Hem_loss	**0,72** **(<0,0001)**	**0,79** **(<0,0001)**	**0,75** **(<0,0001)**	**0,79** **(<0,0001)**	**0,7** **(<0,0001)**	**0,47** **(0,0055)**	**-0,7** **(<0,0001)**	**-0,77** **(<0,0001)**	**-0,79** **(<0,0001)**	**-0,76** **(<0,0001)**
Cell_loss	0,16 (0,372)	0,14 (0,4248)	0,22 (0,2133)	0,14 (0,4249)	0,13 (0,4717)	0,06 (0,7494)	-0,15 (0,3951)	-0,14 (0,4288)	-0,18 (0,3144)	-0,12 (0,4884)
Lig_loss	0,18 (0,3093)	0,07 (0,7111)	-0,14 (0,4386)	0,03 (0,8882)	0,26 (0,1386)	**0,43** **(0,0116)**	0,06 (0,7492)	0,05 (0,765)	-0,01 (0,9404)	-0,15 (0,4059)

Table 4.5. Spearman rank correlations of green leaf traits related to a) macronutrients and b) C fractions contents (%) in fresh (t0) and litter remaining (t4) after decomposition and with their losses (% or g) during decomposition for tree species naturally regenerating in active neotropical pasturelands

a)	Green LDMC	Green LCC	Litter C_t0	Litter C_t4	Green LPC	Litter P_t0	Litter P_t4	Green LNC	Litter N_t0	Litter N_t4
LCC	**0,43 (0,0042) 42**	1	**0,84 (<0,0001) 40**	**0,86 (<0,0001) 33**	**-0,38 0,0022) 62**	-0,25 (0,1148) 40	**-0,4 (0,0194) 33**	-0,0048 (0,9703) 62	0,06 (0,699) 40	0,16 (0,3663) 33
LDMC	1	**0,43 (0,0042) 42**	**0,38 (0,0276) 35**	**0,38 (0,0305) 33**	**-0,43 (0,004) 42**	-0,21 (0,2359) 35	**-0,44 (0,0105) 33**	**-0,32 (0,0421) 42**	0,08 (0,661) 35	-0,06 (0,7276) 33
Green	**0,43 (0,0042) 42**	1	**0,84 (<0,0001)40**	**0,86 (<0,0001) 33**	1	**0,42 (0,0063) 40**	**0,53 (0,0015) 33**	1	**0,50 (0,0012) 40**	**0,59 (0,0003) 33**
t0	**0,38 (0,0276) 35**	**0,84 (<0,0001) 40**	1	**0,83 (<0,0001) 36**	**0,44 (0,0043) 40**	1	**0,66 (<0,0001) 36**	**0,5 (0,0012) 40**	1	**0,77 (<0,0001) 36**
t4_%	**0,38 (0,0305) 33**	**0,86 (<0,0001) 33**	**0,83 (<0,0001) 36**	1	**0,53 (0,0015) 33**	**0,66 (<0,0001) 36**	1	**0,59 (0,0003) 33**	**0,77 (<0,0001) 36**	1
t4_g	**0,39 (0,0271) 33**	**0,71 (<0,0001) 33**	**0,70 (<0,0001) 36**	**0,80 (<0,0001) 37**	0,05 (0,7689) 33	0,18 (0,293) 36	0,21 (0,2094) 37	**0,29 (0,101) 33**	**0,37 (0,0244) 36**	**0,32 (0,0539) 37**
loss_g	-0,28 (0,1161) 32	-0,28 (0,115) 32	-0,17 (0,3112) 36	**-0,4 (0,0183) 36**	**0,43 (0,0139) 32**	**0,88 (<0,0001) 36**	**0,50 (0,0018) 36**	**0,38 (0,0314) 32**	**0,72 (<0,0001) 36**	**0,49 (0,0024) 36**
loss_ %	**-0,35 (0,0515) 32**	**-0,60 (0,0003) 32**	**-0,54 (0,0015) 36**	**-0,68 (0,0001) 36**	0,25 (0,1751) 32	**0,63 (<0,0001) 36**	**0,28 (0,0936) 36**	0,19 (0,3099) 32	**0,44 (0,0077) 36**	0,26 (0,127) 36

b)	Green LDMC	Green LCC	Litter C_t0	Litter C_t4	Green LPC	Litter P_t0	Litter P_t4	Green LNC	Litter N_t0	Litter N_t4
SOL _t0	**-0,35 (0,0538) 32**	**-0,3 (0,0984) 32**	**-0,44 (0,0094) 36**	**-0,44 (0,009) 36**	0,27 (0,1336) 32	**0,39 (0,02) 36**	**0,48 (0,0028) 36**	0,12 (0,5108) 32	0,03 (0,8785) 36	-0,05 (0,7632) 36
HEM _t0	-0,2 (0,277) 32	**-0,33 (0,0671) 32**	**-0,38 (0,0209) 36**	**-0,35 (0,0338) 36**	0,07 (0,714) 32	0,11 (0,5237) 36	**0,29 (0,0901) 36**	0,13 (0,4715) 32	0,12 (0,4843) 36	0,19 (0,2673) 36
CEL _t0	-0,04 (0,8224) 32	-0,03 (0,8758) 32	0,06 (0,7182) 36	0,17 (0,3208) 36	0,01 (0,9713) 32	**-0,47 (0,004) 36**	-0,20 (0,2338) 36	**-0,33 (0,0655) 32**	-0,26 (0,1215) 36	-0,12 (0,4849) 36
LIG _t0	**0,41 (0,024) 32**	**0,64 (0,0001) 32**	**0,78 (<0,0001) 36**	**0,72 (<0,0001) 36**	**-0,42 (0,0176) 32**	**-0,28 (0,0981) 36**	**-0,48 (0,0028) 36**	-0,1 (0,5796) 32	0,05 (0,7866) 36	0,13 (0,4672) 36
SOL _t4	-0,25 (0,1889) 29	**-0,34 (0,0743) 29**	**-0,41 (0,0206) 33**	**-0,48 (0,0067) 33**	0,2 (0,3014) 29	**0,45 (0,0084) 33**	**0,44 (0,0105) 33**	-0,06 (0,7577) 29	**-0,3 (0,0908) 33**	-0,23 (0,1952) 33
HEM _t4	0,01 (0,9788) 29	-0,19 (0,3243) 29	-0,27 (0,1218) 33	-0,22 (0,2187) 33	-0,01 (0,9685) 29	-0,04 (0,8066) 33	0,08 (0,6478) 33	**0,46 (0,0112) 29**	**0,55 (0,0009) 33**	**0,48 (0,0045) 33**
CEL _t4	0,24 (0,2061) 29	**0,4 (0,031) 29**	**0,5 (0,0044) 33**	**0,55 (0,0019) 33**	-0,2 (0,2953) 29	**-0,55 (0,0009) 33**	**-0,48 (0,0048) 33**	-0,28 (0,1368) 29	**-0,29 (0,1025) 33**	-0,14 (0,4385) 33
LIG _t4	0,26 (0,1761) 29	**0,67 (0,0001) 29**	**0,71 (0,0001) 33**	**0,76 (<0,0001) 33**	-0,29 (0,1257) 29	**-0,35 (0,0447) 33**	**-0,4 (0,0211) 33**	-0,23 (0,2345) 29	0,12 (0,5046) 33	0,11 (0,527) 33
SOL _loss	**-0,37 (0,0531) 29**	**-0,44 (0,0164) 29**	**-0,45 (0,0115) 33**	**-0,47 (0,0074) 33**	**0,46 (0,0115) 29**	**0,58 (0,0004) 33**	**0,74 (<0,0001) 33**	**0,32 (0,0865) 29**	**0,47 (0,0062) 33**	**0,46 (0,0075) 33**
HEM _loss	-0,29 (0,126) 29	**-0,39 (0,037) 29**	**-0,32 (0,0684) 33**	**-0,41 (0,0199) 33**	0,24 (0,2191) 29	**0,43 (0,0127) 33**	**0,55 (0,0009) 33**	-0,09 (0,6556) 29	-0,20 (0,2711) 33	-0,03 (0,8636) 33
CELL_ loss_%	**-0,34 (0,0688) 29**	**-0,51 (0,0047) 29**	**-0,56 (0,0007) 33**	**-0,59 (0,0003) 33**	**0,37 (0,0487) 29**	**0,55 (0,0009) 33**	**0,66 (<0,0001) 33**	0,22 (0,2505) 29	0,21 (0,2392) 33	0,27 (0,1349) 33
LIG _loss	-0,26 (0,1671) 29	**-0,42 (0,0217) 29**	**-0,36 (0,0415) 33**	**-0,49 (0,0059) 33**	0,21 (0,2786) 29	**0,46 (0,0074) 33**	**0,62 (0,0001) 33**	0,09 (0,6593) 29	-0,01 (0,9507) 33	0,17 (0,3467) 33

Table 4.6. Spearman rank correlations of green leaf traits related to a) macronutrients with macronutrient and b) C fractions contents (%) in fresh (t0) and litter remaining (t4) after decomposition and with their losses during decomposition for tree species naturally regenerating in active neotropical pasturelands

a)

	SLA	**LA**	**FTF1**
P_t0	-0,13 (0,4777) 34	0,1 (0,5843) 35	-0,24 (0,1506) 36
N_t0	**0,28 (0,104) 34**	**-0,53 (0,0011) 35**	-0,18 (0,2986) 36
C_t0	-0,02 (0,9111) 34	**-0,29 (0,0958) 35**	0,06 (0,7073) 36
P_t4	-0,06 (0,7514) 32	-0,17 (0,3492) 33	-0,28 (0,1144) 34
N_t4	0,16 (0,383) 32	**-0,48 (0,0049) 33**	-0,18 (0,3002) 34
C_t4	-0,06 (0,7518) 32	**-0,31 (0,0798) 33**	0,06 (0,7492) 34
P_t4_g	0,14 (0,4605) 32	**-0,36 (0,0419) 33**	-0,25 (0,1554) 34
N_t4_g	**0,29 (0,1096) 32**	**-0,41 (0,0168) 33**	0,03 (0,8636) 34
C_t4_g	0,11 (0,5339) 32	-0,2 (0,2734) 33	0,13 (0,4609) 34
P_loss_g	-0,14 (0,4366) 31	0,19 (0,3094) 32	-0,26 (0,1391) 33
N_loss_g	-0,01 (0,9442) 31	-0,23 (0,2001) 32	-0,09 (0,6072) 33
C_loss_g	**-0,3 (0,1065) 31**	-0,05 (0,7711) 32	-0,24 (0,177) 33
P_loss_%	-0,16 (0,3855) 31	0,29 (0,1026) 32	-0,12 (0,5131) 33
N_loss_%	-0,12 (0,5312) 31	-0,04 (0,8351) 32	-0,15 (0,3897) 33
C_loss_%	-0,25 (0,1773) 31	0,1 (0,592) 32	-0,18 (0,3073) 33

b)

	SLA	**LA**	**FTF1**
DF_t0	-0,09 (0,6378) 31	0,09 (0,6378) 32	-0,2 (0,271) 33
Hem_t0	-0,14 (0,4476) 31	0,11 (0,5604) 32	-0,17 (0,3479) 33
Cell_t0	0,08 (0,6738) 31	0,02 (0,9238) 32	**0,34 (0,0561) 33**
Lig_t0	0,06 (0,7495) 31	-0,21 (0,2528) 32	0,01 (0,9712) 33
Sol_t4_%	**-0,42 (0,0269) 28**	**0,31 (0,1027) 29**	0,08 (0,6657) 30
Hem_t4_%	0,2 (0,3111) 28	-0,16 (0,4096) 29	0,09 (0,6256) 30
Cell_t4_%	0,13 (0,5139) 28	-0,09 (0,6318) 29	0,14 (0,4708) 30
Lig_t4_%	0,29 (0,1375) 28	-0,3 (0,1192) 29	-0,19 (0,3177) 30
Sol_t4_g	-0,07 (0,7181) 28	0,05 (0,7863) 29	0,11 (0,5759) 30
Hem_t4_g	0,29 (0,1283) 28	-0,25 (0,1886) 29	0,14 (0,463) 30
Cell_t4_g	0,24 (0,21) 28	-0,01 (0,9676) 29	0,09 (0,6549) 30
Lig_t4_g	0,28 (0,1515) 28	-0,19 (0,3313) 29	-0,11 (0,5668) 30
Sol_loss_g	-0,08 (0,6961) 28	-0,11 (0,5871) 29	-0,19 (0,3023) 30
Hem_loss_g	**-0,32 (0,0928) 28**	0,2 (0,2968) 29	-0,06 (0,7374) 30
Cell_loss_g	-0,15 (0,4425) 28	-0,04 (0,8474) 29	**0,42 (0,0207) 30**
Lig_loss_g	-0,16 (0,4286) 28	-0,2 (0,2958) 29	-0,24 (0,2037) 30
Sol_loss_%	-0,01 (0,9405) 28	-0,14 (0,4707) 29	-0,23 (0,2279) 30
Hem_loss_%	**-0,32 (0,098) 28**	0,19 (0,3328) 29	-0,13 (0,5012) 30
Cell_loss_%	-0,28 (0,1558) 28	0,08 (0,6966) 29	-0,01 (0,9622) 30
Lig_loss_%	**-0,35 (0,0716) 28**	0,17 (0,3816) 29	-0,1 (0,6053) 30

The positive relationships of each macronutrient content in green leaves with their content in fresh litter imply that the relative concentrations of C, N, P and C fractions in green leaves amongst species do not change strongly during leaf senescence or indeed during decomposition, as green leaf LDMC, LCC, LPC, LNC and C fractions are good predictors of C, P and N contents in fresh litter (**Figure 4.7**).

Table 4.7. Spearman correlations between a) C fractions contents in green leaves (n = 15) and b) C fractions contents in fresh litter (n = 33) with C fractions contents in fresh litter (t0), remaining litter (t4) and with their looses during decomposition process of tree species naturally regenerating in active neotropical pasturelands

a)

Litter	**Sol_Green**	**Hem_Green**	**Cell_Green**	**Lig_Green**
Sol_t0	**0,53 (0,0326) 17**	**0,44 (0,076) 17**	-0,4 (0,11) 17	**-0,52 (0,0377) 17**
Hem_t0	**0,51 (0,0359) 17**	**0,56 (0,0183) 17**	-0,1 (0,701) 17	**-0,6 (0,0114) 17**
Cell_t0	**-0,49 (0,0522) 17**	-0,07 (0,7687) 17	**0,75 (0,0025) 17**	0,19 (0,4562) 17
Lig_t0	**-0,62 (0,0128) 17**	**-0,45 (0,0697) 17**	0,2 (0,4329) 17	**0,71 (0,0047) 17**
Sol_t4	**0,6 (0,0248) 15**	0,22 (0,4074) 15	-0,31 (0,2505) 15	**-0,54 (0,0422) 15**
Hem_t4	-0,05 (0,8516) 15	**0,47 (0,08) 15**	-0,1 (0,7083) 15	-0,07 (0,7893) 15
Cell_t4	**-0,63 (0,018) 15**	-0,34 (0,1995) 15	**0,61 (0,0223) 15**	**0,51 (0,0543) 15**
Lig_t4	**-0,5 (0,0595) 15**	-0,43 (0,1118) 15	0,2 (0,4543) 15	**0,67 (0,012) 15**
Sol_t0_g	**0,57 (0,0166) 17**	0,37 (0,1392) 17	**-0,45 (0,0725) 17**	**-0,56 (0,0196) 17**
Hem_t0_g	**0,55 (0,021) 17**	**0,49 (0,0475) 17**	-0,15 (0,5698) 17	**-0,67 (0,003) 17**
Cell_t0_g	**-0,52 (0,0334) 17**	-0,08 (0,7682) 17	**0,7 (0,0017) 17**	0,2 (0,4418) 17
Lig_t0_g	**-0,57 (0,0235) 17**	**-0,49 (0,0522) 17**	0,15 (0,5368) 17	**0,64 (0,0102) 17**
Sol_t4_g	**-0,47 (0,077) 15**	-0,0036 (0,9899) 15	**0,67 (0,0059) 15**	0,36 (0,1815) 15
Hem_t4_g	**-0,61 (0,0167) 15**	0,4 (0,1373) 15	0,39 (0,1532) 15	0,33 (0,2368) 15
Cell_t4_g	**-0,65 (0,015) 15**	-0,3 (0,2617) 15	**0,56 (0,0371) 15**	**0,59 (0,0284) 15**
Lig_t4_g	**-0,65 (0,0156) 15**	-0,27 (0,3098) 15	0,39 (0,1416) 15	**0,63 (0,0187) 15**
Sol_loss_g	**0,63 (0,0194) 15**	0,25 (0,3565) 15	**-0,65 (0,015) 15**	**-0,59 (0,0284) 15**
Hem_loss_g	**0,83 (0,0001) 15**	-0,23 (0,4005) 15	**-0,53 (0,0432) 15**	**-0,61 (0,0154) 15**
Cell_loss_g	-0,35 (0,2012) 15	-0,11 (0,6979) 15	**0,58 (0,0241) 15**	0,05 (0,8589) 15
Lig_loss_g	0,11 (0,6939) 15	-0,34 (0,2203) 15	-0,01 (0,9697) 15	0,13 (0,6336) 15
Sol_loss_%	**0,65 (0,0145) 15**	0,17 (0,53) 15	**-0,73 (0,0064) 15**	**-0,55 (0,0383) 15**
Hem_loss_%	**0,75 (0,0048) 15**	-0,16 (0,5565) 15	**-0,48 (0,0733) 15**	**-0,53 (0,0495) 15**
Cell_loss_%	**0,68 (0,0115) 15**	0,12 (0,6592) 15	**-0,48 (0,0733) 15**	**-0,66 (0,0139) 15**
Lig_loss_%	**0,63 (0,018) 15**	-0,03 (0,9043) 15	-0,29 (0,2732) 15	**-0,5 (0,0614) 15**

b)

Litter	**Sol_t0**	**Hem_t0**	**Cel_t0**	**Lig_t0**
Sol_t4_%	**0,73 (<0,0001) 33**	0,14 (0,4526) 33	**-0,44 (0,0128) 33**	**-0,63 (0,0004) 33**
Hem_t4_%	0,1 (0,5775) 33	**0,48 (0,005) 33**	0,09 (0,6299) 33	**-0,41 (0,0169) 33**
Cell_t4_%	**-0,84 (<0,0001) 33**	**-0,38 (0,0278) 33**	**0,65 (0,0003) 33**	**0,73 (<0,0001) 33**
Lig_t4_%	**-0,56 (0,0016) 33**	**-0,45 (0,0085) 33**	0,24 (0,1789) 33	**0,86 (<0,0001) 33**
Sol_t0_g	**0,98 (<0,0001) 36**	0,12 (0,4958) 36	**-0,56 (0,0004) 36**	**-0,71 (<0,0001) 36**
Hem_t0_g	0,15 (0,3699) 36	**0,99 (<0,0001) 36**	-0,03 (0,8498) 36	**-0,48 (0,0029) 36**
Cell_ t0_g	**-0,55 (0,0005) 36**	-0,05 (0,7593) 36	**0,97 (<0,0001) 36**	0,11 (0,5342) 36
Lig_ t0_g	**-0,69 (<0,0001) 36**	**-0,48 (0,0033) 36**	0,06 (0,7221) 36	**0,99 (<0,0001) 36**
Sol_t4_g	-0,13 (0,4625) 33	**-0,48 (0,0051) 33**	0,01 (0,9514) 33	**0,31 (0,0838) 33**
Hem_t4_g	**-0,32 (0,0703) 33**	0,08 (0,6557) 33	**0,28 (0,1098) 33**	0,1 (0,5939) 33
Cell_t4_g	**-0,69 (<0,0001) 33**	**-0,56 (0,0007) 33**	**0,44 (0,0109) 33**	**0,74 (<0,0001) 33**
Lig_t4_g	**-0,58 (0,0004) 33**	**-0,56 (0,0007) 33**	0,27 (0,1248) 33	**0,85 (<0,0001) 33**
Sol_loss_g	**0,8 (<0,0001) 33**	**0,38 (0,027) 33**	**-0,53 (0,003) 33**	**-0,72 (<0,0001) 33**
Hem_loss_g	0,23 (0,2063) 33	**0,74 (<0,0001) 33**	-0,18 (0,3183) 33	**-0,41 (0,0167) 33**
Cell_loss_g	**-0,41 (0,0171) 33**	0,25 (0,1578) 33	**0,83 (<0,0001) 33**	-0,09 (0,6296) 33
Lig_loss_g	**-0,38 (0,0294) 33**	-0,03 (0,8774) 33	0,01 (0,9727) 33	**0,56 (0,0007) 33**
Sol_loss_%	**0,6 (0,0007) 33**	**0,49 (0,0039) 33**	**-0,36 (0,0402) 33**	**-0,62 (0,0004) 33**
Hem_loss_%	**0,31 (0,081) 33**	**0,48 (0,005) 33**	**-0,3 (0,0932) 33**	**-0,35 (0,0486) 33**
Cell_loss_%	**0,52 (0,0021) 33**	**0,61 (0,0002) 33**	-0,2 (0,2539) 33	**-0,72 (<0,0001) 33**
Lig_loss_%	**0,29 (0,0954) 33**	**0,41 (0,0183) 33**	-0,25 (0,1601) 33	**-0,34 (0,0522) 33**

In general, tree species with higher LCC and LDMC had higher C contents in fresh and decomposed at a lower rate. Meanwhile, those tree species with higher green leaf LPC and LNC contents have higher contents in fresh litter and decomposed quickly (**Table 4.7**). In addition, those tree species with the lower LDMC, C and LIG content together with the highest P, SOL and HEM content in green and fresh litter had the higher decomposition rates. Finally, tree species with the cheapest leaf construction (high SLA) have a high N content in fresh litter and tend to have low LA, meanwhile those with a high FTF have higher amounts of CEL in fresh litter but this no-chemical leaf traits were not correlated with decomposition rates.

Relationship of the overall leaf litter decomposition rates with macronutrients and C fractions releases

Decomposition rates were correlated with some of the macronutrients and C fractions contents in the remaining litter at the end of the four months of litter incubation (**Table 4.4**). Tree species with the higher decomposition rates have the lower amounts of P, C, SOL, CEL and LIG (grams or percentages) in remaining litter. Tree species with higher decomposition rates were also negatively correlated with N and HEM amounts (grams) in remaining litter but were not correlated with the proportion of the initial contents in litter of N and HEM (percentage) founded in the remaining litter (**Table 4.4**).

These results suggest that those species with higher decomposition rates and the higher amounts of P, SOL and HEM were releasing the higher amounts and proportions of these components through faster litter decomposition. In addition, these results imply that no matter the lowest amounts of Total C and LIG contents in fresh litter, those species with the higher decomposition rates were also releasing the higher proportion and amounts o these two components during remaining litter. Meanwhile, tree species the higher releases of CEL and N during decay process and with faster decomposition rates were not depending on the amounts of these components in the tree litter.

The measured decomposition rates parameters were also positively correlated with P, N, C, SOL and HEM contents released during decomposition process (**Table 4.4**). These results confirm that those tree species with the higher decomposition rates, release the higher amounts and proportions of the more the labile fractions (P, N, SOL and HEM) and total C during decomposition process. The proportion (%) of the initial amounts of CEL and LIG in fresh litter released during decomposition process were also positively correlated with decomposition rates, meanwhile the amount of LIG losses (grams) was only positively correlated with the decomposition rates during the last month of litter incubation (b4) (**Table 4.4**).

These results show that higher decomposition rates also reflect the lost of a higher proportion of the recalcitrant litter components (LIG and HEM) content in fresh litter, unless a higher proportion (percentage) released of recalcitrant fractions do not represent precisely a highest total amount (grams) released of these components throughout litter decomposition process. Specifically, some tree species having a higher decomposition rates released lowest amounts (grams) of LIG at the end of litter incubation, meanwhile others tree species also with higher overall decomposition rates, released some of the highest total amounts of LIG. Thus, higher percentages of LIG releases can be observed when higher amounts of total LIG are released from litter or when lower amounts are released, depending on the initial amounts of LIG in the fresh litter. This result showed also that the released amounts (grams) of recalcitrant fractions can be highly variable during all litter decomposition process like in case of CEL, meanwhile this variability was observed only for the initial stages of litter decomposition in case of LIG, which showed also higher amounts (grams) with higher decomposition rates at the final month of litter decay.

Macronutrient content in green leaves were also positively correlated with macronutrient concentration in remaining litter and to the amounts released after decomposition process (**Figure 4.8**). These results imply also that the relative concentrations of C, N and P in green leaves amongst species do not change strongly even during decomposition, as green leaf LDMC, LCC, LPC and LNC are good predictors of C, P and N contents in remaining litter after decomposition process and to the amounts of these nutrients released. In general, tree species with higher LCC and LDMC had higher C contents in fresh and decomposed litter and released C at a lower rate. Meanwhile, those tree species with higher green leaf LPC and LNC contents have higher contents in fresh litter and decomposed litter but also released higher amounts of these nutrients (**Table 4.5**).

More specifically, LDMC and LCC in green leaves were both positively correlated with total C concentrations in fresh and remaining litter and were also both negatively correlated with the percentage loss of C mass during litter decomposition. However, LCC was more strongly correlated with C concentrations in litter and with the rate of release during decomposition than was LDMC. LPC and LNC in green leaves were positively correlated to P and N contents respectively (percentages or grams) in fresh and remaining litter and positively correlated to P and N releases (grams) respectively during decomposition process. LPC in green leaves was also negatively correlated to C contents (%) in remaining litter and positively correlated to C looses (percentages or grams) during decomposition. LPC tend also to be negatively correlated to N content (percentage and grams) in fresh litter and remaining litter (grams).

C fractions measured in green leaves were also correlated with C fraction losses during litter decomposition (**Table 4.7**). SOL and LIG contents in green leaves were respectively positively and negatively correlated with the percentage of initial contents of all C fractions released during decomposition. CEL contents in green leaves was strongly and negatively correlated with the initial percentage of SOL released during decomposition, meanwhile negative correlations between CEL with HEM and CELL losses were weakest. SOL in addition to LIG and CEL were positive and negatively correlated respectively with the amounts of SOL and HEM released during decomposition. In contrast, HEM content in green leaves was not correlated at all with any C fraction losses during litter decomposition.

Leaf traits different to the chemical contents in leaf tissues like SLA, LA and FTF were also correlated with macronutrient content in remaining litter and but only with C releases during decomposition (**Table 4.9**). SLA tends to be positively correlated also with N content in remaining litter and negatively correlated with C losses during decomposition process. LA was also negatively correlated with N, P and C contents remaining litter, but again was not correlated with any macronutrients losses during decomposition process.

Changes in content of carbon fractions between green leaves, fresh litter and litter remaining after decomposition

The correlations between macronutrients and foliar C fractions with their contents in the following leaf decay stages like fresh litter and decomposed litter state the relationships and influence that the amounts and proportion of one leaf component have over the precedent i.e. a higher amount of SOL has been found positively related with higher amounts of SOL in litter and decomposed litter. Therefore, the initial amounts of these components in mature leaves covary with the amounts after senescence in fresh litter, and after decomposition process in the remaining litter. However, how each component interact with the other ones within each leaf stages gives additional information about if these previously observed changes over leaf stages are also more stable than others, helping to explain the variability observed in macronutrients and C fractions though senescence and decomposition.

The strength of some relationships amongst the contents of the three macronutrients differed between green leaves, fresh litter and decomposed litter. At all three stages LCC was negatively correlated with LPC but not correlated with LNC. However, LPC was positively correlated with LNC only in green leaves but not in fresh or decomposed litter (**Table 4.8**, **Figure 4.8**). These results showed that some macronutrients relationships were more stable though senescence and decomposition, like the relationships between total C and P. Meanwhile the observed decreasing concentrations of total P and N varies independently from each other through leaf decay.

Table 4.8. Spearman rank correlations between a) C fraction and b) macronutrients contents (%) among green leaves, fresh litter (t0), litter remaining after decomposition (t4) and C fraction looses (% or g) during decomposition process of tree species naturally regenerating in active neotropical pasturelands

a)

Green leaves	**Sol_green**	**Hem_green**	**Cel_green**	**Lig_green**
Hem_green	-0,09 (0,6987) 19			
Cel_green	**-0,63 (0,0077) 19**	0,21 (0,3638) 19		
Lig_green	**-0,73 (0,0019) 19**	-0,36 (0,1308) 19	0,27 (0,2486) 19	
Fresh litter	**Sol_t0**	**Hem_t0**	**Cel_t0**	**Lig_t0**
Hem_t0	0,14 (0,4275) 36			
Cell_t0	**-0,58 (0,0007) 36**	-0,02 (0,9057) 36		
Lig_t0	**-0,72 (<0,0001) 36**	**-0,48 (0,0028) 36**	0,1 (0,5638) 36	
Remainig litter	**Sol_t4**	**Hem_t4**	**Cel_t4**	**Lig_t4**
Hem_t4	-0,19 (0,2852) 33			
Cell_t4	**-0,66 (0,0002) 33**	**-0,29 (0,0984) 33**		
Lig_t4	**-0,78 (<0,0001) 33**	-0,23 (0,2033) 33	**0,66 (0,0002) 33**	
Losses	**Sol_loss_%**	**Hem_loss_%**	**Cell_loss_%**	**Lig_loss_%**
Hem_loss_%	**0,48 (0,0071) 33**			
Cel_loss_%	**0,85 (<0,0001) 33**	**0,65 (<0,0001) 33**		
Lig_loss_%	**0,58 (0,0011) 33**	**0,76 (<0,0001) 33**	**0,76 (<0,0001) 33**	

b)

Green leaves	**LCC_2**	**LPC_2**
LPC	**-0,38 (0,0022) 62**	
LNC	-0,0048 (0,9703) 62	**0,27 (0,0362) 62**
Fresh litter	**C_t0_%**	**P_t0_%**
P_t0	**-0,29 (0,0545) 44**	
N_t0	0,09 (0,5782) 44	0,11 (0,4835) 44
Remainig litter	**C_t4_%**	**P_t4_%**
P_t4	**-0,45 (0,005) 37**	
N_t4	0,14 (0,3977) 37	0,25 (0,1293) 37

Also the strength of some relationships between C fraction contents varied between leaf material degradation states i.e between green leaf, fresh litter and remaining litter (**Table 4.8**, **Figure 4.9**). In green leaves SOL content was negatively correlated with CEL and LIG within green leaves. In addition, C fractions correlations within fresh litter include also a negative correlation between HEM and LIG content. SOL was negatively correlated with HEM and CEL within remaining litter, meanwhile HEM tends to be negatively correlated with CEL and CEL was negatively correlated with LIG. Therefore, negative correlations between SOL with CEL and LIG were found in all the degradation states (more conservative relationships) and were stronger within remaining litter. In contrast, the negative correlation among HEM and LIG was found just in fresh litter (not in green leaves either remaining litter). In addition, the negative correlation between HEM with CEL together with the positive correlation of CEL with LIG, were observed only in the remaining litter. Finally, all the percentages of initial C fraction lost during decomposition process were negatively correlated with each other.

These results indicate that some correlations between C fractions were stable during leaf senescence and litter decomposition processes, while the rate of mass loss of other C fractions was more variable through both processes. Tree species with higher contents of soluble compounds had lower amounts of celluloses and lignin in green litter, after leaves senescence and after litter decomposition. In contrast, those tree species having reduced amounts of hemicelluloses after senescence process had higher amounts of LIG in fresh litter but lowest contest of CEL after decomposition, no matter HEM contents were not directly related with LIG or CEL contents in green leaves. In addition, those species with higher amounts of LIG after decomposition had higher amounts of celluloses in remaining litter, unless CEL contents were not related with LIG contents in green or fresh litter.

Relationships of plant traits with decomposition rates, tree litter quality and nutrient release

Plant traits were correlated with litter decomposition rates

Whole plant, leaf and dispersal traits of tree species naturally regenerating in active neotropical pasturelands were correlated with leaf litter decomposition rates (**Table 4.9**). The whole plant trait H_max was negatively correlated with partial and monthly decomposition rates but not with overall decomposition rate. Negative correlations were found between H_max and decomposition rates during the latest months of litter incubation (b3, b4). In contrast, WD and PHE were not correlated with any measured decomposition rate. These results mean that taller tree species also have the lowest decomposition rates toward the end of the decomposition process. Taller tree species has been found also correlated with other whole plant traits like PHE, leaf traits and with particular dispersal traits and tree natural regeneration capacity (see Chapters 1 and 2).

Dispersal traits of tree species were also negatively correlated with decomposition rates and positively correlated with remaining litter mass (**Table 4.9**). Vol_see, Mass_see and Vol_fru were similarly correlated negatively with i) overall decomposition rates (strongly to those calculated using the quadratic model) and ii) partial and monthly decay rates during the first two months of litter decomposition (b1, b2). However, they were positively correlated with remaining litter mass at the end of the second and third months of litter incubations (T2, T3). The strongest correlations were observed for Vol_see, Mass_see and Vol_Fru with decomposition rates and remaining litter mass during the first month. Only Mass_see was correlated with decomposition rates during the first month of litter decay.

Whole plant traits were correlated with litter quality

Whole plant traits like H_max, WD and PHE were correlated with the macronutrient and C fraction contents of fresh litter and their release during the litter decomposition process (**Table 4.11**). H_max was positively correlated with total carbon contents in remaining litter and tended to be negatively correlated with the percentages of initial total C and N released during litter decomposition. In addition, H_max was positively correlated with the mass of total P and C within the remaining litter. WD tends to be negatively correlated with the P concentration in the remaining litter. In contrast, PHE was not correlated with any macronutrient content or losses either in fresh or litter remaining after decomposition.

H_max was negatively correlated with HEM and positively correlated with LIG content in fresh litter and in remaining litter and was also positively correlated with CEL contents in remaining litter (**Table 4.11**). WD tends to be positively correlated with HEM content in fresh litter. PHE was also negatively correlated with HEM in remaining litter but not with any other C content in fresh litter. In addition, any of these whole plant traits H_max, WD or PHE were correlated with C fraction losses.

Table 4.9. Spearman rank correlation coefficients of overall (Beta_5), partial (Beta_4) monthly decomposition rates (b1, b2, b3, b4) and percentages of litter mass remaining after decomposition (T1, T2, T3, T4) with vegetative, leaf and dispersal traits of tree species commonly found in active neotropical pasturelands

	BETA_5	**BETA_4**	**b1**	**b2**	**b3**	**b4**	**T1_Rem**	**T2_Rem**	**T3_Rem**	**T4_Rem**
H_max (n=36)	-0,25 (0,1366	**-0,31** **(0,0648)**	-0,1 (0,5744)	-0,22 (0,1948)	**-0,34** **(0,043)**	**-0,48** **(0,003)**	0,24 (0,1667)	0,17 (0,3143)	0,22 (0,192)	0,27 (0,1179)
WD (n=30)	0,07 (0,707)	0,02 (0,898)	0,05 (0,7934)	0,06 (0,7493)	0,05 (0,8047)	0,06 (0,7691)	-0,15 (0,4308)	-0,06 (0,7343)	-0,07 (0,7118)	-0,05 (0,7962)
PHE (n=34)	0,15 (0,4098)	0,09 (0,6095)	0,21 (0,2271)	0,19 (0,2823)	0,05 (0,7763)	-0,05 (0,7673)	-0,07 (0,6759)	-0,2 (0,2519)	-0,18 (0,2995)	-0,11 (0,5387)
SLA (n=32)	-0,16 (0,368)	**-0,29** **(0,0928)**	-0,1 (0,5688)	-0,15 (0,4028)	-0,22 (0,2345)	-0,14 (0,4462)	-0,01 (0,9414)	0,08 (0,6502)	0,16 (0,3692)	0,17 (0,3482)
LA (n=33)	0,09 (0,6333)	0,13 (0,4774)	0,13 (0,4853)	0,1 (0,5944)	0,08 (0,6755)	0,02 (0,9167)	-0,03 (0,8701)	-0,14 (0,4502)	-0,08 (0,6421)	-0,1 (0,5674)
LDMC (n=33)	**-0,4** **(0,0195)**	**-0,37** **(0,0366)**	**-0,39** **(0,0266)**	**-0,4** **(0,0195)**	**-0,4** **(0,0211)**	**-0,32** **(0,0665)**	**0,39** **(0,0266)**	**0,42** **(0,0161)**	**0,4** **(0,0231)**	**0,41** **(0,0212)**
LCC (n=34)	**-0,55** **(0,001)**	**-0,51** **(0,0025)**	**-0,54** **(0,0013)**	**-0,57** **(0,0006)**	**-0,5** **(0,0029)**	**-0,34** **(0,0506)**	**0,45** **(0,0082)**	**0,58** **(0,0003)**	**0,58** **(0,0004)**	**0,55** **(0,001)**
LPC (n=34)	**0,48** **(0,0044)**	**0,51** **(0,0026)**	**0,43** **(0,0119)**	**0,49** **(0,004)**	**0,48** **(0,0049)**	**0,33** **(0,0596)**	**-0,35** **(0,0453)**	**-0,51** **(0,0026)**	**-0,47** **(0,0057)**	**-0,49** **(0,0036)**
LNC (n=34)	0,09 (0,6272)	-0,08 (0,664)	0,21 (0,2401)	0,09 (0,6203)	-0,02 (0,8933)	-0,15 (0,4161)	**-0,35** **(0,0448)**	-0,17 (0,3487)	-0,09 (0,6038)	-0,08 (0,6659)
FTF (n=34)	-0,16 (0,3786)	-0,11 (0,5244)	-0,09 (0,6103)	-0,17 (0,3281)	-0,14 (0,4192)	-0,16 (0,3553)	0,14 (0,4211)	0,2 (0,264)	0,15 (0,4076)	0,17 (0,3322)
Sha_Fru (n=26)	-0,14 (0,5048)	-0,27 (0,1771)	-0,04 (0,8505)	-0,11 (0,5763)	-0,18 (0,3811)	-0,12 (0,5549)	-0,06 (0,7608)	0,11 (0,5804)	0,12 (0,5646)	0,15 (0,4709)
Mas_Fru (n=25)	-0,12 (0,563)	-0,06 (0,778)	-0,14 (0,5106)	-0,1 (0,649)	-0,01 (0,9598)	0,11 (0,6085)	0,09 (0,6576)	0,16 (0,4385)	0,11 (0,5979)	0,1 (0,6397)
Sha_See (n=20)	-0,34 (0,1479)	-0,36 (0,1168)	-0,36 (0,1229)	-0,32 (0,1699)	-0,22 (0,3494)	-0,13 (0,573)	0,23 (0,3223)	**0,37** **(0,1069)**	**0,42** **(0,0676)**	0,27 (0,2355)
Mas_See (n=22)	-0,32 (0,1521)	-0,28 (0,1998)	**-0,41** **(0,0596)**	-0,34 (0,1203)	-0,21 (0,353)	-0,0044 (0,9845)	0,21 (0,3383)	**0,39** **(0,0734)**	0,32 (0,1478)	0,29 (0,1833)
Vol_Fru (n=20)	**-0,39** **(0,0872)**	**-0,41** **(0,076)**	**-0,43** **(0,0574)**	**-0,38** **(0,0961)**	-0,27 (0,2475)	-0,1 (0,6895)	0,23 (0,319)	**0,44** **(0,0533)**	**0,42** **(0,0654)**	0,35 (0,1289)
Vol_See (n=20)	**-0,39** **(0,0927)**	**-0,37** **(0,1099)**	**-0,48** **(0,0343)**	**-0,41** **(0,0758)**	-0,28 (0,2236)	-0,07 (0,7765)	0,25 (0,2784)	**0,44** **(0,05)**	**0,41** **(0,073)**	0,36 (0,1172)

These results showed that taller species have fresh leaf litter with higher percentages of lignin but reduced contents of hemicelluloses. The remaining litter of taller tree species has the same patterns together with higher percentages of total carbon and cellulose, releasing low percentages of the initial total carbon during decomposition. Meanwhile, tree species with dense wood tend to have fresh litter with higher contents of hemicellulose while having lower contents of phosphorus within the remaining litter, but were not correlated with any macronutrient and C fraction losses. In addition, the strongest deciduous tree species also have lower percentage of hemicelluloses in the remaining litter fresh litter but didn’t show a clear pattern in macronutrients and C fractions losses or contents in fresh litter.

Table 4.10. Spearman rank correlation coefficients of a) total nutrient and b) C fraction contents (%) in fresh (t0), remaining litter (t4) and looses (% or g) during litter decomposition process with whole plant traits of tree species commonly found in active neotropical pasturelands

a)

	H_max	**WD**	**PHE**
P_t0	0,13 (0,4081) 43	-0,1 (0,5759) 36	0,15 (0,3584) 38
N_t0	-0,14 (0,3801) 43	0,26 (0,1291) 36	-0,23 (0,1697) 38
C_t0	0,23 (0,1429) 43	-0,01 (0,9548) 36	-0,14 (0,3954) 38
P_t4	-0,02 (0,9184) 36	-0,08 (0,6707) 30	0,22 (0,2135) 34
N_t4	-0,11 (0,5247) 36	0,14 (0,475) 30	-0,11 (0,5499) 34
C_t4	**0,36 (0,0312) 36**	0,14 (0,4598) 30	-0,08 (0,6666) 34
P_t4_g	**0,41 (0,0122) 36**	**-0,34 (0,0688) 30**	0,14 (0,4455) 34
N_t4_g	0,26 (0,1209) 36	-0,04 (0,8408) 30	-0,16 (0,3676) 34
C_t4_g	**0,37 (0,0256) 36**	-0,06 (0,7622) 30	-0,1 (0,5799) 34
P_loss_g	-0,04 (0,8257) 35	-0,15 (0,4325) 29	0,1 (0,5881) 33
N_loss_g	-0,19 (0,2629) 35	-0,0049 (0,9798) 29	-0,07 (0,7161) 33
C_loss_g	-0,22 (0,197) 35	-0,0037 (0,9848) 29	0,07 (0,7035) 33
P_loss_%	-0,18 (0,3016) 35	-0,05 (0,7897) 29	0,01 (0,9492) 33
N_loss_%	**-0,29 (0,093) 35**	-0,01 (0,9686) 29	-0,01 (0,9761) 33
C_loss_%	**-0,3 (0,0781) 35**	0,0017 (0,9929) 29	0,11 (0,526) 33

b)

	H_max	**WD**	**PHE**
Sol_t0	-0,18 (0,3094) 35	-0,13 (0,4945) 29	0,2 (0,2706) 33
Hem_t0	**-0,46 (0,0059) 35**	**0,34 (0,0742) 29**	-0,05 (0,7801) 33
Cell_t0	0,1 (0,5657) 35	0,05 (0,8153) 29	-0,0015 (0,9933) 33
Lig_t0	**0,33 (0,055) 35**	-0,03 (0,8709) 29	-0,22 (0,2113) 33
Sol_t4	-0,11 (0,5313) 32	-0,19 (0,3519) 26	0,14 (0,4693) 30
Hem_t4	**-0,32 (0,0766) 32**	0,24 (0,2399) 26	**-0,35 (0,0583) 30**
Cell_t4	**0,37 (0,0399) 32**	0,04 (0,8305) 26	0,04 (0,8406) 30
Lig_t4	**0,3 (0,093) 32**	0,1 (0,6439) 26	-0,06 (0,7728) 30
Sol_t4_g	0,28 (0,1244) 32	-0,18 (0,3825) 26	0,15 (0,444) 30
Hem_t4_g	-0,06 (0,7495) 32	0,24 (0,2455) 26	**-0,35 (0,0555) 30**
Cell_t4_g	**0,31 (0,0814) 32**	0,02 (0,9193) 26	-0,03 (0,882) 30
Lig_t4_g	**0,35 (0,0514) 32**	0,04 (0,8343) 26	-0,05 (0,7891) 30
Sol_loss_g	-0,18 (0,3154) 32	-0,09 (0,662) 26	0,11 (0,5499) 30
Hem_loss_g	-0,25 (0,1682) 32	0,12 (0,5604) 26	0,08 (0,6897) 30
Cell_loss_g	0,02 (0,9182) 32	-0,16 (0,4494) 26	-0,03 (0,8693) 30
Lig_loss_g	0,04 (0,8462) 32	-0,06 (0,7598) 26	-0,05 (0,7918) 30
Sol_loss_%	-0,26 (0,149) 32	-0,01 (0,9735) 26	0,03 (0,8731) 30
Hem_loss_%	-0,23 (0,2135) 32	-0,01 (0,963) 26	0,2 (0,2927) 30
Cell_loss_%	-0,27 (0,1299) 32	-0,07 (0,7435) 26	0,08 (0,6846) 30
Lig_loss_%	-0,28 (0,1231) 32	-0,05 (0,8008) 26	-0,01 (0,9726) 30

Dispersal traits were correlated with litter quality

Dispersal traits were correlated with macronutrient contents in fresh and remaining litter and were also correlated with macronutrient release during litter decomposition (**Table 4.11**). Sha_Fru was positively correlated with N content in fresh litter and with C and N contents in remaining litter, but was not correlated with rates of loss of any macronutrients during decomposition. Sha_see, Mass_Fru and Vol_Fru were positively correlated with C contents in fresh and remaining litter and only Vol_Fru and Sha_see tended to be negatively correlated with C loss during decomposition. Sha _see was also positively correlated with N content (grams) in remaining litter and tended also to be negatively correlated with N losses. Mass_see and Vol_see were not correlated with any macronutrient contents in fresh or remaining litter but both were negatively correlated with P losses. Vol_see also tended to be positively correlated with C contents (grams) in remaining litter.

These results show that tree species with the biggest and heaviest fruits have higher C content in fresh and remaining litter and higher rates of C loss during litter decomposition. Tree species with longer fruits also have higher amounts of nitrogen in fresh litter (tending to be legumes) and higher nitrogen and carbon contents in remaining litter, meanwhile those tree species with longer seeds also had higher rates of nitrogen and carbon release during litter decomposition. Finally those species with the biggest and heaviest fruits had higher rates of phosphorus release during decomposition.

Dispersal traits were also correlated with C fraction contents in fresh and remaining litter but were not correlated with C fraction release during decomposition (**Table 4.11**). Mas_Fru and Vol_fru were positively correlated with LIG percentages in fresh and remaining litter and were negatively correlated with CEL percentages in remaining litter. Mas_fru tends also to be negatively correlated with SOL percentages in fresh litter. Mass_see and Vol_see were negatively correlated with HEM percentage in fresh litter and Vol_see tended also to be positively correlated with LIG percentages in remaining litter. Sha_fru, in contrast, was not correlated with any C fraction in fresh or remaining litter.

These results show that tree species with bigger and heavier fruits have higher amounts of lignin in fresh and remaining litter, together with higher contents of CEL in remaining litter and lower soluble compounds in fresh litter. Fruit length, in contrast, was not correlated at all with content of litter fractions; however those tree species with the longest seeds had higher LIG contents in the remaining litter. Finally those species with the biggest and heaviest fruits have lower contents of HEM in fresh litter but higher contents of LIG.

Table 4.11. Spearman rank correlation coefficients of a) total nutrient and b) C fraction contents in fresh litter with fruit and seed traits of tree species commonly found in active neotropical pasturelands

a)

	Sha_Fru	Mas_Fru	Sha_See	Mas_See	Vol_Fru	Vol_See
P_t0	-0,24 (0,1828) 32	-0,16 (0,3959) 30	-0,24 (0,2678) 24	-0,07 (0,7177) 26	-0,31 (0,1357) 24	-0,01 (0,9771) 24
N_t0	**0,5 (0,0035) 32**	-0,002 (0,9991) 30	0,21 (0,3152) 24	-0,04 (0,8643) 26	0,12 (0,5916) 24	-0,18 (0,4055) 24
C_t0	0,27 (0,131) 32	**0,5 (0,0073) 30**	**0,52 (0,0129) 24**	0,11 (0,6075) 26	**0,83 (0,0001) 24**	0,11 (0,5877) 24
P_t4	-0,21 (0,3029) 26	-0,17 (0,4205) 25	-0,28 (0,2296) 20	-0,09 (0,6764) 22	-0,24 (0,2994) 20	-0,09 (0,7131) 20
N_t4	**0,61 (0,001) 26**	0,13 (0,5294) 25	0,3 (0,1939) 20	-0,03 (0,879) 22	0,33 (0,1551) 20	-0,11 (0,6335) 20
C_t4	**0,43 (0,0283) 26**	**0,6 (0,0034) 25**	**0,65 (0,0049) 20**	0,24 (0,2625) 22	**0,91 (0,0001) 20**	0,31 (0,1707) 20
P_t0_g	-0,24 (0,1907) 32	-0,21 (0,2694) 30	-0,28 (0,1794) 24	-0,02 (0,9069) 26	-0,28 (0,1886) 24	0,01 (0,955) 24
N_t0_g	**0,49 (0,0049) 32**	-0,03 (0,8904) 30	0,14 (0,4993) 24	-0,0017 (0,9934) 26	0,11 (0,582) 24	-0,15 (0,4681) 24
C_t0_g	0,25 (0,1666) 32	**0,48 (0,01) 30**	**0,36 (0,085) 24**	0,08 (0,6878) 26	**0,79 (0,0001) 24**	0,05 (0,8089) 24
P_t4_g	-0,12 (0,5435) 26	-0,31 (0,126) 25	-0,11 (0,6276) 20	0,15 (0,4962) 22	0,03 (0,9113) 20	0,19 (0,4089) 20
N_t4_g	**0,55 (0,0038) 26**	0,11 (0,603) 25	**0,48 (0,0377) 20**	0,3 (0,1647) 22	**0,64 (0,0051) 20**	0,3 (0,1877) 20
C_t4_g	**0,33 (0,1039) 26**	0,32 (0,117) 25	**0,55 (0,0156) 20**	0,35 (0,1139) 22	**0,68 (0,003) 20**	**0,41 (0,0757) 20**
P_loss_g	-0,24 (0,2294) 26	-0,25 (0,2264) 25	-0,31 (0,1812) 20	**-0,37 (0,0891) 22**	-0,28 (0,2278) 20	**-0,38 (0,0959) 20**
N_loss_g	0,22 (0,2789) 26	-0,12 (0,5642) 25	-0,16 (0,4954) 20	-0,05 (0,8259) 22	0,01 (0,953) 20	-0,1 (0,6605) 20
C_loss_g	0,01 (0,9564) 26	-0,01 (0,9489) 25	-0,18 (0,4354) 20	-0,18 (0,418) 22	-0,05 (0,8339) 20	-0,19 (0,4089) 20
P_loss_%	-0,15 (0,453) 26	-0,16 (0,4354) 25	-0,19 (0,3978) 20	**-0,42 (0,0552) 22**	-0,27 (0,246) 20	**-0,46 (0,047) 20**
N_loss_%	-0,09 (0,6768) 26	-0,27 (0,1822) 25	**-0,37 (0,104) 20**	-0,24 (0,2647) 22	-0,34 (0,1385) 20	-0,32 (0,1667) 20
C_loss_%	-0,16 (0,4289) 26	-0,18 (0,3698) 25	**-0,4 (0,0801) 20**	-0,28 (0,2058) 22	**-0,41 (0,0725) 20**	-0,31 (0,1769) 20

b)

	Sha_Fru	Mas_Fru	Sha_See	Mas_See	Vol_Fru	Vol_See
Sol_t0	-0,1 (0,611) 26	**-0,35 (0,0871) 25**	-0,07 (0,7481) 20	-0,08 (0,7152) 22	-0,32 (0,1588) 20	-0,1 (0,6701) 20
Hem_t0	-0,02 (0,926) 26	-0,03 (0,901) 25	-0,18 (0,4201) 20	**-0,38 (0,0853) 22**	-0,35 (0,13) 20	**-0,48 (0,0354) 20**
Cell_t0	0,11 (0,6016) 26	0,09 (0,6484) 25	-0,03 (0,8957) 20	-0,04 (0,8583) 22	0,01 (0,9739) 20	0,02 (0,9373) 20
Lig_t0	0,18 (0,3848) 26	**0,43 (0,0361) 25**	0,35 (0,1219) 20	0,33 (0,1288) 22	**0,69 (0,0026) 20**	**0,39 (0,0883) 20**
Sol_t4	-0,3 (0,1702) 23	-0,22 (0,3217) 22	-0,23 (0,3517) 17	0,05 (0,8233) 19	-0,34 (0,1699) 17	0,06 (0,8064) 17
Hem_t4	0,16 (0,4669) 23	-0,29 (0,1793) 22	-0,13 (0,6033) 17	-0,23 (0,3259) 19	-0,35 (0,1639) 17	-0,28 (0,2679) 17
Cell_t4	0,23 (0,2979) 23	**0,43 (0,0501) 22**	0,34 (0,1761) 17	0,01 (0,9822) 19	**0,47 (0,0625) 17**	0,08 (0,7612) 17
Lig_t4	0,19 (0,3858) 23	**0,37 (0,0862) 22**	**0,41 (0,1016) 17**	0,17 (0,4749) 19	**0,66 (0,0081) 17**	0,25 (0,3269) 17
Sol_t0_g	-0,07 (0,7462) 26	**-0,34 (0,0931) 25**	-0,12 (0,5909) 20	-0,07 (0,7503) 22	-0,29 (0,2106) 20	-0,08 (0,7283) 20
Hem_t0_g	0,0044 (0,9828) 26	-0,04 (0,8636) 25	-0,21 (0,3849) 20	**-0,4 (0,0663) 22**	-0,35 (0,127) 20	**-0,5 (0,0257) 20**
Cell_t0_g	0,07 (0,745) 26	0,1 (0,6296) 25	-0,07 (0,753) 20	-0,05 (0,8299) 22	0,04 (0,8544) 20	0,02 (0,9425) 20
Lig_t0_g	0,19 (0,3443) 26	**0,44 (0,0282) 25**	0,35 (0,1263) 20	0,34 (0,1216) 22	**0,69 (0,0007) 20**	**0,4 (0,0836) 20**
Sol_t4_g	0,02 (0,9286) 23	-0,1 (0,6577) 22	0,14 (0,5989) 17	0,26 (0,2911) 19	0,07 (0,7789) 17	0,33 (0,1922) 17
Hem_t4_g	0,21 (0,3345) 23	-0,2 (0,3652) 22	0,01 (0,9702) 17	-0,11 (0,665) 19	-0,09 (0,7183) 17	-0,1 (0,7148) 17
Cell_t4_g	0,08 (0,708) 23	0,23 (0,3117) 22	0,33 (0,2028) 17	0,09 (0,7234) 19	0,33 (0,1888) 17	0,14 (0,5858) 17
Lig_t4_g	0,17 (0,4324) 23	0,28 (0,2133) 22	**0,46 (0,0602) 17**	0,11 (0,6522) 19	**0,66 (0,0041) 17**	0,21 (0,422) 17
Sol_loss_g	-0,03 (0,8843) 23	-0,16 (0,4577) 22	-0,14 (0,5696) 17	-0,13 (0,592) 19	-0,15 (0,5498) 17	-0,2 (0,4214) 17
Hem_loss_g	-0,15 (0,4809) 23	0,15 (0,511) 22	-0,4 (0,1143) 17	-0,17 (0,4974) 19	-0,3 (0,2413) 17	-0,28 (0,2749) 17
Cell_loss_g	0,11 (0,6066) 23	0,11 (0,6414) 22	-0,29 (0,2617) 17	-0,05 (0,8331) 19	-0,05 (0,8553) 17	-0,01(0,9963) 17
Lig_loss_g	0,16 (0,4556) 23	0,25 (0,2669) 22	0,1 (0,6906) 17	0,32 (0,1874) 19	0,29 (0,2599) 17	0,37 (0,1448) 17
Sol_loss_%	-0,02 (0,9447) 23	-0,09 (0,6694) 22	-0,17 (0,505) 17	-0,22 (0,3445) 19	-0,15 (0,5564) 17	-0,29 (0,2433) 17
Hem_loss_%	-0,2 (0,3562) 23	0,08 (0,7307) 22	-0,33 (0,1923) 17	-0,13 (0,5869) 19	-0,24 (0,3318) 17	-0,23 (0,3619) 17
Cell_loss_%	-0,06 (0,7709) 23	-0,09 (0,6884) 22	-0,35 (0,1609) 17	-0,17 (0,4612) 19	-0,34 (0,1761) 17	-0,19 (0,4444) 17
Lig_loss_%	0,02 (0,9144) 23	0,12 (0,578) 22	-0,06 (0,8216) 17	0,09 (0,7042) 19	-0,01 (0,9609) 17	0,12 (0,6379) 17

Relationships between abundances of tree natural regeneration and leaf litter quality, decomposition rates and nutrient release.

Tree species regeneration abundance was correlated with decomposition rates in active pasturelands

The population density in three life stages of tree species commonly found in active pasturelands was positively correlated with leaf litter decomposition rates. BETA_4, b3 and b4 were positively correlated with abundance of seedlings, saplings and adult trees (**Table 4.13**). In addition, the percentages of remaining litter at the end of litter incubations were negatively correlated with species population density in all three life stages, strongly for adult abundances and T4.

Tree regeneration abundance was correlated with chemical quality of fresh litter

Tree species population density in three life stages was positively correlated with total P and N contents in fresh leaf litter but was not correlated with total C content (**Table 4.13**). Population densities in all three life stages were positively correlated with P contents in fresh litter and only sapling density was positively correlated with N contents in fresh litter. In contrast population densities were not correlated at all with total C contents in fresh litter.

In addition, population density was negatively or positively correlated with some of the C fraction contents in fresh leaves litter (**Table 4.14**). Population density at all three life stages was negatively correlated with CEL content in fresh litter; however only tree sapling abundance was positively correlated with LIG content in fresh litter and with LDMC in green leaves. Population densities were not correlated with SOL or HEM contents in fresh litter.

Table 4.12. Spearman rank correlation coefficients between population densities at three life stages of tree species in active anthropogenic neotropical pasturelands and leaf litter decomposition rates

Descomposition rates	**Seedlings**	**Saplings**	**Adults**
BETA_4	**0,17 (0,0701) 37**	**0,19 (0,0427) 37**	**0,2 (0,0392) 37**
BETA_5	**0,15 (0,105) 37**	*0,15 (0,1268) 37*	**0,17 (0,0829) 37**
T1_Rem	-0,02 (0,8124) 37	-0,01 (0,9175) 37	-0,03 (0,7164) 37
T2_Rem	-0,11 (0,2544) 37	-0,06 (0,5289) 37	-0,13 (0,1834) 37
T3_Rem	-0,13 (0,1763) 37	-0,13 (0,1717) 37	**-0,15 (0,1091) 37**
T4_Rem	**-0,18 (0,0615) 37**	**-0,17 (0,0679) 37**	**-0,18 (0,0554) 37**
b1	0,08 (0,4073) 37	0,03 (0,7871) 37	0,09 (0,3704) 37
b2	0,14 (0,1346) 37	0,13 (0,1823) 37	**0,16 (0,09) 37**
b3	**0,19 (0,0464) 37**	**0,22 (0,0177) 37**	**0,19 (0,0451) 37**
b4	**0,16 (0,1011) 37**	**0,24 (0,0122) 37**	**0,16 (0,1015) 37**

Table 4.13. Spearman rank correlation coefficients for relationships between fresh litter total macronutrients contents and tree species population densities in three life stages in active pasturelands

	Seedlings	**Saplings**	**Adults**
LDMC	**0,15 (0,07) 47**	**0,23 (0,0063) 47**	0,1 (0,2496) 47
P_t0	**0,28 (0,0012) 44**	**0,22 (0,0099) 44**	**0,29 (0,0007) 44**
N_t0	0,13 (0,1237) 44	**0,24 (0,0051) 44**	0,09 (0,3135) 44
C_t0	0,02 (0,7825) 44	0,11 (0,1906) 44	-0,07 (0,4109) 44
P_t4	**0,3 (0,0016) 37**	**0,27 (0,0049) 37**	**0,25 (0,0087) 37**
N_t4	**0,26 (0,0056) 37**	**0,4 (<0,0001) 37**	**0,25 (0,0087) 37**
C_t4	0,13 (0,1815) 37	**0,17 (0,0789) 37**	0,08 (0,426) 37
P_t0_g	**0,26 (0,003) 44**	**0,19 (0,0269) 44**	**0,28 (0,0012) 44**
N_t0_g	0,12 (0,1666) 44	**0,22 (0,0108) 44**	0,08 (0,3642) 44
C_t0_g	-0,01 (0,9145) 44	0,06 (0,5118) 44	-0,06 (0,4795) 44
P_t4_g	**0,2 (0,0345) 37**	0,14 (0,1312) 37	**0,28 (0,0028) 37**
N_t4_g	-0,06 (0,5241) 37	-0,02 (0,8473) 37	-0,03 (0,7247) 37
C_t4_g	-0,09 (0,3701) 37	-0,07 (0,4507) 37	-0,08 (0,3776) 37
P_loss_g	**0,25 (0,0095) 36**	0,15 (0,1324) 36	**0,27 (0,0052) 36**
N_loss_g	**0,2 (0,0355) 36**	**0,22 (0,0235) 36**	**0,32 (0,0006) 36**
C_loss_g	0,13 (0,1817) 36	0,13 (0,1746) 36	**0,19 (0,053) 36**
P_loss_%	0,11 (0,2636) 36	0,0035 (0,9715) 36	0,11 (0,2454) 36
N_loss_%	**0,17 (0,0877) 36**	0,14 (0,1589) 36	**0,27 (0,0054) 36**
C_loss_%	0,11 (0,2605) 36	0,08 (0,4248) 36	**0,17 (0,0726) 36**

Table 4.14. Spearman rank correlation coefficients of the relationships between fresh litter C fraction contents and tree species population densities in three life stages in active pasturelands

	Seedlings	**Saplings**	**Adults**
LDMC	**0,15 (0,07) 47**	**0,23 (0,0063) 47**	0,1 (0,2496) 47
Sol_t0	0,07 (0,4493) 36	0,04 (0,7046) 36	0,11 (0,2432) 36
Hem_t0	0,01 (0,9296) 36	0,09 (0,3716) 36	0,08 (0,4367) 36
Cel_t0	**-0,27 (0,005) 36**	**-0,3 (0,0015) 36**	**-0,23 (0,0149) 36**
Lig_t0	0,12 (0,2213) 36	**0,16 (0,0891) 36**	0,02 (0,8118) 36
Sol_t4	**0,2 (0,0507) 33**	**0,17 (0,1012) 33**	**0,24 (0,0157) 33**
Hem_t4	-0,06 (0,5583) 33	0,11 (0,2786) 33	-0,02 (0,8184) 33
Cell_t4	-0,14 (0,1556) 33	**-0,21 (0,033) 33**	**-0,2 (0,0528) 33**
Lig_t4	-0,03 (0,7743) 33	-0,03 (0,7579) 33	-0,12 (0,2307) 33
Sol_t0_g	0,01 (0,8873) 36	-0,03 (0,7903) 36	0,08 (0,399) 36
Hem_t0_g	0,0048 (0,9607) 36	0,09 (0,3491) 36	0,09 (0,3728) 36
Cell_t0_g	**-0,33 (0,0005) 36**	**-0,35 (0,0002) 36**	**-0,29 (0,0024) 36**
Lig__t0_g	0,14 (0,1413) 36	**0,19 (0,0541) 36**	0,05 (0,5898) 36
Sol_t4_g	0,03 (0,7681) 33	-0,02 (0,8454) 33	0,01 (0,8989) 33
Hem_t4_g	-0,16 (0,1154) 33	0,0012 (0,9903) 33	**-0,18 (0,0745) 33**
Cell_t4_g	**-0,22 (0,0264) 33**	**-0,25 (0,013) 33**	**-0,32 (0,0011) 33**
Lig_t4_g	-0,12 (0,2304) 33	-0,11 (0,2757) 33	**-0,18 (0,0678) 33**
Sol_loss_g	**0,18 (0,0759) 33**	**0,18 (0,0755) 33**	**0,27 (0,0065) 33**
Hem_loss_g	0,06 (0,5453) 33	0,06 (0,5647) 33	0,12 (0,2326) 33
Cell_loss_g	**-0,18 (0,0795) 33**	**-0,17 (0,093) 33**	-0,03 (0,7369) 33
Lig_loss_g	**0,36 (0,0002) 33**	**0,44 (<0,0001) 33**	**0,34 (0,0006) 33**
Sol_loss_%	0,16 (0,1186) 33	**0,18 (0,0777) 33**	**0,24 (0,0181) 33**
Hem_loss_%	0,08 (0,4471) 33	0,03 (0,7953) 33	0,15 (0,1424) 33
Cell_loss_%	**0,18 (0,0744) 33**	**0,19 (0,0609) 33**	**0,28 (0,0047) 33**
Lig_loss_%	**0,3 (0,0026) 33**	**0,33 (0,001) 33**	**0,33 (0,0009) 33**

These results show that those species with higher population densities of seedlings, saplings and adults had higher contents of phosphorus and lower contents of cellulose in fresh leaf litter. Meanwhile the tree species with the higher densities of tree saplings had fresh litter with higher contents of nitrogen and lignin. In addition those species with higher population densities of both early life stages (seedlings and saplings) had higher green leaf dry matter content. Finally, total contents of carbon, soluble compounds and hemicelluloses in fresh litter were variable amongst species with different population densities.

Tree regeneration abundance was correlated with litter nutrient release during litter decomposition

Tree population density was positively correlated with the amounts of P, N and C in remaining litter and with the rate of release of the same macronutrients during decomposition (**Table 4.13**). Population density in all three life stages was positively correlated with the concentrations of P and N in remaining litter after four months of litter decomposition. Only the density of tree saplings was positively correlated with the percentage of total carbon in remaining litter. Seedling, sapling and adult densities were also positively correlated with the amounts of N and P in grams released during decomposition, meanwhile, just adult density was positively correlated with the total amounts of carbon (grams and percentages) released. In addition, only seedling and adult densities were positively correlated with the percentage of initial N released during the four months of litter decomposition process.

Population densities of trees in active pastures were also positively or negatively correlated with different C fractions in remaining litter and with release of C fractions during decomposition (**Table 4.14**). Densities in all three life stages were positively correlated with SOL contents and negatively correlated with CEL contents in the remaining litter. Stronger correlations were found for densities at seedling and adult stages with SOL, and at sapling and adult stages with CEL. LIG and HEM contents in remaining litter were not correlated at all with population densities. The percentages of initial SOL, CEL and LIG contents released during decomposition were positively correlated with populatino densities at all three stages, being strongest for adult densities. Population densities were not correlated at all with HEM rereleases during leaf litter decomposition.

These results show that those species with higher population densities of seedlings, saplings and adults in active pasturelands had the highest contents of total nitrogen, phosphorus and soluble carbon but also the lower contents of cellulose in their remaining litter. In addition, those tree species with higher sapling densities had higher amounts of total carbon within their remaining litter. Tree species with higher densities at all three life stages had higher percentages of nitrogen, soluble carbon compounds, celluloses and lignin released during litter decomposition. Finally, higher amounts of carbon released from litter were observed for those species with the higher adult densities. However, the proportion of initial P content released from litter during decomposition was not correlated with tree population densities.

These results indicate that those tree species with higher population densities in active pasturelands had a faster rate of release of total N, C and SOL during leaf litter decomposition independently of the contents of these components in their fresh litter. Meanwhile, these species also showed higher rates of release of total P and higher rates of decomposition of LIG together with lower rates of decomposition of CEL matching the concentrations of those fractions in fresh litter. Therefore, P release was high for abundant tree species which have also the high P content in their fresh litter. The case of N was different, because independently of the absence of significant correlations between population abundance and total N content in fresh litter, the most abundant species had the highest rates of released of N during litter decomposition.

4.5 DISCUSSION

Leaf litter decomposition rates and leaf quality of trees commonly found in active pasturelands

Differences in decomposition rates between tree species

As expected, there are significant differences in the remaining litter masses (Rem %) and decomposition rates (Beta) of tree species commonly found in active pasture sites. The community of broadleaved tree species commonly found in tropical active pasturelands decompose in average half of their leaf litter in four months having even a tendency to faster decompositions rates. Litter decomposition rates have an approximated normal distribution with most of the range the species formed a continuum of decomposition rates: some species were clustered around the modal value of ca. 55% like *Platymicium parviflorum, Tabebuia rosea* and *Enterolobium* *cyclocarpum*; meanwhile have some tree species with higher or lower decomposition rates.

This normal distribution has a slight tendency to have more number of tree species with faster rates of litter decomposition (average Rem ≤ 40%) of beyond the main range of species' rates, including species like *Guazuma ulmifolia, Crescentia alata, Maclura tictonia* and *Genipa americana* (ca. 6 species, labelled f, g and h). Variability of slowly decomposition rates was less than variability of faster decomposition rates as only two different groups with statistically significant differences were observed for species with average Rem ≥60%) in contrast to four observed for faster decompositions rates. Slowly decomposition rates were observed for species like *Cordia panamensis, Albizia saman* and *Hymenaea coubaril*. A log-normal distribution has been observed also in decomposition rates for several experiments in North America (Forney and Rothman 2012).

The fact that litter decomposition of tropical tree species found outside the forest distributes normally increase the scope of actual ecosystems models, searching to predict global climate effects on carbon and nutrients cycles. As stated by Forney and Rothman (2012) the ubiquity of log-normally distributed degradation rates suggests that a focus on factors that affect rate heterogeneity, rather than specific rates themselves, will lead to a greater understanding—and improved predictions —of the ways in which the carbon cycle interacts with climate. However, the common use of normally distributed decay rates in ecosystem models to predict carbon turnover and storage still require careful parameterizations of the variability of distribution parameters (u and σ) with climatic, soil and compositional parameters (Brovkin et al 2012).

The inter-specific variability in litter decomposition rates of this tree community is comparable to the variability of decomposition ranges observed inside tropical forest and even between biomes worldwide which include greater number of species and variability of plant growth forms and phylogenies. Decomposition rate of tree species in active pasturelands during the overall 4 months of incubation (Beta 5) varied by a factor of 8.6 from a minimum of 0.78 for *Hymenanea coubaril* to a maximum 0.78 for *Genipa americana* when estimated by specie (n=37), or by a factor of more than 11 when using four regressions (n=148) by specie, ranging from a minimum of 0.08 to a maximum of 0.93 (Table 3.3, Figure 3.2/3.3). Mass remaining percentages (Rem) estimated as the average of the four monthly remaining masses values by specie (Rem 1 to Rem 4) varied by 3.5 orders of magnitude (21%-75%) amongst the species. The percentages of remaining mass after 4 months of litter incubation (Rem 4) varied by a factor of more than 70, ranged from 0.1% to 73% for *G. americana* and *H. coubaril* respectively (Table 3.3, Figure 3.2/3.3). Similar ranges of variability in decomposition rates (10) but lower ranges of variability in mass remaining mass (35) were observed by Santiago et al (2010) in lowland tropical forest on the Caribbean coast of Central Panama (dry season, 3100 mm y^{-1}, 26 °C y^{-1}, 140 masl) during 2 years of litter incubation. Santiago et al (2010) used a wider variety of plant species from contrasting growth forms including together canopy and pioneer trees with lianas, palms and even herbs. Cornwell et al (2008) used a comparison between 818 species from 66 decomposition experiments across the world, founding an average 18.4-fold range in decomposition rates. Again, they used a higher growth and phylogeny diversity for a worldwide comparison mixing diverse growth forms: 580 eudicot species, 118 monocots, 22 species from the Magnoliid lineage, 39 Gymnosperms, 37 Pteridophytes (ferns and fern allies) and 20 Bryophytes (Corwnell et al 2008).

The mean decomposition rates observed in tree community in active pasturelands follows the expected patterns of faster decomposition rates in tropical lands compared to tree litter decomposition in temperate regions. The observed decomposition rates of neotropical tree species are similar to reports for African tree species but faster than temperate trees in Nordic and Austral regions. *Albizia gummifera* and *Cordia africana* decomposed 59% and 43% of its initial litter mass at the end of 16 weeks during the dry season spanning November to March 2000 in a coffee plantation with tree cover in southern Ethiopia with an altitude of ca. 1900 m a.s.l., mean annual rainfall and temperature of 1240 mm and 19.5 °C (Teklay and Malmer 2004). The observed tree decomposition rates were faster that those observed for tree species decomposing in chestnut forests in Cevennes hills on south France with altitudes between 380 – 860 m.a.s.l., mean annual rainfall and temperature between 1212 – 2355 mm and 8.1 – 12.8 °C. *Fagus sylvatica* decomposed 38% of initial litter biomass, *Quercus ilex* and *Q. petraea* decomposed 63-63% and *Castanea sativa* decomposed 65% of leaf litter after 2 years of incubation (Cortez 1997). Lightly narrowed ranges of remaining mass during decomposition have been reported for woody species in northern Argentina. Deciduous and evergreen woody species have lower means and narrowed ranges of Rem values: 20% (0 – 60%) and 40 % (0 – 55%) respectively during 9 weeks of litter incubation (Pérez-Harguindeguy et al. 2000). At the same two months of litter incubations we observed that tree species in tropical conditions: 56 % (13% to 77%)

(Table 3.3). Scots *Pinus* spp. needle litter has lower decomposition rates in *Pinus* spp. forest in Sweden, where 82 to 89% of Rem persist after 7 months of decomposition (Berg and Staff 1980). Decomposition of Mediterranean grasses showed similar ranks of variability in litter decay rates. A total 12 of the most abundant herbaceous species characteristics of three stages of the old-field succession in communities of a Mediterranean successional sere decomposed between 26.5% and 74.2% or litter mass during 8 weeks of incubation (Kazakou et al 2006).

All tree species were fitted significantly to simple exponential decays ($p < 0.0001$; Table 3.3) allowing the direct comparisons between species litter decay curves over the four months of litter incubation using one estimation by specie (BETA5). However, the gradients of decomposition rate did vary considerably between species over time (Fig. 3.3) and there is considerable cross-over between species, evidenced also by the significant interactions species*time in the ANOVA test ($p < 0.0001$). These differences in decomposition rates with incubation time were reflected on the estimated monthly decomposition rates (b1, b2, b3, b4). Average monthly decay rates for the 37 tree species clearly showed that decomposition slowest down by a factor of almost 2 from 0,32 during the first month of litter incubation to 0,17 during the fourth month, decreasing about 1.2 fold per month. Inter-specific differences in decomposition rates depend on time of litter incubation and therefore probably species' early decomposition rate did not predict well subsequent rate. The variability of species' monthly decomposition rates increases with time (Table 3.3.) from a change in a factor of almost 5 during the first month of decomposition (b1) to factors of 7, 14 and almost 100 for the consecutive months (b2, b3, b4 respectively) of litter incubation. The higher Species' differences in the process/trajectory of decomposition, is likely to be linked to differences in their leaf structure/chemistry.

The observed variability on overall litter decomposition values (Rem and Beta5) imply that meanwhile for some tree species only one quarter of the initial biomass have decomposed, others tree species has almost completely decomposed at the end of the same time of incubation under standard environmental (temperature) and substrate conditions (soil moisture and microorganisms) in a tropical environment. The results support the hypothesis that large inter-specific variation exist in leaf decomposability of tree species commonly find active pasturelands when placed under the same environmental conditions. These differences could be related to variations in leaf composition and the higher abundance of faster decomposition rates probably suggest that tree species with a highly quality levels are also more abundant.

Inter-specific variability in leaf and litter quality composition

Macronutrient contents

In general, tree species founded in active pasturelands showed a high variability of macronutrient concentrations in leaves and litter. Five main observations come out from all the observed concentrations of macronutrients in mature leaves, litter and decomposed litter: i) macronutrients contents of these tree species were widely variable at green and litter leaf stages; ii) N and P concentration were more strongly reduced than C from green leaves to litter during senescence; iii) the range of variability of P and N concentrations in leaves of these tree species was lower for litter than for green leaves; iv) the range of variability of P contents was higher than for N contents at both stages and v) C concentrations were higher than N and P but less variable at both leaf stages. This wide variability in the total contents (%) of leaf macronutrients (P, N, C) affect the observed variability in litter decomposition rates.

Macronutrients contents in leaves and litter

Tree species commonly found in active pasturelands showed a high variability of macronutrients concentration in leaves, litter and in the percentage of nutrient looses between mature leaves and fresh litter. Macronutrients concentration of tree species commonly found in active pasturelands were widely variable at green and litter leaf stages. Leaves have in average 0.18 % of P (ranging from 0.04% to 0.33%) and 2.67% of N (1.03 to 3.94), which decreased in 46% to 45% to the average contents observed in fresh litter of 0.10% (0.04% to 0.22%) for P and to 1.47% (0.93% to 2.70%) for N. In contrast to N and P, the highest C contents in green leaves of 46% (41% to 52%) were reduced only 8% to an average 44% (35% to 52%) in fresh litter. These wide ranges of nutrients contents probably influence the also high variability in leaf decomposition rates but also give us a good look to inter-specific variability of nutrient contents in a tropical tree community.

The observed ranges of nutrients concentration in tree leaves and litter traslape with the variability of nutrients concentration reported for other topical species but showed a wider extent. Constantinides and Fowdes (1994) reported that nutrients concentration in tree litter of 12 tree species in Hawaii were varied from 0.86% to

1.62% for N and from 0.02% to 0.12% for P contents. Global studies about the trends in nutrient distributions in different vegetal ecosystems worldwide have found that in general, leaf N and P decline toward the equator as average temperature and growing season length increase for different growth forms including trees (Reich and Oleskin 2004). Leaf N and P increase from the tropics to the cooler and drier mid latitudes because of temperature-related plant physiological stoichiometry (P and N levels increase as a metabolic adaptation to enhance growth rates in cooler environments) and bio-geographical gradients in soil substrate age (tropical soils are considered on average to be older, to be more leached, and to have lower N and P) and then plateau or decrease at high latitudes because of cold temperature effects on biogeochemistry. The leaf nutrient concentrations we observed here for tropical tree species were lower than the contents of N (from 3.4% to 8.5%) of *Pinus* sp. stands in Scotland as reported by Berg and Staff (1980). However, ours results translape partially scot pinus P contents (0.14% to 0.42%). According with the global patterns of nutrients distribution in relation to temperature (Reich and Oleskin 2004), our results probably give additional information to support the idea that tropical tree species have lower nutrients contents than temperate trees, as more similar values of N and P have been observed for other tropical trees than for temperate conifers. However the wide ranges of nutrients variability observed for these tropical species traslape even those values observed for temperate species, especially in case of P concentrations.

The global patterns in nutrients distributions presented by Reich and Oleskin (2004) showed also that N:P ratio increases with mean temperature and toward the equator, because P is a major limiting nutrient in older tropical soils and N is the major limiting nutrient in younger temperate and high-latitude soils. Koerselman and Meuleman (1996) proposed the leaf N:P nutrient limitation breakpoint index which stated that N:P values lower than 14 between imply N-limitation growing and that N:P values higher than 16 indicate P-limitation growing. The average N:P values of this tree community indicate P and N co-limitations and not only P limitations. This community N:P index however do not reflect the condition of the majority of tree species, in contrast is reflecting the occurrence of species within a wide range of variability in possible nutrient growth limitation: from strongly N limited to strongly P limited species. In agreement to the global pattern in leaf nutrients, a higher number of tree species (57%) observed in pasturelands showed N:P ratios in mature leaves greater than 16 (data not shown) indicating a higher frequency tree species with P limited growing as expected in tropics vegetation. A following, number of tree species (33%) however showed N:P ratios lower than 14, indication that also tree species with N limitation growing are frequent in this pasturelands. Only 10% showed a possible growing co-limitation by P and N concentration according to N:P index values between 14 and 16. Once again, the wide variability of N and P concentration and in N:P values in tree leaves quality could be responsible for the variable decomposition rates observed for this species.

Macronutrients variability among mature leaves and litter

In addition the range of concentrations i.e. the ratio between maximum and minimum concentration values, change at different factors between leaves stages (green and litter) and between nutrients (N, P and C). N and P variability was higher in leaves than in litter. P and N concentration varied by factors of 8 and 3.8 respectively in green leaves and just by factor of 5.5 and 2.9 respectively in fresh litter. In contrast, ranges of C contents observed at both leaf stages were narrowed and varied by similar factors in green (1.3) and fresh litter (1.5). The fact that the range of variability is higher for Phosphorus than for nitrogen in both leaves stages probably reflect the higher limitation of phosphorus for these tree species in tropical lands.

Macronutrient losses in senescence

As expected and stated previously, macronutrients contents in litter were lower than those observed for green leaves. We observed that 45% -46% of total phosphorus and nitrogen contents in green leaves together with 7% of total carbon are removed from tree leaves previous to litter production. This reduction in contents of nutrients in litter respect to green leaf responds more probably to nutrient re-allocation during the process of senescence. Nutrient leaching from leaves during senescence could be also responsible for the decreasing values of nutrients from leaves (Aerts and Chapin 2000). However, the proportion of nutrients loosed from mature leaves and fresh litter seem to be reduced in comparison with senescence (Freschet et al 2010). In addition, fresh litter collected for this study was done using weakly harvest (by litter traps and manual selection) during dry season were daily rain was almost scarce (data not shown) to reduce leaching looses after senescence. Therefore we a-priory estimate that the reductions on leaf macronutrients observed in these tree species from mature leaves to litter respond mainly to nutrient recycling during senescence.

The strongest and similar reductions observed for nitrogen and phosphorus concentrations during tree leave senescence reflect the limitation of both nutrients in tropical soils. During leaves senescence, soluble nutrients from old leaves are moved via phloem to new growing tissues (i.e new leaves, flowers or apical stems) or to developed seeds (Himelblau and Amasino 2001). Metabolically, during senescense carbon assimilation (photosynthesis) is replaced by catabolism of chlorophyll and macromolecules such as proteins, membrane lipids, and RNA from which some of the released nutrients can be recycled (Gan and Amasino 1997). This nutrient salvage from older or damaged leaves has the adaptive value of recycling nutrients that may be limiting in the environment or that are energetically costly to acquire (Himelblau and Amasino 2001). At any given time, 95-99% of the potentially available nitrogen in soils is in organic forms, either in plant and animal residues, in the relatively stable soil organic matter or in living soil organisms, mainly microbes such as bacteria and is not directly available for plants. Similarly, P concentration inside plants is well below the potencial (Km) for plant uptake and although bound P is quite abundant in many soils, it is largely unavailable for uptake because it rapidly forms insoluble complexes with cations, particularly aluminum and iron under acid conditions (Vance et al 2002). In fact, N and P are well known to regulate the carbon gain plant efficiency and therefore the efficiency in their reabsortion capacities is especially relevant for tree species fitness and is a key aspect of plant life strategies (Aerts and Chapin 2000).

The lowest percentages of decrease in C levels during senescence could respond to mainly to C mobilization and respiration. The accelerated metabolism of membrane lipids during senescence results in a decline in the structural and functional integrity of cellular membranes (Thompson et al. 1998). Thylakoid membranes provide an abundant source of carbon that can be mobilized for use as an energy source during senescence (Ryu and Wang 1995). Carbon drop could result from C mobilization. However, respiration, to provide energy for senescence, is likely to result in significant CO2 loss (Himelblau and Amasino 2001). As little CO2 assimilation occurs during senescence, respiration can result in a net loss of C (Noodén and Guiamet 1989). It is unclear whether mobilization or respiration or both are responsible for the observed decrease in C levels (Himelblau and Amasino 2001). We agree Vergutz et al (2012) when states that the main cause of mass loss is likely the resorption of C and nutrients, while leaching and even in situ decomposition probably play a secondary role. Taking into account the higher C concentrations in leaf and litter in relation to the other nutrients, this even small C resorption efficiencies can have cause substantial effects on plant fitness beyond the inherent decreases in the total mass of the leaf. However such relationships have been less addressed in related literature.

The observed mean percentages of resorption observed for neotropical trees (45% and 46%) are lower than estimation done by initial models which assume a value of 50% resorption for nitrogen and phosphorus (Aerts and Chapin 2000). However, the variability on the reported reabsortion capacities in literature has been high and this initial model clearly lack resorption data for specific vegetation types, environmental variability worldwide and growth groups like neo-tropical trees. Lim and Cousens (1986) found that in old Scots pine *Pinus sylverstris* stands nutrients resorption efficiency (%) from senescing foliage increases with latitude of pine populations. Nutrients reapsortion supplies about 55% on N and 64% of P in Scotland. Again the observed means of nutrient reapsortion (%) for these neotropical trees are lower than those reported for temperate tree species. Unfortunately the resorption capacity has been less reported for tropical species than for temperate vegetation and only recently efforts to understand the global patterns in nutrients resorption have been reported

Ours results shows that mean nutrient resorption (NuR) for tropical tree species can be even lower than those values proposed by the recent global NuR pattern. The recent observed global patterns in NuR includes values for six plant types: ferns, forbs, graminoids, conifers, and evergreen and deciduous woody angiosperms and states that mean NuR differed substantially among nutrients, growth forms and climate (Vergutz et al 2012). Also states that N and P resorption differed significantly from the commonly used global value of 50%, but in contrast to our observations, mover this mean to higher values of 62.1% and 64.9% respectively. C, N and P resorption values (CR, NR and PR) has been estimated in 18.4%, 50.2% and 61.2% respectively for tropical lands; 23.9%, 61.2% and 58.5% respectively for evergreen woody angiosperms and in 20.8%, 56.1% and 58.4% respectively for deciduous woody angiosperm. Our mean NuR for tropical trees including both evergreen and deciduous species are lowest, especially for CR (18% vs 8%) and PR (46% vs 56.5%) meanwhile NR means were quiet similar (45% vs 46.5%). This observation are in agreement with the general pattern stated in the global NuR distribution when states that C, N and P resorption efficiencies are positively correlated with latitude because of significant negative relationships with mean annual temperature and/or precipitation. Therefore, among the studied climatic groups, dry climates tended to have the highest NuR for most nutrients, while tropical climates had the lowest. However our results states that the lower limits of the global ranges can be ever lower for tropical trees.

The lowest nutrient resorption capacities we observed for tropical tree species probably reflects a wider variability in nutrient contents in leaves and litter. Our mean N and P contents in green and litter were higher than those reported by Vergutz et al (2012) but only by a factor of 1.4 and 1.3 respectively meanwhile the mean C contents at both leaf stages were similar. The highest differences were observed in the extend of the 95% confidence intervals (data not shown) which were around 3 times wider for N and two times wider for P in both green and litter for the tree species we observed. NuR was correlated with greater plant nutrient status and therefore greater resorption efficiency can be expected in fresh leaves with lower nutrient concentrations (Vergutz et al 2012). Therefore as we found tree species with higher but also with very low N and P contents, can be expected that tree species with the lowest values are responsible for the lowest mean PR and NR.

Macronutrient losses variability during senescence

In addition to a wide variability in nutrients contents in mature leaves and litter, also nutrient looses nutrients looses (%) from mature leaves to leaf litter were highly between species and also varied between nutrients. The proportion of leaf N, P and C reallocated during senescence was highly variable between tree species and also between nutrients. Phosphorus losses from leaves to litter (46%) vary by a factor of 8 (ranging from 8% to 68%) meanwhile nitrogen losses (45%) varied by factor of 3 (19% to 68%). In addition, the variability of C looses from green leaves to litter (7%) were surprisingly height and varied similarly than P looses by a factor of 8 (from 2.4% to 20%).

The inter-specific variability of foliar P and C reabsorbed during senescence was higher than those observed for N. High inter-specific variability in nutrients contents and resorption percentages could also be reflecting diverse plant nutrients dynamics associated with diverse plant strategies. However if we compare our mean values of nutrients contents in green, litter and its nutrient reabsortion (NuR) with those observed by Vergutz et al (2012) no so clear relationships seems appear between the nutrient contents in leaves with NuR. Unless both data sets have similar mean C contents in leaves, we observed more than two times lower CR. In contrast, as stated previously we observed highest means of P and N contents in leaves, but meanwhile NR was quiet similar for both studies, PR was quit lower than the observed global pattern. The higher abundance of more acquisitive tree species i.e. more tree deciduous species within this tree community in a dry to sub-humid transition environment in tropical lands could be also pushing down the mean NuR values especially for C and P. However, it is clear that not universal patterns can be drowed for all macronutrients and particular relationships between NuR and leaf chemical composition contents could arise with an increased variability in nutrients contents.

Macronutrients looses during decomposition

Tree species in active pasturelands releases a high variability of total leaf phosphorus, nitrogen and carbon contents. The mean percentages of total P (46%) and N (41%) were similar and lower than the mean percentages of total C released (61%). The range of total P released (2-94%) were slightly higher than the range of total N (8-93%) loosed and both were higher than the range of C contents (32-96%). These results highlighted our initial hypothesis about that tree species in active pasturelands have a wide variability in nutrient releases to the pasture system.

Macronutrient losses variability during senescence and decomposition

The loss of P and N are very similar both during senescence and decomposition, which is perhaps surprising. During senescence the % loss of C is much less; presumably it is mainly proteins that (as well as soluble carbohydrates) that are broken down and withdrawn, leaving most of the C in the remaining structural carbohydrates.

C fraction contents

Tree species commonly found in agricultural lands like active pastureland showed a wide inter specific variability in the range of each C fraction contents and between leaf stages. The mean contents of each C fraction measured in proportion by gram (percentage) or it relative mass within the sample (grams) changed differently in function of time from mature green leaves thought fresh and decomposed litter (**Figure 4.8**). The variability of C fractions contents was high and change also between leaf stages and between species (Table 3.4).

C fractions contents in mature leaves and litter

Foliar C fraction contents of tree species commonly found in active pasturelands differ from general models of carbon fractioning proposed by Berg and McClaughert. (2008) based on boreal tree species. The water-soluble fraction (SOL), a chemically complex group resulting from heterogeneous substrates has been accounting for around 50% of boreal tree leaves and litter. Cellulose (CEL) and Hemicelluloses (HEM), considered the most common polymer carbohydrates compounds in litter, has been estimated between 10 to 50% and between 1 to 10% respectively for boreal litter types. Finally, Lignin (LIG) content may reach even above 50% for boreal species (Berg McClaughert 2008). In agreement with this model, we observed that the mean contents of soluble compounds is the highest fraction (47 and 45%) meanwhile hemicelluloses mean contents are the lowest proportions (8 and 9%) of total carbon content in pre-decomposition leaf stages (mature leaves and fresh litter). In contrast, we observed a lower mean of celluloses and lignin contents than expected, corresponding respectively to the second (22 to 23%) and third (20 and 21%) more abundant components in both pre-decomposition leaf stages.

Substantial variation in the content of foliage and litter C fraction seem to be observed also between these 35 trees species commonly found in active pasturelands on a semi-humid dry forest area, compared with C fraction contents in tree species in a tropical rainforest community. Observed differences are not related only with mean contents but also with C fractions variability according with the range of C fraction contents observed for both tree communities. Hättenschwiler et al (2008) found a community if tropical forest tree species that SOL were also around 32% of total carbon; HEM and CEL means were 15% and 20% and LIG was around 32% for tropical species (Hättenschwiler et al 2008). Our observed means and ranges for HEM (8% from 2 to 18%) and LIG (21% from 6 to 39%) foliar contents were half lower than HEM (15% from 4 to 48%) and LIG (34% from 13 to 61%) contents in the tropical forest. In contrast, our mean estimation of SOL (46% from 29 to 67%) is higher than those observed for humid forest species unless the range of possible values was quite similar (32% from 8 to 48%). Only the mean content of CEL foliage and litter of the pastureland tree community (22% from 11 to 32%) is quite similar than CEL estimations for the humid tropical trees species (20% from 10 to 27%).

C fractions relationships with PHE

The lower variability and mean contents of HEM and LIG in the more semi-deciduous community in active pasturelands in comparison with the forest humid community probably reflect communities' differences in the predominant leaf strategies of tree species growing under different environmental resources and limitations. The studied tree community in active pasturelands has a higher proportion of deciduous species (75% of tree species reduced in 50% their canopy for at least one month) meanwhile the majority of humid forest community belong to the rather well-defined functional group of evergreen trees with long-lived, leathery leaves (Hättenschwiler et al 2008). Variability in lignin and hemicelluloses content has been mostly correlated with leaf phenology, physical and chemical leaf composition affecting plant growth rates, litter decomposition and palatability. In comparison with deciduous species, evergreens generally had innately slow growth, which corresponded to their longer-lived leaves of lower specific leaf area, higher tensile strength and lower palatability to generalist invertebrate herbivores therefore producing more resistant leaf litter (Cornelissen et al 2003).

In fact, different proportions of C fractions like lignin, for example, appears to provide structural strength allowing plants to resist wilting as defense mechanisms against harsh environments, and herbivore damage reducing palatability (Cooper and Smith 1985). Hemicelluloses composition and contents has been found to vary greatly between species and growth forms i.e. deciduous leaves are lower in mannans and the ratios of hemicelluloses to cellulose often seen higher in deciduous litter than in coniferous litter. In addition, the lignin content of deciduous species has been observed generally lower than that of the coniferous ones, although the variation is large in both groups (Berg and McClaughert 2008). Therefore lower mean levels of more recalcitrant fiber components like LIG and HEM can be expected for those semi deciduous communities with a lower proportion of evergreen tree species.

The higher SOL contents in the dry-sub humid pasturelands tree community probably reflect only the indirect effects of increases in correlated components like HEM and LIG (i.e. a decrease in one fraction will result necessarily in an increase by similar proportions of another fraction). However, the lower investments in more insoluble leave components like HEM and LIG and the high availability or more mobile components i.e. simple sugars, lower fatty acids and protein remains such as amino acids and peptides, could be also relevant for nutrient and water conservation strategies in more water limited environments like those of dry semi-seasonal tree communities were deciduous tree species domain. A higher proportion of soluble contents in deciduous tree species probably imply a higher capacity of nutrients mobility to reuse nutrients and water more efficiently previous leaves senescence and litter disposal. In fact, we observed that PHE was positively correlated with SOL contents in green mature leaves and fresh litter but only at significant levels when the extreme deciduous tree species (those with 5 or 6 months of reduce tree canopy) were not included (data not shown). In addition, we observed that the positive correlation between percentages of SOL resorption during senescence (the concentrations changes during the foliar transition from green mature leaf to fresh litter) and PHE were significant only when evergreen and faster deciduous tree species were not included (data not shown). Unless evergreen tree species have low proportions of SOL fractions in leaves and litter, the proportions of SOL resorption were more variable than those observed for deciduous species hiding the significant relationships with PHE. In contrast, SOL content in green and litter and their recycled proportions tend to increase when leaf longevity decreases. Therefore, deciduous tree species did have more SOL contents than evergreen species and such differences could be then reflected on mean SOL contents among tropical dry to humid tree communities and forest humid tree communities.

Only CEL contents were similar between both tropical tree communities reflecting probably the variability in fiber structure development and the functional role of each C fraction. Old accepted models of cell fibbers structure have shown a matrix of lignin and hemicelluloses encrusted in the cellulose fibrils (Kerr and Goring 1975). More recently, has been postulated that the formation of lignin in the fibers (lignification) of the live plant is a slower process than that of cellulose forming, resulting in fibers with different levels of lignifications that probably different among tree species (Berg and McClaughert 2008). In addition, the distribution of hemicellulose parallels that of lignin within the wall surroundings the cellulose microfibrils, and occupies the spaces between the fibrils (Berg and McClaughert 2008). This fiber structure and the slowest process of lignification and hemicelluloses insertion suggest a higher probability of hemicelluloses and lignin variability as components surrounding the primordial cellulose fibers which provides the main strengthen of the cell wall. Probably are this variability in lignifications process and hemicellullose integration to the more stable cellulose fibers the most related with species leaf strategies like evergreens resulting in slow growing rates (that allow more lignified mature leaves) and highest investments of C resources for herbivore defense (via lower digestibility with a higher lignifications levels).

PHE has been found correlated with chemical and physical foliar characteristics in mature leaves and litter. PHE was negatively correlated ($p \leq 0.05$) with FTF and LIG contents (data not shown), positively correlated with LPC and also with a positive tendency with SOL in tree mature leaves, indicating that more deciduous tree species are softer have lower lignin but more P and soluble c contents than evergreen species. Unless we dint find any direct correlation between PHE and C fraction contents in fresh leaf litter when the entire leaf phenological spectrum i.e from evergreen to extremely deciduous species was explored. However, correlations between PHE and C fractions are observed for different sections in the phonological spectrum or phenological types i.e. exclusive evergreens (tree species without canopy cover reductions through the year), evergreens to medium deciduous species (tree species with no one to four months with canopy cover reductions) and medium to extreme deciduous species (species with more than 5 months of canopy reductions). Tree phenological status (PHE) from evergreens to medium deciduous species, has a positive correlation with SOL together with a negative correlation with LIG and a negative tendency with CEL contents in fresh litter (data not shown).

In general there was an increase in soluble compounds together with a reduction in recalcitrant C fractions like CEL and LIG from evergreen to deciduous species. However CEL contents showed two different directions in relations to the phonological status: was negative correlated with PHE from evergreen tree species to middle deciduous (those with 4 months of tree cover reductions) but was positively correlated with medium to extreme deciduous species (those tree species having 3 to 6 months with a reduced tree canopy were). These results imply that in fact more recalcitrant C fractions like CEL and LIG decreases from evergreen through faster and medium deciduous species, until a break point when deciduousness can be combined with high leaf CEL contents. Those species with five or six months with a reduced tree canopy during probably have alternative leaf or whole plant strategies to deal with dry environments like wood water storing. However the inclusion of the entire phonological spectrum with all the possible CEL values to obtain a mean CEL was possible the reason for the similar CEL means among the studied tree community in the dry to sub-humid tropical site when compared with the humid forest tree community.

C fractions were also correlated with total nutrients contents and biomass in fresh litter contents and with leaves physical structure. LIG content was correlated positively with LCC, negatively with LPC and tends to be positively correlated with LDMC. In addition CEL tends to be positively correlated with FTF. Therefore those tree species with higher biomass and total carbon did have more investments on carbon recalcitrant fractions like LIG and CEL developing tougher leaves, but lower P contents. Hemicellullose contents followed however different patterns. HEM content was negatively correlated with LCC in addition correlated with Hmax and tends to be positively correlated with WD and no clear patterns were observed for HEM contents in relation to any phonological group. Hemicelluloses independence from the relationships between other recalcitrant and labile C fractions in relation to leaf characteristics and phenology, probably due to a high variability between species and along the phenological continuum.

Unfortunately to date a global assessment about how foliage C fractions vary with environmental gradients and geographical locations have been not addressed. This is one of the few studies generating values of C fractions for a major number of tree species in tropical and also anthropogenic lands. All this differences probably are reflecting not only climatic and environmental effects over foliar tree quality as plant strategy but also possible anthropogenic management effects. However, there is not a generalized knowledge about how C fractions could change due to anthropogenic management to be able also to differentiated between environmental and the possible anthropogenic induced variation in standing tree foliage quality and ever less it possible implications for carbon and nutrients cycling. We are trying to address how the C fractions contents in tree community are affecting not only litter decomposition rates but also C fraction and nutrient releases.

Leaf lignifications must be higher for evergreen communities due to increased specific values or due to population structure i.e. an increased proportion of evergreen versus deciduous species, which reflect higher mean values at community level in humid forest tree communities that in dry-semi humid transitional forest communities.

Aerts and Chapin 2000) found that litter decomposition rates of evergreen shrubs and trees are significantly lower than those of deciduous shrubs and trees. No difference in leaf litter decomposability between evergreen and deciduous species have been observed for Mediterranean species possible because slow-growing deciduous species also contains high concentrations of hemi-) cellulose, insoluble sugars and lignin (Niemann et al., 1992;

Low litter decomposability and the resulting low rate of nutrient release from that litter, as observed in evergreen species, leads to longer dominance of the evergreen species. This implies that the plant characteristics of evergreens do not only lead to high NUE, but also keep soil fertility low and thereby influence the competitive balance with deciduous species in their favor.

C fractions changes in senescence

The mean content of all C fraction components in tree leaves are similar to those observed in leaf litter (Table). SOL is the higher C fraction, followed by similar proportions of CEL and LIG and finally having HEM the lowest proportions in mature leaves and litter. These results underline that quantitatively dominant groups of polymer carbohydrates and lignin are ubiquitous within a big group of tropical trees and those similar mean proportions of C fractions can be found in green leaves and fresh litter of tree species. The fact that C fractions contents in mature tree leaves are similar to those in their litter confirm the possible afterlife effect that different plant strategies like those reflected in the leaf economic spectrum i.e. conservative vs acquisitive tree species could have over ecosystem processes like litter decomposition, nutrient cycling and soil formation.

C fractions differ in their amounts of carbon recycled during leaf senescence. The similar proportions of mean C fractions founded among green and fresh litter suggest that senescence the proportions reused must be probably similar between C fraction and therefore C fraction proportion didn't change among leaf stages. In contrast, according to the different C fractions nature can be expected that SOL fractions have a higher resorption capacity than recalcitrant fractions. However, the mean percentages of SOL contents loosed during senescence (8%) were not significatively higher than the percentages of LIG loses (9%), CEL (2%) and HEM (20%). In contrast with the expected differences in the recycle capacity of C fraction according with their nature, a considered recalcitrant C fraction like HEM has higher mean proportion of looses from green to fresh litter meanwhile CEL was the more stable C fraction during senescence. In addition, the mean proportions of the water soluble fractions SOL were almost identical to the mean recycled proportions of most recalcitrant fraction LIG. More according with c fraction nature, the mean amounts (grams) of SOL fraction reused during senescence (0.52 g) were followed by HEM (0.20 g), LIG (0.16g) and CEL (0.07g). However, not significant differences were observed probably due to the wider variability in SOL releases. The fact that CEL contents were the less recycled fraction and HEM the more recycled, probably reflects it contrasting structure in cell walls: CEL is a more recalcitrant component according with their fundamental role in the main fiber structure, in contrast with a more labile HEM which surround it.

The recycled amounts of C resources are highly variable between C fractions. The lack of evidence for differences between the mean contents of LIG and SOL loosed during senescence as expected, probably reflect mainly the higher inter-specific variability of this components in green and fresh litter. LIG content has the highest variability coefficients (CV) in mature leaves and litter, when mean contents changed by factors of 5 and 6.5 respectively. Unless SOL varying only by factors around 2 in all leaf stages and showed lowest CV in opposition to LIG mean contents, SOL range values in green leaves and litter were as wider as the range observed for LIG and was even wider for SOL looses than for LIG losses during senescence. Therefore, SOL and LIG were the C fractions with highly variable contents in pre-decomposed leaves and with also variable amounts of losses through senescence avoiding finding differences within it recycle proportions according with their contrasting nature.

In addition, C fraction variability also changed through leaf stages and it looses during senescence do not reflect always the variability in pre-decomposed leaf tissues. The high variability of LIG and SOL contents contrasted with the lower variability of HEM and CEL contents in green leaves and litter. However, the lower variability of these C fractions in mature leaves and litter was only partially reflected on the variability of HEM and CEL looses in senescence, implying that besides inter-specific variability in leaves contents, some components are more stable than others. The range of HEM content in mature leaves and litter was narrowed than the observed range from CEL content unless CV was higher for CEL than for HEM. Therefore, more variable CEL looses during senescence could be expected from a higher variability of CEL contents in leave tissues, but in contrast, CEL loses through senescence were less variable than HEM losses. The narrowed range of CEL looses expressed in percentages probably determine the significant differences among these C fractions losses during senescence; no matter than CEL loses has a higher CV. Therefore, trees recycled considerable less proportions of the initial CEL content in green leaves than from the other C fractions, no matter it higher variability in leaf tissues. Equally, HEM loses during senescence were highly variability unless it contents in pre-decomposed leaf tissues were the less variable C fraction. Tree species recycle around 20% of Hemicelluloses but only 2% of it CEL content, but meanwhile one tree species can recycle up to 71% of HEM content in green leaves only 31% was observed for CEL. The variability of the proportions of HEM recycled was even higher than the variability observed for SOL and LIG, C components with a wide variability in pre-decomposed leaf tissues.

C fractions changes during decomposition

The mean content of C fractions in decomposed litter was different to the C fraction contents in green leaves and fresh litter. The absolute amounts of all C fractions in decomposed litter were lower than C fractions contents in fresh litter (Figure). Absolute amounts (grams) of SOL, HEM and LIG in decomposed litter were reduce nearly to half, meanwhile CEL were reduced more than four times it initial total amounts in fresh litter. However the proportions of C fractions do not always decreased. After four months of litter incubation CEL contents decreased significatively from 22-23% in leaves and litter to 12% in remaining litter. In contrast, SOL contents increased from 47-45% in pre-decomposed tissues to 51% in decomposed litter. In addition, either HEM or LIG contents showed any significant change during the same litter incubation time. In consequence, unless all C fractions contest were reduces, the proportion of C fractions in remaining litter changed differently in comparison with pre-decomposed leaf stages. SOL mean contents continue being the more abundant C fraction (around 50%) and now in addition to HEM, CEL has also the lower C fractions in remaining litter. LIG contents in contras continue having middle proportion within the C fraction partitioning in remaining litter as have been in pre-decomposed leaf stages.

These results imply that Cellulose contents of tree litter have been the C fraction most decomposed, during four months of litter decomposition in tropical environment, drooping initial concentrations to half, no matter it recalcitrant nature. Instead, the proportions of C soluble components in tree leaves do not decrease from fresh litter to remaining litter after the four initial months of litter decomposition in tropical environment. In fact, the concentration of soluble carbon increase probably related with cellulose break down which could release soluble C components to refill continually C soluble pools prior leached to soil environment. In contrast, HEM or LIG contents were the most recalcitrant C components in litter tending in fact to increase they mean concentrations in decomposed litter. However, either Hemicelluloses or Lignin concentrations in remaining litter after 4 months in tropical lands showed difference with pre-decomposed stages.

In addition, variability of C fraction contents in remaining litter differs from pre-decomposed stages and between C components. In general, variance of absolute contents (grams) of all C fraction decreases from fresh to decomposed litter. CEL content showed the highest reduction in variance from in pre-decomposed to remaining litter (by a factor of 0.3) followed by HEM (by a factor of 0.4), and both showed the lowest variability in foliar an litter tissues. In contrast, SOL and LIG contents (grams) showed the highest variability in fresh and remaining litter but the lowest reductions of variance (both by a factor of 0.6) from fresh litter.

These results suggest that different C fraction not only have differences in their contents among leaf stages but also in how variable are their responses to decomposition. Obviously variability of C contents tends to be reduced after decomposition together with biomass reductions, but this reduction varied according with C fraction nature. SOL and LIG have the more variable contents (grams) in pre-decomposed and continue being highly variable in decomposed leaf tissues. CEL and HEM were the less variable components in mature leaves and litters but CEL contents have strongest reduction in variably from fresh to decomposed litter.

The variability of the percentages of the initial C fraction loosed during leaf decay was also different from between leaf stages and C fractions. The variance of C fraction proportion (percentages) increased from fresh to decomposed litter for SOL, HEM and LIG but not for CEL. The higher increases in variance in decomposed litter were observed for HEM and SOL (by factor of 1.5) followed by LIG (by factor of 1.2). Only the variance of CEL concentrations in decomposed litter decrease to half (by a factor of 0.5) showing the highest changes in concentration variability in comparison to fresh litter.

These results suggest that the only fraction showing meanwhile variability in absolute contents decreases with decomposition, the variability of C fractions concentrations in decomposed litter increase, except for CEL. Inter-specific differences in the decomposed fraction tend to reduced, meanwhile in t he other C fraction is tending to increase. Therefore inter-specific variability in leaf quality tends to have also more diverse possible effects after decomposition.

Variability of the amounts of carbon releases during decomposition also changed with C fractions and units expressed. Variability was different when changes in C fraction contents were expressed in absolute amounts of C fraction released (grams) than for the proportion of that those loosed amounts represent from the original stocks in fresh litter of leaves (percentages). Variability of the amounts (grams) of C fraction looses during decomposition (t0 – t4) followed the same patterns that variance of C fraction stocks (grams) in foliar and litter tissues: higher variances for SOL followed by

LIG and lower variances for CEL and HEM. In contrast, the proportion of HEM loosed from fresh litter (percentage) were the most variable C fraction, followed by LIG and SOL, meanwhile the proportion of CEL looses during decomposition were the less variable C fraction. These results means that unless the higher contents (grams or percentages) and variability of SOL in fresh and remaining litter and unless showed the highest and most variable looses (grams) during decomposition, was not necessarily the C fraction with ether highest proportions loosed or either the more variable during decomposition; or in other word the most decomposed and variable fraction during decomposition. In contrast, besides the lowest HEM contents (grams and percentages) and variability in fresh and remaining litter together with its lowest amounts released during decomposition, the proportion that this releases represent in relation to HEM stocks unless also lower like for SOL and LIG, were the most variable. Both CEL and LIG have similar middle contents (grams and percentages) and variability in fresh litter and its looses during decomposition, but the highest proportion loosed from the original stock were significatively higher and less variable for CEL than for LIG. Therefore the more variable responses in decomposition were observed for HEM followed for LIG, SOL and finales the less variable responses to decomposition were observed for CEL.

C fractions decomposition rates

C fractions have different decomposition rates and releases different amounts of C component during four months of litter decomposition. The absolute released amounts (grams) of SOL were higher than the other C fractions as expected. CEL was the recalcitrant fraction releasing higher amounts during decomposition followed by LIG; meanwhile HEM released the lowest absolute amounts. Decomposition rates of C fractions followed similar patterns but showed that CEL components could decomposed as faster as SOL. At the same time confirm also that HEM were the most recalcitrant C fraction decomposing even slowest than LIG. In contrast, the proportions of the initial C fraction content in fresh litter released during decomposition only found significant differences between CEL and the other C fractions. The amounts of CEL released during decomposition represent a higher proportion of the initial CEL stocks in litter than those proportions released for SOL, HEM and LIG. The proportions of C fraction released between SOL, HEM and LIG didn’t show any significant differences between, probably due to the higher variability in initial C fraction concentrations and in its releases. In fact, the variability of the proportions of C fractions releases (percentages) was higher than the variability observed for absolute amounts (grams) loosed from leaf litter stocks. Therefore in addition to carbon soluble compounds, cellulose have the higher amounts released during the 4 months of litter decomposition, meanwhile hemicelluloses were even more recalcitrant fractions than lignin releasing the lower amounts during the first four months of litter decomposition.

It is expected that insoluble components, cellulose, hemicelluloses and lignin degraded at different rates. The decomposition of litter organic components by microbes is selective and the microbial degradability of single components may vary greatly (Berg and McClaughert 2008). Thus, there is a pattern in litter chemical changes over the course of decomposition and it is widely expected that SOL has faster decomposition rates than CEL, HEM and LIG. Unless this common basic pattern may be modified as a result of the initial chemical composition of a given litter type, most of the described patterns have been based on boreal forest systems assuming that has a wider generality (Berg and McClaughert 2008). We found a different pattern of C fraction decomposition for leaf litter of tree species in tropical environment.

Generally, for freshly formed foliar litter, the water-soluble fraction (SOL) is a complex compound with high levels of simple sugars, lower fatty acids and protein remains such as amino acids and peptides. Most of these components can easily be taken up by microorganisms and metabolized and as result, the water-soluble fraction decomposes rather quickly and its concentration decrease faster with time (Berg and McClaughert 2008). Berg et al (2008) estimated that SOL in *Pinnus* sp. decreased approximately 38% its initial content in 12 months of litter decomposition. We observed that a mean of 53% of SOL contents in fresh litter decomposed after only 4 months for the studied tropical tree species in comparison to only 12 % and 29% of SOL decomposition for Scots pine needles and silver birch leaves litter in a boreal system (Berg and McClaughert 2008). These results underline that SOL decomposition for broadleaved tree species in tropical lands is 4 and 2 times faster than SOL decomposition of conifer needles and broadleaves deciduous tree species in boreal conditions.

Leaching may also play a role in the decrease in concentrations of water soluble from litter. Soluble substances are formed during the decomposition of polymer compounds such as holocellulose and lignin, and thus a low level of water soluble compounds is found throughout the decomposition process (Berg and McClaughert 2008). Leaching can be higher in tropical environmental than in boreal environments and a faster replenishment of soluble substances from litter can be expected in tropical sites. However, we found that in tropical lands the SOL with possible higher leaching, the levels of SOL contents in remaining litter after 4 months of litter incubation were similar and even slightly higher than pre-decomposed stages.

The decomposition rates of leaf insoluble C components like Cellulose, Hemicellulloces and Lignin's has been expected to be different and lower than soluble compounds. Berg and McClaughert (2008) have observed that in the early stage of decomposition, cellulose, hemicelluloses and lignin were degraded at different rates and that the concentration of cellulose decreases slowly. Somewhat later in the decay process, the degradation rates of these components were similar. In later stages of decay when lignin dominates the degradation process, the degradation rates of insoluble components decrease and maintain similarly low levels. Thus, during this late stage, the concentrations of cellulose remain rather constant. In addition, Berg and McClaughert (2008) propose that Hemicelluloses starts insoluble decomposition meanwhile the concentration of cellulose decreases slowly.

We have observed a different pattern of C fraction decomposition for leaf litter of neotropical tree species. In contrast to Berg and McClaughert (2008) proposed model of C fractions decomposition, we observed that CEL decomposed almost as faster as soluble compounds and even faster than the insoluble C fractions. In agreement with previous models, we observed different decomposition rates for different C fractions, but specific values of C fraction decomposition rates followed a contrasting model. We observed that CEL mean losses of cellulose during decomposition reach 70% of the original CEL stocks in fresh litter, meanwhile the other insoluble and soluble fractions were around 50%. In addition, the estimated decomposition rate of CEL (0.35 g day-1) was similar to SOL dates (0.32 g day-1) and both were higher than LIG (0.12 g day-1) and HEM (0.04 g day-1).

Decomposition rates of C fractions are higher than temperate and Mediterranean.

The observed patter of C fraction decomposition in leaf litter of tropical tree species differ from boreal models mainly in the fact that concentration of cellulose do not decreases slowly than soluble fractions. Cellulose decomposition rates (0.35 g day -1) can be as faster as soluble compounds rates (0.32 g $^{-day}$) releasing the highest absolute amounts (20 g) and proportions (70%) of C components initial stocks in fresh litter (22%) and reducing almost to half (12%) its concentrations in remaining litter during the four months of litter incubation. Conversely in addition, no matter the different concentrations in fresh litter of LIG (21.5%) and HEM (8%) and they contrasting amounts released during decomposition (0.14 versus 0.49 g respectively) both have slower decomposition rates (0.12 v.s 0.04 g day-1), released similar proportions of initial stocks during decomposition (52 and 54% respectively) but keep concentrations in remaining litter (22.5 and 8.5%) similar to those observed in fresh litter. Therefore, all C fractions start decomposition within the four months of litter decomposition with CEL and SOL releasing different amounts of C components faster than LIG and HEM but decreasing CEL the higher proportions of Total C stock founded in fresh litter.

Also different patterns of decomposability between species have been shown widely variable between tree species in mediterrenean species (Fioretto et al 2005). For these species Cellulose decomposition can start during the early decomposition at similar of higher rate than Lignin. In *Cistus* sp. litter, lignin (36% IOM), decomposition began after 6 months of exposure and continued to the end of the study period meanwhile the holocellulose (34% IOM), began to be degraded only after 12 months of exposure but with a higher rate than that of lignin. Cellulose and lignin (37 and 17% IOM, respectively) did not change significantly in the first 8 months of exposure in *Myrtus* litter. However, in the following 2 months the lignin was reduced to half of the initial content and afterwards showed only a little decrease during the following 26 months of litter exposure, meanwhile Cellulose was degraded at a high rate constant in the same period. In *Quercus* litter, cellulose (38% IOM) was degraded from the first sampling (2 months after exposure) and continued at a constant rate for about 18 months. After 27 months the cellulose decay rate decreased to near zero. Lignin (15% IOM) did not show any significant degradation during the entire decay period.

The differences between LIG and CEL decomposition rates and between species have been explained by the association to N and its variability along the decay loos. Although most of the nitrogen was not lost from litters, its distribution among the litter components changed significantly during decomposition. In *Cistus* sp. and *Myrtus* sp. the nitrogen associated with lignin began to decrease just 4 months after exposure. In Quercus this process was slowed and after 3 years of decomposition 8% of the nitrogen remained associated with lignin or lignin-like substances. The nitrogen associated with cellulose or cellulose-like substances, in contrast, began to decrease from the beginning of cellulose decomposition in all three species.

In addition to previous works in C fraction decomposition, we have been able to explore how frequent such patterns of C fractions releases changed within a tree community. Our observed and different pattern with celluloses starting consistently decomposition during the first four months of litter decomposition meanwhile mean Soluble compounds, Hemicelluloses and Lignin mean concentrations increasing slightly was a general pattern. Most of tree species (87%) showed an increase in the percentage of SOL compounds from litter establishment to end of the four months of litter incubation, only 6 showed the expected decreases in the soluble compound concentrations in decomposed litter. Almost half of the tree species (45%) showed a decrease in the hemicelluloses concentrations. In contrast, all the tree species showed decreases in CEL concentration, meanwhile a reduce proportion of tree species (24%) showed also decreases in LIG concentrations.

In contrast to the model proposed by Berg and McClaughert (2008) was CEL and not HEM the first component which was strongly decreasing during the first stage of litter decomposition after litter shed. In addition, unless a decreasing in the HEM was also observed this was not the most frequent pattern: tree species showing decreases in HEM concentration during the first 4 months of litter decomposition were was even slightly lower (45%) than those which increasing it (55%). Ours results also differ in Berg and McClaughert (2008) model because SOL compound are not consistently decreasing in early decomposition. In fact a higher proportion of tree species showed increases in SOL concentration during the 4 months, resulting probably from higher sugar accumulation during Celluloses and Hemicellullosses degradation. Only LIG fraction showed agreement with Berg and McClaughert (2008) model when a higher frequency of tree species showed LIG contents increase during decomposition (76%).

Comparison of C fractions losses during senescence and decomposition

Losses of C fraction (grams and percentage) were obviously lower during senescence than during 4 months of litter decomposition. CEL releases during decomposition were 27 times higher than during senescence, followed by LIG and SOL which changed by factors of 7 and 5 during senescence, and the lower differences were observed HEM which only double its losses during senescence. Variability of C fraction looses thought senescence and decomposition also differs between leaf decay process and C fractions. In general, the variability of C fractions losses (grams) decreases meanwhile variability of C fraction proportions loosed increase. The amounts (grams) of SOL and HEM were the more and less variable C fractions during senescence and decomposition, meanwhile HEM and CEL showed the more variable proportions of C fractions released. The higher changes in variability between senescence and decomposition were observed for LIG releases amounts (grams) and for the proportion of CEL releases from the original stock (percentages) which increases almost twice the variability observed during senescence. These results imply that C fractions have a different behavior during both leaf decay processes.

Variability of C fraction contents changed between leaves stages and C fractions unless the mean percentages of most C fractions contents in leaves were similar thought leaves senescence and decomposition. In addition, the variance of C fractions losses was different not only after but also during senescence and decomposition and between C fractions. SOL ranges from ca. 0.3 to 0.7 in fresh leaves; from ca. 0.28 to 0.7 in fresh litter; and from ca. 0.28 to 0.78 in remaining litter. Variances in fact increased from in green leaves to decomposed litter. SOL variances however were always higher than the others C fractions. Interestingly SOL did not decrease during decomposition. In fact showed a slight increase from green leaves to decomposed litter. The observed range of SOL contents amongst tree species seemed to change so little between leaf stages.

In addition the range of variability between species of SOL and LIG was wider (38%) than for HEM (12%) and CEL (19%). CEL have the highest mean percentage of losses and the lowest variability meanwhile HEM has the higher variability of interspecific losses during decomposition. These results showed also that tree species has a wide variability in C fractions contents which could be also affecting the wide variability in decomposition rates of tree leaves, having possible relevant implication for soil carbon stocks and dynamics in agricultural lands.

C fractions mean contents losses during senescence

The mean content (measured in grams) of all C fractions were obviously lowest in the lowest mass remaining of decomposed litter. In contrast, the mean proportion of each C fraction in that amounts decomposed litter (percentage) were different from those observed in mature tree leaves are fresh litter. Some C fractions decreased, other increased and other remain similar to the pre-decomposed stages of leaves. HEM and LIG contents in decomposed litter (8% and 22% respectively) are similar to those observed in green and fresh litter (see above or Table 3.4). In contrast; CEL dropped strongly to half (12%) it relative contents in fresh litter (22% and 23%). Contrary to CEL, SOL contents actually increase in comparison to their contents in pre-decomposed but mainly from those contents in fresh litter.

These results showed as expected, that not all the mean C fractions have the same behavior during litter decomposition: mean Hemicelluloses and of Lignin's contents as the more recalcitrant fractions in leaves remains at the same proportion even after 4 months of litter decomposition. The fraction that is more strongly reduced during the same period of litter decomposition is the mean Celluloses content. During these initial 4 months of litter decomposition the more labile fraction, the soluble carbohydrates, in contrast increases their relative proportions in decomposed litter from those observed in fresh litter. These results support the model of decomposition which states that the mean proportions of hemicelluloses and lignins did remain invariable during the initial stages of decomposition as the most recalcitrant fractions. The rapid decreasing of celluloses proportion implies that this was the structural C fraction more actively decomposing during this initial stage of litter decay. It is probably the breakdown of this cellulose compounds which is actually replenishing the increased proportion of soluble fractions in a way that mean proportion in decomposed litter even increase from those observed in fresh litter. These results shows that during 4 months of litter decomposition in tropic lands mostly celluloses is being decomposed meanwhile hemicelluloses and lining proportions still remains intact.

Relationship of tree leaf quality with litter decomposition rates

Decomposition rates of tree species commonly found in Central American active pasturelands are correlated with nutrient and C fraction concentrations in fresh leaves and in fresh litter. Tree species with lower LDMC, C and LIG content together with the highest P, SOL and HEM content in fresh litter had the higher decomposition rates (Table 3.5). Foliar macronutrients and C fractions were good predictors of tree leaf litter quality and decomposition rates. These results followed the decomposition models which described higher litter quality with higher k values by higher contents of nutrients like total P in addition with higher level of labile carbon components like SOL, together with low contents of total C contents, LDMC and more recalcitrant C fractions like LIG. In addition to previous models we found that litter with also higher contents of HEM were related with higher K values meanwhile CEL contents didn’t show any particular relationships with decomposition rates. However, in contrast, we didn’t find any correlation between total N contents in mature leaves or either tree litter with litter decomposition rates during the four initial months of litter incubation.

Decomposition rates were negatively correlated with LDMC, C and LIG content in fresh litter and positively correlated with P, SOL and HEM contents. There was no correlation with N or CEL content in tree fresh litter. Strongly correlations were for lignin contents in fresh litter (LIG) with decomposition rates (-0.53 to -0.69) and remaining litter (0.63 to 0.69) values, followed by hemicelluloses (HEM) (0.45 to 0.64 and -0.55 to -0.62 respectively), total phosphorus (P) (0.32 to 0.58 and -0.43 to -0.60 respectively),Total carbon (C) (0.31 to -0.53 and 0.42 to 0.56 respectively), soluble compound (SOL) (0.34 to 0.53 and -0.45 to 0.52 respectively) and finally with leaf dry matter content LDMC (-0.32 to -0.40 and (0.38 to 0.40 respectively).

All these leaf components especially LIG, LPC, LCC, LDMC and SOL have been found correlated with decomposition rates in different floras and plant species. Decomposition rate has been found to correlate positively with litter nitrogen (Parsons and Congdon 2008), phosphorus (Cornwell et al. 2008) while it correlates negatively with large carbon chains, such as lignin and cellulose (Vaieretti et al. 2005, Kurokawa & Nakashizuka 2008). Decomposer organisms tend to have very high nitrogen and phosphorus contents (Vadstein and Olsen 1989) indicative of high requirements for these nutrients. Therefore litter with high nitrogen and phosphorus content should decompose fast because of the associated fast growth of the microbial populations, whereas excess carbon in the plant litter should lead to nutrient-controlled carbon remineralization (Vadstein and Olsen 1989).

Several studies have demonstrated that a strong negative linear relationship existed between decay rates and the lignin content, the ratio lignin:N, the phenol content or the ratio (lignin+ phenols):N (Aerts 1997, Mesquita et al. 1998). As lignin physically protects most of the cellulose and hemicellulose from enzymatic hydrolysis, neither group of compounds decompose independently (Cooke and Whipps 1993). High contents of lignin have a rate-reducing influence on litter decomposition both in the early and later stages, in particular, when associated with high N content, because new and stable complexes are formed (Berg and Ekbohm, 1991; Couˆteaux et al., 1995). Nevertheless, high nitrogen content generally regulates the early stages by enhancing the growth of microorganisms that degrade labile compounds, and repress the formation of lignolytic enzymes (Keyser et al., 1978). In a high N environment, the growth of many microorganisms able to decompose lignin, such as the basidiomycetes, is reduced, because such slow-growing fungi are unable to compete with fast-growing microbes and are eliminated from the decomposer community (Couˆteaux et al. 1991). The high variability of such lignin concentrations and N contents open a high variability effects on decomposition rates.

Fewer studies have found additional effects of other insoluble C fractions over decomposition rates. Other studies showed that the long-term decomposition rate was increased by high cellulose content (i.e. Berg and McClaugherty 2008). The role of both cellulose and lignin as regulating factors of litter decomposition rate have been reported mainly in temperate and boreal coniferous and deciduous forests (Berg et al. 1996, Couteaux et al. 1998) and some in for Mediterranean ecosystems (Rutigliano et al. 1996, Di Nardo et al., 2001). In contrast, HEM content was positively correlated with litter decay meanwhile we didn't find any strong correlation between CEL contents with litter decomposition rates. Either N concentrations in fresh litter or no-chemical foliar traits like SLA, LA or FTF didn't predict tree litter decomposition rates. The absence of such significant correlations between these traits frequently related with decomposition rates could be reflecting the wide variability in leaf phenology in this tree community.

Deferent rates of decomposition have been found for tree species with contrasting leaf phonological status related with lignin, nitrogen and phenols. Lower decomposition rates of evergreen leaves species has been also correlated with high lignin content. In Tazmania (Wedderburn and Carter 1999) found that high rate of litter decay was linked to high amounts of microbial activity affected by the differences in N and lignin content of the leaves. The leaf litter which exhibited the most rate of rapid decay and cycling of nutrients was that from the deciduous N-fixing tree species, which contained low amounts of lignin and C and high amounts of N. Also different decomposition fraction has been found correlated with particular decomposition stages in tree species of semi-evergreen tropical forests in French West Indies (Loranger et al 2002). Between 1 month and 2.5 months, the mass loss was correlated negatively with the initial phenol content and with initial lignin:N and (lignin+phenol):N ratios. From 2.5 to 5.5 months, the mass loss was correlated negatively with the initial phenol content and positively with the initial cellulose content. At later stages of decomposition (9–14 months), the mass loss was correlated negatively with the initial tannin content (Loranger et al 2002). However wider explorations of the relationships with other foliar traits related with leaf phenology and decomposition rates are scarse.

Unless not directly correlated with decomposition rates leaf phenology was correlated with leaf and litter quality and C fraction contents in remaining litter. These correlations probably have particular effect their relationships with litter decay rates. Tree species with the cheapest leaf construction (high SLA) tend to have a high N content in fresh litter and tend to have a low LA meanwhile those with a high FTF have higher amounts of CEL in fresh litter but were not correlated with decomposition rates. PHE was negatively correlated with FTF and positively with LPC, and unless was not correlated with any macronutrient content or losses either in fresh or litter remaining after decomposition, PHE also negatively correlated with HEM in remaining litter. Specific evaluations of the relationships between each phenological status in this tree community and its correlations with decomposition rates of biomass, macronutrients and C fractions probably give us strongest correlations with those chemical and no chemical leaf traits with low correlations like CEL, N, SLA, LA or FTF.

These results support our previous hypothesis stating that foliar quality of tree species in active pastureland predicts decomposition rates. In addition, we observed that foliar nutrient and C fraction concentrations are tightly correlated with fresh litter concentrations across species and therefore the same correlations observed between litter quality and fresh litter are extended to chemical foliar quality in green mature leaves. In addition to the ecological implications of these correlations, these results are relevant for the increasing actual research on plant traits at regional scales suggesting that foliar chemical quality can be used to make inferences about the patterns on biomass decomposition and nutrients releases.

Relationships of plant traits with decomposition rates, tree litter quality and nutrient release

SLA, LA and FTF were correlated with macronutrient content in remaining litter but only with C releases during decomposition.

Only SLA was negatively correlated with C losses during decomposition process, tending to be also positively correlated with N content in remaining litter. SLA was negatively correlated with SOL in remaining litter and tends to be negatively correlated with HEM and LIG losses. LA was negatively correlated with N, P and C contents remaining litter, but again was not correlated with any macronutrients losses during decomposition process. LA tends to be positively correlated with SOL in remaining litter. FTF was positively correlated with CEL contents in fresh litter and with the CEL amounts released during decomposition.

These results imply that leaf traits like SLA, LA and FTF could be related with total C and C fraction losses but not necessarily predict leaf decomposition rates. In addition, tree species with bigger leaves have low N in fresh and remaining litter together with lower amounts of P and higher SOL amounts in remaining litter, but not necessarily predict N either P releases. Only tree species with more expensive leaf construction tend to have a lower decomposition rate and to have lower SOL in remaining litter and tend to have lower losses of HEM and LIG during decomposition process. Meanwhile tree species with more hard leaves have higher contents of CEL in fresh litter but higher amounts of CEL loosed during a faster leaf decomposition.

Whole plant and dispersal traits were also correlated with leaf litter decomposition rates and with nutrient releases during litter decay.

Whole plant and dispersal traits were correlated with decomposition rates. H_max was negatively correlated with monthly decomposition rates during the third and four months of litter incubation. Meanwhile Mass_see, Vol_fru and Vol_see were negatively correlated with decomposition rates during the first month of litter incubation. Whole plant traits were correlated with C fractions but not with macronutrient contents in fresh litter, were correlated with both quality of remaining litter and tend to be correlated with macronutrients but not with c fractions releases during decomposition.

H max was positively correlated with P and C amounts within remaining litter, negatively correlated with C percentages in remaining litter, and tend to be only negatively correlated with percentages of N and C looses during decomposition. WD tends only to be negatively correlated with P contents in remaining litter. PHE was not correlated with macronutrients contents in fresh, remaining litter or with macronutrient losses.

H max, WD and PHE were correlated with HEM contents in fresh or remaining litter: H_maxand PHE were negatively correlated with HEM in fresh and/or remaining litter, meanwhile WD was positively correlated HEM in fresh litter. H_max was in addition positively with LIG content in fresh litter and with CEL and LIG contents also in remaining litter. However, no one of these vegetative traits was correlated with any C fraction losses during decomposition process.

Dispersal traits were also correlated with both macronutrients and C fractions contents in fresh and remaining litter and with macronutrients releases during decomposition, but not with C fractions releases. Mass_fru, Vol_fru and Sha_see were positively correlated with C contents in fresh litter, and together with Sha_fru were also positively correlated with C contents in remaining litter. Mass_see and Vol_see tend to be positively correlated with C contents in remaining litter. SHa_fru was positively correlated with N content in both fresh and remaining litter, and together with Sha_see and Vol_fru also with N in remaining litter.

Mass_see and Vol_see tendi were negatively correlated with P losses, meanwhile just Sha_see and Vol_fru tend to be negatively correlated with C and N loses during decomposition. Vol_see and Mass_see were negatively correlated with HEM in fresh litter, Mas_fru and VOl_Fru in addition to VOl_see were positively correlated with LIG, meanwhile Mass_fru tend to be negatively correlated with SOL. Vol_fru, Mass_fru and Sha _see tend to be positively correlated with LIG in remaining litter. Mass_Fru and Vol_fru were positively correlated also with CEL contents. However dispersal traits were not correlated at all with C fractions losses during decomposition.

These results means that taller tree species have lower decomposition rates at the end of decomposition process related with lower percentages of C loses resulting from high LIG and low HEM contents in fresh litter, together with higher amounts of total P, C, CEL and LIG but low HEM in the remaining litter. Tree species with denser woods and more deciduous canopies had leaves with low HEM contents and were not related with litter decomposition either with nutrient or C fraction releases.

Tree species with bigger dispersules and heaviest seeds have lower decomposition rates during the first month of decomposition. Tree species with bigger and heaviest fruits and longest dispersule have higher percentages of total C and N in fresh litter and remaining litter, but just those with bigger fruits and longest seeds tend to have lowest percentages of initial total C and N released during decomposition. Tree species with heaviest and biggest seeds had the lower percentages of initial P released during decomposition, but not particular relationships were observed with fresh and remaining litter quality. Tree species with biggest and heaviest fruits have higher percentages of LIG in fresh litter and remaining litter; and tend to have lower contents of SOL in fresh litter and higher CEL content in remaining litter. Tree species with bigger and heaviest seeds were more related with lower percentages of HEM in fresh litter, but not with C fractions patterns in remaining litter or C fraction losses during decomposition.

These results support our previous proposed hypothesis stating that plant traits measuring non-foliar tree organs like whole-plant and dispersal traits were correlated with foliar litter quality and decomposition rates. This result express also important trade-off between leaf qualities with other plant organs linked to the plant resource use-conservation axis.

Relationships between abundances of tree natural regeneration and leaf litter quality, decomposition rates and nutrient release.

Abundance of tree natural regeneration was also correlated with decomposition rates, leaf litter quality and macronutrients and C fractions releases through decomposition process.

Abundance of tree natural regeneration at all developmental stages (seedlings, saplings and adults) were positively correlated with tree litter decomposition rates Correlations were strongly with monthly decomposition rates during the late decomposition stages (third and four months of litter incubation). Decomposition rates of leaf litter from adult trees were more strongly correlated with saplings abundances than with seedlings and adults abundances.

These results showed that tree species with higher regeneration capacity in active pasturelands have also higher decomposition rates of leaf litter. In addition, those species with more abundance of seedlings and saplings were those with the higher capacity to persist in active pasturelands and were also the species with the higher decomposition rates during the late stages of tree litter incubation.

These results imply that possible changes in species composition of tree community in active pasturelands due to the negative effects of pasture management on seedlings abundances affect also other important ecosystems processes like tree litter decomposition rates. The possible local extinction of those tree species with a higher lower decomposition rate could potentially increase decomposition rates in active pasturelands. This changes in litter decomposition rates affect mainly the early stages of decomposition process but could have potentially stronger effects over the second phase of litter decomposition beyond 4 months of litter decomposition.

The abundance of tree natural regeneration in active pasturelands was correlated with macronutrients litter quality and releases.

Abundances of tree species in all developmental stages were positively correlated with percentages of total P in fresh litter, with N and P contents in remaining litter and with total N releases during litter decomposition process. Adult and saplings abundances were also correlated with total P contents in remaining litter Only adults abundances were correlated with higher total carbon looses during decomposition.Higher LDMC and N contents in fresh litter were strongly correlated with saplings abundances together with the higher C contents in remaining litter.

These results imply that those species with more capacity to regenerate in active pasturelands are those having higher litter quality and releasing also the higher amounts of nutrients during a faster litter decomposition process. These results imply also that changes in tree species abundances could potentially affect N, P and C releases to the pasturelands. Both results are implying that effectively a higher litter quality including high levels of N and reducing C contents in leaves were related with species survivorship within these agro ecosystems and at the same time that was affecting this system decomposition rates and nutrient cycling.

Abundance of tree natural regeneration in active pasturelands was also strongly correlated with C fractions content and releases from tree litter.

Abundances of all developmental stages were negatively correlated with CEL in fresh litter, CEL and SOL in remaining litter and with CEL and LIG looses during decomposition. Saplings abundances were also positively correlated with LIG percentages in fresh litter, CEL in remaining litter and together with adults also with SOL looses.

These results imply that those tree species with the higher capacity to regenerate in active pasturelands have higher percentages of recalcitrant's C fractions like LIG and CEL in fresh litter. higher proportions of Carbon recalcitrant fractions in leaves of the more abundant species in active pasturelands could help them to survive the water and herbivore stress within these environments.

In addition, the more abundant tree species were those releasing the higher amounts of LIG and SOL but releasing the reduced amounts of CEL during decomposition process. These higher releases of LIG and SOL could be explaining the higher decomposition rates during the late stages of decomposition process.

These results seem to be implying also that tree survivorship within this agro ecosystem is related with high lignified leaves construction to overcome droughts and herbivores attack. Finally also those more abundant tree species are affecting also C nutrient cycling releasing higher amounts of recalcitrant's fractions to these systems through leaves litter decomposition.

Finally, we are awarded that there is not a simple relationship between the rate of litter decomposition and its impact on ecosystem (net primary) productivity. Slow rate of release from litter, during the growing season, of a nutrient whose availability is a key limiting factor to growth may limit productivity. On the other hand, rapid release of a nutrient (beyond the capacity for growing plants to take it up) especially in wet conditions, may well result in greater rates of leaching of that nutrient from the system. This may reduce longer-term ecosystem productivity. Soil organic matter is essentially composed of litter that has not fully decomposed and, of course its high concentration may be vital for retention of moisture and nutrients. However to know how much the inter-specific variability of tree species in relation to it litter quality affects the nutrient decomposition rates helps to be set a more strong mechanistic understanding of nutrient cycling/soil (organic matter) functioning.

4.6 CONCLUSIONS

Tree species in active pasturelands have a wide array of different decomposition rates and litter qualities. More specifically:

> The percentage of leaf litter mass remaining vary between 20 to 74% (mean of 53%) during four months of litter incubation, with overall decomposition rates (BETA 5) varying from 0.09 to 0.78 (mean 0.26) for 37 tree species. Monthly decomposition rates (b1, b2, b3, b4) also vary between tree species with faster decomposition rates occurring in the first month of litter incubation (0.32) and slowest during the fourth month (0.17). Macronutrients and C fractions contents varied also between species: mean Phosphorus content varied from 0.04 to 0.22% (mean 0.10%), Nitrogen content from 0.93 to 2.7% (mean 1.5%), Carbon content from 35 to 52% (mean 44%), Soluble compounds varied from 29 to 67% (45%), Hemicelluloses from 2 to 13%(mean 8%), Celluloses from 12 to 32% (mean 23%) and Lignin from 6 to 39% (21%).

The variability in decomposition rates and nutrient releases of tree species in active pasturelands are strongly related with the leaf variability spectrum but also with reproductive and whole plant traits and with tree abundances.

Our results confirm and extend the afterlife effect of the leaf economic variability for a wide sample of tree tropical species. Tree species with acquisitive leaves having high P, N but low C and also high SOL, HEM but low LIG in green leaves and fresh litter, decompose faster and release more N, P, C, SOL, HEM and LIG than more conservative tree species.

In addition, the variability of whole plant and reproductive traits of tree species commonly found in active pasturelands are also related with tree species differences in decomposition rates and nutrient releases. Particularly,

> Taller tree species with low HEM but high LIG content in fresh leaves and litter decompose slowly during the last months of litter incubation and release the lowest amounts of C and N than shorter tree species.
>
> Tree species with expensive (big, heavy, long) fruit and seeds construction have leaf litter (with more C, N and more C and recalcitrant fractions like LIG but low C soluble compound like SOL and HEM) that decompose slowly during the first months of litter incubation releasing less C, P and N than litter from tree species with cheap constructed fruit and seeds (small, light, spherical).

Finally, the relationships among tree species variability in decomposition and nutrient release with tree abundances show that tree species with active capacity to naturally regenerate in active pasturelands have faster decomposition rates in the last months of litter decay releasing more N and LIG than tree species with limited regeneration capacity. More specifically,

> Tree species with abundant adult populations have leaf litter with high P, low CEL decomposing faster and releasing higher N and LIG amounts than tree species less abundant in adult tree cover.
>
> Instead, tree species with more abundant saplings population have litter with more N and LIG, faster decomposition rates in last months of litter decay and release lower C, CEL and SOL amounts than those tree species with more abundant adult population.

Therefore, the high variability of leaf, reproductive and whole plant traits of the tree cover commonly found in active pasturelands is related with different decomposition rates of tree litter which directly affect nutrient and C fractions releases and cycling in tropical agricultural lands.

Our findings indicate that plant characteristics are linked with ecosystem processes such as litter decomposition and tree natural regeneration with implications for the sustainability of ecological services that could be offered by trees in agricultural systems.

CHAPTER 5. GENERAL DISCUSSION

5.1 INTRODUCTION

Land use changes, largely driven by expansion of agricultural lands in tropical areas, imply intense and abrupt habitat transformations from massive natural vegetation to simplified ecological systems increasing global biodiversity loss. Generally, land use change results in vast areas of agricultural land and strong forest fragmentation limiting the capacity of species to restore their populations in the landscape. The consequential disruptions of ecological processes providing ecological services are strongly related to biodiversity loss and forest fragmentation. Trees outside the pristine forest have an important role in restoring ecosystem processes at landscape level such as increasing habitat diversity, food availability for local fauna, pollen interchange and dispersal patterns. Conventional management practices are reducing actual tree cover diversity in tropical agricultural landscapes but we have no information on the functional characteristics of the relative high taxonomical diversity of tree species that persist today after land use change from forest to pastures and their potential effects on ecosystem processes.

Understanding the variability of functional diversity of tree species outside pristine forest after land use change helps us to understand i) how tree species respond to anthropogenic land disturbances so widely spread world-wide and ii) how the maintenance of reduction of such functional variability in managed areas can affect ecological processes providing ecological services offered by natural diversity. In a novel approach, we try to address the link among tree characteristics or plant traits and ecosystem processes outside pristine forest borders. Our results can help improve the sustainable management of a globally-considerable land use cover as pasturelands. The following lines recall the three main questions addressed during this research and summarize and integrate the key finding of each chapter specially focusing on their cross-links.

5.2 Tree functional strategies in Central American active pasturelands

In the first chapter we asked which are the plant strategies of tree species commonly found in active pasturelands. We show that tree species commonly found in active pasturelands have diverse and inter-linked whole-plant, leaf and reproductive traits, that combined define different "trees functional strategies" (**Figure 5.1**). This result is especially relevant because this is the first approximation to describe the plant functional strategies of an important group of tropical tree species outside forest remnants in agricultural landscapes. We previously knew that a considerable proportion of the tropical taxonomical biodiversity can be found in agricultural lands but we had no information about the functional profile of such remnant or emergent biodiversity. Today we have an extended description of the tree functional strategies outside pristine forest remnants.

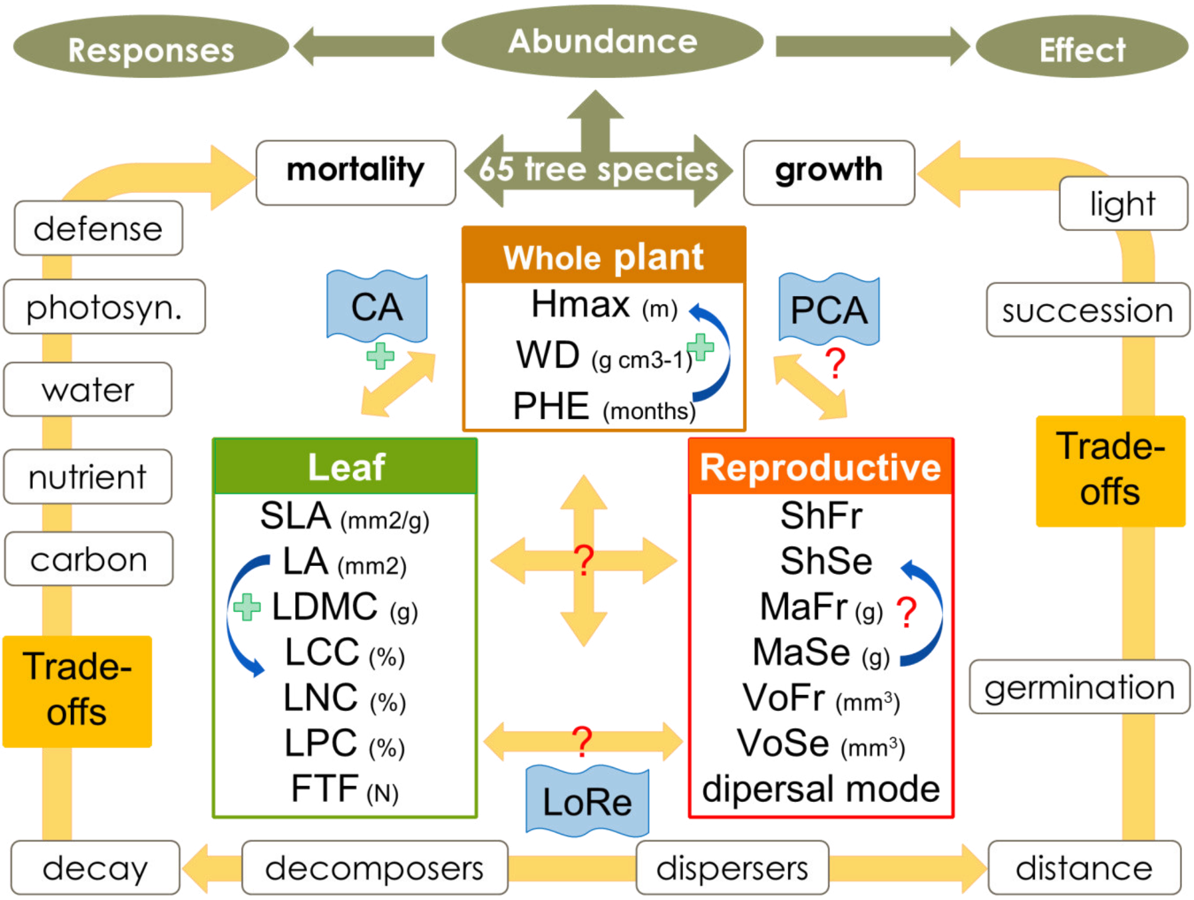


Figure 5.1. Methodological approaches used to describe the tree functional strategies as particular combination of plant traits strongly related with the main dimensions of plant variability i.e. leaf, whole plant and reproductive traits, for 65 tree species commonly found in active pasturelands (chapter1). Intra and inter-dimensional relationships among plant traits were tested with correspondence analyses (CA) for paired correlations, principal components analyses (PCA) for multiple correlations and logistic regressions (LoRe) for paired correlations with categorical traits.

The methodological scheme in **Figure 5.1** shows how the understudied relationships of reproductive traits with other plant dimensions give us new insights on species location in the trade off continuum among mortality to growth rates. This helps increasing today holistic understanding about relative the tree species investments to different dimensions of life history development. for example; it is not new that a high investment in leaf carbon and leaf defense to reduce plant mortality, probably imply slow decay rates and slow growth rates. However, it is still not clear how these strategies are related with either species fruit and seeds characteristics (expressing differences on disperser's attraction investments, dispersion distances, germination and establishment rates) or with light requirements during a particular tree successional stage. The identification of tree functional strategies (Chapter 1), in the following research steps integrating the species abundance component, helps us understand how tree species responds to natural or anthropogenic disturbances like agricultural activities (Chapter 2) as well as their possible effects on ecosystems processes (Chapter 3).

At least four main key findings must be outlined from the results in this first chapter: 1) the four main spectrums of plant traits variability (leaf, height, wood and reproductive spectrums) are correlated for tree species in agricultural lands. 2) The highest proportion of tree species variability was explained by several main axes linking together different whole plant, leaf and dispersal traits. 3) Tree dispersal mode is correlated not only with reproductive traits but also with whole plant and leaf traits. All these information combined together allowed us to describe the functional strategies of tree species commonly found in anthropogenic environments. In these respect, tree dispersal modes were good examples of tree strategies that split species' traits variability with particular combinations of the main spectrums of variability i.e. leaf, wood, height and reproductive spectrums. The following lines extend in more detail these key finding for chapter 1 describing tree functional strategies in active pasturelands.

We confirm the presence of two main spectrums of species variability and their close inter-relationship: i) the leaf variability spectrum which split apart conservative leaf species (high LDMC, LCC, FTF but low SLA and LPC) from those with more acquisitive leaves (conservative - acquisitive); and ii) the tree phenology and stem variability spectrum showing that taller deciduous trees have softer woods than shorter evergreens (deciduous softer – denser evergreen). Both spectrums are interlinked in a iii) Leaf and phenology spectrum, confirming that deciduous tree species with short leaf life span have fragile acquisitive leaves with low investments in carbon but high contents of nutrients like P than evergreen species which have conservative leaves (deciduous, softer, acquisitive vs evergreens, denser, conservative).

A novel result was to find that tree species vary also in a iv) fruit and seed investment spectrum, which split apart tree species with bigger and heavier fruits from those with small and lighter fruits and seeds (cheap – expensive). This fruits and seed investment spectrum was also correlated with leaf, stem and phenology spectrums. Acquisitive leaves have cheap fruits and seeds in a v) leaf and reproductive investment spectrum (acquisitive and cheap) in contrast to conservative tree species with expensive fruits and seed construction. finally, a vi) phenological, stem and reproductive spectrum split apart deciduous trees with softer woods, small and lighter seeds from evergreen tree species with denser woods and more expensive fruits and seeds (deciduous trees with softer woods and cheap fruits and seeds).

Another novel result is that a holistic association occurs in several diverse axes of plant traits variability. More than 70% of tree species variability was explained at least by 5 main axes, each one explaining between 10 to 20% of tree species variability when all plant traits were placed together in a unique principal component analyses. This observation implies that the complexity of the pattern of plant trait associations do not show a tendency to form tightly-defined “functional groups”, in contrast diverse spectra of variability are linking together whole plant, leaf and reproductive traits. These diverse multidimensional interactions were better described by tree “dispersal modes”, which being correlated with all plant traits, make good examples of the tree functional strategies in active pasturelands, displaying each one a particular combination of the main spectrums of plant traits variability. Tree species dispersed by wind were taller, deciduous with rich phosphorus leaves, bigger and longest fruits carrying lighter seeds. Tree species dispersed by local fauna were shorter with big but cheap constructed leaves (low LCC) carrying small, lighter and spherical fruits with spherical seeds. In contrast, tree species dispersed by big mammals like cattle, have strong and expensive leaves (high LDMC and LCC), low nutrients contents (LPC and LNC) and big and heavy fruits with heavy seeds. Tree species with parental dispersion have dense woods but fragile nutrient rich leaves (high LNC) having longest fruits.

5.3 Tree population responses to anthropogenic disturbances

In the second chapter we test whether functional morphology of tree species is related to the capacity to maintain their populations through natural regeneration in active pasturelands (**Figure 5.2**). We hypothesized that tree species' capacity to naturally regenerate in active pasturelands is associated to those plant traits that are related to the four different main trait dimensions namely i) leaf variability spectrum, ii) stem density spectrum, iii) variability on canopy height at maturity and iv) reproductive investment spectrum, as well as to adult tree abundances. Our findings support this hypothesis showing that leaf, reproductive and whole plant traits together with adult tree abundances are correlated with the abundances at early developmental stages of tree species typically founded in agricultural lands. This is the first time to date that the persistence in anthropogenic environments of a representative sample of tropical tree species is predicted by seedlings and saplings abundances using a wide array of plant traits and adult abundances.

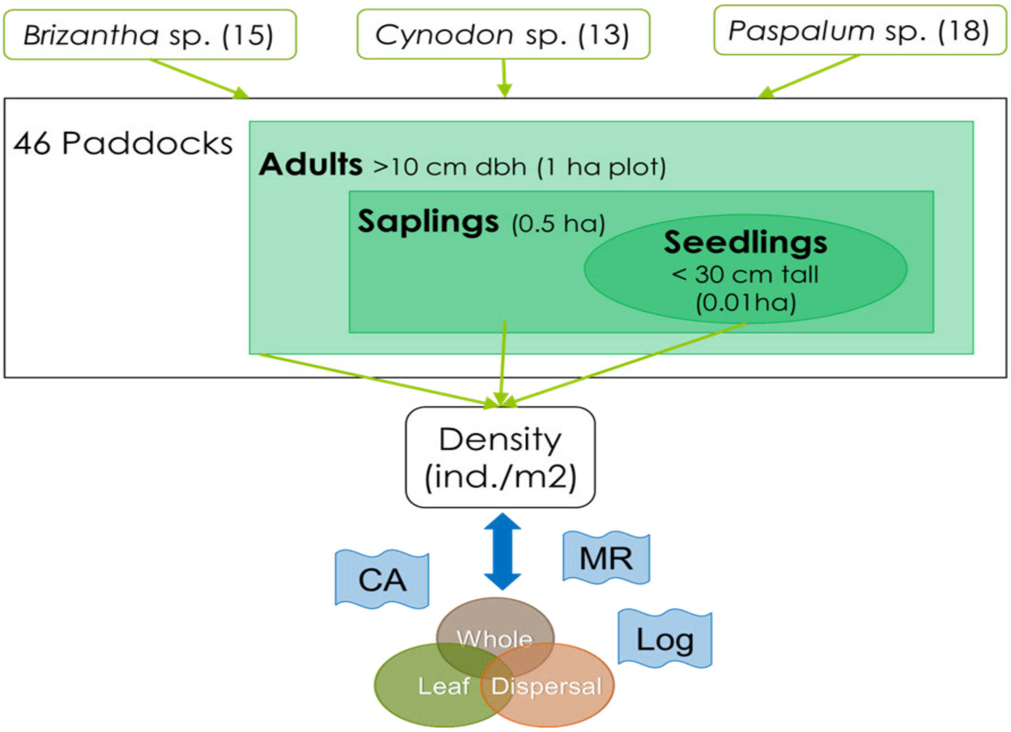


Figure 5.2. Methodological approaches used to evaluate the relationships between tree capacities to naturally regenerate under anthropogenic disturbances and the main dimensions of plants variability i.e. leaf, whole plant (stem height and density) and reproductive traits for 65 tree species commonly found in active pasturelands (Chapter 2).

The scheme in **Figure 5.2** shows that tree density at 3 different developmental stages like seedlings (germinated plants under 30 cm tall), saplings (woody plants with stem diameter at breast height (DBH) fewer than 10 cm but more than 30 cm height) and adult trees (dbh higher than 10 cm) were sampled on nested plots inside a total of 46 active managed pastures (paddocks) using exotic (Brizantha sp. and Cynodon sp.)

and naturalized grasses (Paspalum sp.) commonly found in Central American region. Relationships among tree densities and plant traits were tested using Correspondence Analyses (CA) for paired correlations with quantitative variables, and Logistic Regressions (LoRe) for paired correlations with categorical traits. Adult tree densities and plant traits capacity to predict seedling and saplings abundances were tested using Multiple Regression Analyses (MRA).

Five key findings can be outlined from the results of the second chapter: 1) leaf, reproductive and whole plant traits are correlated with tree species abundances in active pasturelands, 2) the strength of these relationships between plant traits and species abundances depend on tree developmental stages, 3) tree dispersal modes are consistently correlated with the abundances of tree species in all developmental stages, 4) adult tree abundances are the strongest predictor of tree seedlings and saplings abundances in active pastures, and therefore, 5) adult tree species abundances and plant traits explained together a higher variability of seedlings and sapling abundances in these areas in comparison to only plant traits. These results are especially relevant in the context of diversity conservation outside forest ecosystems in tropical regions where agricultural uses domain landscapes at expenses of the reductions of the original forest remnants. The following lines expand these key finding for chapter 2 and their relevance to understand tree population responses to anthropogenic disturbances.

First, we showed that the most abundant tree species in active pasturelands have a particular combination of leaf, whole plant and reproductive traits. Only those taller deciduous trees with softer woods having also small and more conservative leaves (low sla, high lcc) toguether with expensive (big, heavy) and longest fruits carrying big and longest seeds dispersed mainly either by wind or cattle, are the most abundant species of the adult tree cover. The tree species most abundant at early developmental stages show some similar traits. Taller tree species with conservative leaves (high LDMC) and expensive fruits dispersed by cattle were also more abundant at both saplings and seedlings stages. These results indicate that present tree cover in pasturelands is dominated by particular tree characteristics in response to historical and ongoing both natural or anthropogenic disturbances and this affect also the functional composition of future tree community cohorts.

Secondly, we observed that relationships among tree abundances and some plant traits were different at early developmental stages in comparison to adult tree cover.

Tree species with denser woods, P poor leaves and expensive seeds (heaviest) have more sapling abundances, instead those tree species with C and N rich leaves have more abundant seedlings. As stated previously, tree adult's stages were dominated by species with softer woods with a high variability in leaf macronutrients contents and seed masses. This result shows that not only the characteristics of the most abundant adult's tree species are spreading successfully having more abundant seedlings and saplings populations. In contrast, these results suggest that actual pasturelands management and environmental conditions are also filtering tree species abundances at early developmental stages, favoring species of future tree populations with particular plant traits independently from those observed in the most abundant adult trees species. A reduce mortality at early stages due to higher resistance to plant damages by cattle grazing and browsing could be achieved by tree species with denser woods (Poorter et al 2008). In addition, tree species with higher parental resources in seeds, faster growing rates and higher photosynthetic rates together with a low palatability of leaves are probably favoring a higher population of saplings in active pasturelands to overcome the low fertility soils, the full sun exposures and herbivorous damages (Kitajima 2002).

Thirdly, we observed that dispersal mode of tree species is consistently related with abundance of trees at all developmental stages. Only the species dispersed by big mammals like cattle have more abundant seedlings and saplings populations, despite those dispersed by wind are also the more abundant adult's trees. In contrast, tree species dispersed by local fauna were limited in all developmental stages.

These results confirm that the fragmented agricultural landscapes impose barriers for successful natural tree regeneration, additional to the reduced amount of mature trees already present as seed source inside these areas, which tree species have to confront having different functional strategies. The reduction of the vertical structure for example, the high soil temperatures and the excessive grass cover in pastureland could represent examples of such filters by reducing the seed rain of already reduced community of tees species dispersed by local fauna inside these areas. No matter the high abundance of wind dispersed tree species inside the pastures, those dispersed by mammals have more abundant seedlings and saplings populations. Although not yet fully tested, several reasons can increase the probably of cattle dispersed seeds to have more abundant populations: a higher number of fruits can be eaten by animals increasing the seed rain in these areas, cattle reach longer dispersal distances increasing the probability to colonize new adequate microenvironments, cattle dungs reduce grass competition during the early seedlings´ establishment and can provide additional nutrients sources to soils for the early growth phases of saplings.

Fourthly, ours results show that adult tree abundances were the strongest predictor of tree seedlings and saplings abundances in active pasturelands. Correlation and regression coefficients between adults´ abundances and seedlings´ and saplings´ abundances were higher (0.55 and 0.51 respectively) than those among plant traits and early stages abundances (whole plant traits = 0.15 to 0.25; leaf traits = 0.13 to 0.23; reproductive traits = 0.12 to 0.36). These results showed that the abundance of seed sources inside agricultural lands is the strongest independent predictor of natural regeneration abundances, simply because a higher density of mature trees increases seed rain and thus the probability to successfully develop seedlings and saplings of this species inside the managed areas. This result is particularly relevant for conservation purposes because reinforces the importance of maintaining an abundant and diverse adult tree cover within managed areas to encourage tree natural regeneration in agricultural lands.

Finally, both adult's tree cover abundances and plant traits explain together the highest proportion of variability in saplings and seedlings relative abundances. Between 60 and 67% of species abundance variability was explained by adult tree abundances and plant traits, meanwhile whole plant, leaf and dispersal traits explain only 55 and 56% of saplings and seedlings abundances respectively. Therefore, although adult abundances are the per se the strongest predictors of tree natural regeneration abundances, tree plant traits increase the prediction capacity of tree species variability in composition and abundances at early tree developmental stages. The variability of saplings and seedlings population of tree species in active pastures is better predicted by most abundant adult trees together with highest contents of leaf dry matter or total carbon and longest fruits or seeds. Abundant adult tree populations inside pastures assure the availability of abundant seed sources; longest fruits and seeds are correlated with successful dispersal modes in open grasslands like mammalochory which increase seed rain and seed germination; meanwhile stronger leaves reduce mortality risk due to herbivorous damages like during cattle grazing. Together all this tree characteristics define an optimal plant strategy to successfully overcome the limited dispersal, early establishment and growth of tree species in active pasture sites.

All these results in the second chapter define clearly that some of the tree functional strategies observed in the first chapter for the actual tree cover in active pastures, are successfully maintaining tree populations in agricultural lands meanwhile others are not. Now we have a clear understanding of the characteristics of those tree species having active or having limited natural regeneration after strong disturbances caused by deforestation for pasturelands establishment and livestock production. As a consequence of this disturbance, present tree cover is dominated by particular tree characteristics like taller deciduous trees with softer woods, small and more conservative leaves (low SLA, high LCC) with expensive (big, heavy) and longest fruits carrying big and longest seeds dispersed mainly by wind and cattle. Trees with these characteristics are more abundant seed sources and therefore are more able to regenerate. However only those abundant tree species with also strongest leaves (high LDMC or LCC) and dispersed by cattle (longest fruits or seeds) have also abundant seedlings and saplings populations, possibly dominating future tree cover. In contrast, the populations of tree species with contrasting characteristics like those dispersed by wild fauna, will probably continue to decrease inside active pasturelands. These results suggest that the diversity of actual tree functional strategies in active pastureland will decrease possibly affecting other ecosystems process more directly linked with the productive system like litter decomposition and nutrient cycling.

5.4 Tree effects on ecosystem processes

In the final third chapter of results we test if tree functional diversity and natural regeneration capacity is related to differences in decomposition rates and nutrient releases of tree species in active pastures (**Figure 5.3**). We hypothesized that tree species in managed pasturelands have different litter and nutrient decomposition rates related to the previously identify tree functional strategies and natural regeneration capacities. The fact that tree species have different decomposition rates related with their life strategies and natural regeneration capacities, imply that the productivity of the agricultural system and not only tree cover diversity per se, will be affected with the reduction of actual tree functional strategies. These results are highly relevant by providing for the first time in agricultural landscapes, a better understanding of the direct links among tree characteristics and ecosystem functioning for a wide sample of tropical tree species.

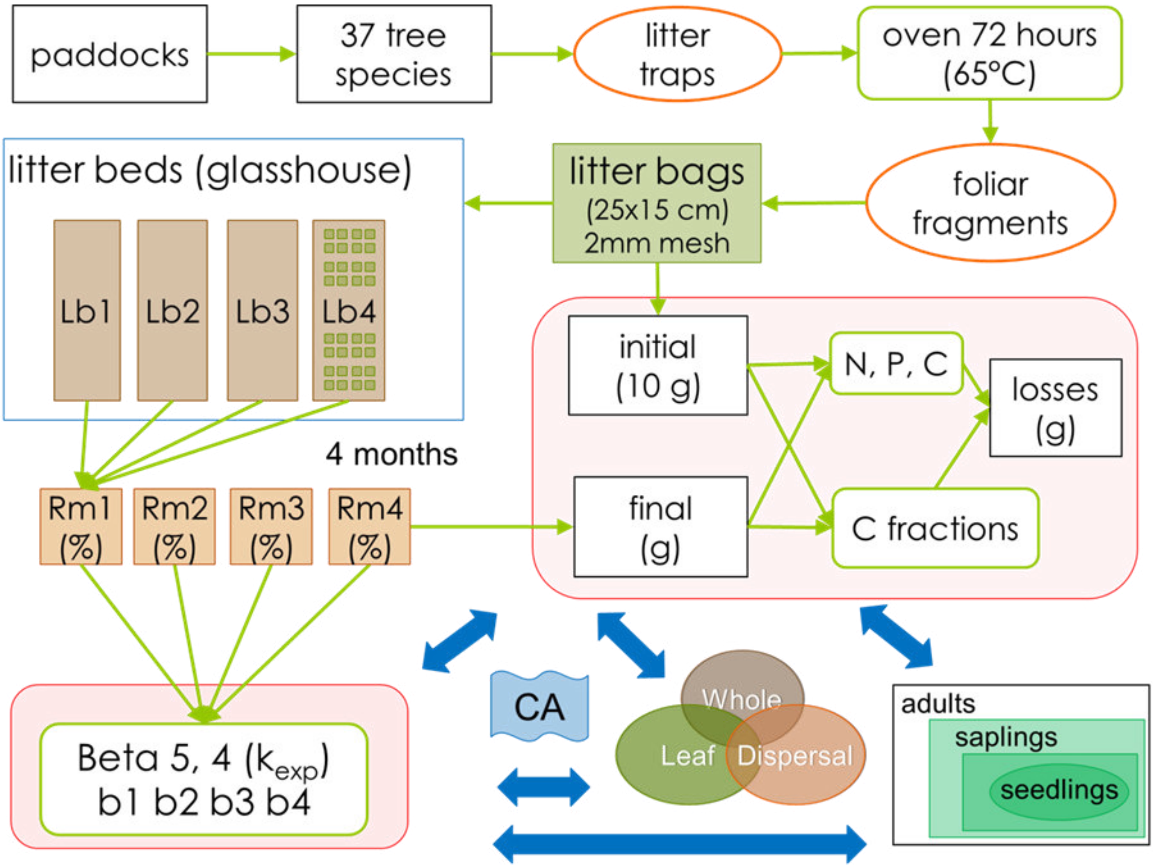


Figure 5.3. Methodological approaches to evaluate the relationships between the variability of tree species in litter quality, decomposition and nutrient releases rates with the main dimensions of plants variability (leaf, whole plant and reproductive traits) and tree capacities to naturally regenerate for 37 tree species commonly found in Central American active pasturelands (Chapter 3).

The scheme in **Figure 5.3** shows the standard decomposition experiment method used in chapter 3. Here, tree litter collected by litter traps in pastures were used to fill litter bags (375 cm 2 nylon bags with 2mm mesh) with 10 grams of foliar litter fragments (app. 4 cm2 each), incubated in a block design arrangement on litter beds. These beds were filled with pasture soils inside a glasshouse with homogenized environmental conditions (temperature and moisture). Four litter bags by species (one from each litter bed) were harvested monthly to measure i) the percentage of remaining litter mass during 4 consecutive months (Rm1, Rm2, Rm3, Rm4) and ii) fit decay curves to simple exponential models and obtain the overall decomposition rates (BETA 5), partial (Beta 4) and monthly decomposition rates (b1, b2, b3, b4). Samples from initial (fresh litter) and final remaining litter at the end of 4 months of litter incubation (decomposed) were used to measure total macronutrients (N, P, C) and C fractions contents (initial litter quality) so that their difference was used to calculate nutrient losses during decomposition process (releases). The relationships between litter decomposition rates, quality and nutrient releases with the main dimensions of plants variability (leaf, whole plant and reproductive) and with tree capacities to naturally regenerate under anthropogenic disturbances were tested using correspondence analyses (CA) for paired correlations.

The links among decomposition rates, plant traits and regeneration capacity of this tree community in active pasturelands can be summarize it into five key results: 1) tree species in active pasturelands have a wide array of different decomposition rates and litter qualities. 2) a wide sample of tree tropical species and leaf traits show the afterlife effect of their leaf economic variability, 3) in addition to leaf traits, whole plant traits and reproductive traits are both related with differences in litter quality, decomposition rates and macronutrients releases during decomposition. 4) more abundant tree species have faster decomposition rates in late months of litter decay than less abundant tree species; and, finally, 5) the strength of the correlations among tree abundances, litter quality, decomposition rates and nutrient releases depend on tree developmental stage. Therefore, litter quality of those tree species more abundant at early developmental stages and more probability to succeed naturally in these areas, is different from the litter of more abundant of adult's tree species, probably affecting future decomposition rates and nutrient releases. These results are particularly relevant in the context of the biodiversity conservation and its effects on ecosystems processes linking the importance of tree cover maintenance in agricultural lands with nutrient cycling.

The following lines expand on the key finding of chapter 3 and their relevance to improve our understanding on the effects of tree functional diversity on ecosystem processes. Tree species commonly found in active pasturelands have a wide variability in litter quality, decomposition rates and nutrient releases. Macronutrients and C fractions contents varied also widely among species. On average, half of litter mass decomposed during four months ranging from 20 to 74% for 37 tree species. Overall and monthly decomposition rates vary also between species from 0.09 to 0.78, with faster decomposition rates during the first month (0.32) and slowest during decay rates during the fourth month (0.17). This high variability imply that tree cover commonly found in active pastures can have also variable effects over ecosystems processes like nutrient cycling and soil carbon formation according to tree functional strategies.

Our results extend the scope of the afterlife effects of leaf variability spectrum from macronutrients to C fractions contents of green leaves. We confirm that tree species with high P, N, C in green leaves have also high P, N, C in fresh litter. However, we find in addition that tree species with high C fractions in green leaves have also high C fractions in fresh litter. Therefore, leaves of tree species with acquisitive leaves, high SOL and HEM, but low LIG contents decompose faster and release more N, P and C, particularly more SOL, HEM and LIG than those of more conservative tree species. These results show that leaf characteristics of trees have clear effects on ecosystems processes far beyond their effects on living tree strategies, potentially influencing other system components like soil fertility and grass productivity.

Whole-plan and plant and reproductive traits were also correlated with decomposition rates and nutrient releases' variability. Taller tree species with high LIG but low HEM contents in litter have slow decomposition rates during the last months of litter incubation and releases lowest C and N than shorter species. Leaf litter of tree species with expensive fruits and seeds construction and with more longest dispersules have more C, N and LIG but low SOL and HEM, decompose slowly during the first months of litter incubation and release low C, N and P contents than cheap and more spherical dispersules. These results show that other spectrums of plant variability like i) tree phenology and stem variability and ii) fruits and seeds investment (which are more related with growth rates and reproduction capacity) are also related with the afterlife effect of leaf variability. According to these results, tree natural regeneration capacity after disturbances could be also related with decomposition rates variability affecting nutrient cycling and carbon storing according with the functional strategies of the tree cover capable to maintain their populations in agricultural lands.

In fact, abundances of tree species commonly found in active pasturelands were correlated with litter quality, decomposition rates and nutrient releases. Tree species with abundant populations (i.e. with high capacity to naturally regenerate in these areas) showed faster decomposition rates than less abundant tree species. Leaf litter of the more abundant tree species have high P but low CEL contents and release higher amounts of N and LIG during its faster decomposition than less abundant tree species. In addition, the strength of correlations between tree abundances at early developmental stages with litter quality, decomposition rates and nutrient releases, differ from those at adult stages. Tree species with larger saplings population, for example, have litter with more N and LIG contents, faster decomposition rates only during the last months of litter decay and release less CEL than those tree species showing more abundant adult populations, faster overall decomposition rates and larger P, C and SOL releases. These results imply that actual tree cover dominated by tree species with faster decomposition rates might be replaced by a tree cover with species with slower early-decomposition rates due to higher N and LIG litter contents. This change in tree cover composition might affect macronutrients cycling and soil carbon due to a more variable P, C and Sol release rates and lower CEL rates and higher N and LIG releasing rates. Together all these results provide strong evidence of the links between tree species characteristics, population dynamics and ecosystems processes in agricultural lands.

5.5 PRACTICAL RECOMMENDATIONS

The livestock sector, a major driver of land use change in neo-tropical areas, accounts for 30% of global land area (Havlík et al. 2013) while only15% is covered by globally protected forest areas (Lindenmayer et al 2012). The remaining and sometimes high diversity tree cover outside fragmented forest in agricultural lands represent a high proportion of regional diversity (Harvey and Saenz 2008) but is also endangered worldwide (Fisher et al 2009). The different capacities of tree species to reproduce and maintain viable population within managed areas is predicted to reduced by half of the actual tree diversity in Central America (Esquivel et al 2008).

Non-sustainable management pactices of tropical pastures such as eliminating or reducing original tree cover in favor of extensive natural or exotic grasslands have often to deal with a gradual decline in soil fertility and forage yields some years after pasture establishment (Fearnside and Barbosa 1998). Maintaining or increasing tree cover in active pasturelands can potentially increase productivity and avoid degradation of pasturelands by providing nutrients and organic matter to soils while providing additional goods and services such as wood and fruits, reduced cattle heat-stress (Velasco et al 1999). Since agricultural production is a major driver of the tropical deforestation, improvements in agricultural productivity should be a part of the strategy for addressing deforestation (i.e. given the potential reduction in the need to expand to new areas after degradation-induced abandonment of pasturelands), a significant global source of greenhouse gas emissions and an historical contributor to climate change (Rose et al 2013). Given the reduced area of protected forests and the continuous high rates of deforestation, finding management approaches that will sustain the multiple environmental and economic values of the tree cover remaining into the vast agricultural lands is imperative.

Agroforestry Systems are alternative agricultural land uses which grow herbaceous plants (crops and grasses) and animal production (cattle) in association with different woody species (shrubs and trees) in diverse spatial arrangements. Silvopastoral Systems (SPS) include specifically the different spatial and temporal associations among woody species and grasses to maintain or increase pasture productivity. These sustainable livestock production systems vary widely in terms of spatial arrangements, density and diversity of the woody components and therefore in their implementation costs. Some of the most common SPS consist in one or a combination of practices such as isolated trees in pastures, live fences, cattle grazing in forest plantations, tree-grasses alley farming, high wood-density systems for cattle browsing and forage banks. The intensification of SPS in products, management and investment also vary incrementally from isolated trees where naturally-growing trees are protected to obtain forage, fruits, woods and shadow for cattle to protein and energy forage banks where woody species with high quality leaves are sown in dense plantations, harvested and feed to stabled cattle. All these systems have widely been reported to increase livestock productivity and sustainability, while helping to reduce the negative effects of forest-fragmented agricultural landscapes on connectivity and regional biodiversity (Harvey et al 2004).

To expand the adoption of SPS, some issues related to resources needed for establishment and available knowledge guiding management decisions should be considered. More specifically, farmers' decisions to convert conventionally-managed pastures to SPS depend, among many factors, also on establishment costs. In this respect, conventional methods for reintroducing trees in pasturelands have relied largely on costly forestry methods starting by growing saplings in greenhouses and then planting them in the field. The management of tree natural regeneration has been proposed as a cheapest strategy for the the maintenance of isolated trees in active pasturelands and the establishment of SPS. However, our knowledge to date is mainly based on research focusing on ecological interactions among SPS components such as light and soil nutrient competition among a limited number of trees and grasses. In this respect, the lack of understanding on the relationship at different spatial and temporal scales (and the correspondent benefits provided) among tree cover variability and their ecological interactions with SPS components (grasses, soils and cattle) has limited the dissemination of this strategy and thus farmers' adoption, although they have been proposed as cheap way for the establishment of these systems. In this context ours results can help to improve our understanding on sustainable pasture management at different levels.

The description of tree plant functional strategies increases our knowledge ~~the~~ on which are the characteristics of species commonly found in active pasturelands and how one more obvious tree characteristic like ldmc is associated with another like wood density or fruit and seed masses. This knowledge about tree characteristics associations could help farmers to determine the multidimentional effects of tree species over the pasture, as well as the investments required to maintain such species within the system. The identification of a “leaf variability spectrum” for tree species commonly found in active pastures, which split apart conservative leaf species from those with the opposite characteristics (i.e. acquisitive) will help to identify tree species with potential forage uses. Tree species in pastures with high leaf quality for example, can be desired for potential cattle consumption fortending to have low leaf dry matter contents, low total carbon and low recalcitrant fractions which increases rumen digestibility and palatability of leaves.

The identification of a “stem and phenological variability spectrum” (i.e. stating that taller deciduous trees have softer woods than shorter evergreens) help also to identify properly the pros and cons of including particular tree canopies into pastures. For example, when high quality woody resources are desired inside pastures, potential higher increases in light interference (i.e. affecting grass growth) can be expected with the evergreen tendency of denser wood species, probably reducing to some extend grass productivity. These relationships are particularly relevant to model and predict properly the productivity of each component of the system (grasses and trees) previous any particular decision making.

The identification of a “fruit and seed investment spectrum”, splitting apart tree species with bigger and heavier fruits from those with small and lighter fruits and seeds (cheap – expensive) help also to identify tree species with different capacities to naturally colonize disturbed areas for SPS or even forest restoration purposes. Tree species with small, light and more spherical dispersules disseminated by local fauna require more assistance to reach open pasture sites due to the reduced availability of maternal sources thus decreasing their chances to successfully germinate and establish at early developmental stages. In fact, seed rain and seedling banks of these tree species with cheap spherical dispersules has been found mainly restricted to microsites like under-canopy areas of previously established isolated trees frequently visited by birds and bats. In contrast, those tree species with expensive (big and heavy) and longest dispersules are those requiring a reduced dispersal assistance mainly due to their cattle-based wide dispersion of their seed banks in open pastures.

The observation that these leaf, stem and reproductive variability spectrums, and whole plant traits are associated increases the capacity to predict other unknown tree characteristics from other few and most commonly available traits. Moreover, our findings on the interactions among traits of diferent dimensions can help to make inferences about over holistic effects of tree species in sps and to better calculate the investments required to maintain useful tree species using tree natural regeneration management. For example, those tree species with higher nutrient contents but fragile acquisitive leaves tend also to be also the more deciduous tree species with a shorter leaf life associated to their low carbon investments in leaves and woods (deciduous-softer-acquisitive). Tree species with acquisitive leaves have also cheapest fruits and seeds as evidenced by their reproductive investment spectrum (acquisitive and cheap fruit and seeds) in contrast to conservative tree species with more expensive fruits and seed construction. Finally, a phenological, stem and reproductive spectrum split apart deciduous tree species with small and lighter seeds from evergreen species with more expensive fruits and seeds (deciduous cheap fruits and seeds).

These results are relevant for the selection of tree species in SPS according not only to forage but also to additional tree services offered to cattle during dry season such as wood, shadow and fruits. The identification of tree species with higher investments in carbon (e.g. those evergreen species with denser woods and conservative leaves) helps also to distinguish the reltive potential of SPS on environmental services like carbon sequestration. More specifically, evergreen tree species with conservative leaves and expensive fruits are probably presenting higher carbon investments, with potential interest for environmental payments schemes interested in mitigation of climate change in agricultural landscapes.

The fact that the fruits and seed investment spectrum were correlated with leaf, stem and phenology spectrums provides additional insights on adequate mechanism for the establishment and management of tree species in pasturelands. Dispersal modes were correlated with leaf, whole plant and reproductive traits providing directions about the requirements for tree species establishment as well as of their tree adult characteristics affecting the productive system. Tree species dispersed by wind were taller, deciduous with rich phosphorus leaves, bigger and longest fruits carrying lighter seeds. Tree species dispersed by local fauna were shorter with big but cheap constructed leaves (low LCC) carrying small, lighter and spherical fruits with spherical seeds. In contrast, tree species dispersed by big mammals like cattle, have strong and expensive leaves (high LDMC and LCC) with low nutrient content (LPC and LNC) and carried big and heavy fruits with heavy seeds. Tree species with parental dispersion have dense woods but fragile nutrient rich leaves (high LNC) having the longest fruits. Tree species dispersed by cattle will require lower investments by farmers than tree species with richer forages but mainly dispersed by wind and local fauna.

This research results provide guidance to promote low cost establishment of tree cover in SPS given the correlation among tree species capacity to naturally regenerate and those plant traits strongly related with the three main dimensions of plant variability (leaf, stem and phenology, and reproductive investment spectrums), as well as to adult tree abundances is especially relevant to develop management schemes which assure the sustainability of diverse SPS at low expenses.

Under actual management practices overlooking the importance of maintaining tree cover diversity, the highly variable characteristics of tree species in active pasturelands will not persist in the following tree cover generations. The present adult tree cover is dominated by tree species characteristics such as taller deciduous with softer woods, small and more conservative leaves with expensive and longer fruits, carrying bigger and longer seeds dispersed by wind and cattle. Since more abundant tree species in these agricultural lands have a higher probability to regenerate due to higher seed availability, the future tree cover will continue to be dominated by some of these characteristics (i.e.conservative leaves and expensive fruits dispersed by cattle), associated to tree species with more abundant seedlings and saplings banks. If more nutritive forages are desired for future tree cover in agricultural lands then management schemes should promote species providing more seed rain, seedlings banks and saplings survivorship .

The fact that both adult tree abundances and plant traits were predicting a higher proportion of the early relative abundances and composition is relevant for landscapes conservation and management. Adult tree abundances and plant traits explained between 60 and 67% of species abundance variability. Increases in adult abundance of tree species with limited natural regeneration (e.g. dispersed by wind, local fauna or parental trees are required to increase the probability of this species to persist inside agricultural landscapes. In contrast, tree species dispersed by big mammals like cattle which have active and abundant natural regeneration in active pastures can be managed to increase their additional potential incomes to the grazing systems designing more structured SPS.

Tree species in managed pasturelands have different litter and nutrient decomposition rates, related to tree functional strategies and natural regeneration capacity. This result is of huge relevance to point out how tree diversity and characteristics have direct link to ecosystems services like biomass decomposition, nutrient and carbon cycling inside agricultural lands. The fact that also the natural regeneration capacity of trees is linked to decomposition and plant characteristics suggests that farmers can potentially manage tree cover to stir tree diversity and composition towards a desirable nutrient and carbon cycling performance for sustainable production.

The afterlife effect of the leaf variability spectrum for this wide sample of tree tropical species underline~~d~~ that quality of tree leaves are not only strong predictors of litter decomposition rates but also predictors of nutrient and carbon cycling. Therefore, acquisitive tree species with a high leaf litter quality decomposes almost 4 times faster than tree species with the more conservative leaves with low litter quality. The implementation of pasture management strategies increasing the abundance of tree species with faster decomposition rates will probably speed up grasslands' litter decomposition increasing perhaps the turnover of nutrients from trees, to soil and grasses. In contrast, management practices promoting the opposite tree cover composition i.e. tree species with more conservative leaves, will probably slow down grasslands' decomposition, tending to increase carbon stocks in soils.

The fact that not only leaf traits, but also other tree characteristics were related with differences in litter quality, decomposition rates and macronutrients releases implies that SPS-management decisions affecting the provision of tree cover services like wood, shadow or fruits forages can also have direct effects on carbon and nutrient cycling. Taller tree species which can be desired to reduce pasture shadow have leaves with low hem and high lig which decomposed slowly during the third and fourth months of litter incubation and release less c and n than shorter tree species. Tree species with expensive fruit and seed construction can be desired as alternative forage for cattle having more C, N and LIG but low SOL, HEM and P in leaf litter, decomposing slowly during the first months of litter incubation and releasing less C, N and P than cheap constructed fruit and seeds (small light spherical fruits/seeds).

The observation that also tree regeneration capacity is related with decomposition rates and macronutrients releases during decomposition gives us insight about the actual and futures states of such ecosystems processes in active pasturelands. The most abundant adult tree cover have litter with high P and low CEL decompose faster and release higher LIG, P, N, C and SOL amounts than less abundant adult tree species. However, decomposition rates and macronutrients releases from leaf litter of the more abundant tree species in adult stages are different from those tree species having more abundant early developmental stages. Tree species with a higher capacity to naturally regenerate under actual management practices (most abundant seedlings and saplings populations) have more N and LIG in leaf litter, more variable initial decomposition but higher decomposition rates during the last months of litter incubation. Therefore, decomposition dynamics and nutrient releases will probably change in further generations of tree cover, releasing less CEL and more variable P, C and SOL than those tree species with more abundant adult populations today but making more N and LIG relesesreleases. These results show that the management of tree natural regeneration is an accessible practice to drive actual and future nutrient cycling services searching to maintain or increase soil fertility or carbon stocks in active pasturelands.

Our results show clearly that altering the variability of tree characteristics has a direct effect on the functioning of ecosystems processes like decomposition, carbon and nutrient cycling which are relevant for fertility replenishment and productivity in managed pasturelands. The effects of the variability in tree decomposition rates and nutrient releases on grass litter decomposition, soil fertility and grass productivity remains unknown (being beyond the scope of this research) but are imperative to fulfill understanding of tree variability effects on grasslands ecosystems. However, the relationships between decomposition rates and nutrient releases with plant traits and species abundances outline a clear link between tree species characteristics and ecosystem processes. Present tree cover has wide differences in litter quality tending to faster decomposition rates for more abundant tree species. Decreases of tree cover functional diversity due to the limited regeneration capacity of less abundant tree species with particular relationships with leaf, reproductive and whole plant traits probably decrease decomposition rates of tree leaves affecting nutrient and carbon cycling in Central American pasturelands.

5.6 GENERAL CONCLUSIONS

Plant strategies: Tree species in active pasturelands have wide variability of plant traits. These plant traits interact in several plant spectrums defining different plant strategies where investments in fruit and seed construction are related with leaf and whole plant traits like i) leaf - reproductive and the ii) phenology – stem – reproductive investment spectrums.

Tree responses: Tree capacity to naturally regenerate in active pasturelands is related with leaf, reproductive and whole plant traits, being adult abundances the main predictors of early stages abundances. Adult abundances are dominated by taller deciduous trees with conservative leaves and expensive investments in fruits and seeds dispersed mainly by wind and cattle. However tree species with denser woods, low P, high N and more expensive seeds dispersed by cattle have more abundant early development stages in response to disturbances.

Ecosystem effects: The variability in decomposition rates and nutrient releases of tree species in active pasturelands are strongly related with leaf spectrum but also with reproductive and whole plant traits as well as with tree abundances. Tree species with more conservative leaf decompose slowly and release less SOL, HEM and LIG. Taller tree species decompose slower at the last months meanwhile those with higher investments on fruits at seed tend to decompose slowly during the first months, releasing less nutrients and C fractions. The most abundant adult tree species were related with faster decomposition rates at the end of litter incubation time, but litter quality of tree species with more abundant saplings have more N and LIG resulting in less CEL and more variable P, C, SOL releases.

Therefore this links between plant traits, species responses to disturbances and ecosystems processes imply that tree species with contrasting functional strategies have different capacity to naturally regenerate in Central America pasturelands and have contrasting effects on litter decomposition and nutrient driven future ecosystems services in SSP.

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