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Growth and inter-specific interactions in young silvopastoral systems with native timber trees in the dry tropics of Costa Rica

Hernán Jair Andrade Castañeda

Growth and inter-specific interactions in young silvopastoral systems with native timber trees in the dry tropics of Costa Rica

By

Hernán Jair Andrade Castañeda

Thesis submitted to the consideration of the Graduate School to opt for the degree of Doctor of Philosophy at the CATIE – UWB joint PhD Program

Tropical Agricultural Research and Higher Education Centre (CATIE),
Turrialba, Costa Rica
School of Agricultural and Forest Sciences, University Of Wales (UWB),
Bangor, Gwynedd, United Kingdom

March 2007

Doctoral Advisory Committee

Dr. Muhammad Ibrahim (Major Advisor)

Department of Agriculture and Agroforestry, CATIE

Dr. Robert Brook (Co-advisor)

Lecturer, School of the Environment and Natural Resources, University of Wales, Bangor

Dr. Philippe Vaast (Committee member)

CIRAD (Centre de coopération Internationale en Recherche Agronomique pour le Développement)

Dr. Francisco Jiménez (Committee member)

Department of Natural Resources and Environment, CATIE

Dr. Fergus L. Sinclair (Committee member)

Senior Lecturer, School of the Environment and Natural Resources,
University of Wales Bangor

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Dedication

To my parents who worked hard to give me an impulse in my professional and personal life.

To my wife Milena and our son Juan Camilo for their love, patience and permanent support in this phase of our lives

To my sisters, brothers, nephew and nieces.

To Colombia, I hope we can stop the stupid fight against ourselves.

Acknowledgements

This thesis was produced with the partial financial support of the Cerbastan Project, which was an agreement between CATIE and Hacienda La Pacifica to promote the establishment of trees in grassland in the dry forests of Costa Rica. Special thanks to Ph.D. Candidate Outi Myatt-Hirvonen who supported the fine root and carbon sequestration study through the Project on Land Use Change and Carbon Flows in Central America (LUCCAM; University of Helsinki / CATIE).

First of all, I wish to thank my supervisors Dr. Muhammad Ibrahim (CATIE) and Dr. Robert M. Brook (UWB) for their guidance, dedication and patience during the production of this work. They were more than advisors; they have been friends who supported me in the academic and personal life. Thanks to my committee members Dr. Francisco Jiménez, for his patience, support and reviewing of the writing; Dr. Philippe Vaast for his support and interest; and Dr. Fergus Sinclair for the arrangements in Bangor. To the past and present coordinators of the Cerbastan Project: Dr. Andrea Schlönvoigt, Dr. Mario Piedra and Dr. Guillermo Navarro, who always supported me in this research adventure. I would like to thank to my wife Milena who supported me working many hours in the edition of the document.

I wish to mention especially to Dr. Eduardo Somarriba for his support, interest and good advice. To Dr. John Beer, for his patience as the head of the Department of Agriculture and Agroforestry at CATIE. I am grateful to Dr. Glenn Galloway and the staff of the Graduate School at CATIE. Thanks are due to the people of the Orton library. I wish to thank to Dr. Fernando Casanoves and M.Sc. Gustavo López at CATIE for their support in statistics and SAS programming, respectively.

To Don Fernando Estrada (General Manager of La Pacífica) whose support was fundamental for the development of this research. To the rest of the La Pacifica's staff mainly to Nestor Boniche, Werner Martinez, Elvin Rios, Harvey Alvarado,

Andrés Hidalgo and Alejandro Sánchez; and all hotel’s personal: Ronald, Cristina, Ilena, Yadira, Alfredo, Daisy, Yudith and Francisco. To For. Eng. Leonardo Mora, for his support and interest in the work. To all field workers, mainly Fernando, Mauricio and Henry.

I would like to thank many people, I hope nobody is forgotten. To M.Sc. Jairo Rojas, who carried out his thesis in the same experiment. To laboratory and office assistants: Yaneth Sánchez, Guisella Montoya, Ney Ríos, Mario Martinez, Mónica Salazar, Amparo Ostos and Alexander León whose work was key for the development of this thesis. Special acknowledgement to Sue Pattinson, who reviewed the english of the entire thesis.

To all colleague current and former PhD students: Tangaxuhan, Humberto, Angel, Maria Helena, Rudy, Pedro, Wataru, Juan Carlos and Leigh. To all our friends at Turrialba: Giovanni, Claudia, Lorena, Gabriel, Liliana, Maria Fernanda, Gaby Robles, Gaby Ávila, Marilyn and Elias.

Biography

Hernán Jair Andrade Castañeda, a national of Colombia and Costa Rica, was born in Chaparral (Tolima - Colombia) on July 22th 1973. He concluded his high school education in 1989 and obtained his Agronomical Engineering degree at the University of Tolima (Ibagué – Tolima – Colombia) in 1995. He was working as young researcher in the Colombian Corporation of Agricultural Research (CORPOICA) from January 1996 to December 1997, working in silvopastoral systems and improved grasslands. Hernán obtained his MSc degree in Tropical Agroforestry in the Tropical Agricultural Research and Higher Education Center (CATIE) in December 1999. Between January 2000 and March 2001, he was working at CATIE as researcher in the Electronic Platform on Livestock and Enviroment. During his time at CATIE, Hernán has had a wide participation in the academic and research life at this institution as professor of the course "Agroforestry with annual and perennial crops", guess editor for two special issues of "Revista Agroforestería en las Américas", committee member of seven MSc students, and instructor of several training courses. In April 2001, he was awarded with a scholarship from Cerbastan Project (CATIE – Hacienda La Pacifica) to start his PhD. In January 2007, he concluded his PhD under the CATIE-University of Wales (Bangor) joint program. His research interests are ecological interactions in agroforestry systems such as water and radiation competition and carbon sequestration. His permanent contact address is handrade@catie.ac.cr.

Summary

Silvopastoral systems, win-win technologies to enhance productivity and providing environmental services, may play an important role in retaining trees (Ibrahim et al. 1999, Gobbi and Ibrahim 2004), and to mitigate the deforestation process attributed to cattle production in the last decades. *Brachiaria* grasses are the most widely planted tropical forage grasses in Latin America. It is calculated that the area under *Brachiaria* grasses in Brazil ranges between 30 and 70 million hectares (Miles et al. 1998). Tree-grass associations with *Brachiaria* species are becoming frequent in the dry tropics; however, there is little information about how compatible these grasses are in silvopastoral mixtures with native timber tree species. Understanding the ecological and biophysical interactions in these systems is the key for designing and managing silvopastoral systems for sustainable production (meat, milk and timber) and generation of environmental services. Three native timber tree species (*Pithecellobium saman, Diphysa robinioides* and *Dalbergia retusa*) were planted with an improved grass (*Brachiaria brizantha*) and a naturalised grassland dominated by *Hyparrhenia rufa*. The central aim of this study was to understand the main tree-grass interactions in silvopastoral systems in the dry tropics. Tree growth, grass production, fine root interactions, water and radiation competition were studied to evaluate the most important biophysical interactions in dry tropics.

D. robinioides was the fastest growing species, and *P. saman* the slowest; while *B. brizantha* produced three times the aboveground and twice the belowground biomass as *H. rufa*. Trees had no effect upon grass yield. *P. saman* grew more slowly in *B. brizantha* than in *H. rufa* treatments, but there was no effect of pasture species upon the other two tree species. The carbon in phytomass varied between 7 and 13 Mg C ha^{-1} in no-tree pastures and silvopastoral systems, respectively, and soil organic carbon (SOC) averaged 100 Mg ha^{-1} for the top 60 cm of soil. *B. brizantha* appeared to stimulate tree root production, which in turn was highly correlated with the light fraction of soil organic carbon, resulting in increments in SOC of up to 9.9 Mg ha^{-1} year^{-1}.

Tree fine roots grew more than grass, responding more rapidly to increase in water availability, increasing the possibility of their establishment in grasslands. The fact that trees tended to have higher root competitive capacity in soil deeper layers and under canopy positions, and grass was more competitive in intermediate positions (away from trees) and superficial layers demonstrated the niche differentiation of this association. The introduction of improved and drought tolerant grass species such as *B. brizantha* enhances the root development of whole systems, increasing the coexistence of components in region with seasonal water deficits. The increment of soil nitrogen content by tree component, attributed to their nitrogen fixing capacity, is an advantage of these silvopastoral systems.

The transmission through the canopy of photosynthetically active radiation varied between 46.6 and 68.0% for *D. robinioides* and *P. saman*, respectively. Grass species did not affect the sap flow velocity of *D. retusa* and *D. robinioides*; whereas *P. saman* presented a higher sap flow velocity associated with *B. brizantha* than with *H. rufa*. Tree species did not affect the water use of grasses. At a plot level, these young trees used less water than grasses (on average, 0.11 vs 1.2 mm day^{-1}, respectively), showing the importance of selection of compatible grass species in these dry conditions. *D. robinioides* and *D. retusa* proved to be adapted species to seasonal drought via their adaptation in regulating water use according to soil and climatic conditions.

The silvopastoral systems evaluated showed great productive and environmental benefits such as the promotion of tree growth through the establishment of drought tolerant and productive grass species; the dry matter production of grass species was not affected by trees after four years; a relative high carbon sequestration in biomass and soil; nitrogen fixing of tree timber species; niche differentiation in terms of soil exploration; and the adaptation of evaluated species to seasonally dry environments.

The future research on silvopastoral systems in the dry tropics should be focussed on the evaluation of management practice to reduce tree-grass competition and to improve timber quality. Similarly, more attention needs to be directed to the estimation of the evapotranspiration of grasses, which is the main componente of the water use in these silvopastoral systems, and about phosphorus interactions because it was know the potential of these tree native species to improve soil nitrogen.

Resumen

Los sistemas silvopastoriles, tecnologías ganar-ganar para mejorar la productividad y proveer servicios ambientales, pueden jugar un papel importante en retener árboles (Ibrahim et al. 1999, Gobbi e Ibrahim 2004), y mitigar el proceso de deforestación atribuido a la producción ganadera en las ultimas décadas. Las especies de *Brachiaria* son las pasturas tropicales más ampliamente distribuidas en América Latina. Se calcula que el área con pasturas *Brachiaria* en Brasil varía entre 30 y 70 millones de hectáreas (Miles et al. 1998). Las asociaciones árbol-pasto con especies de *Brachiaria* están convirtiéndose cada vez más frecuentes en los trópicos secos; sin embargo, existe poca información sobre la compatibilidad de estos pastos en mezclas silvopastoriles con especies maderables nativas. El entendimiento de las interacciones ecológicas y biofísicas en estos sistemas es clave para el diseño y manejo de sistemas silvopastoriles para la producción sostenible (carne, leche y madera) y la generación de servicios ambientales. Tres especies maderables nativas (*Pithecellobium saman, Diphysa robinioides* y *Dalbergia retusa*) fueron plantadas con una especie de pasto mejorado (*Brachiaria brizantha*) y una pastura naturalizada dominada por *Hyparrhenia rufa*. El objetivo central de este estudio fue entender las principales interacciones en sistemas silvopastoriles en el trópico seco. El crecimiento de árboles, la producción de pasto, la interacción de raíces finas, la competencia por agua y radiación fueron estudiados para evaluar las más importantes interacciones biofísicas en el trópico seco.

D. robinioides fue la especie de más rápido crecimiento, y *P. saman* fue la mas lenta; mientras que *B. brizantha* produjo tres veces la biomasa arriba del suelo y dos veces la biomasa abajo del suelo que *H. rufa*, y los árboles no tuvieron efecto en la producción de pasto. *P. saman* creció mas lentamente en tratamientos de *B. brizantha* que en éstos de *H. rufa*, pero no hubo efecto de especies de pasto sobre el crecimiento de las otras dos especies de árboles. El contenido de carbono en fitomasa varió entre

7 y 13 Mg C ha^{-1} en pasturas sin árboles y en sistemas silvopastoriles, respectivamente, y el carbono orgánico del suelo (COS) promedió 100 Mg ha^{-1} en los primeros 60 cm de suelo. *B. brizantha* pareció estimular la producción de raíces de los árboles, lo cual estuvo altamente correlacionado con la fracción liviana del carbono orgánico del suelo, resultando en incrementos de hasta 9,9 Mg ha^{-1} año^{-1}.

Las raíces finas de los árboles crecieron más que las de los pastos, respondiendo más rápido a incrementos en disponibilidad de agua, incrementando las posibilidades de su establecimiento de praderas. El hecho que los árboles tendieron a tener una mayor capacidad competitiva en capas más profundas de suelo y en posiciones bajo su copa; y el pasto fue más competitivo en posiciones intermedias (lejos de los árboles) y en capas superficiales demostró la diferenciación de nichos de esta asociación. La introducción de especies de pastos mejoradas y tolerantes a sequía tal como *B. brizantha* mejora el desarrollo radicular de todo el sistema incrementando la coexistencia de componentes en regiones con déficit estacional de agua. El incremento en el contenido de nitrógeno del suelo por el componente arbóreo, atribuído a su capacidad de fijación de nitrógeno, es una ventaja de estos sistemas silvopastoriles.

La transmisión a través del dosel de radiación fotosintéticamente activa varió entre 46,6 y 68,0% para *D. robinioides* y *P. saman*, respectivamente. Las especies de pasto no afectaron la velocidad de flujo de savia de *D. retusa* y *D. robinioides*; mientras que *P. saman* presentó una mayor velocidad de flujo de savia cuando estaba asociado a *B. brizantha* que cuando lo estaba a *H. rufa*. Las especies arbóreas no afectaron el uso de agua de los pastos. A nivel de parcela, estos árboles jóvenes usaron menos agua que los pastos (en promedio, 0,11 vs 1,2 mm dia^{-1}, respectivamente), mostrando la importancia de la selección de especies de pastos compatibles en estas condiciones secas. *D. robinioides* y *D. retusa* probaron estar adaptadas a sequía estacional por medio de su plasticidad en regular su uso de agua de acuerdo a las condiciones edáficas y ambientales.

Los sistemas silvopastoriles evaluados mostraron grandes beneficios productivos y ambientales tal como la promoción del crecimiento de árboles a través del establecimiento de especies de pastos productivas y tolerantes a la sequía; la producción de materia seca de los pastos no fue afectada por los árboles después de cuatro años; un relativo alto secuestro de carbono en biomasa y suelo; fijación de nitrógeno de las especies arbóreas; diferenciación de nicho en términos de exploración de suelo; y la adaptación de las especies evaluadas a ambientes estacionalmente secos.

La investigación futura sobre sistemas silvopastoriles in el trópico seco debería estar enfocada en la evaluación de prácticas de manejo para reducir la competencia árbol-pastura y mejorar la calidad de la madera. Similarmente, es necesario dirigir más atención en la estimación de evapotranspiración en pasturas, lo cual es el principal componente de uso de agua en estos sistemas, y sobre disponibilidad de fósforo debido a que se conoció el potencial de estas especies arbóreas nativas en el mejoramiento del contenido de nitrógeno del suelo.

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CHAPTER I

1. INTRODUCTION

1.1. GENERAL INTRODUCTION AND RATIONALE

The deforestation process, one of the most important environmental problems in the world; causes the loss of around 13 million hectares of forests per year; most of this area becomes agricultural lands (FAO 2005). Permanent pastures covered most of the agricultural lands in Central America and Costa Rica (63 and 82%, respectively) in 2003 (FAO 2006a). This type of land use, mostly conventionally managed using fire and low inputs, has been increasing in the region in the last decade (0.1% year^{-1}; FAO 2006a); however, pastures degrade over time decreasing their productivity and causing environmental degradation. The tropical dry forest in Costa Rica has experienced a fragmentation process during the last four decades, caused mainly by cattle ranching practices (Arroyo-Mora et al. 2005). A tendency to replace naturalised grass with more aggressive and drought tolerant grass species is also occurring in Costa Rica and its dry zone. Improved grasses (*Brachiaria brizantha* and *B. decumbens*) cover 72% of the pasture area and 56% of total agricultural areas in Cañas (Esquivel et al. 2003). Between 1990 and 2003, 18.7% of the permanent pastures in Costa Rica have been established using *Brachiaria* species, contributing to about 55% of the national milk production and almost 18% of the beef production in 2003 (Holmann et al. 2004).

Well designed and managed silvopastoral systems are win-win technologies. These systems enhance productivity and provide environmental services and may play an important role in retaining trees (Ibrahim et al. 1999, Gobbi and Ibrahim 2004). Most farmers manage natural regeneration of trees in pastures because it is a very cost effective way to introduce tree component in grasslands. Trees in grasslands are able to provide a number of environmental and productive benefits such as improvement of productivity and nutritional quality of fodder, carbon sequestration, improvements in soil characteristics such as fertility, physical structure, water infiltration and nutrient cycling, soil conservation through reduced erosion, microclimate improvements, weed, pest and disease control, and conservation of biodiversity (van Noordwijk et al. 1991, Ong and Huxley 1996, Ibrahim et al. 1999, Ong and Leakey 1999, Ong et al. 2002, Beer et al. 2003, Harvey et al. 2004, Abule et al. 2005). However, benefits from the inclusion of trees in agricultural landscapes are often eclipsed by intense water competition (Smith et al. 1997) mainly in top layers.

Some studies have demonstrated increased growth of tropical grasses under tree canopies of moderate densities (Wilson 1998, Marlats et al. 1999, Andrade et al. 2004) mainly attributed to increased fertility or nitrogen availability under the tree canopy. Overall productivity and/or sustainability of agroforestry can be achieved by identifying and minimising competition for the most limiting resource in the system through proper selection and management of species combinations (Schroth 1995). However, the partitioning of resources between components is still not well understood (Lafolie et al. 1999). There are strong limitations to the implementation of these systems in arid and semiarid conditions, due to the lack of water availability in some seasons (Droppelmann et al. 2000); and this problem may contribute to low adoption of new silvopastoral systems in Central America (Dagang and Nair 2003).

Fine root dynamics is a key process for understanding the competition and dynamics of agroforestry systems (Dhyani and Tripathi 2000). Fine roots are the most active belowground component in terms of their dynamics (production and mortality), carbon and nutrient cycling and resource acquisition (Hooker et al. 2000), particularly in dry and/or infertile conditions (Schroth 1999, García-Barrios and Ong 2004). Although some root characteristics are generalized at species level, the actual root pattern is highly dependent on soil type, management and climate (van Noordwijk et al. 1996). Niche separation through spatial differentiation, where for example deep-rooted tree species could use resources outside the reach of crop roots or where there is temporal differentiation (Anderson and Sinclair 1993, Emmerman and Dawson 1996, Breman and Kessler 1997, Lehmann et al. 1998, Ong and Leakey 1999, Gyenge et al. 2002) may allow complementarity in resource sharing which will affect the success of the agroforestry systems.

The *Brachiaria* species introduced in the seasonally dry areas are more drought and shade tolerant than the naturalised grass species (*Hyparrhenia rufa*) and support higher stocking rates and animal productivity (Lascano 1991, Pizarro et al. 1998, Guenni et al. 2002). However, there is little information about how compatible these *Brachiaria* grasses are in silvopastoral mixtures with native timber tree species. This information is essential for designing and managing silvopastoral systems for sustainable production (meat, milk and timber) and generation of environmental services. Most studies on traditional systems have focused on inventory of tree species and system composition and structure. However, few studies have been conducted to evaluate the tree-grass interactions in terms of fine root development, water and radiation use, growth and productivity.

1.2. CONTEXT OF THE RESEARCH

This study was carried out in the seasonally dry zone of Costa Rica, which covers around 1056 km^2 (about 2.7% of national territory; Figure 1; ITCR 2000). The tropical dry forest is a biome that extends into other countries and regions. However, the dry region where the study was carried out is the onlyone in the non-coastal area and covers 54% of the dry tropics of Costa Rica. This area has historically been one of the hubs of cattle ranching in the country (Flores 2005, Monterroso 2005). Other important activities are irrigated rice and fish production. Around 58% of land is adequate for permanent crop systems, such as grasslands; whereas 27% of the area is devoted to forestry and 15% to annual crops. Tree resources are an important component of cattle farms in the Cañas zone because around 20% of their area is covered by forest and most of the pastures have trees (Flores 2005) mainly due to natural regeneration areas (Flores and Monterroso 2001). However, current tree structure in the zone may not be sustainable because natural regeneration is by the low proportion of small trees in pastures (Monterroso 2005).

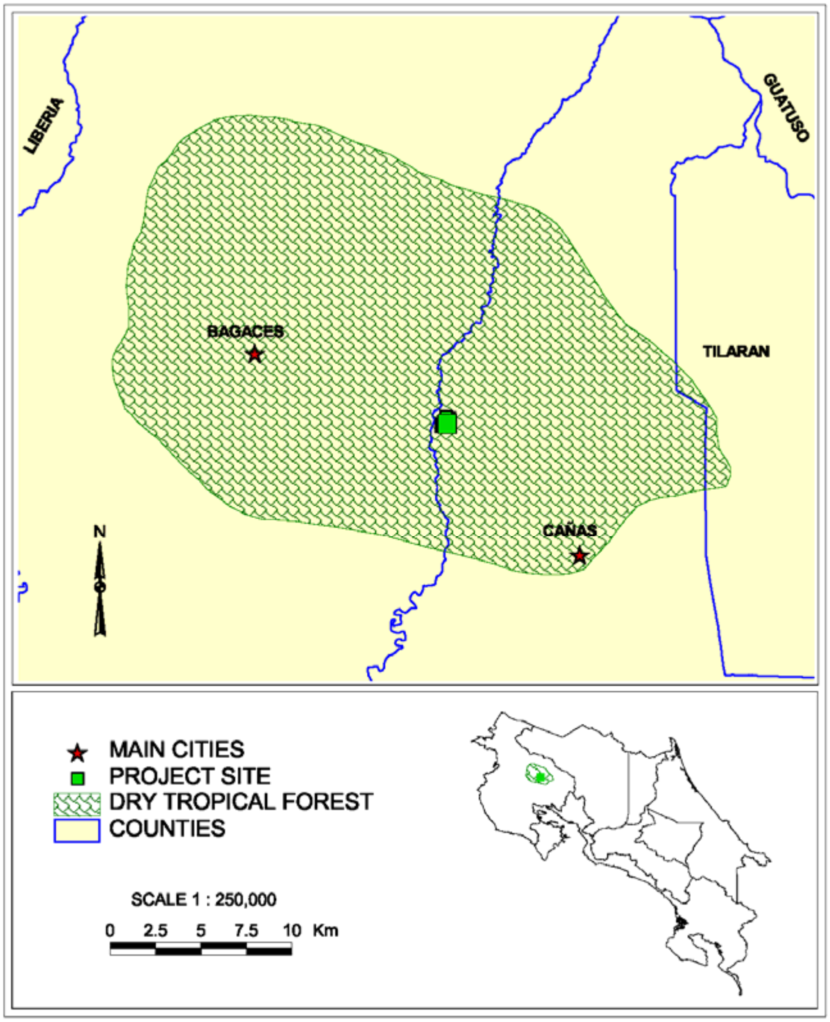

Figure 1. Location of the dry region of Costa Rica.

Tree resources in pastures have an enormous influence on the cattle production systems in the study zone. Farms with dispersed trees in pastures generate 35% more profits than pure cattle production (Monterroso 2005). However, the adoption of silvopastoral systems as opposed to dispersed trees in pastures or live fences is low mainly due to lack of knowledge about these systems and the expectation of receiving incentives from establishment of forest plantations (Flores 2005). Low financial capital and the lack of access to credit are the main constraints in livestock farms, which are mainly in small and medium sized properties (Flores 2005). The promotion of better tree management could be the best initial policy action for increasing tree cover and promoting higher rural incomes (Monterroso 2005).

The dry zone of Costa Rica lies at an altitude between 0 and 500 m, with the most of the land between 100 and 200 m (60%; ITCR 2000). The topography of the zone consists of plains and of hillsides with slopes between 30 and 60%, this covers 66% of the area (ITCR 2000). The region has a mean rainfall of 1500 mm year^{-1} with a poor distribution throughout the year as 85% of this rain falls between May and November. The mean temperature is around 28^{O}C, with minimum and maximum values of 23 and 36^{O}C, respectively. The relative humidity varies between 60% in the dry season, and 85% in the wet season (IMN 2003). The potential evapotranspiration in the area estimated by open pan, according to Taboga, is 1800 mm year^{-1} (unpublished data). The most dominant soils are inceptisols and entisols (ITCR 2000). The soil of the experimental site is classified as a Lithic Ustorthent - Lithic Dystropept Complex, belonging to the complex Bagaces-Liberia series. The parental material of the soil is volcanic ash and its texture is loam (20% clay; Herrick 1993).

The central aim of this study was to evaluate the main tree-grass interactions in silvopastoral systems with native timber tree species (*Pithecellobium saman, Diphysa robinioides* and *Dalbergia retusa*) and naturalised pasture dominated by *Hyparrhenia rufa* and improved (*Brachiaria brizantha*) grass species in the dry tropics. The fine root interactions, and water and radiation competition are some of the most important biophysical interactions in the dry tropics, and have primary importance in determining growth and productivity, which are fundamental for the success of silvopastoral systems.

1.3. OBJECTIVES

This study comprises three experimental chapters to address the following specific objectives:

- To evaluate early growth of trees, grass production and carbon sequestration in six silvopastoral associations (Chapter IV).
- To assess the fine root development of interacting components in terms of biomass and length (Chapter V).
- To estimate the water and radiation interaction in tree-grass systems and water use efficiency (Chapter VI).
- To evaluate the drought tolerance of tree and grass species in different silvopastoral combinations (Chapter VI).

1.4. HYPOTHESES

1.4.1. Chapter IV

- Early tree growth varies between tree species and it is affected by the grass species
- Grass production differs between grasses and tree species affect it
- Concentration of carbon in biomass varies between plant component and species
- Carbon sequestration in soil and in biomass components are different and it is affected by the silvopastoral combinations
- Light fraction of soil organic carbon is affected by fine root biomass of the silvopastoral associations

1.4.2. Chapter V

- Fine root biomass and length is dependent of the season, soil depth and position respect to trees
- Fine root competitiveness depends on soil depth and associated species
- There is a niche separation or complementarity in the exploration of soil by fine roots of each component (grass and tree species)
- Tree species promote the accumulation of nitrogen in soil
- There is a correlation between soil nitrogen and fine root biomass

1.4.3. Chapter VI

- Tree canopy cover varies between tree species and it is affected by associated grass species
- Leaf area index of tree species and the transmission of photosyntetically active radiation through their canopies are different among trees species and this is affected by season and associated grass species
- Tree and grass species have an intrinsic water use which is affected by the associated species
- Season and associated grass species affect the transpiration of tree species
- Tree and grass species have different water use and water use efficiency, which area affected by the associated species
- Tree and grass species have different strategies to tolerate drought conditions

1.5. GENERAL OUTLINE OF THE THESIS

This dissertation has been divided into seven chapters; three of which correspond to complete papers (Chapters VI, V and VI). Chapter I gives a general introduction including the problem statement, rationale, the context of the research, the objectives and hypotheses. Chapter II reviews the most relevant and recent theoretical and methodological aspects regarding growth, production and biophysical interactions in silvopastoral systems. Chapter III is the general material and methods section, which includes information about the approaches used to carry out the study and the sampling dates. Chapters IV (growth, production and carbon sequestration), V (fine root interactions) and VI (water and radiation interactions) are extended complete papers in formats suitable for submission to refereed journals. Chapter VII, the general discussion and recommendation section, provides synthesis including the most important findings of the three experimental chapters. The reference section, Chapter VII, contains references from Chapters I, II, III and VII only.

CHAPTER II

2. LITERATURE REVIEW

2.1. DEFINITION OF SILVOPASTORAL SYSTEMS

Agroforestry occurs when trees and crops are grown together; however, current definitions include detail about the nature of this mixture. Lundgren and Raintree (1982) define agroforestry as “a collective name for land-use systems and technologies where woody perennials are deliberately used on the same land management unit as agricultural crops and/or animals, in some form of spatial arrangement or temporal sequence”.

Silvopastoral systems are an important type of agroforestry systems where the tree component is mixed with livestock and grasslands in the same terrain (Nair 1993). Other definitions include additional characteristics: “a silvopastoral system is an option of livestock production, which involves perennial woody plants, and it interacts with traditional components (herbaceous fodder and animals), under integral management” (Somarriba 1992, Pezo and Ibrahim 1998). The most important silvopastoral systems in Central America include live fences, protein and/or energy banks, alley farming, dispersed trees on pastures, grazing in forestry plantations and windbreaks (Ibrahim et al. 1999).

2.2. PRINCIPLES OF CAPTURE OF RESOURCES IN AGROECOSYSTEMS

In mixed systems, such as agroforestry practices, one of the most important issues is the management of interactions between components, mainly in terms of resource capture. The principle of resource capture is a key in this area; it refers to complementary or competitive interactions among species and depends on their ability to capture and use restrictive resources for growth (Monteith 1981). In inter-specific interactions, the model can be expressed in terms of transpiration by each plant component (Ong et al. 1996):

$$W = e_w \sum E_t \qquad \text{Equation 2.1}$$

Where;
W: Dry matter production (DM; g)
e_w: Relationship of water use efficiency (g DM mm^{-1} H_2O)
E_t: Accumulated transpiration (mm H_2O)

2.3. IMPORTANCE OF WATER FOR PLANTS

Water, which is the most abundant component of living plant cells, constitutes between 80 and 95% of the mass of growing tissues (Taiz and Zeiger 1991). At the cellular level, water is the major medium of transporting metabolites through the cell; and at the whole-plant level, water is the medium that transports the raw materials (carbohydrates and nutrients) as well as the phytohormones that are required for growth and development, from one plant organ to another (Lambers et al. 1998).

Unlike many other substances in the plant cell, a water molecule is temporary resident (Taiz and Zeiger 1991). Plants continuously absorb and lose water and they require water in large quantities; however, less than 1% of the water absorbed by plants is retained in biomass: the remainder is lost by transpiration. This inefficient use of water is as a consequence of photosynthesis. The opening of stomata allows CO2 to enter the leaf for photosynthesis, also provides a pathway for water loss (Lambers et al. 1998).

2.4. MOVEMENT OF WATER THROUGH THE SOIL-PLANT-ATMOSPHERE CONTINUUM

Water moves in the soil-plant-atmosphere continuum through a widely variable medium and the mechanism of transport also varies with the type of medium: cell wall, cytoplasm, lipid bilayer (Taiz and Zeiger 1991). Water moves through the plant either along a water potential gradient, hydrostatic pressure or partial water vapour pressure. As soils dry out, there are parallel decreases in soil and plant water potentials both immediately before dawn and at midday (when water stress is minimal and maximal, respectively). The steepest gradient in the soil-plant-atmosphere continuum occurs at the leaf surface, which indicates that the stomata are the major control point of plant water relations (Lambers et al. 1998).

The status of water in soils, plants and the atmosphere is commonly described in terms of water potential (ψ_w), which is the algebraic sum of the osmotic potential (ψ_π) and hydrostatic pressure (ψ_p; Lambers et al. 1998). The osmotic potential is the chemical potential of water in a solution due to the presence of dissolved materials; whereas, the hydrostatic pressure refers to the physical pressure exerted on water in the system. By definition, the water potential of pure, free water at atmospheric pressure and at a temperature of 25°C is 0 MPa[1] (Lambers et al. 1998).

In the soil and xylem, water moves by bulk flow in response to a pressure gradient. In the vapour phase, movement is primarily by diffusion, at least until water reaches the outside air, where convection becomes dominant. The driving forces of water transport in membranes are the water potential gradients across them. Water flow is a passive process where water tends to move from regions of high water potential (soil and roots) to regions of low water potential (leaves and air; Taiz and Zeiger 1991).

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[1] 1 Pa = 1 kg · m s^{-2} = 10^{-5} bar = 9.87 x 10^{-6} atm

At soil level, plant available water in the soil is normally held in pores of 50-0.2 μm at potentials between -10 kPa (field capacity) and -1500 kPa (permanent wilting point; Russell 1988). These suction limits are arbitrary because they were determined in the laboratory using a sunflower plant. Nevertheless, they provide a useful guideline from which the plant-soil-water relationship can be defined. Field capacity refers to the water content of a soil after it has been saturated with water and excess water has been allowed to drain away. At the permanent wilting point, water delivery to the roots is too slow to allow overnight rehydration of plants that have wilted during the day (Taiz and Zeiger 1991). Clay and organic soils, which have small particles, generate very negative pressure (large suction tensions). The clay soils have higher water availability than sandy soils because of the difference in size of pores between these types of textures (Lambers et al. 1998).

Water in the soil may exist as a film adhering to the surface of soil particles or may fill the entire channel between particles, so its content and rate of movement depend to a large extent on soil type. In sandy soils, the spaces between particles are so large that water tends to drain and remain only on the particle surfaces and at interstices between particles. Whereas in clay soils, the channels are small so water does not freely drain but is held tightly (Taiz and Zeiger 1991). As long as the upper soil is fairly moist, plants tend to absorb most of their water from shallower soil regions, where roots are concentrated. As soil dries out, relatively more water is absorbed from deeper layers (Lambers et al. 1998). Similarly, soil water status will also affect leaf water status. Depending on the hydraulic conductance in the flow path through the plant, there will be a change in the root and in the leaf xylem water potential with progressive soil drying (Schulze 1986).

2.5. INTERACTIONS IN AGROFORESTRY SYSTEMS

Interaction can be defined as the effect of one component of a system on the performance of another component and/or the overall system (Nair 1993). There are many interactions between tree and crop components in agroforestry systems, the following being the most important: increased productivity, improved soil fertility, changes in nutrient cycling, soil conservation improvements, microclimate improvements, increased competition, the occurrence of allelopathy, changes in weed growth and changes in levels of sustainability, stability, pests and diseases (Ong and Huxley 1996). Two causes of complementary interaction have been identified: better resource capture and more efficient resource utilisation (Young 1997).

The success of multi-species systems depends primarily on minimising the negative interactions between trees and crops, both above (mainly for light) and belowground (for water and nutrients) (Jose et al. 2000). Competition between crops and trees for the same resource is higher when the components are growing closer together, even though the magnitude of the belowground competition is not apparent (Singh et al. 1989). In conditions with water deficit, which occurs in arid and semiarid zones, one of the most important interactions in agroforestry systems is water competition; however, this is still not understood well, mainly because there are several measuring and modelling problems (Thornton et al. 1990, Willey 1990, Lafolie et al. 1999). For this reason, in agroforestry systems such as alley cropping, competition for water and nutrients is the main reason for failure in semiarid tropics (Ruhigwa et al. 1992, Govindarajan et al. 1996).

In the distribution of resources in agroforestry systems four hypotheses have been considered: 1) possible increase in efficient resource use by combining species with different uptake patterns; 2) competition for below-ground resources is inevitable and it is best managed by manipulating the interface between species in a mixture; 3) tree phenology can be selectively used to create temporal complementarities; and 4) trees cause a redistribution of resources within the landscape (Ong and Leakey 1999). Another known advantage of silvopastoral systems is a separation of niches, where grasses utilise the topsoil water while tree roots have exclusive access to deeper water. This niche separation provides an an explanation for the higher efficiency in the use of resources in these systems of production (Ong and Leakey 1999).

2.6. WATER RELATIONS IN AGROFORESTRY SYSTEMS

Water is the most limiting factor of plant production in arid to semiarid regions, because the acquisition of this resource directly determines the biomass production (Droppelmann et al. 2000). The effect of trees on the biomass production of grasses due to water availability is not the only interaction affecting crop production. In the case of silvopastoral systems, differences in productivity between under-crown and open-grasslands habitats have been attributed primarily to three factors: 1) improved fertility and structure of soils under canopies, 2) improved water relations of shaded plants, and 3) competition between trees and under story plants for soil moisture and nutrients (Belsky 1994). The magnitude of the pasture response to tree clearing is dependent on tree-grass competition for soil water. In regions where wet season rainfall is generally reliable, there is less competition between trees and grasses for soil moisture during the growing season (Jackson and Ash 1998).

Water sharing is the result of exploration by shoot and root systems, as well as interactions between environmental conditions and plant growth. The canopy structure determines the sharing of intercepted radiation and the partitioning of evaporative demand between the two components. Moreover, the ability of each component to satisfy its own evaporative demand will depend on soil water availability, root characteristics, and biophysical regulation of water flow (Ozier-Lafontaine et al. 1998). Zinke (1962) developed the idea that individual trees have an influence roughly proportional to their crown area projected on the soil surface.

In general, agroforestry systems have some advantages in water use with respect to monoculture crops (Ong et al. 1991):

- Annual crops are unable to use all the water stored in the soil
- Tree-crop combination can greatly enhance water use
- Total productivity of agroforestry systems could be increased through higher water use in comparison with annual crop systems
- There is less competition between tree and crop species that develop differently, especially in terms of canopy cover
- Water competition in agroforestry systems can be reduced by modifications of tree space arrangement.

Trees may influence the water balance in silvopastoral systems in two ways, directly or by through soil or microclimatic conditions:

2.6.1. Direct effects: increase in water use of mixed systems

Crop or grass systems in semi-arid regions often use less than half of the rainfall, because water may be substantially lost by soil evaporation, runoff and drainage. Drainage loss is one water balance component which may be more easily modified by trees, because they use water that annual crops cannot use because it is away from their root systems or it is in a different growth season (Huda and Ong 1989). Improvements in rainfall use may be realized when agroforestry systems substantially reduce runoff losses (Wallace 1996), especially on sloping lands (Young 1989). However, a possible disadvantage of the inclusion of trees in agricultural or livestock systems is that the interception losses can be around 10 and 30% (Ong and Black 1994); moreover, trees may also decrease water availability for use by crops (Wallace 1996).

The effect of trees on crop transpiration does not only depend on the effects of water availability. It also depends on the restrictive resources in the specific environment and on the effect of the trees on availability to those restrictive resources. If water is abundant, the monocrop and the crop in agroforestry systems can transpire at their own maximum rates (Kho 2000). Studies developed in the semi-arid area of India demonstrated that the inclusion of trees in crop systems can increase precipitation use. However, trees spread to compete with crops for moisture, which depresses the crop yields (Ong et al. 1991).

In the water relationship of the crop-tree interface there is an important process attributed to some tree species, which is the hydraulic lift. Some trees take up water hydraulically from the deeper soil layers and they distribute it on the soil surface to dry environmental conditions, this water can be used by other species (Emmerman and Dawson 1996, Dagang and Nair 2001). This occurs primarily at night, when stomata are closed and the plant is at equilibrium with root water potential (Lambers et al. 1998). Moreover, Burgess *et al* (1998) suggested that the fine roots in dry soil maintain a hydraulic lift. They indicated that an active root system allowed the use of available water in deeper soil layers, maximizing the water acquisition during drought conditions. Consequently, hydraulic lift could have important benefits for silvopastoral systems, mainly in arid and semi-arid zones.

2.6.2. Indirect effects: improvement of soil condition and microclimate

The high canopy of trees in agroforestry systems may be able to modify the microclimatic conditions, resulting in an increment of total water use efficiency for crops. This may be due to (Ong et al. 1991, Wallace 1996):

- Reduction of soil evaporation by shading of the ground
- Lower vapour pressure deficit under the canopy
- Reduction of crop transpiration without a proportional reduction of its photosynthesis
- Lower soil surface and air temperatures

- Improved soil physical conditions

According to Ong et al. (1991), in monoculture crops there is an inefficient use of water. A study from the Indian plateau showed that the best cropping systems only used 40% of annual rainfall, while the rest was lost as runoff (26%) and deep percolation (33%). On the other hand, in the semi-arid region of Middle East and West Africa, 30-60% of rainfall is directly evaporated (Cooper et al. 1983). During the period between rainfall seasons, the distribution of water in the soil is crucial for plant survival. Vertical distribution of moisture in the soil profile after a rainfall event varies with infiltration, soil surface evaporation and plant activity while horizontal redistribution is mainly affected by plant root activity (Pidgeon 1972). Initial soil moisture content at the beginning of the rainy season is a key issuse, because it may determine how much is available for crop establishment in slow-starting seasons in semi-arid regions (McIntyre et al. 1997).

Trees in grasslands modify the soil moisture distribution compared to areas without trees. This influence is affected by tree density, crown size and distribution and microclimatic conditions. Marlats et al. (1999) argued that the effect of trees on water availability was higher in the lower layers; whereas, in intermediate horizons the soil moisture was similar between silvopastoral systems and a pasture without trees. In seasons with a water deficit, the trees in the silvopastoral systems also contributed to conserve water in the upper layers because of their litter deposition and protection against radiation. In those layers where grasses grew, trees improved soil water availability (Marlats et al. 1999).

The growth of tropical grasses was increased under tree canopies at moderate density. These responses are attributed largely to an increased fertility, organic matter, nitrogen availability and low cover under the tree canopy (McIvor et al. 1995, Wilson 1998, Marlats et al. 1999). High tree density may give an excessive shade and provide detrimental competition to pasture (Braziotis and Papanastasis 1995, Jackson and Ash

1998, Wilson 1998). In isolated trees in grasslands with low tree density, there are two ecological components: an open herbaceous layer dominated by annual species, and an area affected by the tree canopy which includes an herbaceous stratum (Gonzalez Bernaldez et al. 1969). Braziotis and Papanastasis (1995) have demonstrated that soil moisture is increased with decreasing tree density in all seasons; this response is attributed to a higher rainfall received by the soil in combination with a partial shade in the open stands. In contrast, other studies concluded that the canopy area of live trees did not affect the grass yield of the systems (Jackson and Ash 1998).

Grass production varies with distance from the tree. Wilson (1998) found that the distances from trees did not affect the grass yield for *Acacia stenophylla* and *Albizia lebbeck*; but it did affect *Eucalyptus argophloia* and *Leucaena diversifolia*. Sharrow (1991) noted that biomass yield of pasture was lower under the canopy of *Pseudotsuga menziessi* (Douglas –fir) trees and increased with distance from the tree to open pasture. This response is associated with the loss of understory vegetation due to the intense competition with trees for moisture, nutrients and light.

Drought tolerant grass species can better cope with the effect of trees on water availability. Hake et al. (1984) evaluated the water stress in seven tall grasses (*Andropogum gerardi, Schizachyrium scoparium, Panicum oligosanthes, Sporobolus asper, Ambrosia psilostachya, Psoralea tenuiflora* and *Solanum eleagnifolium*) in Oklahoma. All species decreased their seasonal water potential, concurrent with increased temperatures and water stress. There were differences in water potential reduction, where *S. scoparium*, and to a lesser extent, *P. oligosanthes*, were much greater than that for the other species. *A. gerardi* was less affected by soil water depletion in the upper soil profile than was *S. scoparium*. Both *S. scoparium* and *P. oligosanthes* have shallow root systems, thus as the upper soil dried, water availability decreased causing higher degrees of stress. *A. gerardi* apparently avoided dehydration by having a deep root system, whereas *S. scoparium* survived in spite of a high degree of dehydration.

In the same way, climatic conditions affect the water competition in grasslands with trees. Trees had a more positive effect on herbaceous production in drier than in wetter environments (Belsky et al. 1993), and the magnitude of the pasture response depended on tree-grass water competition. In regions without water deficit during growth season, there was less competition between trees and grasses (Jackson and Ash 1998). This response also depends on seasonal changes. In dry seasons, water competition may depress pasture yields (Jackson and Ash 1998) but pasture quality may be higher under trees. In wetter seasons, pasture yields may reflect the fertility gradient of trees, while pasture quality may not be influenced (Jackson and Ash 1998).

The effects of soil water availability on grass productivity have been evaluated in some studies. Wilson (1998) found differences in the behaviour of grasses under different tree species; the growth of *Panicum maximum* under *Acacia stenopfhylla* and *Albizia lebbeck* was not reduced, but in the final year, it was significantly reduced under *Leucaena diversifolia* (25%) and under *Eucalyptus argophloia* (33%). In silvopastoral systems, the proportion of *P. maximum* was consistently higher than in the monoculture pasture, especially in the more heavily shaded eucalyptus plots (Wilson 1998).

In the third year of a silvopastoral system with *Pinus radiata*, total yields of the pasture species in the agroforestry plots were reduced by an average of 3.5% for Lucerne and ryegrass/clover species compared to their yields in the open plots; whereas ryegrass (*Lolium perenne*) species did not suffer any yield reduction in the agroforestry plots (Yunusa et al. 1995). Other researchers have found increments in grass productivity in the silvopastoral mixture with *Acacia mangium* (Bolivar et al. 1999) and this is consistent with data reported by other authors. These authors noted that managing *Brachiaria humidicola* at a spatial configuration of 8 m x 4 m permitted sufficient sunlight for the growth of the grass. In humid conditions, the production of *B. humidicola* was 25% higher in silvopastoral systems with *A. mangium* than in monoculture (Bustamante et al. 1998).

2.7. WATER USE IN AGROFORESTRY SYSTEMS

Studies on water competition usually calculate two important indicators: water use and water use efficiency. Evapotranspiration or water use is the combination of two separate processes: evaporation and transpiration (Allen et al. 1998). Evaporation is the process whereby liquid water is converted to water vapour and removed from the evaporating surface; while transpiration consists of the vaporization of liquid water contained in plant tissues and transference to atmosphere (Allen et al. 1998). The transpiration stream is necessary for (1) nutrient uptake from the soil and transport to other organs, especially the leaves, and (2) transpirational cooling in hot, arid environments (Allen 1999).

Several researchers have estimated evapotranspiration based on water balances (Benzarti 1999, Droppelmann et al. 2000), sap flow measurements (Namirembe 1999, Vose et al. 2000), use of potential evapotranspiration or vapour pressure deficit (Yunusa et al. 1995, McIntyre et al. 1997, Souch and Stephens 1998, De Montard et al. 1999, Vose et al. 2000) and lysimeters (Ozier-Lafontaine et al. 1998). At a plant community level, transpiration is affected by both stomatal and boundary layer conductance in the canopy. These terms refer to the rate of passage of either water vapour or carbon dioxide through the stomata and through boundary layer (a thin film of air hugging the surface of leaf (Taiz and Zeiger 1991)). Stomatal conductance has far less effect on canopy water loss than would be expected from a study of single leaves; thus transpiration from leaves in canopies requires consideration of both diffusion and leaf energy balance (Lambers et al. 1998). If canopies affect the gas exchange properties of individual leaves, then the water use efficiency of the canopy cannot simply be calculated by summation of individual leaves measured under prevailing bulk air conditions (Lambers et al. 1998).

In agroforestry systems, the effect of trees on crop transpiration depends on the restrictive resources in the specific environment. If water is abundant, crops in monoculture and agro forestry systems will have their own maximum transpiration rates (Kho 2000). In this type of system, it is necessary to measure water loss in two ways: in crops, including grasses and in trees. Tree transpiration is measured in water volume per time, which should be converted using the plot or canopy area (Narain et al. 1998). The uptake of water in a mixed system is not the sum of total of potential exploitation achieved by each of its components in monocultures (Brown and Stott 1984), as it is affected by sharing spatially or temporally the root occupancy of soil.

2.8. WATER BALANCE

One of the most important tools for estimating water use in agroecosystems is water balance, which is a detailed expression of the mass conservation law. In agroforestry systems, it can be explained through the following equation (Jiménez 1986):

$$T_t + T_c = R - I_t - I_c - E_t - E_c - D_s - R_t - R_c + R_{on} - \delta\theta_t - \delta\theta_c \quad \text{Equation 2.2}$$

Where:
T: Transpiration of tree (t) and crop (c)
R: Total rainfall
I: Rainfall interception of tree (t) and crop (c)
E: Evaporation of tree (t) and crop (c)
D: Drainage of soil
R: Runoff of tree (t) and crop (c)
Ron: Runon from neighbouring areas
δθ: Water contents in tree (t) and crop (c)

In water studies in monoculture crops, the water use or evapotranspiration is usually estimated as the difference between inputs and outputs in the system. However, in mixed systems such as silvopastoral systems, there are two different components, and so it is necessary to separate the transpiration by component. To reach this objective, three main methodologies can be used (Ong et al. 1996):

- Transpiration by each component can be estimated using transpiration models based on the light interception by component
- Total water use of the community and transpiration of a component can be measured, and then the transpiration for another component can be calculated by the difference; and
- Transpiration of each component can be measured separately.

The second option is the most realistic method because there are several techniques to accurately measure tree or crop water use. However, a simplified water balance may be used, and evapotranspiration may be estimated by the difference between the precipitation and the change of soil water content, when there is no water loss by either runoff or leaching. In this case, it is supposed that when the soil is saturated and it starts to decrease in moisture, all reduction in soil water storage is caused by evapotranspiration (Eastham et al. 1990, Huber and López 1993, Naeth and Chanasyk 1995).

2.8.1. Components of water balance

2.8.1.1. Soil water storage

Soil water content, which is a very important component of water balance, is usually estimated using several techniques such as gravimetric methods (Braziotis and Papanastasis 1995, Ozier-Lafontaine et al. 1998, Smith et al. 1998), time domain reflectancy (TDR; Sun et al. 1995, McIntyre et al. 1997, Miller and Gaskin 2000), neutron probes (Hake et al. 1984, Joffre and Rambal 1993, Govindarajan et al. 1996, Jose et al. 2000) and gypsum blocks (Wilson 1998).

The soil water storage is the amount of water contained in a certain soil profile. This variable can be calculated as the numerical integration of the soil water content profile (Joffre and Rambal 1993), using the following equation:

$$Hs = \frac{\%Hs * da * Ps}{100}$$

Equation 2.3

Where;
Hs: Soil volumetric moisture content (mm)
%Hs: Soil gravimetric moisture (%)
Bd: Bulk density (g cm^{-3})
Ds: Soil depth (mm)

For mixed production systems (e.g. agroforestry), the water content profile can be calculated through measures of soil moisture in tree and crop bands, as the following equation explains (Narain et al. 1998):

$$Sw_t = \frac{Q_c W_c + Q_r W_r}{W_c + W_r}$$

Equation 2.4

Where;
Sw_t: Water content in the system
Q: Water content in the crop (c) and tree (t) area
W: Width of the crop (c) and tree (t) band

2.8.1.2. Gravimetric method

The estimation of soil moisture through the gravimetric method is the most accurate technique. This involves the extraction of soil samples directly from the sampling site. The samples are weighed in humid (current) condition and oven-dried (105°C) to reach a constant weight (dry), and the gravimetric moisture is calculated using following equation:

$$\theta_g = \frac{M_w}{M_s} \times 100 \qquad \text{Equation 2.5}$$

Where;
θ_g: Gravimetric soil moisture (%)
M_w: Mass of water (humid weight minus dry weight) (g)
M_s: Dry soil mass (g)

In the water balance, the volumetric moisture, which is calculated by multiplying the gravimetrical moisture with the bulk density of the soil (Equation 2.6), is used:

$$\theta_v = \theta_g * \rho_s \qquad \text{Equation 2.6}$$

Where;
θ_v: Volumetric soil moisture (%)
θ_g: Gravimetric soil moisture (%)
ρ_s: Bulk density of soil (g cm^{-3})

2.8.1.2. Time domain reflectancy (TDR)

The TDR employs the apparent dielectric constant to estimate volumetric moisture (Miller and Gaskin 2000). An example of the equipment used is the Theta probe, which measures volumetric soil moisture content (1 % accuracy). This equipment is easy to calibrate for specific soils, it has easy data logger connection (DC in DC out) and excellent temperature stability, is usable in very saline soils (up to 2000 ms m^{-1}) and performs well in most soil types, including clays. The equipment is formed by a sensor (5-15 V DC at 20mA), which can be buried up to 5 m and is connected to a data logger, and the volumetric soil moisture is calculated by the following equation:

$$\theta_v = \frac{\left(\sqrt{\varepsilon - a_o}\right)}{a_1}$$ Equation 2.7

Where;
ε: Apparent dielectric constant
a_o and a_1: Constant dependent on soil type

2.9. WATER USE OF TREES

Water use of trees has been widely studied using sap flow methods. Xylem sap flow, which is an accurate method for determining transpiration, relates actual transpiration to actual growth on a tree basis under *in situ* conditions (Lindroth et al. 1995). This method uses heat as a tracer for sap movement. Sap flow has been used in herbaceous plants and trees by determining the rate of ascention of sap through the stem (Grime et al. 1995).

Measuring sap flow in individual stems and scaling up to standard level is a direct way of measuring plant water use compared to use of meteorological data (Vose et al. 2000). However, there is an effect of tree density on sap flow (Rakkibu 1998). Sap flow measurement is most appropriate in regions where transpiration rates are low compared to the atmospheric demand of water (Hatton et al. 1995), which is usually the case if soil water is limited. Methods available for determining sap flow on individual stems involve use of heat transfer: the heat balance, the steady-state heat balance and the heat pulse.

2.9.1. Stem heat balance method

The stem heat balance method involves supplying a volume of stem with a known amount of heat, using a heater wound or wrapped around a section of the stem

(Sakutarani 1981). Thermocouples are used to measure heater temperature and sap temperature on entering and on leaving the heated stem section. From the heat balance within the stem, the heat transported by moving sap, Qf, is calculated as:

$Q_f = c_w F(T_d - T_u)$ Equation 2.8

Where;

c_w: specific heat capacity of sap (or water)

F: flow rate of water

$T_d - T_u$: temperature difference between water entering and that leaving the heated stem segment.

2.9.2. Steady-state temperature method

This method involves the supply of heat to the stem to maintain a constant temperature by varying power input rather than in pulses. An example is the Granier's gauge (Granier 1985, 1987), where two metal probes are inserted into the wood. This method is based in the temperature difference between the upper heated and the lower reference probes. It is assumed that the maximum difference in temperature is reached at zero sap flow; whereas, the higher flow is obtained when the difference of temperature between probes is minimum (Granier 1985, 1987, Lu et al. 2004, Roupsard et al. 2006). The probes are protected against weather, animals and direct sunlight. Sap flow is derived as a function of the rate of heat loss from a heater in comparison to the environmental sap temperature recorded by a second sensor far upstream on the stem. Sap velocity is calculated as:

$$\upsilon = \alpha \left[\frac{\Delta T_o - \Delta T_i}{\Delta T_i} \right]^{\beta}$$ Equation 2.9

Where;

υ: Sap flow velocity (m s^{-1})

ΔT_o and ΔT_i: Daily maximum and current temperature difference between the two sensors of the probe (^oC), respectively

α and β:	Parameters of the model (1.19×10^{-4} and 1.231, respectively for the Granier's empirical equation)

2.9.3. Heat pulse velocity method

Heat pulse velocity measurement involves the determination of sap flux within the whole trunk by integrating various point measurements within conducting wood. These measurements assume that wood is thermally homogeneous, vessels conduct sap at uniform velocity, and that interstitial spaces between vessels are small enough to allow transverse heat transfer to occur between moving sap and stationary wood in negligible time (Marshall 1958). Heat transfer calculations are based on maximum temperature or temperature equilibration between two sensors. Heat pulse velocity is computed from the time, t_m, it takes a single sensor at a known distance downstream from the heater to reach maximum temperature (Cohen et al. 1981, Erickson et al. 1986).

$$V = \sqrt{(x^2 - 4kt_m)}/ t_m \qquad \text{Equation 2.10}$$

Where;

V: heat velocity

x: distance between the heater and the sensor

k: thermal diffusivity of the wood (Cohen et al. 1981).

Heat velocity is converted to sap velocity using the Marshall equation (1958).

$$V_s = V_h. (\rho_{sm}C_{sm})/(\rho_s C_s) \qquad \text{Equation 2.11}$$

Where;

$V_{h:}$ heat velocity

ρ_s - C_s: density and specific heat capacity of sap (assumed to be equal to that of water)

ρ_{sm} - C_{sm}: density and specific heat capacity of green wood.

The density and heat capacity of green wood is obtained by determining moisture content, volume (W_i) and oven-dry weight (W_d) of wood. Then heat capacity and density of green wood are computed as the sum of the proportion of each multiplied by its heat capacity or density respectively (Edwards and Warwick 1984).

$F_l = (W_f - W_d)/ W_d$ Equation 2.12
$F_m = W_d/(1.53W_i)$ Equation 2.13
$P_{sm} = (1530F_m + 1000F_l)\ \mathrm{kg/m^3}$ Equation 2.14
$C_{sm} =((1.53F_mC_m)+(C_sF_l))/(F_l+1.53F_m)\ \mathrm{kJ/kg/^0C}$ Equation 2.15

Where,
W_f - W_d: weight of green and oven dry wood, respectively
W_i: volume of wood sample
F_l - F_m: volumetric fractions of water and the woody matrix, respectively.

2.10. WATER USE OF GRASSES

Some authors have used small lysimeters to evaluate the transpiration in pastures (Eastham et al. 1988). Therefore some models have also been developed to predict transpiration. However, the main progress in this field is the use of porometers, which are used to study the behaviour of stomata at individual leaf level. Nevertheless, a few studies have shown that the porometry can be used to measure transpiration of complete vegetation canopy in temperate and semi-arid climates.

One of the most commonly used methods for estimating water use in grass species is the use of the change in soil water content between consecutive evaluation periods using water balance (Guenni et al. 2002, Fernandez 2003, Edraki et al. 2004). Alternative methods include correlations between plant water potentials and soil water potential (moisture) at different depths (Peláez et al. 1994, Montaña et al. 1995).

2.11. ESTIMATIONS BASED ON CLIMATIC CONDITIONS

Climatic conditions have been used to estimate water use in plants. The difference in vapour pressure between leaf and air determines transpiration, but in the same way, it may decrease stomatal conductance affecting transpiration. The water flux is determined by both the gradient between two points and the resistance to flow between these points, according to the following equation (Lambers et al. 1998):

$$J = L_p * \Delta \psi_w \qquad \text{Equation 2.16}$$

Where;
J: Water flux ($mm^3\ s^{-1}$)
L_p: Conductance ($mm^3\ s^{-1}\ MPa^{-1}$)
$\Delta\psi_w$: Gradient in water potential (MPa)

Potential evapotranspiration (Eo), which is the maximum rate of water use for prescribed environmental conditions, defines the upper limit of actual evapotranspiration (Et). Even though atmospheric conditions determine potential evaporation, the characteristics of vegetation limit transpiration and consequently the evapotranspiration in environments with water limitations (Ong et al. 1996). In mixed systems, transpiration of each component can be calculated using a modified Penman-Monteith equation (Monteith 1965), including the fractions of incident radiation intercepted by the component crops (Wallace 1996).

2.12. WATER USE EFFICIENCY (WUE)

Water use efficiency refers to the amount of water lost during the biomass production or the fixation of CO_2 in photosynthesis (Tlof 1976). It is defined in two terms: water use efficiency for productivity (ratio between gain in biomass and loss in water) or photosynthetic water use efficiency (ratio between carbon gain and water loss in transpiration). In both cases, leaf conductance of CO_2 and water vapour (g_c/g_w) can be used (Lambers et al. 1998).

A plant's water use efficiency depends on both stomatal conductance and the difference in vapour pressure between the leaf's intercellular air spaces and that in the air. The temperature is another factor, because it affects the vapour pressure in the leaf. The major differences in water use efficiency are found between physiological groups (C_3, C_4 and CAM; Lambers et al. 1998). Water use efficiency depends on tree density (Droppelmann et al. 2000) and on the air saturation deficit (Tanner and Sinclair 1983) then the same plant grown in semi-arid environments produces less dry matter per unit of water transpired than in humid conditions. When water is limited, plant yields decrease linearly with increasing vapour pressure deficit (Howard et al. 1997).

Leaf area also affects the water use efficiency; the more leaf area that is transpiring at or near maximum potential rate, the greater the water use efficiency. A leaf area index (leaf area per unit of ground area) greater than 3 results in increased assimilation without much increase in transpiration thus in increased water use efficiency (Ritchie 1972); whereas, leaf area index of less than 1.5 also results in increased WUE because of controlled transpiration. In the case of a drought, a decrease in shoot: root ratio resulted in decreased WUE (Passioura 1988).

Several equations have been proposed for the evaluation of WUE. Droppelmann et al. (2000) defined it as the conversion efficiency of the vegetation cover to utilise water resources:

$$WUE = \frac{BP}{WU} \qquad \text{Equation 2.17}$$

Where;
WUE: Water use efficiency (g mm^{-1})

BP: Biomass production (g m^{-2} day^{-1})
WU: Water use (mm day^{-1})

Additional to WUE, other authors have included other variables. Tanner and Sinclair (1983) have proposed the transpiration efficiency (TE), which is calculated based on the following equation:

TE = k/(VPD) Equation 2.18

Where;
K: crop specific constant
VPD: vapour pressure deficit

Thus agroforestry systems consisting of species with a high k value should be more productive than systems of species with low crop constant. The k is taken as the slope of regression of DM vs. Ep/VPD with the line forced through the origin (Walker 1986), and was used to calculated Ep for the whole growing season.

2.13. PHYSIOLOGICAL INDICATORS OF PLANT WATER STATE

Plant species, including woody species, had marked differences in tolerance to water stress, which affected their metabolism, physiology and morphology (Sun et al. 1995). Leaf water status and stomatal behaviour responded to water status and or to evaporative conditions in the atmosphere. A change in water vapour concentration between a leaf and its surrounding air, may affect the leaf simultaneously in three different ways: 1) via a change in stomatal and cuticular transpiration; 2) via a direct effect on leaf conductance; and, in some cases, 3) via effects of humidity on the photosynthetic apparatus (Schulze 1986). In this context, physiological indicators are important tools for studying water interactions in agroforestry systems.

2.13.1. Leaf water potential

Leaf water potential is considered to be a reliable parameter for quantifying plant water stress response. Several authors (Hake et al. 1984, Yunusa et al. 1995, Stoneman et al. 1996, Angeles et al. 1997, Ozier-Lafontaine et al. 1998, De Montard et al. 1999, Vose et al. 2000, Puri and Swany 2001) have studied water competition by measuring this physiological indicator. Water potential, which measures the energetic status of water inside the leaf cells (Yamasaki and Rebello Dillenburg 1999), is frequently measured by Scholander pressure chamber (Scholander et al. 1965). The best time time for this evaluation is at predawn because during the night the plant-soil system trends to return to equilibrium, as the stomata are closed and the transpiration rate is very low (Angeles et al. 1997).

The integral water stress (IWS) can join the values of leaf water potentials at different times. According to Myers (1988), it is formulated as the following equation:

$$IWS = \left| \sum \left[\left(\psi_i + \psi_{i+1} \right) / 2 - c \right] n \ \right| \qquad \text{Equation 2.19}$$

Where;
IWS: Water stress integral
$(\psi i + \psi i+1)/2$: Mean water potential of any interval i to i+1
c: Maximum potential (less negative) during the whole station
n: Interval length in days

A daily maximum level of Ψx, measured early in the morning and presumed to correspond to the condition of equilibrium between soil and plant water potentials, was always defined as the base potential (Ψb) despite the time of observation (Sellin 1996). Depression potential (Ψd) was expressed as a difference between the current level of Ψx and Ψb.

To evaluate the role of soil drying versus atmospheric evaporative demand in the development of tree water stress, an empirical model predicting the daily evolution of Ψx from the current vapour pressure deficit and Ψb (taken as an index of the soil water availability) was developed (Sellin 1996). To eliminate a variation in Ψx due to height, the gravitational component of water potential was subtracted from the values obtained with the pressure chamber. The gravitational potential was calculated from the height of the sampled shoots aboveground surface. Depression potential (Ψd), which is another water stress indicator derived from water potential, expresses the difference in daily maximum level of water potential (Ψx) and the base potential (Ψb), measured early in the morning and presumed to correspond to the condition of equilibrium between soil and plant water potentials (Sellin 1996).

2.13.2. Leaf relative water content

Relative water content (RWC) of leaves, which expresses the relative amount of water present on the plant tissues, is another important indicator of water status of plants. It refers to the current water content in relation to the maximum water content and is intimately related to several leaf physiological variables, such as leaf turgor, growth, stomatal conductance, transpiration, photosynthesis and respiration. The loss of water, when the stomata are open to allow photosynthesis, may lead to a decrease in the relative water content (RWC) of the leaf, if the water supply from roots does not match the loss from leaves. The decline in RWC may directly or indirectly affect photosynthesis (Lambers et al. 1998). Sinclair and Ludlow (1985) proposed that leaf relative water content was a better indicator of water status than water potential.

Measurements of tissue water content expressed as a basis of fresh or dry mass has been mostly replaced by measurements based on the maximum amount of water a tissue can hold (Yamasaki and Rebello Dillenburg 1999). Several authors have used this method (Tlof 1976, Sinclair and Ludlow 1985, Schonfeld et al. 1988), which is relatively easy. Leaves are sampled at midday and stopper flasks with water must be prepared and accurately weighed previously. The cut-off leaves are put into these flasks, which at the end of the sampling were weighed again, the difference being the fresh weight of the leaves at the time of sampling. After staying over-night in the flasks, the leaves are assumed to be fully turgescent, and they are taken out, carefully blotted and weighed. Then they are dried 24 h in the oven and weighed again (Tlof 1976).

$$RWC = \frac{CWC}{TWC} * 100 \qquad \text{Equation 2.20}$$

Where;
RWC: Relative water content (%)
CWC: Current water content (%)
TWC: Turgid water content (%)

2.13.3. Gas exchange and other indicators

The gas (O_2 and CO_2) exchange activity is another indicator of water status in plants and in many cases helps to estimate water loss. Several authors (Yunusa et al. 1995, Ozier-Lafontaine et al. 1998) have employed this technique with porometers. Changes in transpiration will affect the water potential in mesophyll cells where the water evaporates. Intrinsic photosynthesis also decreases under conditions of soil drought, but the effect is species and treatment specific. Generally, stomata are more sensitive to changes in the root environment and function than photosynthesis (Schulze 1986). However, stomata respond to several stimuli, which are coupled directly or indirectly with evaporative conditions in the atmosphere or soil water status (Schulze 1986). Similarly, leaf temperature (Yunusa et al. 1995) and canopy temperature (Sinclair and Ludlow 1985, Siddique et al. 2000) can be used to estimate the water status of plants.

2.14. ROOT INTERACTIONS IN AGROFORESTRY SYSTEMS

Root interactions determine the water and nutrient competition in plant communities. The length density of fine roots has primordial importance in nutrient diffusion from soil (Marschner 1997). Plant species have different patterns in root dynamics. Dry matter accumulation by root systems of annual crops typically follows the sigmoidal pattern commonly observed with shoots; while in legumes, the situation is less certain because the degree of determinacy may influence the pattern of carbohydrate allocation to the root system (Gregory 1996). However, tree roots may die due to aging, which is a genetically controlled process, or due to environmental stress and/or management (such as shoot pruning). Root presence can be measured as root counts per unit area, root biomass or root length density (per unit volume of soil). Root biomass is easier to determine than root length density, but it is not very sensitive to changes in the fine root fraction and does not give information about the actual distribution of roots within the soil (Gregory 1996).

The study of roots in agroforestry systems may be made more difficult because of the difficulties of distinguishing the fine roots of trees from those of crops. Measurements of root mass and length are few with little attempt to determine seasonal patterns of production and turnover. Substantial variation between species has been demonstrated in both the quantity and distribution of roots produced by trees suggesting that suitable combinations of trees and crops might be achieved to optimise resource utilisation. However, it is also evident from the results that, with a few exceptions, most trees will be competing with crops for both water and nutrients particularly in the upper 0.5 m of most soils (Gregory 1996).

There are several methods available for studying roots (Böhm 1979). Four methods are commonly used for investigating tree root systems: rooting profiles (counting roots in a trench; Ruhigwa et al. 1992, Ozier-Lafontaine et al. 1998, De Montard et al. 1999); pin board analysis (trenching); core sampling (Govindarajan et al. 1996, Jose et al. 2000); and the use of mini-rhizotrons. A fifth method, involving the washing out of entire root systems, can give absolute information about the form and disposition of roots (Böhm 1979, Jonsson et al. 1988) but it is extremely laborious and inappropriate for tree-crop interface situations. Determination of root length from cored samples has been simplified by various forms of computer-assisted image analysis (Harris and Campbell 1989).

Fractal methods are another important technique for studying root interactions, as they quantify the total length of tree root systems. These methods worked well with the permanent structural root system of trees but seriously underestimated the length of fine roots (<2 mm diameter; Ong et al. 1999). Indices of shallow rootedness and fractal methods of root system study were combined with sap flow monitoring to determine whether these "short-cut" methods could be used to predict tree competition with crops and complement belowground resources use in an agro forestry trial in semiarid Kenya (Ong et al. 1999).

2.15. MODELLING OF WATER RELATIONS

The modelling of plants and crops has two main aims; first is to increase the knowledge in this area of science, and the second, which is more applicable, is directed to the solution of the current problems. In modelling crop growth, the effects of water status on physiological processes such as photosynthesis, leaf area expansion, root: shoot partitioning, growth, respiration, the uptake of nutrients and perhaps nitrogen fixation are required (Thornley and Johnson 2000). The importance of root arrangements in intercrop water-uptake models is actually widely misunderstood, because most assume that roots are completely mixed (Adiku et al. 1995) or fully separated (Kiniry et al. 1992, Kiniry 1995), whereas field situations may be quite different from these extreme cases.

In modelling in agroforestry systems, there is a need to collect the following information (Gregory 1996):

- The temporal and spatial distribution of root systems beneath typical agroforestry systems.
- The relative use of water by each of the components in the agroforestry systems and the relative uptake of water from different depths in the soil profile.
- The uptake of nutrients by the crop and tree species and temporal changes in the soil solution concentration of the major nutrients.

There are some problems in the use of models in mixed systems because they (i) are one-dimensional, whereas both vertical and horizontal fluxes need to be considered to describe water transport (Caldwell 1995), (ii) assume that the two root systems are either fully separated (Kiniry et al. 1992), or completely mixed (Adiku et al. 1995), and (iii) use the concept of “mean distance between roots” to describe root distribution in soil layers (Gardner 1960), whereas geometrical patterns of the root systems can greatly influence the sharing of soil water (Ozier-Lafontaine et al. 1998, Lafolie et al. 1999).

In water studies, researchers have developed models to relate biomass production to soil moisture availability (Braziotis and Papanastasis 1995) and/or water potential (Hake et al. 1984). In most cases the third degree polynomial equations gave the best fit. The equations estimate herbage yield in relation to tree cover and soil moisture content at two depths (Braziotis and Papanastasis 1995). Other important correlations are the significant linear relationships between leaf water potential at mid-day and mean leaf conductance and a linear relationship between mean daily sap flow rates when leaf conductance was lower than 1.5 cm s^{-1}. However, with higher values of leaf conductance no relationship was found between leaf conductance and leaf water potential (Vose et al. 2000).

2.16. OPTIONS FOR MANAGING WATER COMPETITION IN AGROFORESTRY SYSTEMS

The water competition between trees and crops (grasses) may be managed through different options: pruning of tree roots to reduce their dominance, which is not cost effective for low-income farmers (Ong et al. 1989), manipulating the canopy size to reduce tree water use, exploitation of different spatial zones, increase efficiency in the utilisation of a given limited resource, or through demand for a limited resource at different times (Ong and Black 1994). Competition for soil moisture between trees and the herbaceous layer may be reduced in some situations, and indeed soil moisture conditions may be enhanced under canopies due to increased water infiltration associated with higher soil organic matter and litter cover (McIvor et al. 1995), lower evaporation rates due to litter cover and/or to a lower amount of transpiring biomass in the under-canopy zone.

2.17. BIOLOGICAL MATERIAL

2.17.1. Grass species

2.17.1.1. Brachiaria brizantha (A. Rich.) Stapf cv. Toledo

This grass species is known as palisade grass (Samoa), signal grass (East Africa), St Lucia grass (Queensland), ceylon sheep grass (Sri Lanka), upright brachiaria (Zimbabwe), bread grass (South Africa) and estrella de Africa, pasto alambre (Latin America; Skerman and Riveros 1992, Maas 1998). *B. brizantha* is a perennial up to 120 cm high, with stout erect culms and broadly lanceolate leaf-blades. It has two to five racemes, up to 15 cm long, with two rows of almost sessile, overlapping, rounded spikelets 4-6 mm long on the underside. It is native to tropical Africa but now introduced into most tropical countries. It has a wide altitudinal range (sea level to 3,000 m), and its rainfall requirement is more than 500 mm per year. This grass species tolerates a wide range of soils and acid conditions (Skerman and Riveros 1992).

2.17.1.2. Hyparrhenia rufa (Nees) Stapf

Jaragua, faragua or yaragua grass, puntero (South America), veyale (Mali), senbelet (Ethiopia), yellow spike thatching grass (southern Africa) is a very variable perennial from 60-240 cm high. Panicles are loose and narrow up to 50 cm long, with slightly spreading or contiguous racemes with short hairy or nearly glabrous spikelets 3.5-5 mm long. The flowering stems have little leaf. The sheaths of the leaves enclose about half the length of each internode, giving the culm a banded appearance. It is distributed throughout tropical Africa, but widespread in Central and South America. *H. rufa* has an altitude range from sea level to 2,000 m, and it requires a rainfall between 600 and 1,400 mm per year, nevertheless it tolerates a dry season of six months. This grass prefers black clays and latosols (Skerman and Riveros 1992). *H. rufa* is a low quality, drought-tolerant, wind-dispersed grass from Africa (Bogdan 1977).

2.17.2. Tree species.

2.17.2.1. Pithecellobium saman (Jacq.) Benth

This species is a member of Mimosaceae family; its common names including cenizaro, monkeypod, rain tree and saman. The cenizaro is a tall tree that can grow to 30 m and its crown can be 40 m in diameter (León and Poveda 2000). It has a rounded crown, usually broader than tall; leaves with 2-8 pairs of primary leaflets, each of these with 2-7 pairs of ovate to obovate leaflets 3-6 cm long; flowers in loose heads; corolla greenish-yellow, stamens dark pink; pods elongate to 20-24 cm long, thick but compressed, black, pulpy within; and numerous seeds. This species is propagated by seeds. Commonly planted for shade and wood; however, other uses have been identified such as for apicola production, construction, various industrial uses and for ornamentation (Poveda and Sanchez 1999).

2.17.2.2. Diphysa robinioides **Benth**

This tree species is part of Papilionaceae family. The height of this tree usually reaches 15 m (León and Poveda 2000). It has alternate leaves, with stipules; black cortex with many fissures; inflated fruits; and yellow flowers. Guachipelin is a multiple use species, which can be used in handicrafts, bee production, and biological control of pests, fuel, construction, industrial uses, fodder, medicines, oil production and ornamentation (Poveda and Sanchez 1999).

2.17.2.3. Dalbergia retusa **Hemsl**

The common names of this Papilionaceae species are cocobolo and rosewood. Cocobolo is a medium-sized tree which commonly reaches 20 m in height (León and Poveda 2000). It has a straight trunk that is usually cylindrical but somewhat irregular, and which frequently branches near the base. The bark has clear vertical fissures. Leaves are alternate, compound, usually with 9-13 leaflets, including a terminal one. Leaflets are light green or whitish on the underside, rounded, and the tip has a very small indentation. The base of the petiole is swollen, green, and cylindrical, and the stipule green, but readily falls off to leave a scar on the branchlet. Its flowers are white and the fruits have between 1 and 3 seeds whose outlines in the pod are very clear; they are dispersed by wind. The main use of this species is the production of handicrafts, because the wood is hard, heavy and lustrous in colour (Poveda and Sanchez 1999).

CHAPTER III

3. MATERIALS AND METHODS

3.1. DESCRIPTION OF EXPERIMENTAL SITE

This study was carried out at the farm Hacienda La Pacifica (85º9’14.5” W and 10º28’36.8”N; 50 m of altitude) located 5 km at north of the town of Cañas, Guanacaste, Costa Rica (Figure 2). The zone is classified as a dry tropical forest biome (Holdridge 1996), with a mean rainfall of 1500 mm year^{-1}. About 85% of rainfall falls between May and November (wet season); in contrast, between December and April when the evapotranspiration is higher than rainfall (dry season; Figure 3). The mean temperature in the experimental site is around 28ºC (range 23-36ºC) and the relative humidity varies between 60 and 85% for the dry and rainy season, respectively (IMN 2003). The mean potential evapotranspiration, using an open pan, is 1800 mm year^{-1}. The landscape of Cañas has changed dramatically in recent decades from predominantly forests to pasture mainly dominated by jaragua grass (*Hyparrhenia rufa*; Herrick 1993).

The experimental field had an average slope of 4%. The first determination of soil characteristics was conducted in September 2003 and showed that the soil texture was clay, with a mean content of clay of 44%. The soil contained a medium level of organic matter in the 0-20 cm horizon and a low concentration in the 20-60 cm horizon. There was a phosphorus deficiency across the soil profile (Table 1).

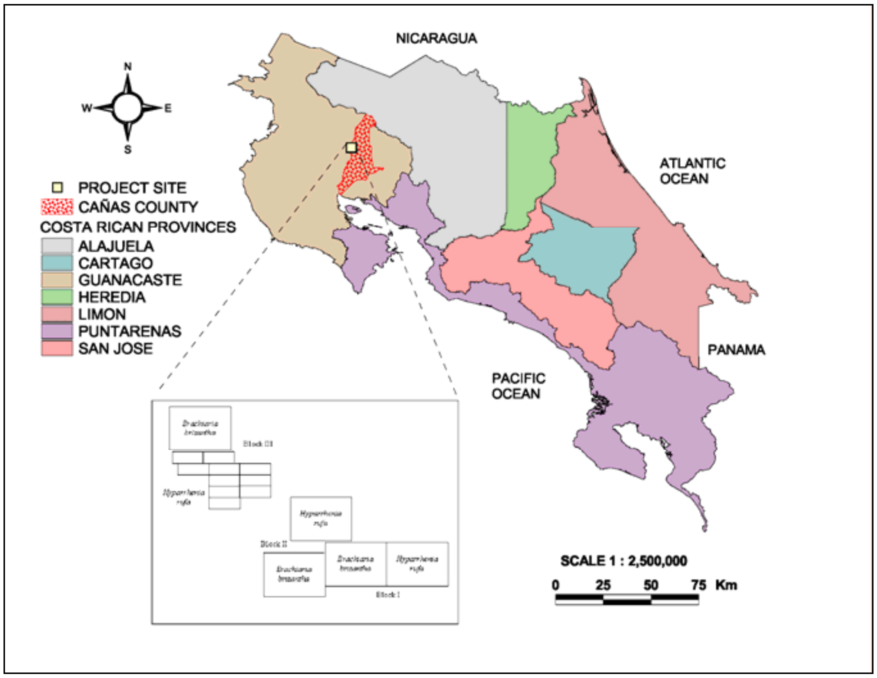

Figure 2. Location of experiment and distribution of experimental blocks.

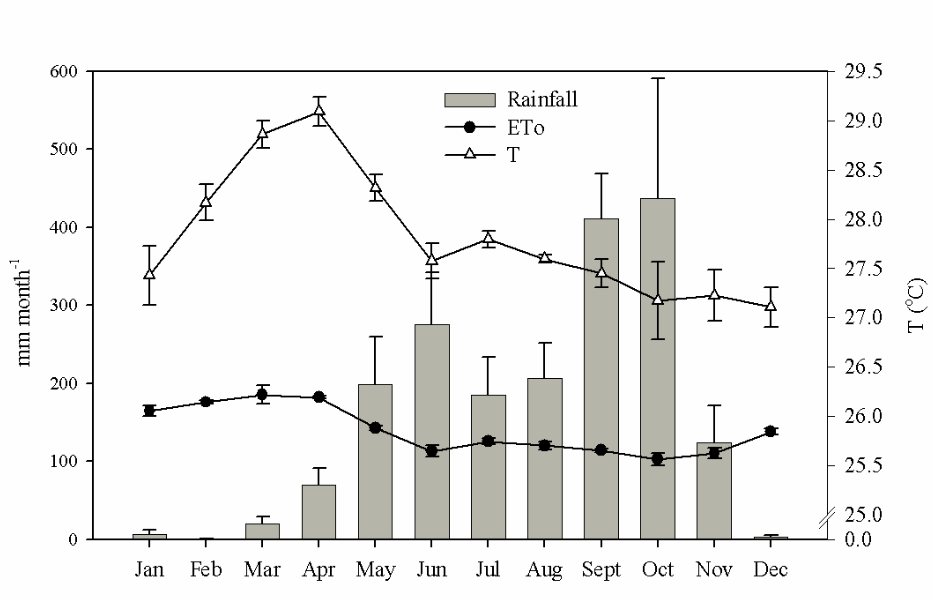

Figure 3. Climatic conditions in the study zone. Temperature (T) and rainfall are mean values between 1985 and 2003; reference evapotranspiration (ETo) by open pan (between 2000 and 2003). Source: Ingenio Taboga, unpublished data.

Table 1. Main soil chemical properties of the experimental site, Hacienda La Pacífica, Cañas, Costa Rica.

Depth	pH	Ca	Mg	K	CEC	Base	P	Cu	Zn	Mn	Fe	OM
cm	Soil water 1:1	cmol(+) kg^{-1}				Sat (%)	mg kg^{-1}					%
0-20	6.7	13.0	4.38	0.64	18.0	0.35	1.02	8.8	0.75	2.32	47.7	3.5
20-40	7.0	13.1	4.34	0.50	17.9	0.44	0.66	8.4	0.22	1.79	32.0	1.9
40-60	7.1	13.8	4.84	0.36	19.0	0.58	0.44	6.1	0.17	1.13	21.2	1.1

3.2. ESTABLISHMENT OF THE EXPERIMENT

A randomized complete block experimental design with three replications was used. The treatments had a factorial structure with a split plot design where two grass species (*Brachiaria brizantha* and a pasture dominated by *Hyparhenia rufa;* Figure 4) formed the main plots with four randomized tree treatments (*Pithecellobium saman*, *Diphysa robinioides, Dalbergia retusa* and no-tree control) in the subplots (Figure 4). Main plots had an area of 8000 m^2; whereas the subplots were 1000 m^2.

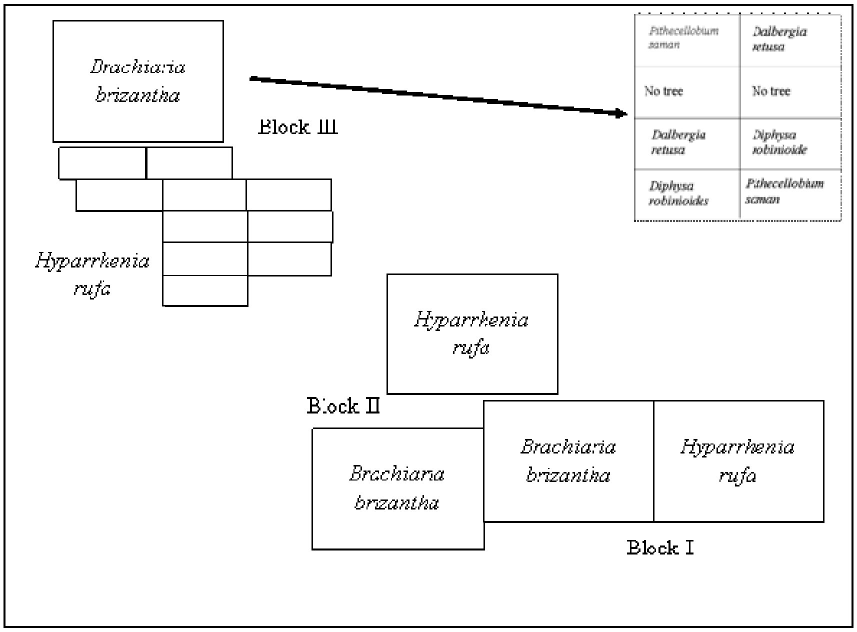

Figure 4. Layout of blocks, main plots (grass species) and subplots (tree species) in the general experiment.

This trial was set out in September 2001 in actively grazed pasture plots which were initially established with *H. rufa* and had been grazed by cattle over the previous 20 years. No fertilizers were used to manage these pasture plots. The treatments were distributed within this pasture area according to the design above. The main plots for *B. brizantha* were prepared with tractor, with a plow and rake; whereas the *H. rufa* was left without preparation because this grass was already established in these plots. The *H. rufa* plots were naturalised pastures dominated by this species. *B. brizantha* pasture was established by sowing 4 kg seeds ha^{-1}. All plots were initially fertilized using a compound fertilizer (12-30-20) at a rate of 180 kg ha^{-1}. Maintenance fertilizer was not applied. Trees were planted in double lines (2 x 2 m) within the pasture plots, leaving a strip of 8 m between lines and were fertilized with the same fertilizer used for the pastures, at a rate of 100 g plant^{-1}. Seedlings were produced in Hacienda La Pacifica, with seeds from the CATIE´s seed bank and soil material from fertile sites on the same farm. Trees were planted at the end of September 2001. Two replantings were done (May and October 2002), replacing all dead plants. Each subplot had a total of 100 trees per plot, giving a tree density of 1000 trees per ha.

3.3. MANAGEMENT OF THE EXPERIMENT

The grazing of the experimental site started when the trees were completely established, around two years old (September 2004). In the first two years, grass was harvested and collected with a tractor to eliminate the need to graze and, hence, avoiding damage to the young trees by the cattle. Young and light weight animals were used (calves with around 80 kg of live weight) for the three first grazing periods, to minimize tree damage. After that, animals with higher weight were used. A system of flexible grazing was used, with around four or five days of occupation and a average of 30 and 50 resting days for rainy and dry seasons, respectively (Photo 1). A mean stocking rate of 2.0 AU ha^{-1} was used and animals always had free access to the entire general experiment.

Photo 1. Grazing in *Brachiaria brizantha* grass of experimental plots in dry season in Cañas, Costa Rica. Photo: H. Andrade

3.4. DATA COLLECTION

The climatic variables of rainfall, temperature, relative humidity, wind speed and global radiation were collected from an automatic climatic station close to the study site, owned by the farm. This station recorded data for every 15 minutes sending the information by a telemetry communication system (Adcon Telemetry) to a central computer to be stored in the software addVANTAGE. This information was used to calculate vapour pressure deficit and reference evapotranspiration.

Tree dimensions (total height, diameters at 30 cm height and at breast height) were recorded every six months (April and November 2003, April and October 2004, May and December 2005; Photo 2). Two perpendicular crown diameters were measured twice (November 2003 and December 2005) from which vertically projected crown area was calculated. Grass dry matter production was estimated at four times in contrasting climatic seasons (March 2005 – dry season and August 2003, June and August 2005 – rainy season) by cutting to 30 cm height drying and weighing.

A preliminary soil study, including chemical and physical properties, was carried out when tree were completely established (September 2003). Soil nitrogen and organic carbon samples were collected for fractionation analysis in February 2005. Soil core samples, for estimating fine root biomass and length, were taken twice (July 2004 and 2005; wet season and early wet season, respectively).

Photo 2. Measurement of tree dimensions a) total height and b) diameter at breast height.
Photo: H. Andrade

Leaf area index and the transmission of radiation to grasses were estimated by hemispherical photographs taken in three contrasting climatic periods (November 2004 –rainy-, August 2005 –transition- and January 2006 –dry seasons) using a digital camera. Transmitted photosynthetically active radiation measured by Sunscan PAR sensor (Delta-T Instruments, Burwell, Cambridge, UK), consisting of a linear array of PAR sensors, was carried out in a dry season (January 2005; Photo 3). Water use in the tree – grass competition control trial was estimated using an event approach, calculating the soil volumetric moisture in four periods of dry season (December 2004 –early dry season-, February 2005 and January 2006 – middle of dry season- and April 2006 –end of dry season; Photo 4).

Photo 3. Measurements of transmission of photosynthetically active radiation by Sunscan
Photo: H. Andrade

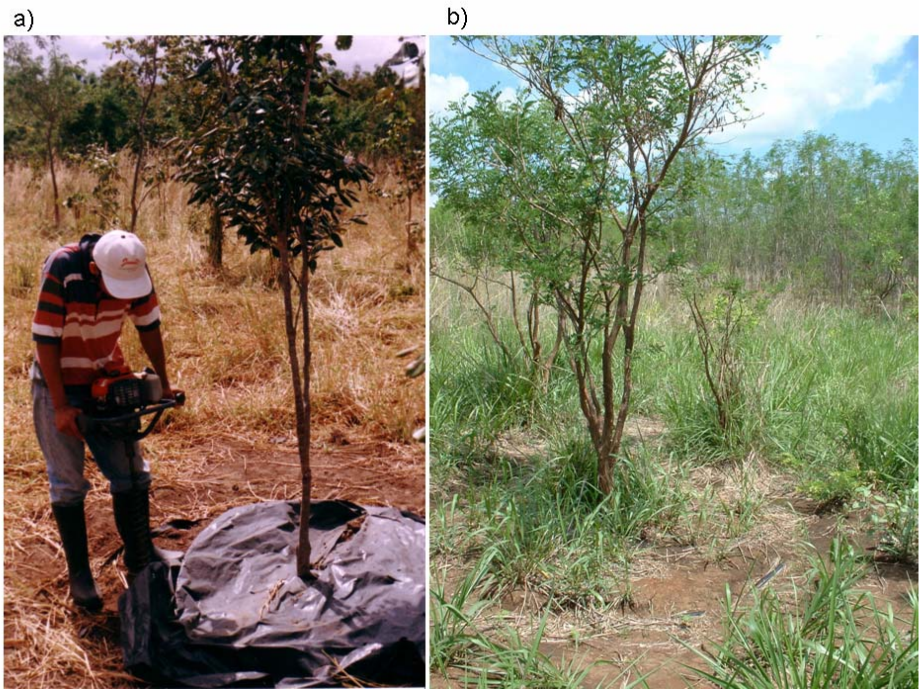

Photo 4. Water use in tree – grass competition control trial: a) estimation of soil moisture in *Dalbergia retusa* without grass in the dry season; b) *Diphysa robinioides* growing in with competition of *Brachiaria brizantha* in the transition season.
Photo: a) H. Andrade; b) R.M. Brook

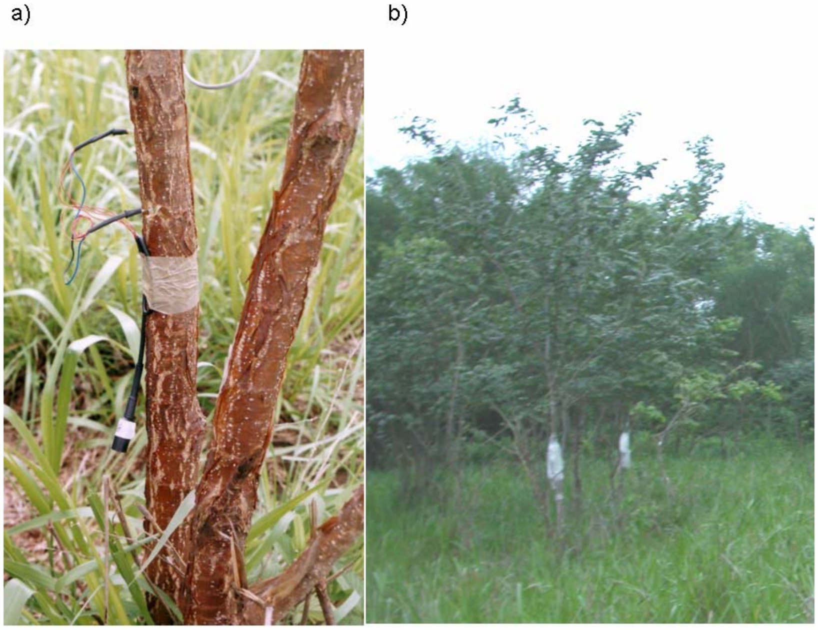

Photo 5. Tree sap flow monitoring: details of a) sap flow gauges and b) monitored trees.
Photo: H. Andrade

Photo 6. Calibration of sap flow gauges with trees growing in pots in a greenhouse at CATIE: a) general view of trial; b) weighing of pots.
Photo: H. Andrade.

3.5. EXPERIMENTAL DESIGN AND STATISTICAL ANALYSES

The general experimental design was a randomized complete block with split factorial arrangement. The factor position had two levels (under canopy and intermediate canopy); whereas, depth had three levels (0-20, 20-40 and 40-60 cm). The factor competition control considered the establishment of subplots with different tree-grass arrangements (grasses alone, trees alone and tree-grass association). However, specific experimental designs were employed according to the evaluated variables as shown in Table 2. Analysis of variance, comparisons of simple and mixed means, T tests correlation analyses, and regression procedures were carried out by SAS (1988) through the following procedures: ANOVA, GLM, MEANS, LSMEANS, TTEST, CORR and REG.

This section has covered the general issues of materials and methods for the whole research programme. Due to the style used for the thesis (i.e. in the form of a series of complete paper manuscripts), there will inevitably be some repetition of materials and methods in each chapter.

Table 2. Summary of used experimental design and treatment arrangements for the statistical analyses.

Experimental design	**Treatment arrangement**	**Source of variation**	**Evaluated variables**
Randomize complete blocks	Split plot	B, G, T, GxT	Tree growth, total carbon storage, tree cover, leaf area index and transmission of radiation to grasses, canopy light extinction coefficient
	Split split plot	B, G, T, GxT, P, TxP, GxP, GxTxP	Grass dry matter production
		B, G, T, GxT, D, TxD, GxD, GxTxD	Soil nitrogen and organic carbon
		B, G, T, GxT, C, TxC, GxC, GxTxC	Soil moisture, water availability and water use, soil in tree – grass competition control trial
	Split split split plot	B, G, T, GxT, P, TxP, GxP, GxTxP, D, GxD, TxD, PxD, GxTxD, GxPxD, TxPxD, GxTxPxD	Fine root biomass and length, tree relative root length and biomass
Completely randomized	N/A	T	Water use in trees growing in pots in a greenhouse
N/A	N/A	G, T	Tree water use by sap flow, leaf water potential

B: Block; G: Grass; T: Tree; P: Position; D: Depth; C: Competition control.

CHAPTER IV

4. GROWTH, PRODUCTION AND CARBON SEQUESTRATION OF SILVOPASTORAL SYSTEMS WITH NATIVE TIMBER SPECIES IN THE DRY TROPICS OF COSTA RICA

Hernán J. Andrade[2]; Muhammad Ibrahim[3]; Robert Brook[4]; Phillipe Vaast[2]; Fergus Sinclair[3]; Francisco Jiménez[5]

Summary

The twin environmental issues of loss of forest cover due to cattle farming combined with pasture degradation leading to low levels of production and leading therefore to more deforestation are serious concerns in Costa Rica. To test the feasibility of combining a more productive pasture with indigenous tree species, a silvopastoral experiment was established on a farm in the seasonally dry lowlands of Cañas, Guanacaste Province. The experiment tested an improved pasture (*Brachiaria brizantha*) against an unimproved pasture dominated by *Hyparrhenhia rufa*. Three indigenous tree species were established: *Pithecellobium saman*, *Diphysa robinioides* and *Dalbergia retusa*. The treatment plots were grazed by cattle for two periods each year. After 51 months, *D. robinioides* was the fastest growing species, and *P. saman* the slowest, while *B. brizantha* produced three times the aboveground and twice the belowground biomass as *H. rufa*, and trees had no effect upon grass yield. *P. saman* grew more slowly with *B. brizantha* than with *H. rufa* treatments, but there was no effect of pasture species upon the other two tree species. The carbon in phytomass varied between 7 and 13 Mg C ha^{-1} in no-tree pastures and silvopastoral systems,

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[2] PhD Candidate, CATIE-University of Wales (Bangor): handrade@catie.ac.cr (Author for correspondence)

[3] Department of Agriculture and Agroforestry, CATIE. Emails:mibrahim@catie.ac.cr; pvaast@catie.ac.cr

[4] School of the Enviroment and Natural Resources, University of Wales (Bangor). Emails: r.m.brook@bangor.ac.uk; f.l.sinclair@bangor.ac.uk.

[5] Department of Natural Resources and Environment, CATIE. Email: fjimenez@catie.ac.cr.

respectively, and soil organic carbon (SOC) averaged 100 Mg ha^{-1}. *B. brizantha* appeared to stimulate tree root production, which in turn was highly correlated with the light fraction of soil organic carbon, resulting in annual increments in SOC of up to 9.9 Mg ha^{-1} year^{-1}. These early results indicate the promising potential of this silvopastoral system.

4.1. INTRODUCTION

Deforestation represents one of the most important problems in the world; it is considered that around 13 million hectares per year are being lost due to conversion of forest to agricultural lands (FAO 2005). On the other hand, forest planting, landscape restoration and natural expansion of forests have significantly reduced the net loss of forest area. In 2003, 12 million hectares (63%) of the agricultural area of Central America was occupied by permanent pastures (FAO 2006a) and 82% in Costa Rica, respectively. In the Central America region, the total area dedicated to permanent pastures has slowly grown in the last decade (0.1% year^{-1}; FAO 2006a); most being conventionally managed using fire and low inputs. These pastures degrade in time resulting in decreases in productivity and environmental degradation. The deforestation in Central America is mostly dominated by the conversion of forests in lowland frontiers (FAO 2006b). In the Chorotega region of Costa Rica, where the dry region is located, a fragmentation process has occurred in the last four decades. Between 1960 and 1980, fragmentation was due forest shrinkage and division mainly attributed to cattle ranching practices; whereas, between 1980 and 2000, fragmented landscape was the result of secondary forest growth and aggregation (Arroyo-Mora et al. 2005).

Silvopastoral systems have been advanced as win-win technologies to enhance productivity and provide environmental services (Ibrahim et al. 1999, Gobbi and Ibrahim 2004). Most farmers manage natural regeneration of trees in pastures because it is a very cost effective way to introduce tree component in grasslands. There is a tendency to replace naturalised grass with more aggressive and drought tolerant grass species. In Cañas, Esquivel et al. (2003) have estimated that improved grasses (*B. brizantha* and *B. decumbens*) cover 72% of the pasture areas and 56% of total agricultural areas. In dry and seasonally dry areas such as Cañas zone, the use of drought tolerant and productive grasses improves the overall productivity of silvopastoral systems. In Costa Rica, between 1990 and 2003, 18.7% of the permanent pastures had been established with *Brachiaria* species in order to improve the milk and beef productivity in the country. About 55% of the national milk production and almost 18% of the beef production in 2003 have been attributed to establishment of *Brachiaria* species (Holmann et al. 2004).

The introduction of trees in pasture ecosystems may improve the total productivity of the system. Some studies have demonstrated increased growth of tropical grasses under tree canopies at moderated density (Wilson 1998, Marlats et al. 1999, Andrade et al. 2004). These responses are mainly attributed to increased fertility or nitrogen availability under the tree canopy. However high tree density or cover may give excessive shade and exert detrimental competition on pasture, therefore reducing carrying capacities of the pasture (Wilson 1998). On the other hand, the economic and ecological importance of silvopastoral systems may increase if livestock grazing is also used to manage the under story vegetation (Braziotis and Papanastasis 1995).

The *Brachiaria* species introduced in the seasonally dry areas are more drought and shade tolerant than the naturalised grass species (*H. rufa*) and support higher stocking rates and animal productivity (Lascano 1991, Pizarro et al. 1998, Guenni et al. 2002). However, there is little information about how compatible these *Brachiaria* grasses are in silvopastoral mixtures with native timber tree species, and this is a key for designing and managing silvopastoral systems for sustainable production (meat, milk and timber) and generation of environmental services. Most studies on traditional systems have focused on inventories of tree species and system composition and structure; nevertheless, a few studies have been conducted, which evaluate how the grass component affects the growth and performance of associated native tree species. This chapter presents results about tree-grass interactions in terms of growth, production, fine root biomass and carbon sequestration in silvopastoral systems in the dry tropics of Costa Rica.

4.2. MATERIALS AND METHODS

4.2.1. Description of Experimental Site

This study was carried out in Hacienda La Pacifica (85º9'14.5" W and 10º28'36.8"N; 50 m of altitude) located 5 km at north of Cañas, Guanacaste, Costa Rica. The zone is classified as a dry tropical forest (Holdridge 1996), with a mean rainfall of 1500 mm year^{-1}. About 85% of rainfall falls between May and November (the wet season); in contrast, between December and April the evapotranspiration is higher than the rainfall (the dry season; Figure 1). The mean temperature in the experimental site is around 28°C (23-36ºC) and the relative humidity varies between 60 and 85% for the dry and rainy season, respectively (IMN 2003). The mean potential evapotranspiration, using an open pan, is 1800 mm year^{-1}. The landscape of Cañas has changed dramatically from predominantly forests to pasture mainly dominated by jaragua grass (*Hyparrhenia rufa*; Herrick 1993).

The experimental field has an average slope of 4%. Initial determinations conducted in September 2003 showed that the soil texture is clay, with a mean content of clay of 44%. The soil contains a medium level of organic matter in the 0-20 cm horizon and a low concentration in the 20-60 cm horizon. There is a phosphorus deficiency in the lower horizons as pH rises (Table 1).

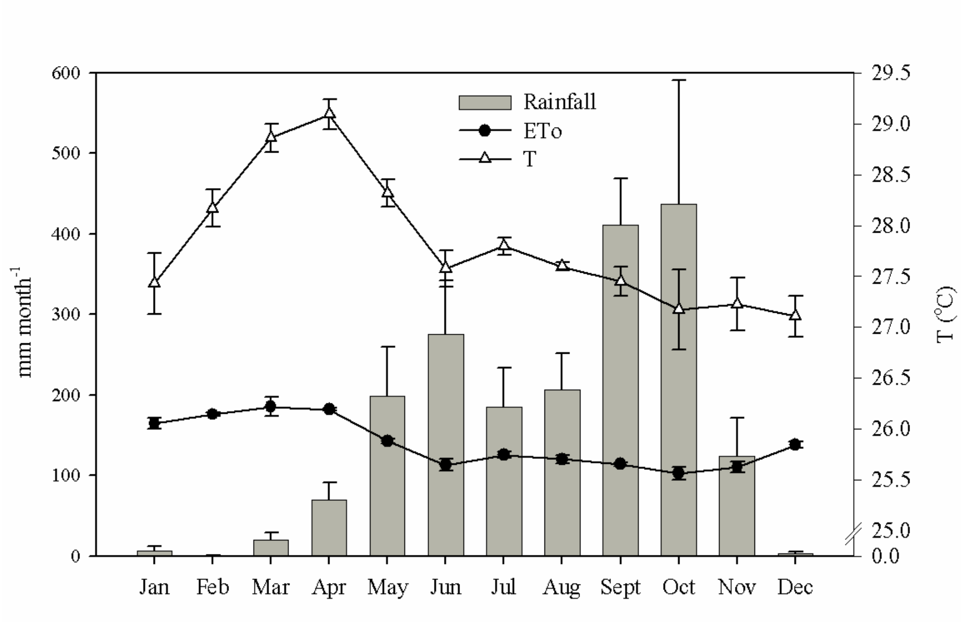

Figure 1. Climatic conditions in the study zone. Temperature (T) and rainfall are mean values between 1985 and 2003; reference (ETo) by open pan (between 2000 and 2003). Source: Ingenio Taboga, unpublished data.

Table 1. Main soil chemical properties of the experimental site, Hacienda La Pacífica, Cañas, Costa Rica.

Depth	pH	Ca	Mg	K	CEC	Base	P	Cu	Zn	Mn	Fe	OM
	Soil					Sat						
cm	water 1:1	cmol(+) kg^{-1}				(%)	mg kg^{-1}					%
0-20	6.7	13.0	4.38	0.64	18.0	0.35	1.02	8.8	0.75	2.32	47.7	3.5
20-40	7.0	13.1	4.34	0.50	17.9	0.44	0.66	8.4	0.22	1.79	32.0	1.9
40-60	7.1	13.8	4.84	0.36	19.0	0.58	0.44	6.1	0.17	1.13	21.2	1.1

4.2.2. Establishment of the experiment

A randomized complete block experimental design with three replications was used. The treatments had a factorial structure with a split plot design where two grass species (*Brachiaria brizantha* and a pasture dominated by *Hyparrhenia rufa*) formed the main plots with four randomized tree treatments (*Pithecellobium saman*, *Diphysa robinioides, Dalbergia retusa* and no-tree control) in the subplots. Main plots had an area of 8000 m^2; whereas the subplots were 1000 m^2.

This trial was set out in actively grazed pasture plots which was initially established with *H. rufa* and had been grazed over the last 20 years. No fertilizers were used to manage these pasture plots. The treatments were distributed within this pasture area according to the design above. The main plots for *B. brizantha* were prepared with tractor, using a plowe and a rake; whereas the *H. rufa* was left without preparation because this grass was established in these plots. *B. brizantha* pasture was established by sowing 4 kg seeds ha^{-1}. All plots were initially fertilized using a compound fertilizer (12-30-20, N-P-K) at a rate of 180 kg ha^{-1}. Trees were planted in double lines (2 x 2 m) within the pasture plots, leaving a strip of 8 m between lines and were fertilized with of the same fertilizer used for the pastures, at a rate of 100 g plant^{-1}. Seedlings were produced in Hacienda La Pacifica, with seeds from the CATIE´s seed bank and soil material from fertile sites in the same farm. Two replantings were carried out (May and October 2002), replacing all dead plants. Each subplot have a total of 100 trees per plot, for a tree density of 1000 trees per ha.

Grazing at the experimental site started when the trees were completely established, around 2 years old (September 2004). In the first two years, grass was harvested and collected with a tractor to avoid grazing and possible damage to the young trees. Young and light animals (calves with around 80 kg of live weight) were used for the three first grazing periods, to minimize tree damage. After that, animals with higher weight were used. A flexible grazing system was used, with around 4-5 days of occupation and an average of 30 and 50 resting days for rainy and dry seasons, respectively. A mean stocking rate of 2.0 AU ha^{-1} was used and animals always had free access to the entire general experiment.

4.2.3. Variables evaluated

4.2.3.1. Aboveground biomass models of trees

A destructive sampling of 27 trees (nine for each species) was carried out to develop the aboveground biomass models. These trees were sampled outside the tree plots. The development of these models was carried out following the approach recommended by Segura et al. (2006) and Segura and Kanninen (2005). Preliminary models for each tree species were developed. These models were statistically compared to determine if there were differences in the intercept and slopes of the three models.

4.2.3.2. Tree growth

The 36 central trees per subplot were measured every six months (total height [TH], diameter at 30 cm height [D30] and diameter at breast height, crown diameter in two directions: N-S, E-W). Mean quadratic diameter (MQD) was calculated using Equation 1, because these tree species usually have more than one stem.

$$MQD = \sqrt{(D_1^2 + D_2^2)} \qquad \text{Equation 4.1}$$

Where;
MQD: Mean quadratic diameter (cm)
D_1 and D_2: Diameter of the two major trunks (cm)

4.2.3.3. Forage production and residual grass biomass

Forage production was estimated by cutting the grasses at a height of 30 cm height using two quadrants (50 x 50 cm) per subplot, one located under canopy and another at the limit of canopy projection. Selected trees had a canopy area similar to the mean canopy area in the subplot. Fresh weight of edible fodder was registered in the field and a sub-sample was collected and dried for 48 h at 60°C to estimate dry matter content. DM production of pasture was measured the day before each grazing cycle, which was 30 days in the rainy and 50 days in the dry season. A regression analysis was carried out to evaluate the effect of tree cover on grass production for both species. Tree canopy cover was estimated using hemispherical photography (Andrade et al. 2007c). Residual grass biomass was considered as the total aboveground biomass up to a height of 30 cm.

4.2.3.4. Fine root biomass

Soil cores were collected from two individual trees and two positions with respect to each tree (under canopy, around 1 m from tree stem and at an intermediate distance from the canopy, around 2m away). The trees to de sample were selected based on their dimensions (diameter at breast height, total height and canopy area). The chosen trees had the mean dimensions of the trees in their subplot. Samples containing roots were collected from three depths (0-20, 20-40 and 40-60 cm) and extracted them with an engine auger (EFCO TR1540, 5 cm in diameter and 60cm in length). This method was necessary because the soil was compacted. The soil samples containing roots were taken to the laboratory for separation from soil and dead material. The roots were stored in a refrigerator (4 °C) until analysis. Roots from core sample were separated by species (tree and grass) based on some differential characteristics such as colour; the grass roots were white contrasting with the brown colour of the tree roots. Root samples for each species were maintained in the laboratory as references. When the amount of roots was high, a subsample of around 40% of the sample was taken for separation; in this case the remnant sample was dried to estimate dry matter. Each sample or subsample was oven dried (65°C for 48 h) to quantify root biomass by component (Jose et al. 2000).

4.2.3.5. Carbon content in biomass

Samples of grass and tree species were collected to estimate the carbon fraction in biomass. From trees, 54 samples were taken from three species by four components (stem, branches, leaves and fine roots) with three replications from the 27 trees sampled in the development of biomass models. The samples were oven dried (65^{o}C for 48 h) and they were pulverised using a mill. In the case of woody components such as stem and branches, the samples were broken into small pieces using a hand drill before being pulverised. Grass samples were also collected to analyze carbon content, taking in account species, position with respect to the trees and component (above and belowground biomass). All samples were analyzed by combustion using a Thermo Finnigan FLASH EA 1112 (Rodano, Milan, Italy) at the CATIE soil laboratory. Data were analyzed using a completely random design with treatments as a factorial arrangement.

4.2.3.6. Soil nitrogen and organic carbon

One sample for each horizon was obtained in February 2005 by mixing around 10 sub-samples collected from three depths (0-20, 20-40 and 40-60 cm). Soil organic matter was fractionated using a chemical dispersant (sodium hexametaphosphate, 5 g l^{-1}) followed by physical separation based on particle sizes (53μm; Cambardella and Elliot 1993). Organic carbon and nitrogen was analyzed for each fraction using a CHN auto-analyzer Thermo Finnigan FLASH EA 1112 (Rodano, Milan, Italy) in the soil laboratory at CATIE. Total and light fraction organic carbon was estimated using the organic carbon concentration and Equation 4.2. Two soil core samples by block from the three studied depths were collected with a metallic ring (4.3 cm in diameter and 4.4 cm in height) to estimate soil bulk density (MacDicken 1997) using Equation 4.3. Soil organic carbon, nitrogen content and fine root biomass (total and by component) were correlated to analyze the relationships between variables.

Accumulation of soil organic carbon was calculated using the sample in September 2003 as the initial state.

$$Bd = \frac{SM}{SV}$$ Equation 4.2

Where;
Bb : Bulk density (g cm^{-3})
SM : Soil mass of sample (g)
SV : Soil volume of sample (cm^3)

$$SOC = CC \times Bd \times Ds$$ Equation 4.3

Where;
SOC : Soil organic carbon (Mg ha^{-1})
CC : Carbon concentration in soil (%)
Bd : Bulk density (g cm^{-3})
Ds : Depth of soil (cm)

4.2.3.7. Total carbon in biomass

Biomass of structural roots of trees was estimated through an equation developed by IPCC (2003) for tropical areas (Equation 4.4). Carbon in aboveground biomass (trees and grasses) and fine and structural root biomass were added to estimate total carbon storage in biomass. Carbon accumulation rates were calculated by dividing total carbon in biomass between 51 months corresponding to the age of the trial.

$$Br = e^{(-1.0587+0.88*\log(Ba))}$$ $R^2 = 0.84$ N= 151 Equation 4.4

Where;
Br : Biomass of roots (Mg ha^{-1})
Ba : Aboveground biomass (Mg ha^{-1})

4.2.4. Statistical analyses

All statistical analyses were carried out using SAS (SAS 1988). Analyses of variance, analyses of correlation, regression procedures and comparison of means were carried out.

4.3. RESULTS

4.3.1. Aboveground tree biomass equations

There was a poor relationship between height of trees and its total aboveground biomass but the use of mean quadratic diameter (MQD) explained a large percentage of the biomass variability ($R^2 = 0.85$; Figure 2): However, the inclusion of total height improved the R^2 of the model (0.92; Table 2). There was no statistical difference among tree species in terms of relationships between total aboveground biomass and tree MQD. A multispecies biomass model for the three tree species was developed with good adjustment indicators (Equation 4.5; Table 2). The parameters for the three preliminary models of each species resulted significantly similar among the tree species (Table 3).

4.3.2. Tree growth

There was an interaction between grass and tree species with respect to MQD and total height of tree species. Mean MQD and height of *D. retusa* was higher combined with *B. brizantha* that with *H. rufa* (4.6 vs 3.7 cm MQD; 3.4 vs 2.5 m height) but with *P. saman* these values were higher with *H. rufa* (2.7 vs 3.7 cm MQD; 2.2 vs 2.7 m height) whereas these growth parameters for *D. robinioides* were not significantly different between grass species (Table 4). *D. robinioides* exhibited the highest growth rates compared to *D. retusa* and *P. saman*. There was a seasonal effect on growth of the tree species: growth rates were higher in the rainy than in the dry season (1.8 vs 0.4 cm year^{-1} of QMD and 0.9 vs 0.3 m year^{-1} in height, respectively; Figure 3). Although there was no statistical differences in tree growth with different grass species, growth of trees in the dry season was better in association with *B. brizantha* than with *H. rufa* (0.6 vs 0.2 cm year^{-1} of MQD, respectively). In the dry season, *P. saman* and *D. retusa* were not affected by the grass; whereas, *D. robinioides* had a higher growth in mixture with *B. brizantha* than with *H. rufa* (1.2 vs 0.3 cm year^{-1} of MQD; Figure 3). In the rainy season, there was no effect of grass species on growth of the trees. Tree aboveground biomass gain was different among tree species ($P<0.01$) and between seasons ($P=0.04$). Although *P. saman* had the lowest biomass gain, this species was less affected by the dry season than of *D. retusa* and *D. robinioides*.

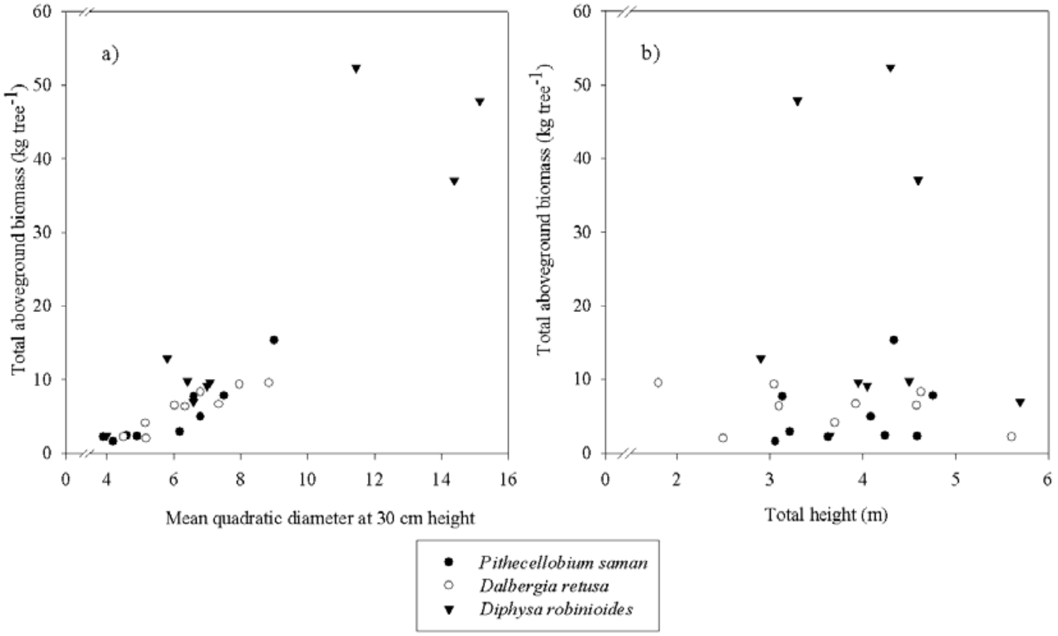

Figure 2. Relationship between total aboveground biomass and a) mean quadratic diameter at 30cm height and b) total height of three native timber tree species (*Pithecellobium saman*; *Dalbergia retusa* and *Diphysa robinioides*) growing in silvopastoril systems in the dry tropics of Costa Rica. Mean quadratic diameter= $\sqrt{(D_1^2 + D_2^2)}$; where D_1 and D_2 are the diameter of the two major trunks in each tree.

Table 2. Best-fit equations to estimate total aboveground biomass of three native timber tree species (*Pithecellobium saman*; *Dalbergia retusa* and *Diphysa robinioides*) growing in silvopastoral systems in the dry tropics of Costa Rica.

Equation/ Model	**RMSE**	**R^2**	**Adj-R^2**	**PRESS**	**FI**
4.5. $\text{Log (TB)} = -1.54 + 2.05 \text{ Log (mqd)} + 1.18 \text{ Log (th)}$	0.12	0.92	0.91	0.45	1.84
4.6. $\text{Log (TB)} = -1.25 + 2.53 \text{ Log (mqd)}$	0.16	0.85	0.85	0.74	2.46
4.7. $\text{Log (TB)} = -0.82 + 0.31 \text{ mqd} - 0.01 \text{ mqd}^2$	0.16	0.86	0.85	3.91	1.55
4.8. $\sqrt{(\text{TB})} = -4.97 + 3.01 \sqrt{\text{mqd}}$	0.62	0.85	0.84	0.82	2.49

TB: Total aboveground biomass (kg tree^{-1}); mqd: mean quadratic diameter at 30 cm height (cm); th: total height (m); RMSE: Root of mean square error; PRESS: Sum of predicted residual squares; FI: Furnival Index.

Table 3. Comparison of aboveground biomass models of three native timber species growing in silvopastoral systems in the dry tropics of Costa Rica.

Variable/comparison between species		**Parameter estimated**	**Standard error**	**P value**
Intercept (a)	*P. saman* vs *D. retusa*	0.63	0.39	0.12
	P. saman vs *D. robinioides*	0.21	0.39	0.59
	D. retusa vs *D. robinioides*	0.42	0.41	0.33
Slope 1 (b; dg)	*P. saman* vs *D. retusa*	-0.20	0.61	0.74
	P. saman vs *D. robinioides*	0.11	0.47	0.82
	D. retusa vs *D. robinioides*	-0.31	0.50	0.54
Slope 2 (c; ht)	*P. saman* vs *D. retusa*	-0.61	0.75	0.42
	P. saman vs *D. robinioides*	-0.21	0.84	0.80
	D. retusa vs *D. robinioides*	-0.40	0.62	0.53

Table 4. Dimensions of three native timber tree species in 51 month old silvopastoral systems with two contrasting grass species in the dry tropics of Costa Rica.

	Tree species					
	Mean quadratic diameter (cm)			Total height (m)		
Grass species	*P. saman*	*D. retusa*	*D. robinioides*	*P. saman*	*D. retusa*	*D. robinioides*
B. brizantha	2.7 (0.4)	4.6 (0.3)	5.8 (0.3)	2.2 (0.2)	3.4 (0.2)	3.4 (0.2)
H. rufa	3.7 (0.4)	3.7 (0.3)	5.6 (0.3)	2.7 (0.2)	2.5 (0.2)	3.5 (0.2)
Mean	3.3 (0.3)	4.1 (0.2)	5.7 (0.2)	2.5 (0.1)	3.0 (0.1)	3.4 (0.1)
Significance level (P)						
Tree species		<0.01			<0.01	
Grass species		0.78			0.39	
Tree x grass		0.01			<0.01	

Values in parenthesis represent standard error of mean.

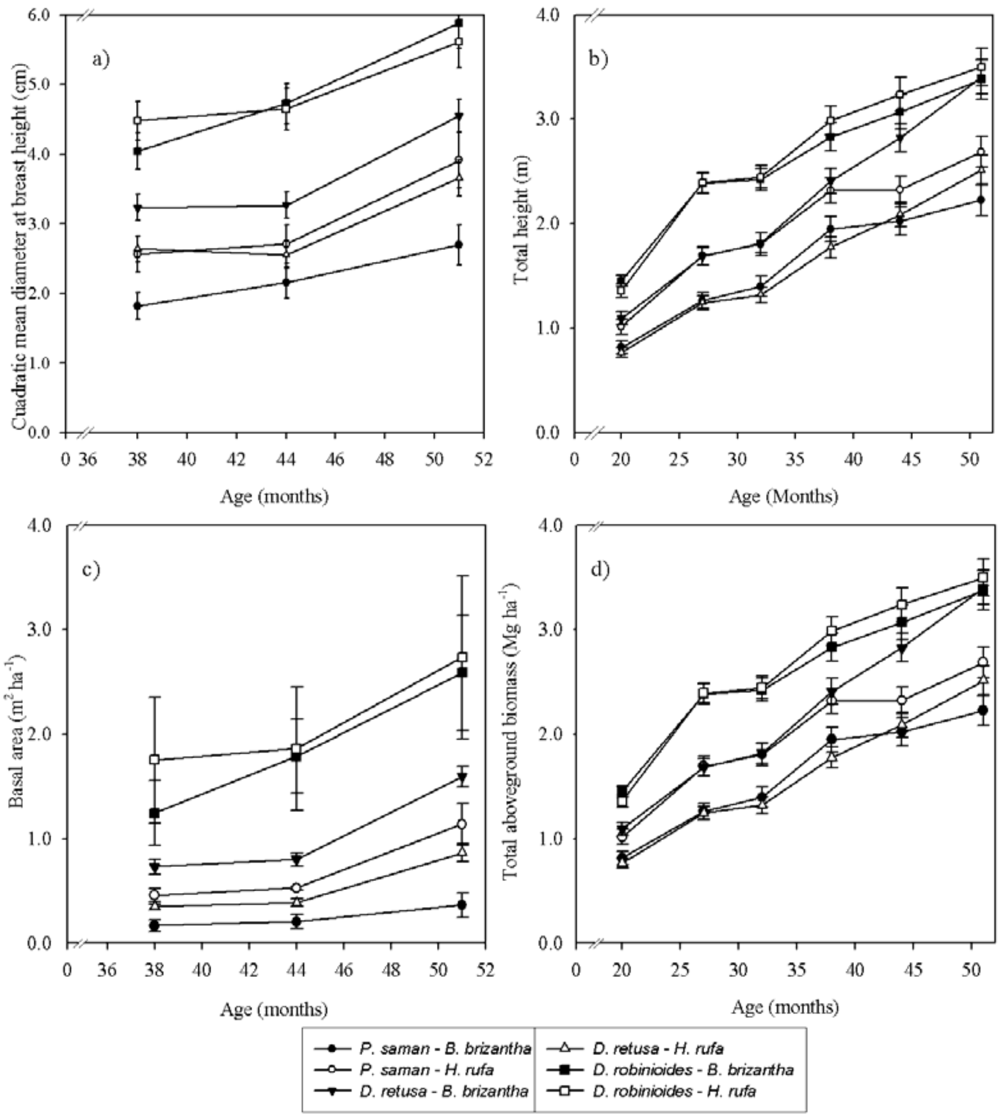

Figure 3. Performance of three native timber tree species in silvopastoral systems with two contrasting grass species in the dry tropics of Costa Rica. a) mean quadratic diameter at breast height; b) total height; c) basal area and d) total aboveground biomass. Error bars correspond to standard error. Dry seasons correspond to periods 27-32 and 38-44 months.

4.3.3. Grass dry matter (DM) production

Mean annual dry matter production of *B. brizantha* was more than double that of *H. rufa* (14.7 vs 5.3 Mg DM ha^{-1} year^{-1}). Tree species did not affect annual grass production (Table 5). As expected, there was a lower mean forage production in the dry than in the rainy season for both species (1.8 vs 3.3 g DM m^{-2} day^{-1}). Dry matter production of *B. brizantha* was always higher than that of *H. rufa* in both seasons with mean of 2.6 and 1.1 g DM m^{-2} day^{-1}, respectively in the dry season and corresponding values of 5.3 and 1.4 g DM m^{-2} day^{-1} for the wet season (Figure 4). Grass dry matter production was statistically similar in both positions with respect to tree canopy for both grasses (Table 5).

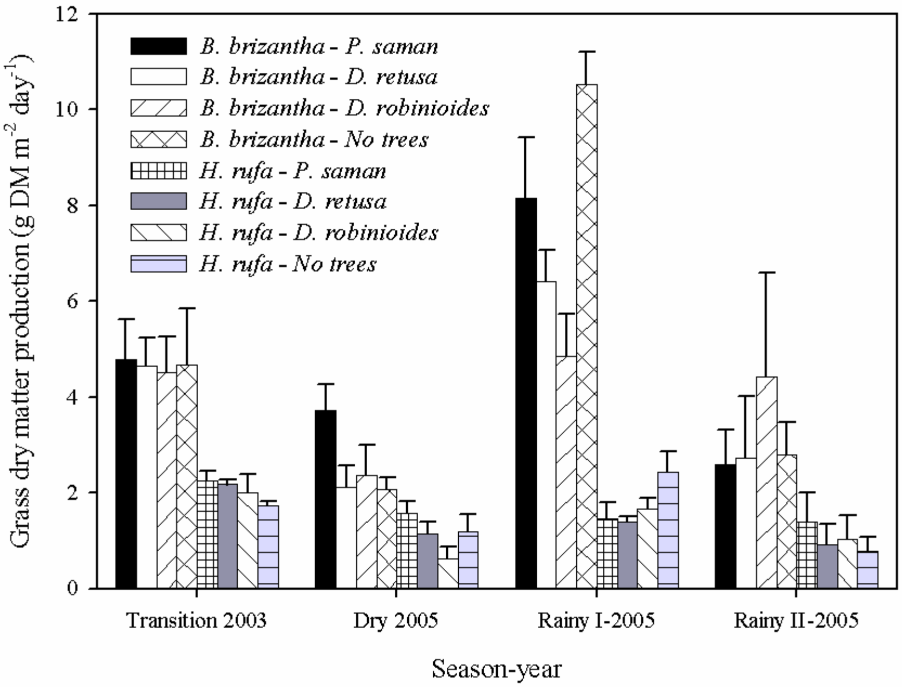

Figure 4. Forage production of two contrasting grasses under three native timber tree species and without trees in silvopastoral systems in the dry tropics of Costa Rica. Error bars correspond to the standard error of the mean.

There was a little effect of the associated tree species on the productivity of grass species. The grasses under *D. robinioides* and *D. retusa* produced less dry matter than under *P. saman* and when grown in monoculture (Figure 4). There was a linear relationship between grass productivity of *H. rufa* and its tree cover which shows that the grass yield decreased with increasing canopy cover (R=0.75, P=0.02; Equation

4.3). In contrast, it seems *B. brizantha* is less affected by tree canopy cover (R=-0.30, P=0.43).

$$DMP = 7.16 - 0.09 * TC \qquad R^2 = 0.56 \qquad \text{Equation 4.3}$$

Where;
DMP : Dry matter production of grasses (Mg DM ha^{-1} $year^{-1}$)
TC : Tree canopy cover (%)

Table 5. Annual grass production of two contrasting grass species in silvopastoral associations with native timber tree species and in open areas in the dry tropics of Costa Rica.

	Annual grass production (Mg DM ha^{-1} $year^{-1}$)		
	Grass species		
Tree species	*Hyparrhenia rufa*	*Brachiaria brizantha*	Mean
Pithecellobium saman	6.2 (0.2) a	16.6 (2.0) a	11.4 (2.5) a
Dalbergia retusa	5.2 (0.3) a	13.1 (1.3) a	9.1 (1.9) a
Diphysa robinioides	4.4 (0.8) a	13.4 (1.4) a	8.9 (2.1) a
Open areas	5.4 (0.3) a	15.6 (1.0) a	10.5 (2.3) a
Mean	5.3 (0.3) A	14.7 (0.8) B	
Position			
Under canopy	6.2 (0.3) a	15.1 (1.7) a	10.7 (1.4) a
Intermediate canopy	4.3 (0.4) a	13.6 (0.8) a	9.0 (1.2) a

Different lower case letters in the same column indicate statistical differences ($P<0.05$). Different upper case letters indicate statistical difference between grass species ($P<0.01$). Values in parenthesis represent standard error of mean.

4.3.4. Fine root biomass

Fine root biomass of trees was significantly higher ($P<0.01$) in association with *B. brizantha* than with *H. rufa* (1.0 vs 0.5 Mg ha^{-1}; Table 6). In contrast, fine roots of grasses were not affected by tree components ($P>0.05$). In all combinations, the fine root biomass was significantly lower in deeper layers ($P<0.01$; Table 6). There was no interaction between tree and grass species for root biomass by component ($P>0.05$).

Table 6. Mean fine root biomass of tree and grass in six silvopastoral systems of two contrasting grasses under three native timber tree species and two monoculture grasses in the dry tropics of Costa Rica. Values in parenthesis correspond to the standard error.

		Mg DM ha^{-1}					
Species		**0-20**		**20-40**		**40-60**	
Grass	Tree	**Tree**	**Grass**	**Tree**	**Grass**	**Tree**	**Grass**
Brachiaria brizantha	*Pithecellobium saman*	2.62 (0.81)	1.36 (0.56)	1.01 (0.56)	0.60 (0.41)	0.52 (0.20)	0.11 (0.02)
	Dalbergia retusa	1.69 (0.37)	1.40 (0.32)	0.48 (0.08)	0.40 (0.12)	0.25 (0.04)	0.19 (0.04)
	Diphysa robinioides	1.80 (0.50)	1.30 (0.34)	0.50 (0.06)	0.28 (0.04)	0.25 (0.03)	0.27 (0.12)
	Monoculture (no-tree control)	0.00	1.60 (0.43)	0.00	0.34 (0.08)	0.00	0.26 (0.08)
Hyparrhenia rufa	*Pithecellobium saman*	0.97 (0.35)	1.27 (0.20)	0.22 (0.05)	0.29 (0.06)	0.10 (0.02)	0.16 (0.03)
	Dalbergia retusa	1.33 (0.42)	0.68 (0.13)	0.47 (0.16)	0.23 (0.06)	0.17 (0.05)	0.12 (0.02)
	Diphysa robinioides	1.22 (0.35)	1.26 (0.37)	0.26 (0.05)	0.18 (0.03)	0.15 (0.03)	0.13 (0.03)
	Monoculture (no-tree control)	0.00	1.08 (0.20)	0.00	0.28 (0.04)	0.00	0.17 (0.02)

	Fine root biomass		
Source of variation	**Tree**	**Grass**	**Total**
	P values		
block	0.53	0.83	0.64
grass	0.30	0.39	0.33
tree	0.01	0.87	0.12
grass*tree	0.23	0.90	0.67
depth	< 0.01	< 0.01	< 0.01
grass*depth	0.32	0.47	0.29
tree*depth	0.05	0.92	0.43
grass*tree*depth	0.92	0.86	0.99

Total root biomass depended on grass species which was higher for *B. brizantha* compared to *H. rufa* (1.7 vs 1.0 Mg ha^{-1} at 0-60 cm depth). There was a little difference in total biomass of fine roots between tree species: *P. saman* had slightly higher values than *D. robinioides* and *D. retusa* (1.5 vs 1.3 vs 1.2 Mg ha^{-1} at 0-60 cm depth; Figure 5). A large percentage (70%) of the fine roots were recorded in the 0-20 cm soil depth and only 20 and 10% of fine roots were found in the 20-40 and 40-60 cm horizons, respectively.

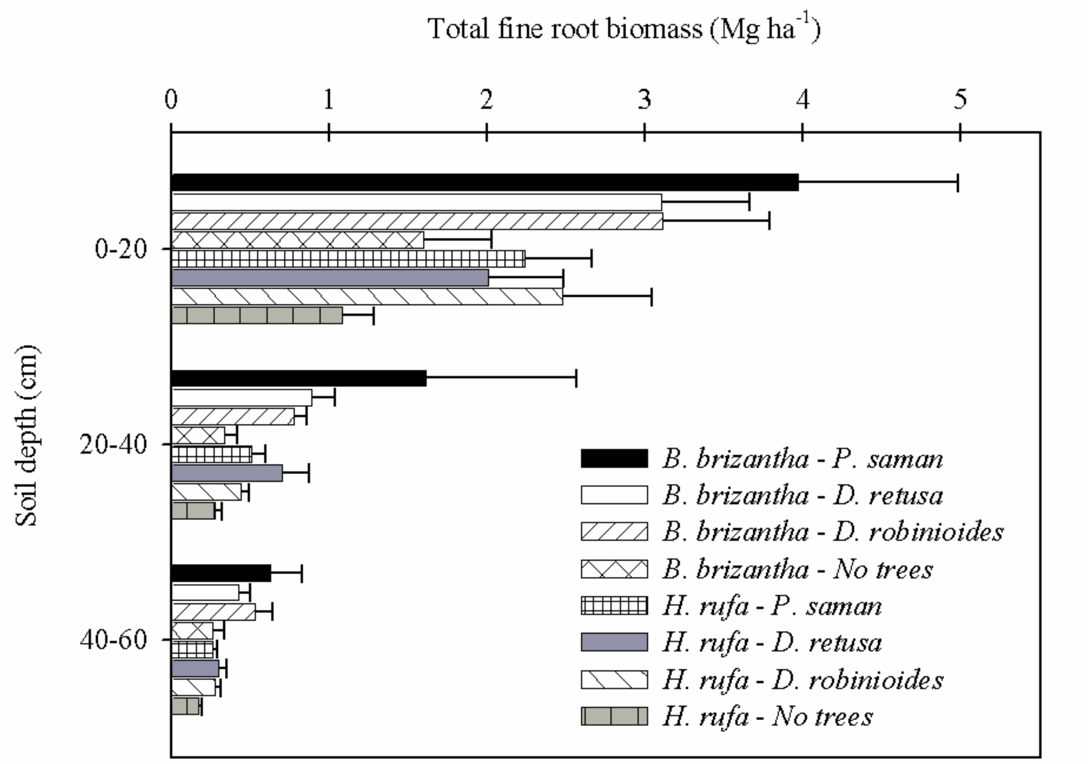

Figure 5. Fine root biomass distribution in six silvopastoral systems of two contrasting grasses (*Brachiaria brizantha* and *Hyparrhenia rufa*) under three native timber tree species (*Pithecellobium saman*; *Dalbergia retusa* and *Diphysa robinioides*) and two monoculture grasses (*B. brizantha* – No trees and *H. rufa* – No trees) in the dry tropics of Costa Rica. Error bars correspond to standard error of mean.

In the control plots (no trees), around 89% of total fine root biomass was found in the first 40 cm soil depth. *B. brizantha* had a higher root biomass than *H. rufa* in the 0-60 cm soil depth (2.2 vs 1.5 Mg ha^{-1}; Figure 5). Although the differences in root biomass were evident, statistical differences between components (tree and grass species) were not found except in trees for tree fine root biomass. This was due to very high variability within treatments, which is common when sampling roots in the field.

4.3.5. Carbon concentration in biomass

Tree species had similar carbon content (45%) in their biomass ($P>0.05$). However, there were significant ($P<0.05$) differences in C concentration between different components of trees. Stems had the highest carbon concentration (Table 7) and fine roots had the lowest. In contrast, carbon fractions in the biomass of the grasses were different between species ($P<0.05$); *B. brizantha* presented a much higher value of carbon content respect to *H. rufa* (43.7±0.3 vs 40.9±0.6%; Table 8). The carbon concentration of grass biomass taken in quadrants further from trees was similar to those taken under the tree canopy and the percentage of carbon was significantly higher belowground than aboveground (43.1±0.7 vs 41.4±0.5%; for belowground and aboveground, respectively; Table 8). The C/N ratio was considerably higher in the aboveground biomass of *H. rufa* than in that of *B. brizantha* (130.4±7.4 vs 46.9±3.0, respectively; Table 8).

Table 7. Carbon concentration in biomass of native timber tree species in the dry tropics of Costa Rica. Values in parenthesis correspond to the standard error of the mean.

	Component				
	Fine roots	**Stems**	**Branches**	**Leaves**	**Mean**
Tree species	**gC 100 g^{-1} biomass**				
Pithecellobium saman	42.4 (0.5)	46.7 (0.5)	45.7 (0.7)	46.4 (0.5)	44.9 (0.5) a
Dalbergia retusa	42.8 (0.5)	46.6 (0.7)	45.2 (0.4)	46.7 (0.4)	44.9 (0.5) a
Diphysa robinioides	43.6 (0.9)	48.0 (0.4)	46.4 (0.1)	43.7 (0.4)	45.3 (0.5) a
Mean	42.9 (0.4) c	47.1 (0.3) a	45.8 (0.3) b	45.6 (0.5) b	

Same letters indicate no statistical differences among components and among tree species ($P>0.05$).

4.3.6. Soil organic carbon

Total (TSOC) and light fraction (LFOC) soil organic carbon was similar in its distribution in the soil to that observed with fine root biomass (Figure 6). On average, the top 60 cm of soil stored approximately 110.3 Mg C ha^{-1} of total soil organic carbon (TSOC). The bulk of OC was found in the first 20 cm soil depth (mean 56 %), and a mean 25 % was found in the 20-40 cm and 19 % in 40- 60 cm depth (60.4, 26.8 and 21.1 Mg C ha^{-1}, respectively; Figure 6). TSOC was not significantly affected ($P>0.05$; Table 9) by treatments (silvopastoral associations and monoculture grasses). However, TSOC was increased by 27, 38 and 43% when *D. retusa*, *D. robinioides* and *P. saman* were included in the systems with *B. brizantha*. No statistical effect of tree species was found with *H. rufa* ($P>0.05$; Table 9). Light fraction organic carbon (LFOC) showed identical vertical distribution than the fine root biomass. On average, 41.2 Mg C ha^{-1} of LFOC (38% of TSOC) was found in the first 60 cm of the soil (Figure 6). As with TSOC, the inclusion of *D. retusa*, *D. robinioides* and *P. saman* in pastures increased the LFOC by 33, 36 and 42%, respectively.

Table 8. Carbon concentration (g C 100 g^{-1} biomass) in aboveground and belowground biomass of contrasting grass species in silvopastoral systems in the dry tropics of Costa Rica. Values in parenthesis correspond to standard error of mean.

	Under canopy		**Open areas**		**Mean**		**C/N ratio**
Grass species	Above	Below	Above	Below	Above	Below	Above
Brachiaria brizantha	43.0 (0.7)	44.3 (0.4)	43.1 (0.2)	44.1 (0.8)	43.1 (0.3) a	44.2 (0.4) a	46.9 (3.0)
Hyparrhenia rufa	39.5 (0.6)	41.8 (1.4)	39.2 (0.4)	42.2 (0.6)	39.4 (0.3) b	42.0 (0.7) a	130.4 (7.4)
Mean	41.3 (1.1) b	43.1 (0.9) a	41.6 (1.0) b	43.2 (0.6) a			

Same letters indicate no statistical differences between components ($P>0.05$).

Soil organic carbon content was strongly correlated with nitrogen concentration in soil ($0.71<R<0.99$; Table 10). Total and light fraction carbon and nitrogen were the most highly correlated variables ($R=0.99$). Nitrogen and carbon parameters are more better associated with total (tree + grass) fine root biomass than with the biomass of the separate components. Fine root biomass of grass species presented a better correlation with soil nitrogen and carbon than fine root biomass of tree species ($0.60<R<0.66$ vs $0.49<R<0.58$; Table 10).

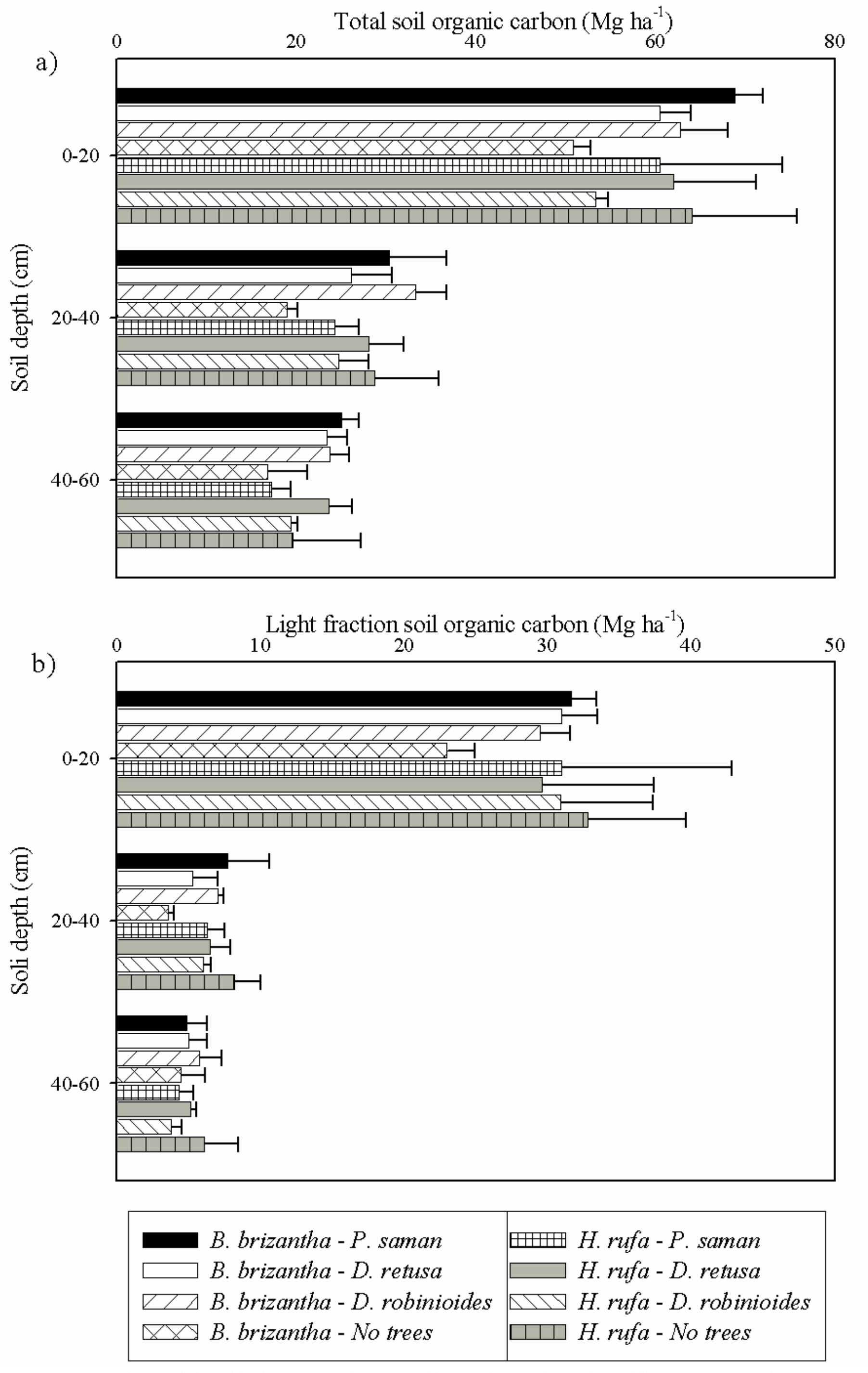

Figure 6. a) Total and b) light fraction soil carbon in six silvopastoral systems of two contrasting grasses (*Brachiaria brizantha* and *Hyparrhenia rufa*) under three native timber tree species (*Pithecellobium saman*; *Dalbergia retusa* and *Diphysa robinioides*) and two monoculture grasses (*B. brizantha* – No trees and *H. rufa* – No trees) in the dry tropics of Costa Rica. Error bars correspond to standard error of mean.

Table 9. Summary of analyses of variance for total and light fraction soil carbon in silvopastoral systems in Cañas, Costa Rica.

Source of variation	Degrees of freedom	Total organic soil carbon	light fraction organic soil carbon
		P values	
Block	2	0.39	0.65
Grass (G)	1	0.76	0.69
Main plot error	2	0.02	0.13
Tree (T)	3	0.61	0.95
G x T	3	0.14	0.51
Sub-plot error	12	0.03	0.32
Depth (D)	2	< 0.01	< 0.01
G x D	2	0.91	0.79
T x D	6	0.84	0.99
G x T x D	6	0.92	0.97
Experimental error	32		

Table 10. Correlation (Pearson coefficient) between soil carbon, nitrogen and root biomass in silvopastoral systems of two contrasting grasses (*Brachiaria brizantha* and *Hyparrhenia rufa*) under three native timber tree species (*Pithecellobium saman, Dalbergia retusa* and *Diphysa robinioides*) and two monoculture grasses in the dry tropics of Costa Rica.

			Soil organic Carbon			**Soil Nitrogen**			**Root biomass**		
			LF	**HF**	**Total**	**LF**	**HF**	**Total**	**Tree**	**Grass**	**Total**
			g 100 g^{-1} soil						Mg ha^{-1}		
Soil organic Carbon	**LF**	g 100 g^{-1} soil	-								
	HF		0.73	-							
	Total		0.96	0.89	-						
Soil Nitrogen	**LF**		0.99	0.71	0.95	-					
	HF		0.71	0.91	0.84	0.70	-				
	Total		0.95	0.86	0.98	0.96	0.88	-			
Fine root biomass	**Tree**	Mg ha^{-1}	0.50	0.58	0.57	0.50	0.53	0.54	-		
	Grass		0.61	0.63	0.66	0.61	0.60	0.65	0.62	-	
	Total		0.60	0.66	0.67	0.60	0.61	0.65	0.93	0.86	-

All Pearson´s correlation coefficient are positive and were significant ($P<0.01$). LF: light fraction; HF: heavy fraction.

4.3.7. Carbon storage and accumulation rates

A grass by tree interaction was found in TSOC accumulation (P<0.05) between September 2003 and February 2005. The TSOC accumulation in *H. rufa* was not affected by tree species (on average, 6.6 ± 1.9 Mg C ha^{-1}; Table 11). In contrast, the tree species had a statistical effect on TSOC change in *B. brizantha* <0.05; Table 11). *B. brizantha* exhibited reduced TSOC in open areas -2.0 Mg C ha^{-1} during the same evaluation period (-1.4 Mg C ha^{-1} year^{-1}). The silvopastoral system combining *P. saman* and *B. brizantha* resulted in the highest soil carbon accumulation (7.4 Mg C ha^{-1} year^{-1}).

Table 11. Total soil carbon accumulation (Mg C ha^{-1}) in 17 month-old silvopastoral systems in the dry tropics of Costa Rica.

	Tree species			
Grass species	***P. saman***	***D. retusa***	***D. robinioides***	**Open areas**
B. brizantha	10.5 (3.2) a	5.8 (2.7) a	9.0 (2.3) a	-2.0 (1.9) b
H. rufa	5.0 (4.8) a	9.0 (3.8) a	3.7 (1.4) a	8.8 (4.4) a

Values in parenthesis correspond to standard error of mean. Different letter indicate statistical differences among tree species (P<0.05).

In these young silvopastoral systems (51 months old), aboveground biomass of grasses were accumulating most of the carbon in biomass in the system, followed by the aboveground biomass of trees, then the fine and structural roots (40.3, 34.8, 21.6 and 3.3 %, respectively; Figure 7). The total organic carbon (TOC) in biomass varied between 2.8 and 14.9 Mg C ha^{-1} in no-tree pastures and silvopastoral systems, respectively (Figure 7). Grass species did not affect the TOC in biomass (P>0.05); but in contrast, tree species statistically affected TOC (P<0.05). Systems with *D. robinioides* had the highest carbon storage in biomass followed by *D. retusa*, *P. saman* and grasses without trees (11.0±1.4, 6.6±0.8, 6.1±0.6, 4.1±0.4 Mg C ha^{-1}, respectively; Figure 7). While carbon storage in *B. brizantha* and *H. rufa* differed little (Figure 7), the inclusion of *P. saman*, *D. retusa* and *D. robinioides* increased carbon storage in phytomass by 45, 76 and 154%, respectively with respect to monoculture *B. brizantha* and by 59, 46 and 194%, respectively with respect to *H. rufa*.

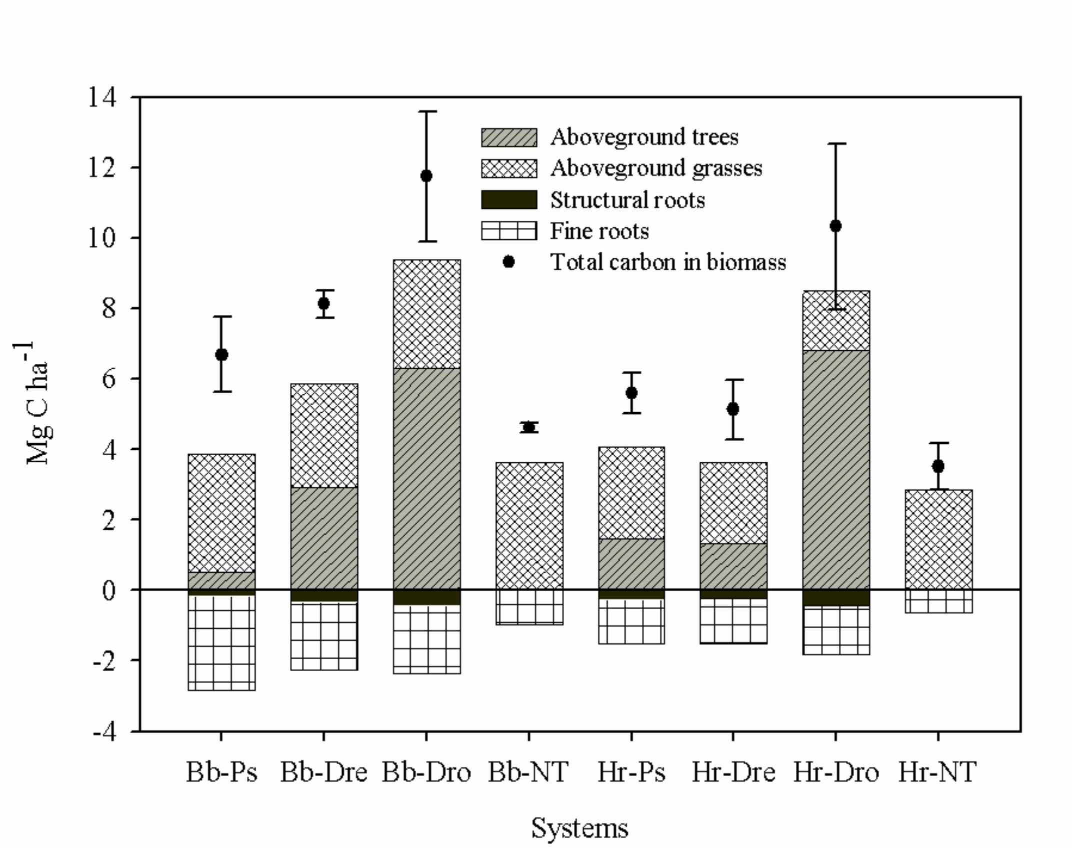

Figure 7. Total carbon storage by biomass components in two contrasting grasses (*Brachiaria brizantha* –Bb- and *Hyparrhenia rufa* –Hr) under three native timber tree species (*Pithecellobium saman* –Ps-; *Dalbergia retusa* –Dre- and *Diphysa robinioides* –Dro) and without trees (Bb-NT and Hr-NT) at 51 months after establishment of silvopastoral systems in the dry tropics of Costa Rica. Below zero bars correspond to root biomass components. Error bars correspond to the standard error of total carbon in biomass.

The carbon accumulation rates in biomass of these pasture-based systems varied between 0.8 and 2.8 Mg C ha^{-1} year^{-1} for monoculture of *H. rufa* and silvopastoral systems of *B. brizantha* with *D. robinioides*, respectively. The mean fixation rates of silvopastoral systems were 95% higher than monoculture grasses. Carbon storage accumulation rates were strongly affected by tree component, with *D. robinioides* as the most important species for storing carbon in its biomass. Carbon accumulation rates were markedly higher in soil (organic carbon) than in other components, with the exception of *B. brizantha* without trees.

4.4. DISCUSSION

4.4.1. Aboveground tree biomass equations

Allometric equations for estimating total aboveground biomass of individual trees using dbh and/or total height give reasonable predictors in woodlots and silvopastoral systems. Many of these allometric equations were developed for trees growing in forest plantations which have systematic arrangement of trees and uniform growth (Bredenkamp 1982, Shiver and Brister 1992, Kanninen and Pérez 2002, Pérez and Kanninen 2003). Although dbh is the most correlated variable with tree biomass, the inclusion of total height generally improve predictability over diameter based equations (Kumar et al. 1998, Segura et al. 2006). The results of this study show that the use of mean quadratic diameter is a good tool for predicting aboveground biomass of native species especially when grown in open spaces and in low densities. Field experiences have shown that native timber and multipurpose tree species have a different growth form when grown in wide spacing compared to dense plantations; in the former they have more branching and/or larger crowns (Clutter et al. 1983, DeBell et al. 1996).

In this study there was a better relationship between mean quadratic diameter (MQD) of trees and biomass compared to that with dbh, probably because some of the tree species had multiple stems especially (*D. robinioides*) with greater stem diameter. The equation, which was developed (Equation 4.5; Table 2) gave good estimates considering the variability in architecture and crown shapes in these native timber tree species. It was possible to use just one equation for all three tree species because the individual curves (a, b and c parameters) for each species were statistically similar. The selected equation presented the highest R^2 (0.92) with a minimal value of PRESS (predicted residual sum of squares), and so it was the best-fit equation with a lowest bias of estimation.

There are only a few studies cited in the literature which evaluate growth of native timber and multipurpose trees in wide spacings in silvopastoral systems and there is a need for more in depth studies to develop allometric equations for these species especially for developing tools for predicting growth of these species in silvopastoral systems and to for quantification of environmental services. Most of the models had been developed for forest plantations and other agroforestry systems (Bredenkamp 1982, Shiver and Brister 1992, Kanninen and Pérez 2002, Pérez and Kanninen 2003, Segura and Kanninen 2005, Segura et al. 2006, Andrade et al. in prep) because of the lack of information about trees in other systems. Ruiz (2002) developed a multispecies model with a relative high determination coefficient (0.94) for six native timber tree species (*Cassia grandis* L.f, *Platymiscium pleistachyum* J.D Smith, *Pithecellobium saman* (Jacq.) Benth, *Cordia alliodora* (Ruiz and Pav.) Oken, *Tabebuia rosea* (Bertol.)) growing in grasslands in Nicaragua

4.4.2. Tree growth

The results in the over five years of measurements showed that there were significant differences in the growth of timber species in the zone. Tree growth of these species in SPS (height 0.6-0.8 m year^{-1} and dbh 0.8-1.3 cm year^{-1}) are slightly lower than those found in pure and mixed plantations with the same native species (0.4-1.2 m year^{-1} and 0.6-2.3 cm year^{-1}; Herrera and Lanuza 1995, Ugalde 1997, Fonseca et al. 2000, Fonseca et al. 2002, Gutiérrez and Fonseca 2002, Piotto et al. 2004) in the dry zone of Central America and the differences in growth may be associated with grass competition. The effect of grass species on tree growth was not significant in this study. The mean aboveground biomass growth (0.5 to 0.8 Mg ha^{-1} year^{-1}) is very low in comparison to those in silvopastoral systems with *Ailanthus triphysa* and *Acacia auriculiformis* in India (4 and 28.1 Mg ha^{-1} year^{-1}; Kumar et al. 1998).

There was an interaction between grass and tree species with respect to tree growth, which is of significance for establishing compatible silvopastoral mixtures with native tree species. It seems that the effect of grass species is dependent on tree size and cover. *D. robinioides*, the tallest species, was not affected by grass species. *B. brizantha* decreased the rate of growth of *P. saman*, the smallest species, whereas, *D. retusa* grew better with *B. brizantha*. This may indicate that there is a critical tree size for successful growth in silvopastoral systems: when the trees reach this size; the competition due to aggressive grasses is less important (Schaller et al. 2003). Other studies have shown the effect of grass species in early growth of trees; natural regeneration of native tress in pastures was not affected by grass species in a study conducted in Muy Muy, Nicaragua (Esquivel 2005); however, the tree and shrub seedling density was higher in improved (*Brachiaria* spp) and naturalised grass respect to star grass (*Cynodon nlemfuensis*) pasture (4, 4 and 3 trees per 7 m^2 of plot). This implies that natural regeneration and, possibly growth, of native timber species do not depend on type of grass but instead on the growth habit of the grasses. Camargo et al. (2000) found a higher survival rate of *Cordia alliodora* in grasses of *Cynodon nlemfuensis* in comparison to *Ischaemun ciliare*, *B. decumbens* and *Hyparrhenia rufa* in silvopastoral systems in Costa Rica.

4.4.3. Grass dry matter production

Annual production of *B. brizantha* was 180% higher than that of *Hyparrenhia rufa* (14.7 vs 5.3 DM ha^{-1} year^{-1}) with a higher production of the former grass species in both wet and dry seasons. This explains why farmers have been converting *H. rufa* pastures to *B. brizantha* pastures: this species is more drought tolerant and can support higher carrying capacities and liveweight gains of cattle (Holmann et al. 2004). A study conducted at a landscape level in Cañas, which is the same area of this study, showed that improved grasses of *B. brizantha* and *B. decumbens* represented 72% of the pasture area and 56% of the area under agricultural use (Esquivel et al. 2003) and other observations in the study area indicate that cattle farmers are continuing to convert *H. rufa* into *B. brizantha* pastures.

In this study, dry matter production of *H. rufa* pastures decreased with increased tree cover but for *B. brizantha* pastures there was no effect of tree cover on grass dry matter production and the differences may be associated to higher shade tolerance of *B. brizantha*. Durr and Rangel (2002) found that grass growing under *P. saman* canopy produced 90% above that of the open grassland in Australia.

Although *B. brizantha* is a C_4 species, with high radiation use efficiency, it is little affected by shade due to its tolerance (Wong 1991). Also, the trees in this study were still small, with sparce canopies at this stage. On average, D. *robinioides* had the highest percentage tree cover, followed by *D. retusa* then *P. saman* ($P<0.01$; 30.6±0.4 vs 27.8±0.5 vs 9.7±0.1, respectively; Figure 3); whereas the transmitted photosynthetically active radiation was between 50 and 66% under the canopies (Andrade et al. 2007c). Studies in the humid tropics showed that annual production of *B. brizantha* was 41% higher in silvopastoral systems with *Erythrina poepigiana,* which was pruned every 6 months compared to production measured in open sun (Bustamante et al. 1998); while according to Andrade et al. (2004), this species raises its production by 10 and 42% in rainy and dry season when grown in 30% shade. In contrast, Andrade et al. (2000) found that *B. brizantha* reduced its production by 35% under tree canopies of *Eucalyptus deglupta* and *Acacia mangium* in the humid tropics of Costa Rica. In another study, conducted in traditional silvopastoral systems in dry zone of Cañas, the results showed that yields of *B. brizantha* pastures were not affected as tree over increased in the range of 0 to 20% (Esquivel et al. in prep). This experiment is less than five years old and it is possible that the trees will have some effect on the production with age as there will be overlapping canopies and greater effects of shading on grass production.

The estimated grass yield of *B. brizantha* in this study was lower than those reported in Brazil under humid tropics (Andrade et al. 2004). These studies reported yields 70 and 100% higher in rainy and dry seasons (5.6 and 3.6 g DM m^{-2} day^{-1}, respectively) compared to the current study. *B. brizantha* in this study was not affected by tree cover (shade); Carvalho (1997) found dry matter production of *B. brizantha* of 7.1 and 6.9 Mg DM ha^{-1} $year^{-1}$ in open areas and in shade, respectively. Improved grasses such as *B. brizantha* may be more competitive if atmospheric CO_2 is increased (Merkel et al. 1999), because they show a relative growth rate twice that of native grasses (0.58 vs 0.25 g g^{-1} $week^{-1}$; Baruch and Jackson 2005). The aggressiveness of invader grasses may promote the establishment and competitive strength in infertile soils in drier climates (Baruch and Jackson 2005).

4.4.4. Fine root biomass

The highest fine root biomass of trees in silvopastoral systems was found in combination with *B. brizantha* and may indicate the stimulation of root production in a water competitive environment. It seems aggressive grasses such as *B. brizantha* may promote a higher root production for the tree, it is possible that the *B. brizantha* roots create channels or pores in the soil that make it easier for tree roots to grow; this soil has high clay content, so pore spaces would be low. Many fine roots can die as a result of grazing, increasing the turnover of roots which agrees with the high accumulation rate of organic carbon in soil. However, in the humid tropics Schaller et al. (2003) found no effect of *Panicum maximum*, *Brachiaria brizantha* and *Saccharum officinarum* barriers in development of deeper tree roots of *Eucalyptus deglupta*. These results contrast with the study by Giraldo et al. (2003) who did not find differences in root biomass in 0-60 cm depth between silvopastoral systems with

Pennisetum clandestinum and *Acacia decurrens* and grass monoculture in andisol soils in a humid zone of Colombia. *Coffea arabica* shows opposite behaviour from the native timber trees evaluated; as fine root decreased dramatically when grown with green herbaceous cover such as *Arachis* spp. and *Desmodium* spp. in the dry tropics of Nicaragua (Bradshaw and Rice 1998). In the current study, it seemed grass roots were decreasing when grasses were grown with trees. These contrasting results can be explained by the differences in water availability in the study zones. When the root biomass levels of the tree component were not affecting grass roots, it can be due to the low quantity of tree roots and their allocation in deeper layers (i.e. niche differentiation). The contrast in the influence of one component on another in the current study agrees with the findings by Fetene (2003) in Ethiopia, who found that the inter-specific competition of *H. hirta* grass on the root yield of *Acacia etbaica* was more than five times greater than vice versa. Eastham and Rose (1988) found that fine root length under pasture at medium and high tree densities was significantly lower than in pasture at low tree density.

Higher growth of *D. retusa* in competition with the aggressive species, *B. brizantha*, can be explained by its higher fine root biomass in the soil profile. Fine root biomass of *D. retusa* was 23% more with *B. brizantha* than with *H. rufa* (2.4 vs 2.0 Mg ha^{-1}) in the 0-60 cm horizon. This increase in roots is explained by a higher concentration in 0-20 cm depth in *B. brizantha* (27%) in contrast with similar root biomass in 20-60 cm depth. The concentration of fine roots in the 0-20 cm horizon (70%) is typical for grass based ecosystems. Veldkamp (1993) found that 79 and 84% of fine root biomass is located in 0-20 cm depth in native (*Axonopus compressus*) and improved grasses (*B. dictyoneura*), respectively. Jackson et al. (1996) reported that tropical grassland/savanna contained on average 57% of root biomass in 0-30 cm depth. Differences in root biomass between grasses were clearly explained by their aboveground biomass accumulation rates. It is interesting to note that though aboveground biomass of trees and height of trees was different between tree species there was little differences in fine root biomass of trees and this could be explained by their need to allocate more resources to roots to explore deeper soil profile for water. Water deficit was associated with a decrease in the percentage of fine roots in superficial soil layers (0-20 cm of depth); Guenni et al. (2002) found a reduction of 27, 24 and 20% in 10-30 cm in *B. brizantha, B. mutica and B. humidicola* under drought, respectively. Soil nutrients and water deficits led to an increase in root biomass, suggesting that the *Brachiaria* increased rooting intensity in response to decreasing nutrient supply from the soil (de Oliveria et al. 2004). In contrast, Hipondoka et al. (2003) found that trees do not explore deeper soil layers looking for water resources when they are growing with grass in arid ecosystems. Easthman and Rose (1988) found that the root length density of *Eucalyptus grandis* growing in pasture dominated by *Setaria sphacelata* was greater in the upper 0.1 m, decreasing with depth. Eighty-three percent of the roots sampled occurred in the upper 0.3 m of the soil profile.

4.4.5. Carbon concentration in biomass

Carbon concentration of timber species ranged between 42.4 and 48.0 g C 100 g^{-1} dry matter, similar to values were reported by other authors (Segura and Kanninen 2002, Lamlom and Savidge 2003, Losi et al. 2003). Cernusak (2006) found very similar concentrations of carbon in dry matter of *D. retusa* seedlings (44.8, 43.1 and 47.6% for roots, stems and leaves, respectively) growing in glasshouse at the same life zone. However, other researchers have reported higher values in timber trees species in other regions (between 7 and 13% higher than current findings; Bert and Danjon 2006, Lamlom and Savige 2006).

However, in this study C concentration was different between plant fractions. These differences between components may be associated with the chemical composition of plant tissues. Woody materials have a higher content of cellulose, hemicellulose and lignin than herbaceous components; According to Ververis et al. (2004), lignin and cellulose content depends on tissue maturity, but does not change significantly within each species. Cellulose has a mean carbon percentage of 42.1%; whereas the carbon content varies between 40-44% and 63-72% in hemicelluloses and lignin, respectively (Lamlom and Savige 2006). The C concentration in leaves is a little lower than that of woody or root material (42, 47 and 52%, respectively; Atjay et al. 1979). Roots of the evaluated timber tree species contained less carbon in their biomass than shoots (42.9 vs 46.2 %, respectively). Bert and Danjon (2006) found a similar pattern in *Pinus pinaster* with a mean carbon concentration of 53.6% in the shoots and 51.7% in the roots. Lamlom and Savige (2003) reported that hardwood species ranged from 46.3-50.0%; whereas in conifers had a range of 47.2-55.2%. They explained the differences as a function of lignin content (around 30 and 20%, respectively). Differences in carbon concentrations in grasses are probably due to differences in chemical composition including lignin concentration.

The differences in C/N ratio of aboveground biomass between grass species had a large impact in their potential decomposition. *B. brizantha* had a lower C/N ratio which means a higher biomass quality because it is more easily decomposed than that of *H. rufa* as suggested by Mafongoya et al. (1998). This implies that litter of *B. brizantha* can be converted more rapidly into soil organic matter than that of *H. rufa* increasing the rate of carbon sequestration in the soil.

4.4.6. Soil organic and total carbon storage and accumulation rates

These silvopastoral systems were storing a mean of 110.3 Mg ha^{-1} of total organic carbon (TSOC) 41 months after tree planting. These values are similar to those found by Brown and Lugo (1992) in the Amazonia (60-115 Mg C ha^{-1}) and by Soepadmo (1993) in tropical lowland dry forests, and lowland subtropical dry forest and tropical premontane and low montane forests (78 and 142 Mg C ha^{-1}). Amézquita et al. (2005) found similar values of organic carbon accumulation in 1m-depth soils in secondary forests, degraded pasture, fodder banks, silvopastoral systems, improved pastures and native forests in the sub-humid tropics of Costa Rica (116, 129, 130, 130, 134 and 185 Mg C ha^{-1}, respectively). Giraldo et al. (2003) found a higher amount of soil carbon in silvopastoral systems of *Pennisetum clandestinum* and *Acacia decurrens* in andisol soils of Colombia (362.2 Mg C ha^{-1}) in the 0-90 cm profile. Tree species had increasing TSOC in associations with *B. brizantha* and this may be due to greater total biomass production compared to those of *H. rufa*. These results are in accordance with the findings of Abril and Bucher (2001) in the Argentinean Chaco; where they reported an accumulation rate of TSOC of 1.9 and 2.8 Mg ha^{-1} $year^{-1}$, when the soil is restored through cattle exclusion for 10 and 20 years, respectively. Trouve et al. (1994) argued that plantations of *Eucalyptus* and *Pinus* could increase TSOC in 9.4 mg C g^{-1} $year^{-1}$ in the Congo in 30 years. Fisher et al. (1994) found approximately 200 Mg C ha^{-1} in the Colombian Savannas.

The higher accumulation of TSOC in *B. brizantha* respect to *H. rufa* agrees with the results of other studies. Ruiz et al. (2004) reported values for soil carbon storage in 60 cm depth of 150 Mg C ha^{-1} for silvopastoral systems with *H. rufa* and 158 Mg C ha^{-1} in silvopastoral systems with improved grasses (*Brachiaria brizantha, Panicum maximum* and *Cynodon dactylon*) in Nicaragua. However, trees did not have an effect on TSOC accumulation in the same study (Ruiz et al. 2004). Studies conducted by da Silva et al. (2004) in similar condition in Brazil showed that well managed pastures of *B. brizantha* with *Stylosanthes* (110.3 to 113.0 Mg C ha^{-1}) had higher TSOC than degraded pastures of *B. decumbens* (97 Mg ha^{-1}) and there was a loss in carbon stocks in native and degraded pastures following deforestation. The major difference in C accumulation between introduced and native grasses was a result of high net primary productivity of the introduced species (Trujillo et al. 2006).

The predominant concentration of TSOC in the top 20 cm (60.4% of the total found in 0 - 60 cm) agrees with results in other forestry and grassland based systems. In contrast, Giraldo et al. (2003) found 40% of the total soil carbon in the 0-30 cm soil horizon in silvopastoral systems. This was probably due to low biomass inputs and low O_2 availability for microorganisms (Trujillo et al. 1997). In the current study, the higher contribution to soil organic carbon was due to the dieback of grass adventitious roots because the contribution from tree leaf fall was low at this stage. In most pasture systems, the major mechanism for depositing C at a depth beyond the top few centimetres is through root production, mortality, and decomposition (Trujillo et al. 1997).

The light fraction is the soil carbon component most affected by land use changes. In a study conducted in the Argentinian Chaco, in degraded areas and sites with exclusion of 10 and 20 years, the light fraction represented 38, 47 and 98% of TSOC, respectively (estimation based on work of Abril and Bucher 2001), indicating a close relationship between LFOC and fine root biomass. According to Trujillo et al. (1997), TSOC is highly correlated with root biomass and microbial activity. Rosell and Galantini (1997) argue that perennial pastures increase TSOC mainly in coarse-textured Haplustolls, probably due to a high production of humifiable residues from roots.

Carbon storage in these grass based systems was low at the termination of this investigation due to its age (51 months) compared with the potential stocks in agroforestry systems (16 - 233 Mg C ha^{-1}; Ibrahim 1994, Torres 1995, Houghton 1995, Abarca 1996, Albrecht and Kandji 2003, Beer et al. 2003). Lu et al. (2004) estimated a mean carbon fixation rate of 0.2 Mg C ha^{-1} year^{-1} in the first 50 years of a growth simulation of pine in a wetland ecosystem in Florida and Minnesota. However, the carbon accumulation rates in biomass (0.8-2.8 Mg C ha^{-1} year^{-1}) of this research are more comparable to those of agroforestry systems in other conditions (Andrade 1999, Albertch and Kandji 2003, Beer et al. 2003, Segura 2005). In silvopastoral systems described in the literature, the contribution of tree biomass ranged between 7 and 62% of carbon in total biomass, which is the most permanent carbon sink in these systems.

Increments in soil organic carbon in silvopastoral systems from the current experiment (2.6-7.4 Mg C ha^{-1} $year^{-1}$) were much higher than those in biomass due to recycling of high biomass and a possible higher root turnover in grass species. However, a key issue in carbon sequestration is the permanence of accumulated carbon. The permanence refers to the time between carbon sequestration by forests (or other forestry ecosystems) and its re-emission to the atmosphere (Subak 2003). Carbon sequestered in the terrestrial biosphere may lack permanence because biomass may be harvested for timber and used to produce short-lived products or cleared for other purposes and wild fires can release large amounts of sequestered carbon (Sedjo and Marland 2003). Carbon permanence depends on management and decisions about land use; carbon stored in biomass may be less permanent than carbon stored in soil, mainly in deeper layers. Removals vegetation may lead to an increase in soil carbon content (de Moraes et al. 1996).

The literature indicates lower rates of C accumulation in systems (Lu et al. 2004) and in grassland, Long et al. (1992) found a mean soil carbon accumulation rate of 0.1 Mg C ha^{-1} $year^{-1}$ in grasslands of Mexico, Kenya and Thailand without fires. In this study, trees had the highest impact on changes in TSOC (2.6 to 7.4 Mg C ha^{-1} $year^{-1}$) in comparison to the grass only effect (-1.4 to 6.2 Mg C ha^{-1} $year^{-1}$). Young (1989) estimated a decrease of TSOC of 0.5 Mg C ha^{-1} $year^{-1}$ in 50 years of agricultural use; in contrast, Fassbender et al. (1991) found net accumulation of TSOC of 1.7 Mg C ha^{-1} $year^{-1}$ in agroforestry with cocoa in humid tropics of Costa Rica.

4.4.7. Application of results

Human interventions, especially those related with cattle production in Cañas zone, have resulted in fragmented landscapes and a reduction of native timber species. One way of diversifying cattle farms and of conservating of native species is the establishment of silvopastoral systems.

In general, farmers use low densities of trees, often using only isolated trees in pastures, to reduce competition with grasses. In these situations, the native timber species tend to produce several stems from the base of the trunk. However, if the objective is to produce high quality timber, silvicultural management will be required to have trees with single and straight trunks. Some management strategies can be applied in these systems such as thinning and early pruning. Some management practices for the establishment and management of trees in pastures in Australia and New Zealand have been documented (Anderson et al. 1988, Knowles 1991). These practices include tree arrangement, grass control with herbicide to establish trees, grazing management, protection of trees from livestock and pruning and thining of trees.

In this experiment, grass species affected the growth of the timber species. The results suggested the need to consider management strategies, which reduce competition in silvopastoral systems according to the interacting species. The tree-grass interaction must be considered as the behaviour of tree species depends on accompanying grass. Grass control by weeding can be considered as a strategy in the early stages in some associations. Cornejo-Oviedo et al. (1992) found that, after three years, the factor most significantly affecting growth of *Prosopis glandulosa* var. *glandulosa* trees was removal of the understory. Holl (1998) demonstrated that vegetation clearing had a strong positive effect on seedling height and biomass of *Calophyllum brasiliense* (Camb.) in abandoned tropical pasture in the humid zone of Costa Rica. According to Griscom et al. (2005), herbicide application and cattle exclusion had a positive effect in growth rates on seedlings of *Cedrela odorata* and *Enterolobium cyclocarpum* in the Pacific region of Panamá. Another strategy may be to manage the trees as a taungya system and then introduce *B. brizantha* in the third year after establishment.

The inclusion of improved grasses in silvopastoral systems increased the availability of grass dry matter for animal consumption. This factor may cause a mitigation of the animal damage to trees for feeding, improving the tree growth in these conditions. Improved grasses also can stimulate the establishment of trees due to increase of soil porosity by grass root exploration and increased in soil organic matter due to root dieback. In spite of this, native trees were slow growing. Well managed silvopastoral systems may be able to enhance temporary storage of carbon by pastures and permanent carbon sink from carbon fixed in trees. In degraded soils, carbon sequestration in soils due to silvopastoral practices is more important than carbon in biomass.

4.5. CONCLUSIONS

The aboveground biomass model developed for these native timber trees had a relatively high level of prediction using mean quadratic trunk diameter and tree total height. Early tree growth in these systems is a key point in establishment; the use of aggressive grasses such as *Brachiaria brizantha* can considerably reduce the development of slow growing native trees. Timber trees growing together with aggressive and drought tolerant grass species in the dry tropics produce more roots than when they were growing in association with naturalised grasses. The competition of trees with improved grasses seems to induce change in the shoot:root ratio to increase allocation of carbon assimilates to the root systems. *Dalbergia retusa* had higher growth with *B. brizantha* than with *H. rufa* due to the production of more fine roots mainly in the 0-20 cm horizon, which enabled the tree to have a higher competitive ability with respect to the grass. The establishment of these land use strategies should involve some management practices, such as weeding around young trees, to enhance success. The inclusion of *B. brizantha*, a shade tolerant grass species, in SPS in dry tropics has enormous potential due to its elevated forage production and ability to grow under tree canopies.

Fine roots distribution would be influenced by lack of a particular growth resource; in dry conditions, drought tolerant species were using more carbon assimilates to explore deeper soil horizons. The fine root biomass was the most important factor in soil carbon accumulation, especially the light fraction of soil organic matter. Deeper root allocation in dry regions could enhance the carbon sequestration in more stable sinks such as the deeper layers of soil. Tree components in silvopastoral systems have more impact in carbon sequestration than grasses due to higher biomass accumulation and higher carbon contents in wood. However, carbon sequestration by grass should focus on roots because they have a higher carbon content than the shoot component. According to these results, *B. brizantha* could reduce soil carbon quantities when the system is not well managed.

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CHAPTER V

5. TREE-GRASS ROOT INTERACTIONS IN SILVOPASTORAL SYSTEMS WITH NATIVE TIMBER TREE SPECIES IN THE DRY ZONE OF COSTA RICA

Hernán J. Andrade[6]; Robert Brook[7]; Muhammad Ibrahim[8]; Phillipe Vaast[3];
Fergus Sinclair[2]; Francisco Jiménez[9]

Summary

The interaction of fine roots at the tree-grass interface in silvopastoral systems in the seasonally dry area of Costa Rica was evaluated through soil core sampling. The experiment tested an improved pasture (*Brachiaria brizantha*) against an unimproved pasture dominated by *Hyparrhenhia rufa* in combination with three indigenous tree species (*Pithecellobium saman*, *Diphysa robinioides* and *Dalbergia retusa*). Soil core samples were collected at three soil depths (0-20, 20-40 and 40-60 cm), two positions with respect to trees (under and intermediate canopy) and two seasons (rainy 2004 and 2005) for two average individual trees in each sub-plot. Fine roots, separated from soil and sorted by species, were scanned to analyse length using Rootedge, and then oven dried to obtain dry mass. The relative tree fine root length and biomass was estimated to evaluate the potential competitiveness of trees at the grass-tree interface. Soil nitrogen content was also estimated and correlated to fine root parameters. Trees tended to have higher competitive root capacity in deeper layers and in under canopy positions; whereas grasses are more competitive in intermediate canopy and superficial layers, resulting in niche differentiation. The introduction of improved and

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[6] Ph.D. Candidate, CATIE-University of Wales (Bangor): handrade@catie.ac.cr (Author for correspondence)

[7] School of the Environment and Natural Resources, University of Wales (Bangor). Emails: r.m.brook@bangor.ac.uk; f.l.sinclair@bangor.ac.uk.

[8] Department of Agriculture and Agroforestry, CATIE. Emails: mibrahim@catie.ac.cr; pvaast@catie.ac.cr

[9] Department of Natural Resources and Environment, CATIE. Email: fjimenez@catie.ac.cr.

drought tolerant grass species such as *B. brizantha* enhanced the root development of the whole system, improving the coexistence of components in regions with seasonal water deficits. The increase in soil nitrogen content, attributed to the nitrogen fixing capacity of the tree component, is an advantage of these silvopastoral systems.

5.1. INTRODUCTION

Trees in grasslands are able to improve productivity, the nutritional quality fodder, carbon sequestration, soil fertility, physical structure of the soil, water infiltration, nutrient cycling, soil conservation through reduced erosion, the microclimate, weed, pest and disease control, and the conservation of biodiversity (Ong and Huxley 1996, Ibrahim et al. 1999, Beer et al. 2003, Harvey et al. 2004, Abule et al. 2005, Andrade et al. 2007a). In spite of the advantages of maintaining trees on grasslands, generally Central American livestock producers are not adopting silvopastoral systems and technologies (Dagang and Nair 2003). One of the most important reasons for this lack of adoption may be the perception of strong competition between plant components (Ruhigwa et al. 1992, Govindarajan et al. 1996). Roots of young trees, which are confined to the shallow rooting zone, can compete strongly for nutrients and water (Dupraz et al. 1998, Smith 2000) and when trees grow and expand their canopies they will eventually dominate the site, decreasing the pasture production (Pollock et al. 1997).

The study of fine roots is highly relevant in the understanding of the competition and dynamics of agroforestry systems because they are the most important belowground biomass component. Fine roots are the most active in terms of production and mortality, carbon and nutrient cycling, and resource acquisition (Hooker et al. 2000). Fine root length density is an important parameter for the acquisition of water and nutrients particularly in dry conditions (Schroth 1999). Dhyani and Tripathi (2000) argued that an understanding of tree root patterns is essential for evelopment and management of these systems. Although some root characteristics are generalized at species level, the actual root pattern is highly dependent on soil type, management and climate (van Noordwijk et al. 1996). In tropical regions, where drylands and/or unfertile soils are predominant, competition for water and nutrients is critical (García-Barrios and Ong 2004).

The zone of Cañas and Bagaces, which covers 54% of the dry tropics of Costa Rica, has historically been one of the hubs of cattle ranching in the country (Flores 2005, Monterroso 2005). Tree resources are important component of cattle farms in Cañas zone because around 20% of their area is covered by forest and most of the pastures have trees (Flores 2005). However, current tree structure in the zone may not be sustainable because natural regeneration is limited due to the low proportion of small trees in pastures (Monterroso 2005). The promotion of better tree management could be the first policy action for increasing tree cover and promoting higher rural incomes (Monterroso 2005).

The main objective of this study was to examine the dynamics of fine roots at the tree-grass interface in silvopastoral systems in seasonal dry area of Costa Rica. An index to evaluate the potential competitive ability of fine tree root in grass-tree systems was calculated. This paper presents the spatial distribution of fine roots of trees and grasses, in terms of biomass and length, in tree-grass associations.

5.2. MATERIALS AND METHODS

5.2.1. Description of experimental site

This study was carried out in Hacienda La Pacifica, Cañas, Costa Rica. Details of location, soil and landscape characteristics, establishment of the trial are given in materials and method section in Chapter IV. The mean climatic conditions for the study zone are found in Figure 1 of Chapter IV.

5.2.2. Experimental design

The basic experimental design was the same as that used as in the first study (Chapter IV). However, two additional sources of variation were added to produce a randomized complete block experimental design with a strip-strip-split plot factorial arrangement. Grass species (*Hyparrenhia rufa* dominated or newly established *Brachiaria brizantha*) formed the main plots, tree species (*Pithecellobium saman*, *Diphysa robinioides, Dalbergia retusa*) formed the subplots, and position with respect to tree stem and soil horizons were located in strips. The factor position, with respect to tree stem, had two levels (under and intermediate canopy positions) while three soil depths were sampled (0-20, 20-40 and 40-60 cm horizons). Errors for strips (positions and depths) were tested against error for their respective interaction. In the case of non-significance of error, the design was regarded as a classic split-split plot with a factorial arrangement (position x depth) in the sub-subplots for the purposes of analyses of variance.

5.2.3. Sample collection

Soil cores were collected at two sampling dates in the same month (July 2004 and 2005; wet seasons). Two trees of mean size were selected in each subplot (grass - tree combinations). The mean was established by measuring diameter at breast height and total height of all the trees in each subplot. Positions with respect to trees were established according to distance from selected trees: under canopy and intermediate canopy which corresponded to 0.5 and 1.0m away from the tree trunk. Six cores were collected from within the rooting zone of each sampled tree, using the two positions for each of the three depths. In total, 216 samples (3 blocks x 2 grass species x 3 tree species x 2 individual trees x 2 positions with respect to tree trunk x 3 depths) were collected in each year of the study.

Soil cores for fine roots (diameter < 2 mm) were collected using an engine-powered auger (EFCO, TR1540; 5 cm internal diameter and 70 cm length), due to the high clay content and consequent hardness of the soil in dry conditions. Real soil volume was estimated by collecting two sub-samples per sample, for gravimetrical moisture and bulk density determinations. Both samples were oven dried to constant weight (65 ^{o}C).

Roots were separated from the soil and dead material in the laboratory. The separation of grass and tree roots was carried out by contrasting morphological characteristics such as colour. The roots of the grass species in this study were white, contrasting with the brown tones of tree roots. The samples that could not be analyzed immediately were preserved in a 15% alcohol solution and stored in a refrigerator (4 – 7 ^{O}C).

5.2.4. Variables recorded

5.2.4.1. Fine root length

After the separation of roots, these samples were scanned using a conventional scanner (Canon model LIDE 20) creating black and white images in Tagged Image File Format (TIFF) with a 300 dpi resolution. Scanned images were analyzed with Rootedge software version 2.3b (2001; Kaspar and Ewing 1997, Ewing and Kaspar 1998) in order to estimate total fine root length. According to Himmelbauer et al. (2002) Rootedge provides correct measurements of root parameters. The software was calibrated using cotton thread of various known lengths and colours. When the soil core contained too many roots, a sub-sample was taken to accurately estimate their length. Total fine root length per sample was divided by soil sample volume to calculate fine root length density (RLD in cm cm^{-3}).

5.2.4.2. Fine root biomass

After the scanning process, all roots collected in each sample were oven dried (65 ^{O}C for 48 h) to quantify total fine root biomass. Biomass in each sample was divided by soil sample volume to obtain root biomass density (RBD in mg cm^{-3}).

5.2.4.3. Specific fine root length

Total fine root length by component was divided by total fine root biomass in order to calculate specific fine root length (SRL in cm mg^{-1}) for each sample.

5.2.4.4. Tree relative root length (RTRL) and biomass (RTRB)

The relative tree root length (RTRL) was calculated by dividing the RLD of the tree component by the total (tree plus grasses) RLD. A similar calculation was carried out for the estimation of the relative tree root biomass (RTRB). These variables were calculated to estimate the potential competitiveness of trees in the grass-tree interface.

5.2.4.5. Soil organic carbon and nitrogen content

One sample was obtained by mixing approximately 10 sub-samples collected from all evaluated experimental units (3 blocks x 2 grasses x 3 trees x 3 depths). Soil organic matter was fractioned using a chemical dispersant (sodium hexametaphosphate, 5 g l^{-1}) followed by physical separation based on particle sizes (53μm; Cambardella and Elliot 1993). Organic carbon and nitrogen were analyzed for each fraction using a CHN auto-analyzer Thermo Finnigan FLASH EA 1112 (Rodano, Milan, Italy) in the soil laboratory of CATIE. Total nitrogen was calculated for each mixed treatment (grass x tree) using the concentration of nitrogen, the bulk density and depth of the soil layer. Carbon and nitrogen concentration were correlated to total, tree and grass root biomass and length. The accumulation rate of nitrogen by tree species was calculated using the percentage of tree canopy cover of each subplot (Andrade et al. 2007c) and taking the no-tree subplots of each main plot as the baseline. It was assumed that initial nitrogen content in each subplot was similar to that in no-tree subplots.

5.2.5. Statistical analyses

The experimental design was analyzed using SAS (1988) through the ANOVA Procedure. At the first stage, a strip-strip-split plot arrangement of treatments was tested. If errors for strips (position and depth) were not significant then a traditional split-split-split plot allocation of degrees of freedom was used. As the fourth order interaction (grass x tree x position x depth) was not significant, then a second analysis was carried out excluding this source of variation, improving the efficiency by increasing the residual error term. The same procedure was carried out for non-significant third order interactions. When analyzing non-randomized soil horizons, although there was a potential problem of dependence of samples from different depths, a complex symmetry was assumed where the correlation between pairs of horizons was equal for all combinations. Means were compared using the least square means (LSMEANS) procedure of SAS. Linear regressions with transformed and non-transformed variables were carried out to evaluate the relationship between fine roots and depth and soil nitrogen content using the SAS (SAS 1988) GLM procedure.

5.3. RESULTS

5.3.1. Climatic conditions in sampling seasons

The climatic conditions of both seasons (wet season 2004 and early wet season 2005) varied highly (Figure 1). The rainfall that occurred in the three months before the sampling periods (May, June and July) was considerably higher in 2005 than in 2004 (712 vs 498 mm, respectively). The mean ETo was similar in both seasons (131 vs 126 mm month^{-1}; Figure 1). Mean temperature and relative humidity were also similar in both periods (27.9 vs 27.9 °C and 77.2 vs 73.3% for wet season 2004 and early wet season 2005; Figure 1).

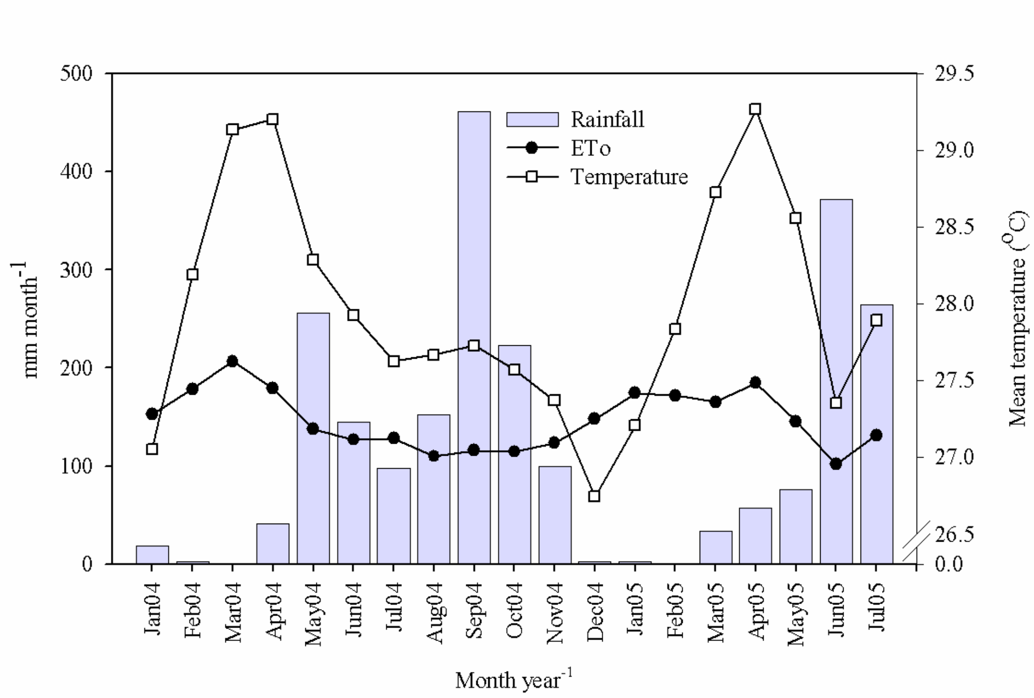

Figure 1. Climatic conditions in the study zone for the sampling period in Cañas, Costa Rica.

5.3.2. Fine root biomass density

5.3.2.1. Wet season 2004

The total (grass and tree) fine root biomass of *B. brizantha* was statistically higher than that for *H. rufa* ($P<0.05$; 0.6±0.06 vs 0.4±0.05 mg cm^{-3}, respectively). This disparity was due to differences in tree biomass rather than grass roots. Mean tree root biomass was strongly affected by grass species ($P<0.01$; Table 1), with more tree roots in *B. brizantha* than in *H. rufa* (0.3 ± 0.03 vs 0.1±0.02 mg cm^{-3}; Table 2). There was an interaction for tree x grass ($P<0.05$) for tree root biomass; *P. saman* and *D. robinoides* had more root biomass in *B. brizantha* than in *H. rufa* ($P<0.01$); in contrast with *D. retusa* which was not affected by grass species ($P>0.05$; Table 2). Grass root biomass was not affected by tree or grass species; there was no grass x tree interaction ($P>0.05$; Table1).

Tree and grass fine root biomass decreased sharply with increasing soil depth ($P<0.01$; Tables 1 and 2; Figure 2). Trees tended to have greater root biomass in deeper horizons compared to grasses. Around 61% of tree roots were in the first 20 cm of soil; whereas this proportion was 72% for grasses. The root distribution in the soil profile was statistically similar between both grasses evaluated; about 9% of the fine grass roots reached the 40-60 horizon (Table 2; Figure 2). Although trees produced more roots in association with *B. brizantha*, they allocated a slightly higher proportion of roots in deeper layers with *H. rufa* compared with *B. brizantha* (14 vs 11%), although this interaction was not significant.

Table 1. Summary of P values for fine root biomass and length by component (tree and grass) and tree relative biomass and length for two sampling dates (2004 and 2005) in silvopastoral systems in Cañas, Costa Rica.

	2004								**2005**							
	Biomass				**Length**				**Biomass**				**Length**			
Source*	Tree	Grass	Total	TRB	Tree	Grass	Total	TRL	Tree	Grass	Total	TRB	Tree	Grass	Total	TRL
Block	0.097	0.152	0.110	0.218	**0.011**	0.562	0.948	0.147	0.576	0.652	0.629	0.116	0.691	0.802	0.786	0.184
Grass (G)	**0.005**	0.414	**0.018**	**0.029**	**0.049**	0.479	0.372	0.322	0.482	0.524	0.496	**0.024**	0.841	0.657	0.740	0.118
Tree (T)	0.433	0.355	0.211	0.714	0.800	0.089	0.126	0.341	0.441	0.538	0.349	0.488	0.873	0.542	0.817	0.880
G x T	**0.047**	0.062	0.553	**<0.001**	0.339	**0.011**	**0.046**	0.156	0.113	0.616	0.167	**0.033**	0.277	0.489	0.356	**0.022**
Position (P)	**0.005**	0.682	0.325	**<0.001**	**<0.001**	0.564	0.259	**<0.001**	0.107	0.333	0.477	**<0.001**	0.292	0.852	0.741	**<0.001**
T x P	0.849	0.087	0.105	0.697	0.773	0.087	0.104	0.986	0.494	0.399	0.582	**0.019**	0.932	0.577	0.703	0.063
G x P	0.321	0.780	0.822	0.863	0.631	0.649	0.845	0.668	**0.029**	0.700	0.159	0.517	0.208	0.638	0.815	0.289
Depth (D)	**<0.001**	**<0.001**	**<0.001**	**0.049**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**	0.452	**<0.001**	**<0.001**	**<0.001**	0.343
G x D	**<0.001**	0.666	**0.016**	0.921	0.911	0.534	0.571	0.281	0.541	0.750	0.575	0.377	0.819	0.770	0.805	0.732
T x D	0.531	0.441	0.362	0.882	0.353	0.407	0.238	0.451	0.997	0.855	0.951	0.817	0.776	0.590	0.772	0.464
P x D	0.457	0.977	0.748	0.221	0.133	0.967	0.786	**0.043**	0.598	0.364	0.920	0.585	0.924	0.438	0.647	0.215
T x P x D	0.996	**0.043**	0.106	0.365	0.490	**0.009**	**0.033**	0.201	0.983	0.073	0.578	0.223	0.834	0.440	0.555	0.304

TRB: Tree relative biomass; TRL: tree relative length. *Non significant source of variation were eliminated from the original analysis of variance.

Table 2. Fine root biomass density (mg cm^{-3}) by component in silvopastoral systems with native timber tree species in Cañas, Costa Rica.

Grass species	**Tree species**	**0-20 cm**		**20-40 cm**		**40-60 cm**	
		Tree	**Grass**	**Tree**	**Grass**	**Tree**	**Grass**
		2004					
Brachiaria brizantha	*P. saman*	0.75 (0.11)	0.49 (0.11)	0.25 (0.06)	0.14 (0.05)	0.11 (0.02)	0.07 (0.02)
	D. retusa	0.44 (0.08)	0.78 (0.23)	0.21 (0.05)	0.17 (0.05)	0.08 (0.02)	0.09 (0.02)
	D. robinoides	0.60 (0.14)	0.90 (0.20)	0.31 (0.05)	0.17 (0.03)	0.12 (0.02)	0.11 (0.05)
Hypharrhenia rufa	*P. saman*	0.18 (0.05)	0.78 (0.14)	0.07 (0.03)	0.21 (0.05)	0.05 (0.01)	0.09 (0.02)
	D. retusa	0.24 (0.05)	0.34 (0.05)	0.14 (0.04)	0.14 (0.05)	0.06 (0.02)	0.06 (0.01)
	D. robinoides	0.27 (0.08)	0.74 (0.29)	0.08 (0.02)	0.13 (0.02)	0.05 (0.01)	0.08 (0.02)
		2005					
Brachiaria brizantha	*P. saman*	1.87 (0.78)	0.86 (0.56)	0.76 (0.56)	0.46 (0.40)	0.41 (0.20)	0.04 (0.01)
	D. retusa	1.25 (0.32)	0.62 (0.23)	0.28 (0.06)	0.23 (0.11)	0.16 (0.04)	0.10 (0.04)
	D. robinoides	1.19 (0.48)	0.42 (0.26)	0.19 (0.03)	0.10 (0.04)	0.13 (0.03)	0.16 (0.11)
Hypharrhenia rufa	*P. saman*	0.79 (0.33)	0.49 (0.13)	0.15 (0.03)	0.09 (0.02)	0.05 (0.01)	0.07 (0.02)
	D. retusa	1.09 (0.39)	0.34 (0.12)	0.33 (0.16)	0.09 (0.02)	0.11 (0.04)	0.06 (0.02)
	D. robinoides	0.96 (0.32)	0.52 (0.24)	0.18 (0.05)	0.05 (0.01)	0.10 (0.02)	0.05 (0.02)

Values in parenthesis correspond to standard error. N= 12.

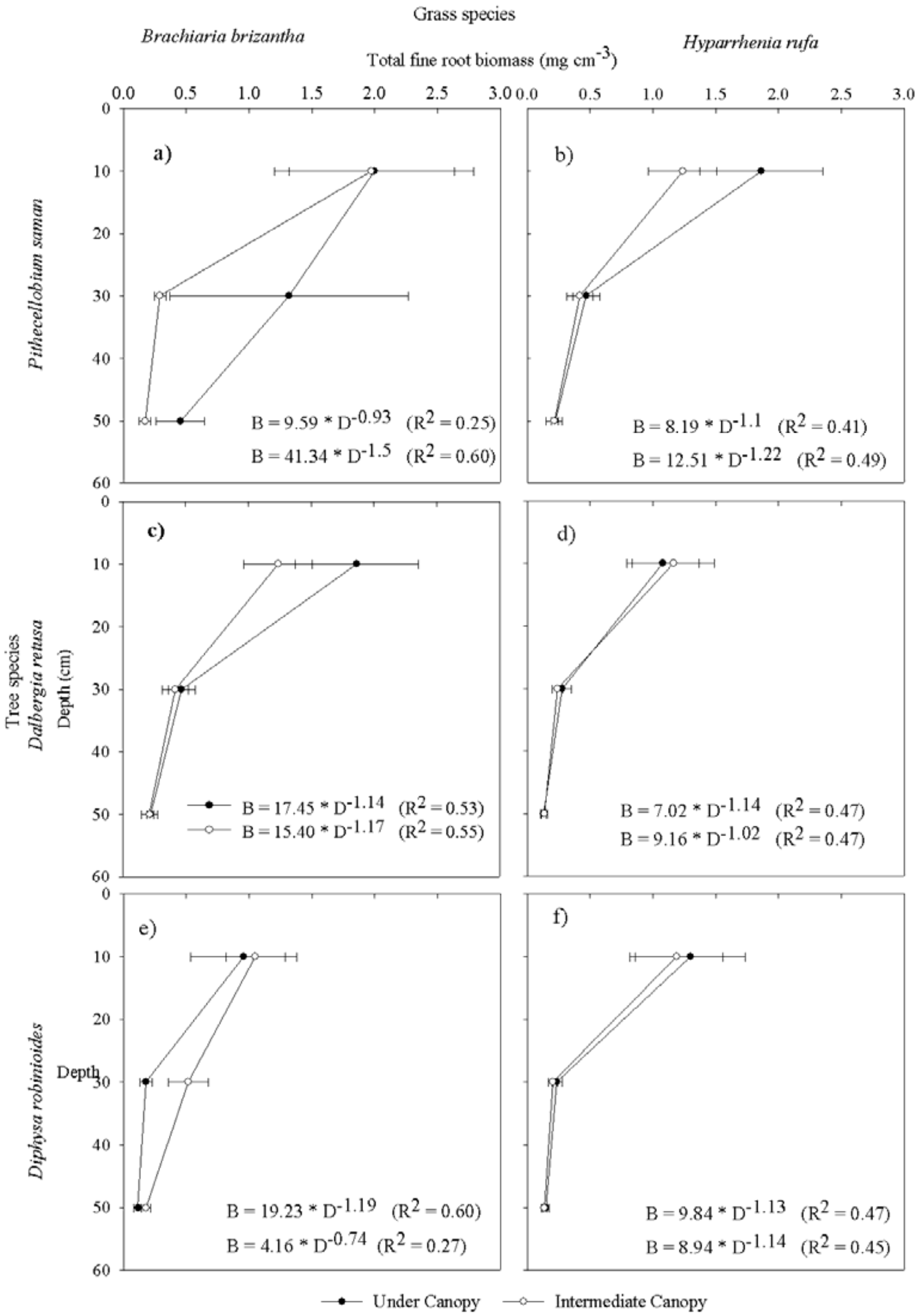

Figure 2. Total fine root biomass (tree plus grass) in silvopastoral systems in 0-60 cm of soil depth in six silvopastoral combinations with native timber tree species in the dry tropics of Costa Rica. Values correspond to means for two sampling periods (2004 and 2005). Error bars correspond to standard error. N= 12.

Total root biomass was not statistically different between under canopy and intermediate canopy sampling positions ($P>0.05$; Table 1). However, tree root biomass under the canopy was significantly higher than in the intermediate canopy position ($P<0.01$; Table 1; 0.3±0.03 vs 0.2±0.02 mg cm^{-3}; Figure 2). All tree species showed the same tendency. Grass fine root biomass was not affected by position with respect to trees.

5.3.2.2. Wet season 2005

There was no significant effect of treatments upon total root biomass ($P>0.05$; Table 1). Although statistically significant differences between grasses were not detected, total root biomass with *B. brizantha* was in fact 69% higher than that with *H. rufa* (1.0±0.2 vs 0.6±0.1 mg cm^{-3}; Table 2). Trees represented 68% of the total root biomass in the sampled positions. Despite there being no differences in root biomass among tree treatments, *P. saman* had slightly higher biomass than *D. retusa* and *D. robinoides* (1.0±0.3 vs 0.8±0.1 vs 0.7±0.1 mg cm^{-3}; Table 2). As in the first sampling, differences could be attributed more to tree species than to grasses.

Root biomass declined steeply with depth ($P<0.01$; Table 1), with around 70% found in the top 20 cm whereas the 20-40 and 40-60 cm horizons each had 20 and 10% of total root biomass (1.7±0.2, 0.5±0.2, 0.2±0.04 mg cm^{-3}; Table 2; Figure 2). The proportion of tree root relative biomass was not affected by depth ($P>0.05$; Table 1), with between 65 and 69% of total fine roots originating from tree species. In spite of the statistical similarity between grasses, *B. brizantha* allocated more fine roots than *H. rufa* in the deepest sampled layer (0.4±0.02 vs 0.1±0.01 mg cm^{-3}).

Total and grass root biomass was not affected by position with respect to trees ($P>0.05$; Table 1) with values of 0.9 (±0.2) and 0.8 (±0.1) mg cm^{-3} of total root biomass for under and intermediate canopy positions, respectively (Figure 3). There was an interaction for grass species x sampling position in tree biomass in 2005 ($P<0.05$; Table 1). There were no statistical differences in grass and total root biomass in the two positions for each grass ($P>0.05$; Table 1); however, total root biomass at the under canopy position was higher in *B. brizantha* than in *H. rufa* (1.2±0.3 vs 0.5±0.1 mg cm^{-3}; Figure 2). There was a grass x position interaction for tree root biomass ($P<0.05$; Table 1); tree root biomass was statistically higher under canopy than in the intermediate canopy position in *B. brizantha* ($P<0.01$; 1.0 ± 0.2 vs 0.4±0.1 mg cm^{-3}) in contrast with no differences in *H. rufa* ($P>0.05$; 0.4±0.1 vs 0.5±0.1 mg cm^{-3}).

5.3.2.3. Profile root patterns

The relationship between fine root biomass and depth was weak in all silvopastoral combinations ($0.25<R^2<0.60$; Figure 2) when lineal models, with logarithmic transformation, were tested. The determination coefficients were similar for the two grasses, *B. brizantha* and *H. rufa*, with a mean R^2 of 0.47 (±0.07) and 0.46 (±0.03), respectively. Similarly, tree species did not affect the determination coefficients, with values of 0.51 (±0.02), 0.45 (±0.05) and 0.44 (±0.07) for *D. retusa*, *D. robinoides* and *P. saman*, respectively (Figure 2).

According to the models developed (linear with logarithmic transformation), the total fine root biomass at the soil surface (1 cm of soil depth; intercept of the models) ranged between 4.2 and 41.3 mg cm^{-3} (13.6±2.8 mg cm^{-3}; Figure 2). The total fine root biomass decreased with depth, the slope of the regression varying between -1.5 and -0.7 (mean -1.1±0.05). However, the slope did not differ between the evaluated systems. Systems with *B. brizantha* had a markedly higher total root biomass in the surface than with *H. rufa* (17.9±5.2 vs 9.3±0.5 mg cm^{-3}; Figure 2). In contrast, the slope of the equation was similar for both grasses. *P. saman* had the highest estimated root biomass at the surface compared to *D. retusa* and *D. robinoides* (17.9±7.9 vs 12.3±2.4 vs 10.5±3.2 mg cm^{-3}; Figure 2).

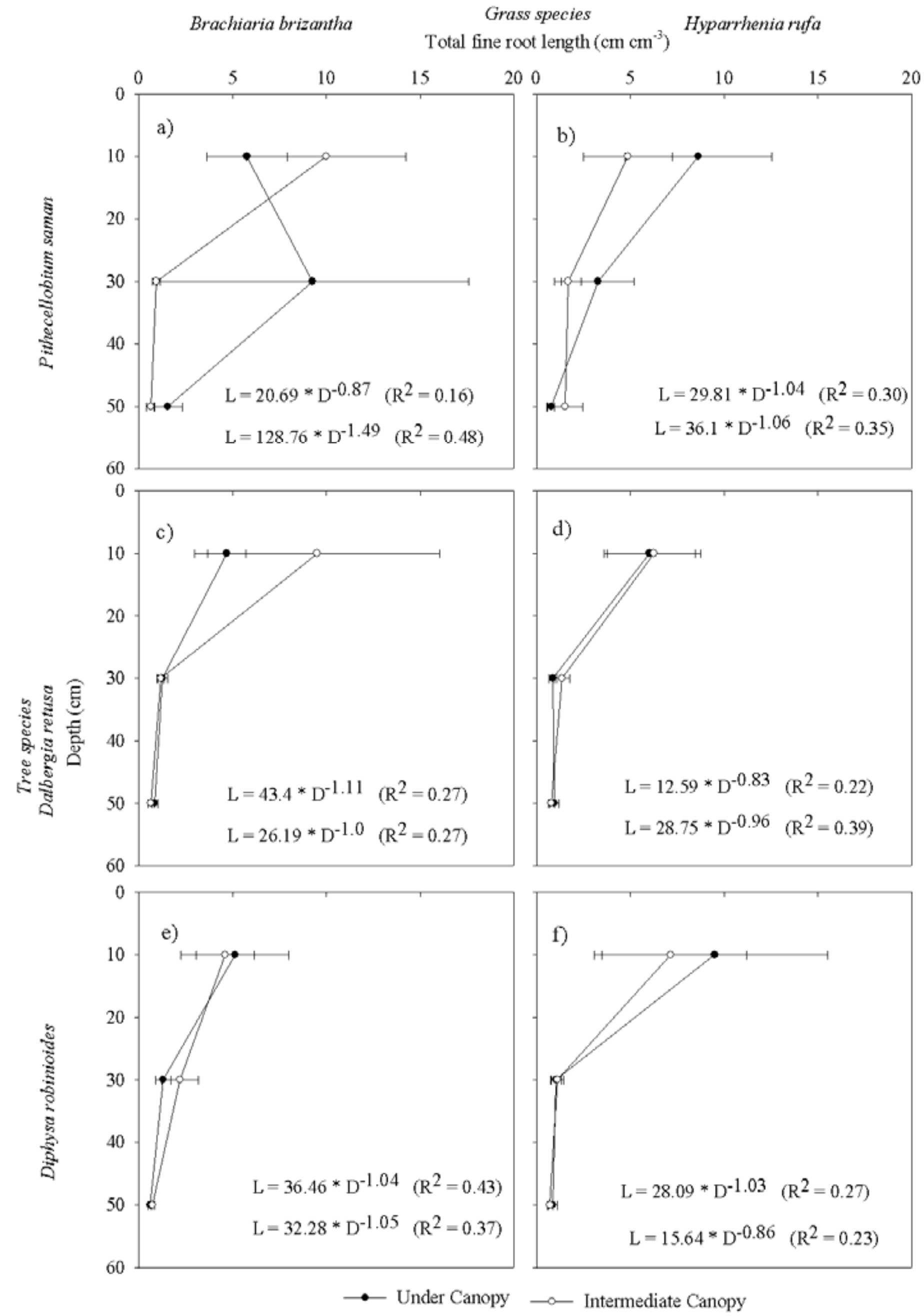

Figure 3. Total fine root length density (tree plus grass) in the soil depth 0-60 cm in six silvopastoral combinations with native timber tree species in the dry tropics of Costa Rica. Values correspond to means for two sampling periods (2004 and 2005). Error bars correspond to standard error. N= 12.

Total and grass fine root length density was statistically similar for the two sampling positions ($P>0.05$; Table 1). However, a big difference was found in tree roots ($P<0.01$; Table 1); where the tree biomass was statistically higher at the under canopy sampling position than the intermediate canopy position ($P<0.01$; 0.5±0.06 vs 0.3±0.03 cm cm^{-3}; Figure 3).

5.3.3.2. Wet season 2005

Root length density showed similar behaviour to biomass wherein statistical differences due to grass and tree species were not detected ($P>0.05$; Table 1). However, total fine root (grass plus trees) length was slightly higher with *B. brizantha* than with *H. rufa* (5.9±1.4 vs 4.4±1.0 cm cm^{-3}; Table 3). This contrasted with results of the 2004 season, where the proportion of tree root length was fairly similar (44 and 50% for *B. brizantha* and *H. rufa*, respectively). The proportion of grass root length was dramatically reduced in this sampling.

Total, tree and grass root length densities were strongly affected by depth ($P<0.01$; Table 1). Root length was statistically greater in the 0-20 cm horizon than 20-40 and 40-60 cm ($P<0.01$; 11.1±1.9 vs 3.1±1.4 vs 1.2±1.8 cm cm^{-3}; Table 3; Figure 3). The contribution of grass to total root length was fairly similar among depths (53, 56 and 49% for 0-20, 20-40 and 40-60 cm, respectively).

Positions with respect to tree canopy did not statistically affect the root length ($P>0.05$; Table 1), although root length at the under canopy position was rather higher than for intermediate canopy ($P>0.05$; 5.4±1.3 vs 4.9±1.1 cm cm^{-3}). The under canopy position had a higher proportion of tree fine roots than intermediate canopy (51 vs 41%, respectively).

Table 3. Fine root length density (cm cm^{-3}) by component in silvopastoral systems with native timber tree species in Cañas, Costa Rica.

Grass species	Tree species	0-20 cm		20-40 cm		40-60 cm	
		Tree	**Grass**	**Tree**	**Grass**	**Tree**	**Grass**
		2004					
Brachiaria brizantha	*P. saman*	0.79 (0.03)	1.85 (0.10)	0.36 (0.03)	0.72 (0.06)	0.17 (0.01)	0.34 (0.02)
	D. retusa	0.56 (0.04)	1.73 (0.08)	0.27 (0.02)	0.78 (0.11)	0.14 (0.01)	0.35 (0.04)
	D. robinoides	0.55 (0.03)	2.77 (0.16)	0.56 (0.03)	1.02 (0.05)	0.27 (0.02)	0.37 (0.03)
Hypharrhenia rufa	*P. saman*	0.59 (0.06)	2.60 (0.15)	0.24 (0.02)	0.85 (0.06)	0.12 (0.01)	0.57 (0.04)
	D. retusa	0.38 (0.02)	1.32 (0.05)	0.61 (0.09)	0.52 (0.07)	0.19 (0.01)	0.30 (0.01)
	D. robinoides	0.67 (0.08)	1.56 (0.13)	0.23 (0.02)	0.53 (0.03)	0.16 (0.01)	0.35 (0.02)
		2005					
Brachiaria brizantha	*P. saman*	5.25 (0.46)	7.86 (0.96)	3.37 (0.83)	5.76 (1.57)	1.31 (0.21)	0.37 (0.05)
	D. retusa	5.78 (0.78)	5.43 (0.72)	1.97 (0.31)	1.94 (0.28)	0.58 (0.05)	1.23 (0.24)
	D. robinoides	4.48 (0.56)	6.42 (1.38)	0.31 (0.02)	0.55 (0.04)	0.47 (0.04)	0.38 (0.02)
Hypharrhenia rufa	*P. saman*	3.49 (0.46)	5.62 (0.54)	0.49 (0.08)	0.68 (0.05)	0.42 (0.03)	0.64 (0.05)
	D. retusa	5.60 (0.62)	2.44 (0.38)	1.33 (0.17)	1.05 (0.11)	0.45 (0.04)	0.39 (0.02)
	D. robinoides	6.50 (0.91)	7.92 (1.05)	0.78 (0.06)	0.63 (0.07)	0.53 (0.04)	0.57 (0.04)

Values in parenthesis correspond to standard error. N= 12.

5.3.3.3. Profile root patterns

Total fine root length was poorly explained by depth, with the R^2 ranging between 0.16 and 0.48 (Figure 3), lower than for biomass models. As for the biomass models, the correlations for the two grass species were similar (0.33±0.05 vs 0.29±0.03, respectively). Values of R^2 for trees were almost the same (0.33±0.05 vs 0.32±0.07 vs 0.29±0.04) for *D. robinoides*, *P. saman* and *D. retusa*, respectively (Figure 3).

B. brizantha based systems supported higher total root lengths at the surface than *H. rufa* systems (48.0±20.2 vs 25.2±4.5 cm cm^{-3}; Figure 3). The slope of models varied between -1.5 and -0.8 with no differences between grasses or trees. Similar to root biomass density, the total root length at surface was considerably higher in *P. saman* than *D. robinoides* and *D. retusa* (53.8±25.2 vs 27.7±6.3 vs 28.1±4.5 cm cm^{-3}, respectively).

5.3.4. Tree-grass root competitiveness

5.3.4.1. Wet season 2004

Relative tree root length (RTRL) was affected by neither tree nor grass species ($P>0.05$; Table 1), although trees in *B. brizantha* plots tended to have greater competitive ability than in *H. rufa* as shown by their higher mean RTRL (36.6±2.5 vs 30.9±2.3%; Figure 4). In contrast, relative tree root biomass (RTRB) was statistically different between grasses ($P<0.05$; 56.5±2.5 vs 37.8±2.6%, for *B. brizantha* and *H. rufa* respectively; Figure 5). Additionally, a grass x tree interaction in RTRB was detected; *P. saman* and *D. robinoides* decreased their RTRB with *H. rufa* with respect to *B. brizantha*; whereas *D. retusa* was not affected by grass species.

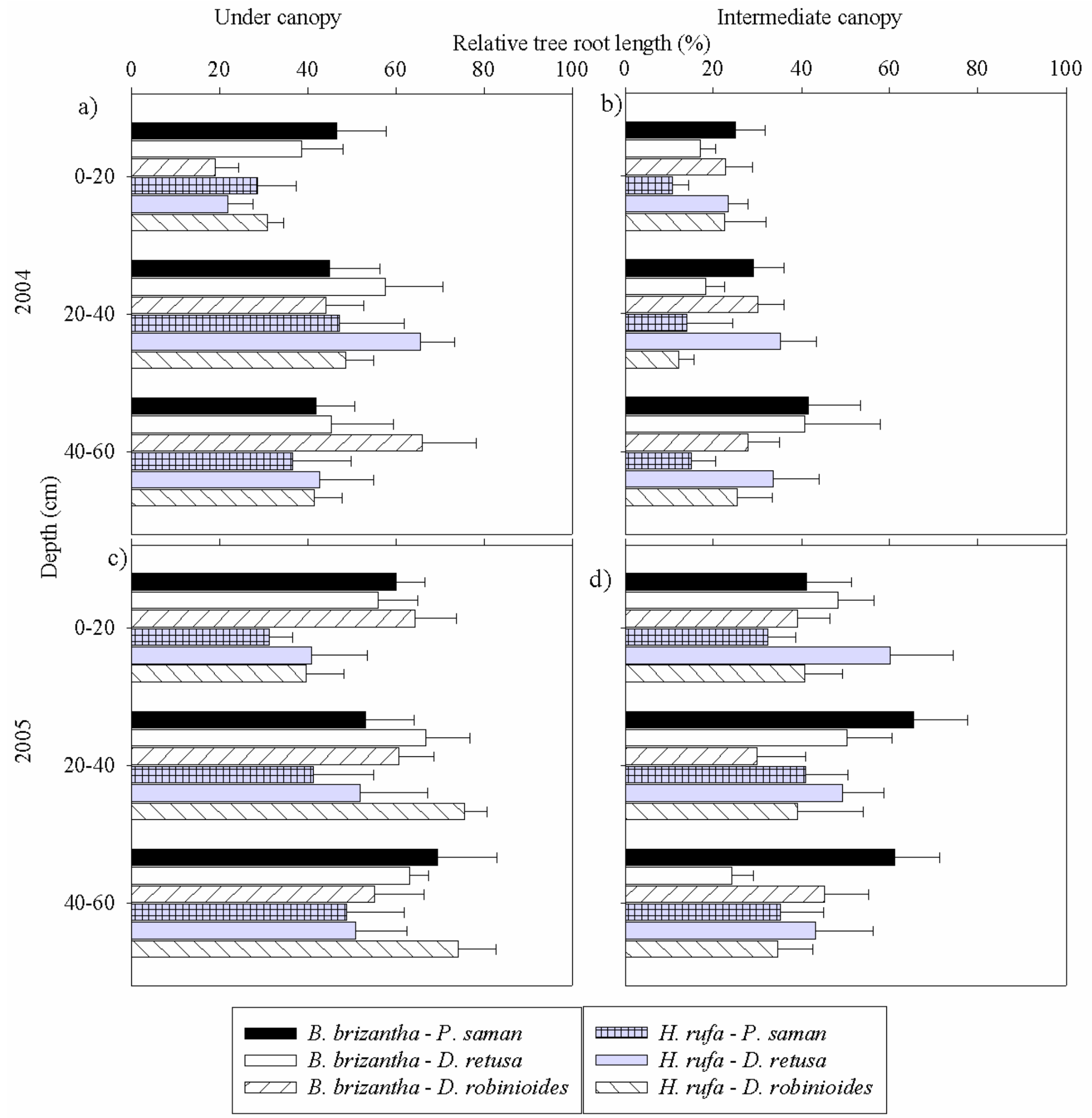

Figure 4. Relative tree root length of native timber trees in six silvopastoral associations in the dry tropics of Costa Rica. Error bars correspond to standard error. N= 6. a) under canopy 2004; b) intermediate canopy 2004; c) under canopy 2005; d) intermediate canopy 2005.

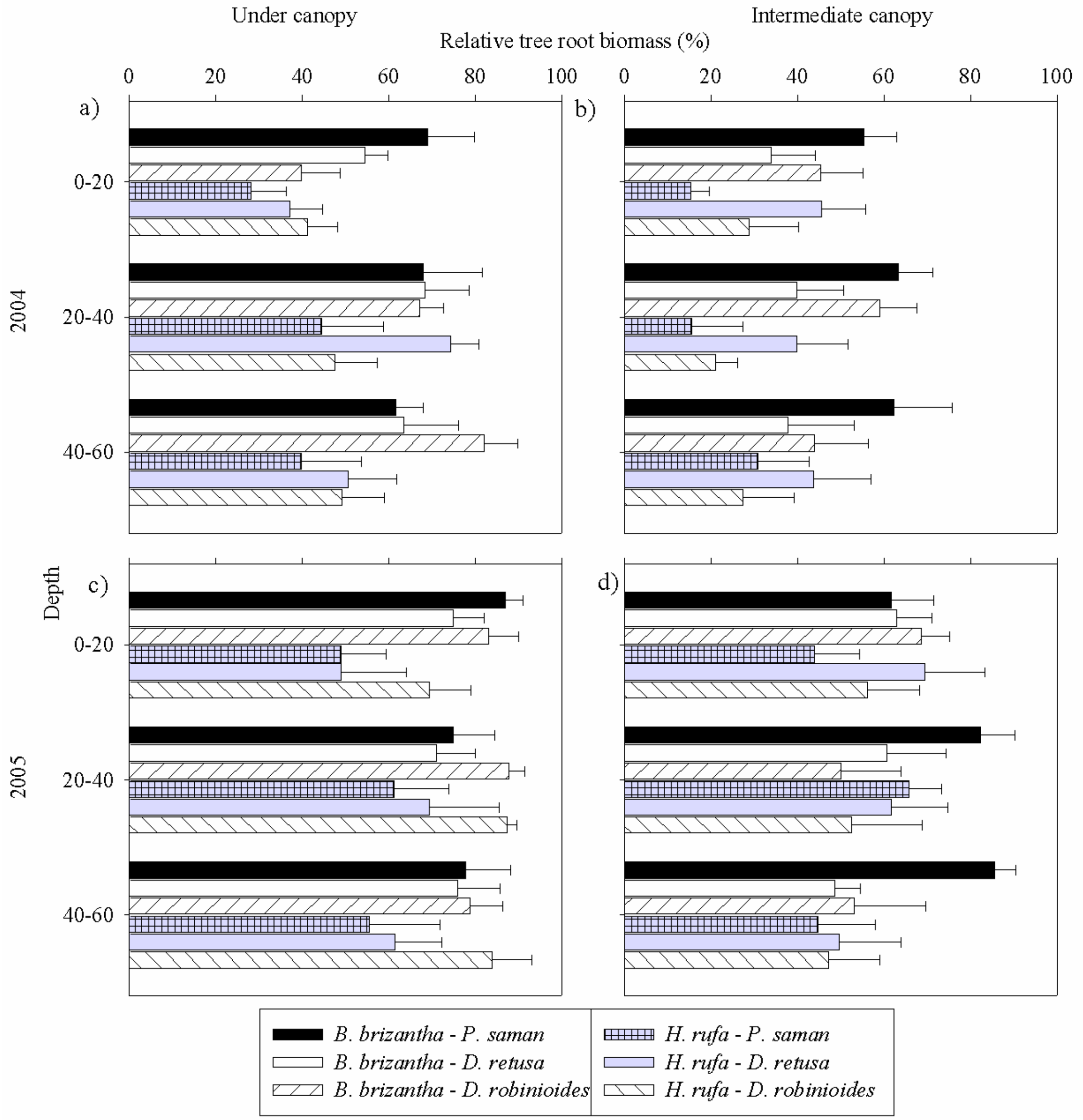

Figure 5. Relative tree root biomass of native timber trees in six silvopastoral associations in the the dry tropics of Costa Rica. Error bars correspond to standard error. N= 6. a) under canopy 2004; b) intermediate canopy 2004; c) under canopy 2005; d) intermediate canopy 2005.

RTRL was significantly lower in the 0-20 cm horizon compared to 20-40 and 40-60 cm ($P<0.05$; 25.6±2.2 vs 37.5±31. vs 38.2±3.3%, respectively; Figure 4); in contrast, depth did not affect RTRB ($P>0.05$; Table 1). RTRL was highly affected by position ($P<0.01$; Table 1). In the under canopy position, trees had a statistically higher relative root length than in the intermediate canopy position (42±2.5 vs 24.6±2.0%, respectively; Figure 4). Similarly, RTRB was higher under canopy than in the intermediate canopy sampling position (54.9±2.5 vs 39.2±2.7%, respectively, Figure 5).

5.3.4.2. Wet season 2005

A grass x tree interaction was detected in RTRL ($P<0.05$; Table 1), whereas *P. saman* RTRL was statistically higher with *B. brizantha* than with *H. rufa* (58.4±4.4 vs 38.4±3.9%, respectively; Figure 4); no differences were found for *D. retusa* and *D. robinoides* ($P>0.05$). The same interaction was found for TRB with similar results (Figure 5).

There were no statistical differences of RTRL or RTRB between soil depths ($P>0.05$; Table 1). RTRL varied between 50.5 and 46.1% (Figure 4), whereas RTRB ranged between 63.5 and 68.7% (Figure 5). Sampling position significantly affected RTRL and RTRB ($P<0.01$; Table 1), being much higher under canopy than in the intermediate canopy position (55.8±2.5 vs 43.3±2.4 and 72.1±2.5 vs 59.2±2.8 %, under and intermediate canopy, respectively; Figures 3 and 4).

5.3.5. Soil nitrogen content and its relationships with root density

There was no statistical effect of silvopastoral components (grass or tree) on soil total nitrogen ($P>0.05$; Table 4). The soil nitrogen concentration ranged from 1.2 to 1.5 g N kg^{-1} soil in all silvopastoral combinations including grasses in no tree plots (Table

4). Soil nitrogen concentration, however, did show statistical differences according to soil depth; a peak at 0-20 cm soil depth was found followed by a strong decrease in the deeper layers at 20-40 and 40-60 cm (2.2±0.06, 1.1±0.05 and 0.89±0.04 g N kg^{-1} soil, respectively; Table 4). The whole profile (0–60 cm) soil nitrogen content was also statistically similar between grass species and among tree species ($P>0.05$, Table 4). However, there was a slightly higher quantity of soil nitrogen in tree plots with respect to no tree control plots (between 9.9 and 10.1 Mg N ha^{-1}, for trees and 9.1 Mg N ha^{-1} for no tree plots; Table 5), suggesting an impact of tree species in soil nitrogen. Considering the total nitrogen content in monoculture grasses in each main plot as the base line for all subplots, the highest rate of nitrogen increment was seen in *D. robinioides* followed by *D. retusa* and *P. saman* (76, 74 and 23 kg N ha^{-1} year^{-1} at 60 cm of depth).

Table 4. Soil nitrogen concentration in silvopastoral systems with native timber tree species in the dry tropics of Costa Rica.

Source of variation		**N**	**Mean nitrogen concentration (g N kg^{-1} soil)**
Factor	**Level**		
Grass species	*Brachiaria brizantha*	36	1.38 (0.10) a
	Hyparrhenia rufa	36	1.37 (0.11) a
Tree species	*Pithecellobium saman*	18	1.39 (0.16) a
	Dalbergia retusa	18	1.42 (0.15) a
	Diphysa robinioides	18	1.41 (0.13) a
	No trees	18	1.27 (0.15) a
Soil Depth (cm)	0 - 20	24	2.15 (0.06) a
	20 - 40	24	1.08 (0.05) b
	40 - 60	24	0.89 (0.04) c

Different letters for the same factor correspond to statistical differences in means ($P<0.05$).

Root biomass had, in all treatments, a positive correlation with the nitrogen levels in soils. However, soil nitrogen content was more highly correlated with roots in *B. brizantha* than for *H. rufa* ($0.76<R<0.95$ vs $0.46<R<0.91$; Table 6; Figure 6). Soil nitrogen content in silvopastoral systems with *B. brizantha* was more affected by total root biomass than by grass or tree root biomass (on average, R=0.90 vs 0.83 and 0.82). This contrasted with *H. rufa*, where there was a higher correlation of soil nitrogen content with tree root biomass than total and grass root biomass (R=0.68, 0.67 and 0.62, respectively; Figure 6).

Table 5. Total soil nitrogen in silvopastoral systems with native timber tree species in the dry tropics of Costa Rica.

Source of variation		**N**	**Mean N content**
Factor	**Level**		**(Mg N ha^{-1} at 60 cm of depth)**
Grass species	*Brachiaria brizantha*	12	10.1 (0.3) a
	Hyparrhenia rufa	12	9.4 (0.6) a
Tree species	*Pithecellobium saman*	6	9.9 (0.7) a
	Dalbergia retusa	6	10.1 (0.5) a
	Diphysa robinioides	6	10.0 (0.6) a
	No trees	6	9.1 (1.0) a

Different letters for the same factor correspond to statistical differences in means (P<0.05).

Root biomass had, in all treatments, a positive correlation with the nitrogen levels in soils. However, soil nitrogen content was more highly correlated with roots in *B. brizantha* than in *H. rufa* (0.76<R<0.95 vs 0.46 <R<0.91; Table 6; Figure 6). Total root biomass was better correlated to soil nitrogen content than grass or tree root biomass (on average, R=0.90 vs 0.83 and 0.82, respectively). This was in contrast with *H. rufa*, where there was a higher Pearson's correlation coefficient higher for tree with respect to total and grass root biomass (R=0.68, 0.67 and 0.62, respectively; Figure 6).

Soil nitrogen content had a much higher correlation with root length in systems based on *B. brizantha* respect to those based on *H. rufa* (0.47<R<0.92 vs 0.03<R<0.79, respectively; Table 6; Figure 7). As for root biomass, the highest correlation was detected between nitrogen and total root length in *B. brizantha* (R=0.83; Table 4). In

H. rufa, the best correlation was found with grass root length (R=0.65; Table 4; Figure 7). It seems that nitrogen content was not affected by tree root length in *B. brizantha-D. retusa* systems.

Table 6. Pearson's correlation coefficient (R) of root biomass density (mg cm^{-3}) and length density (cm cm^{-3}) with soil nitrogen (%) in six silvopastoral systems in the dry tropics of Costa Rica.

Grass species	Tree species	Biomass			Length		
		Grass	**Tree**	**Total**	**Grass**	**Tree**	**Total**
Brachiaria brizantha	*Pithecellobium saman*	0.79 (0.011)	0.87 (0.002)	0.89 (0.001)	0.75 (0.020)	0.78 (0.012)	0.81 (0.008)
	Dalbergia retusa	0.76 (0.017)	0.82 (0.007)	0.87 (0.003)	0.66 (0.052)	0.77 (0.015)	0.76 (0.017)
	Diphysa robinioides	0.95 (0.001)	0.76 (0.016)	0.95 (<0.001)	0.91 (0.001)	0.47 (0.205)	0.92 (0.001)
Hyparrhenia rufa	*Pithecellobium saman*	0.68 (0.046)	0.58 (0.101)	0.68 (0.045)	0.59 (0.097)	0.39 (0.303)	0.56 (0.115)
	Dalbergia retusa	0.91 (0.001)	0.65 (0.058)	0.82 (0.006)	0.79 (0.012)	-0.03 (0.938)	0.54 (0.130)
	Diphysa robinioides	0.46 (0.213)	0.64 (0.065)	0.51 (0.162)	0.57 (0.111)	0.53 (0.141)	0.56 (0.118)

Values in parenthesis correspond to P value.

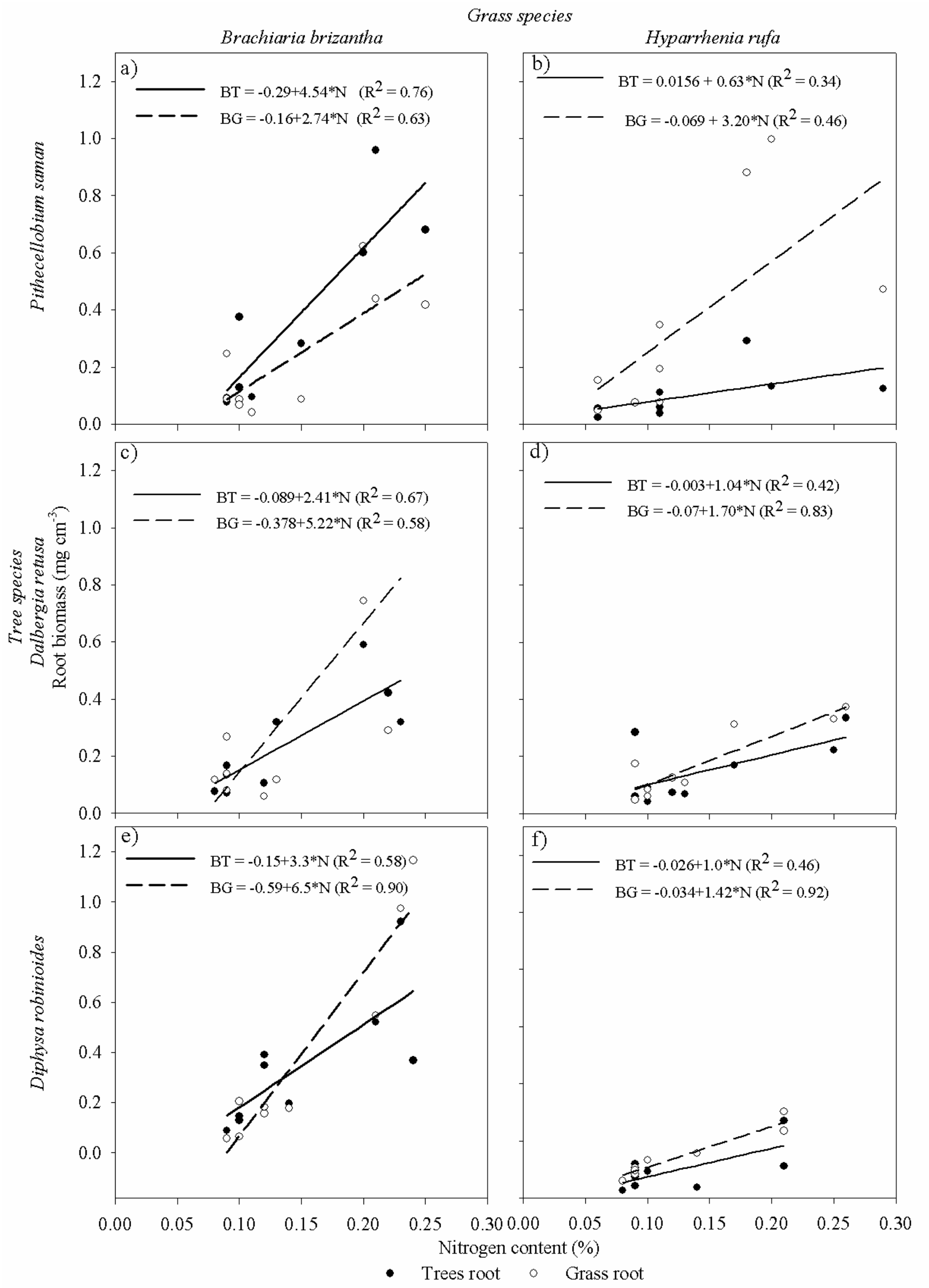

Figure 6. Relationship between tree (BT) and grass (BG) root biomass and soil nitrogen content in the soil depth 0-60 cm in six silvopastoral combinations with native timber tree species in the dry tropics of Costa Rica.

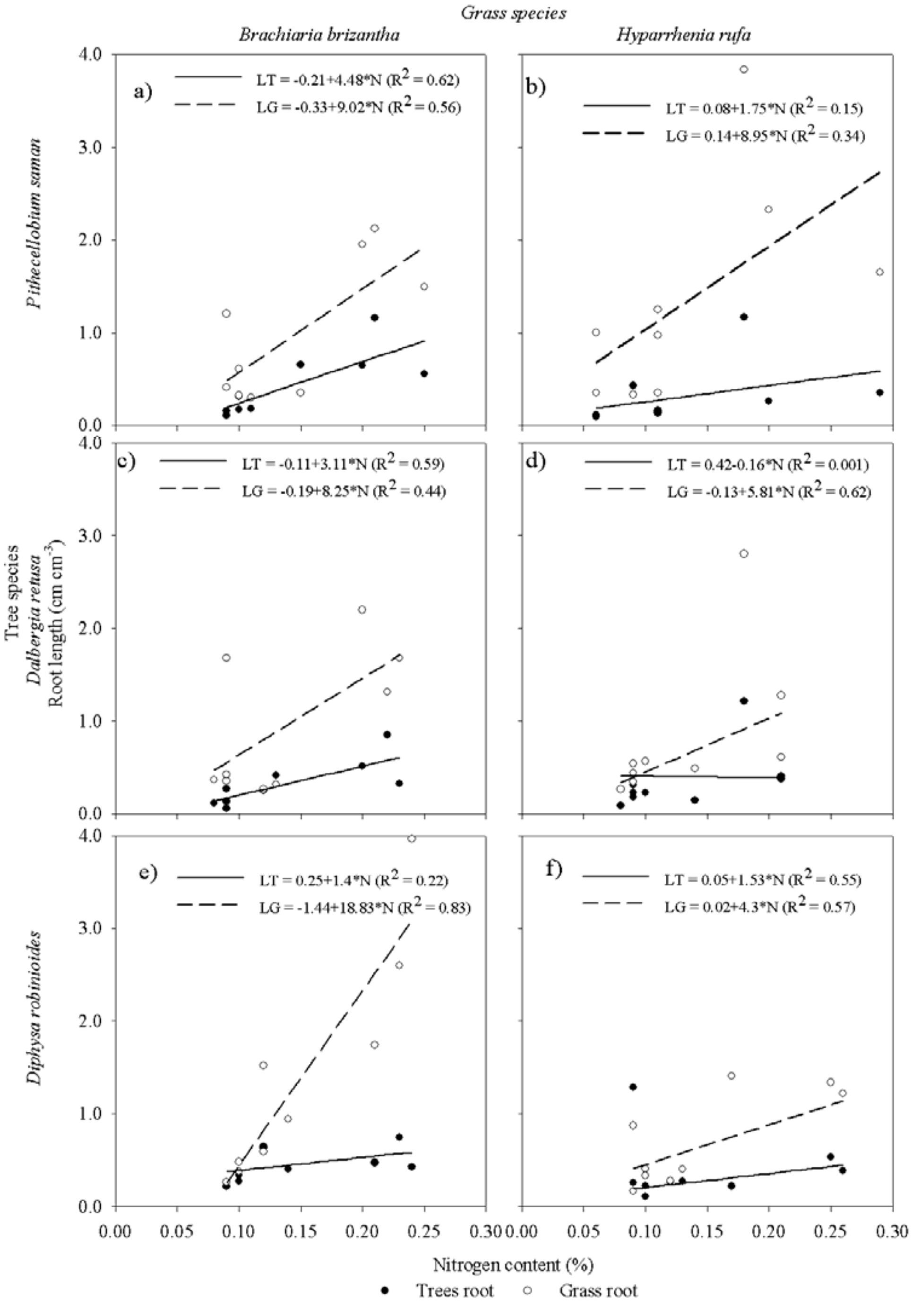

Figure 7. Relationship between tree (LT) and grass (LG) fine root length and soil nitrogen content in the soil depth 0-60 cm in six silvopastoral combinations with native timber tree species in the dry tropics of Costa Rica.

5.4. DISCUSSION

5.4.1. Fine root biomass density

A difference was found in mean root biomass density between seasons in these silvopastoral systems, from 0.53 (±0.04) mg cm^{-3} in wet season (2004) to 0.82 (±0.11) mg cm^{-3} in wet season (2005). Tree root biomass displayed active growth, increasing by 0.33 mg cm^{-3}, from one year to the next, while grass roots decreased by 0.04 mg cm^{-3}. Tree roots increased by 150% (0.56±0.02 vs 0.22±0.02 mg cm^{-3}, respectively), and this difference was unlikely to be attributed to an active tree root development.

In both sampling seasons, silvopastoral systems with *B. brizantha* had more fine roots than those with *H. rufa*. This difference was due to a disparity in tree roots rather than in grass roots. However, a difference in responses of trees between seasons was observed. In wet season 2004, *B. brizantha* systems promoted the root growth in *P. saman* and *D. robinoides* contrasting with no effect in *D. retusa*; whereas there were no differences between trees in wet season 2005. Several other studies have revealed the broad effect of components in fine root development. No effect of understory vegetation was observed by Dhyani and Tripathi (2000) who found that tree fine root biomass was similar or higher in four tree species (*Citrus reticulata*, *Alnus nepalensis, Prunus cerasoides* and *Paraserianthes falcataria*) in agroforestry systems with respect to the same no-crop situation.

Holl (1998) found a higher fine root biomass of *Calophyllum brasiliense* (Camb.) in abandoned pastures than in actively grazed grasslands (29%). The aboveground clearing of grass vegetation increases the ability of the tree to compete through the production of more fine roots, enhancing the success of tree establishment in grasslands. Guinea grass (*Panicum maximum*), in the humid tropics reduced the number of tree roots of young *Eucalyptus deglupta* trees (Schaller et al. 2003). These same authors found a different response in the number of roots of *E. deglupta* for different grass species; an increase of the width of contour grass strips of *Brachiaria brizantha* caused a decrease in the number of roots in *E. deglupta* trees; in contrast there was no effect due to *Saccharum officinarum* strips.

Rooting depth determined the plants' capacity to use resources from subsoil strata. Deep roots allowed plants to be more independent of topsoil resources usually occupied by crops or pasture species. At the same time, deep-rooted plants are less affected by root competition or mechanical disturbance (Schroth 1999). The ideal vertical root distribution in agroforestry systems implies the occupation of more or less separated soil layers for each component. This situation may reduce overall root competition improving the utilisation of soil resources (Schroth 1999).

In the current experiment, total, tree and grass fine root biomass rapidly decreased with soil depth in both sampling seasons in all silvopastoral systems. The proportion of fine roots in the top 20 cm ranged between 61 and 72% with respect to the whole 0-60 cm soil profile sampled. Trees produced more roots in *B. brizantha* systems, however, trees with *H. rufa* grass tended to have a slightly higher proportion of roots in deeper layers. Systems with *B. brizantha* allocated more roots in the deepest layer (40-60 cm) compared to *H. rufa* in an apparently more water limiting season (wet season 2005), in contrast with no differences in periods with water availability. At the evaluation times, the plant components seemed to exhibit a degree of niche differentiation, which is widely discussed in literature (Schroth 1999), with trees occupying the deeper layers of the soil.

According to Gautam et al. (2003), *Medicago sativa* cover did not affect the vertical exploration of coarse roots of *Pinus radiate,* compared to no understory in a subhumid climate. The concentration of root biomass in shallow soil layers has been widely observed. However, it appears that the proportion of tree roots in the top soil is lower than the proportion for crop plants. This difference is mainly attributed to a deeper exploration by trees. Rao et al. (1992) found that *Cassia siamea* and *Leucaena leucocephala* in Kenya reached 2 m in depth. *L. leucocephala* penetrated the soil beyond 1.7 m of depth in alley systems with maize in Kenya (Govindarajan et al. 1996). Brook et al. (2004) found that *Gliricia sepium* roots were more prolific in the top 30 cm in a wet season in Malawi than in the dry. However, in the dry season, roots were found descending to 5.4 m, but only to 3.6 m in the wet season. Roots of *Pinus ponderosa* were deeply distributed in afforested stands, compared with grazed and non-grazed stands in Patagonia. The top 0-10 cm contained 24, 26 and 4% of total root biomass for grazed, non-grazed and afforested stands, respectively (Nosetto et al. 2006). In contrast, the root contribution from the 1.5–2 m zone was 0.6, 4 and 9% for grazed non-grazed and afforested stands (Nosetto et al. 2006). In dry South African savannah, with very sandy soils, the root length of three tree species (*Burkea africana*, *Ochna pulchra* and *Terminalia sericea*) was concentrated between 10 and 40 cm depths; whereas for the grasses *Eragrostis pallens* (in open areas) and *Digitaria eriantha* (under the trees) the concentration occurred at 0-10 cm.

Dhyani and Tripathi (2000) reported that the bulk of the fine roots of *Citrus reticulata*, *Alnus nepalensis, Prunus cerasoides* and *Paraserianthes falcataria* were concentrated in the upper 10 cm soil layer (38 to 47%). Similarly, the bulk of the root volume of crops is located in the top layers. According to Pietola and Alakukku (2005), 74% of root biomass of *Lolium multiflorum* was found in the first 20 cm with respect to the 0-60 cm soil profile in Nordic fields. Frank (2002) found that root biomass in a prairie and a seeded western wheatgrass [*Pascopyrum smithii* (Rybd) Löve] was mainly located in the upper 30 cm with a proportion of 80 and 69%, respectively. Schaller et al. (2003) found that tree roots of *E. deglupta* were more superficial in association with more competitive grass species. Root competition did not encourage deeper tree root development in wet regions but this effect in drier conditions could be possible (Schaller et al. 2003). A slightly opposite result was found by Gautam et al. (2003) who found that *Pinus radiata,* in a sub-humid temperate silvopastoral system, produced higher numbers of fine root tips in the 10–

30 than in the 0–10 cm depth (2.4 vs 1.3 tips dm^{-2} day^{-1}), whereas, O'Grady et al. (2005) argued that there were no significant differences in fine root biomass of *Eucalyptus globulus* (Labill.) in the deeper soil horizons.

Despite there being a common tendency for decreasing root density in deeper layers, the fine root biomass of these silvopastoral systems can not be well explained by soil depth, due to medium level of adjust (R^2) in the developed model. It seems other factors are affecting root allocation. However, these models indicated a high difference in fine root biomass at surface level for all silvopastoral combinations, but the reduction of this value with increasing in depth (slope) was similar. The combination of *B. brizantha* and *P. saman* seemed to have the highest root biomass at surface level. The same behaviour, exponential decrease of roots with depth, was found by Ozier-Lafontaine et al. (1999) in *Gliricidia sepium* associated to *Digitaria decumbens* in Guadeloupe.

The total and grass root biomass did not differ between the intermediate and under canopy sampling positions in either sampling season. However, the ratio of the tree to grass roots components did vary with position, being much higher under the canopy. Moreover, systems with *B. brizantha* produced more tree roots under canopy in both sampling periods; however, in the wet season sampling (2005), there was no difference between sampling positions in *H. rufa* pastures. These results agree with Sundarapandian and Swamy (1996) where differences in root biomass according canopy conditions were found in forest ecosystems in India. Very fine root biomass was higher in the open than within the closed canopies in moist deciduous forest. Dhyani and Tripathi (2000) found the opposite results where the maximum accumulation of fine root biomass of *Citrus reticulata*, *Alnus nepalensis, Prunus cerasoides* and *Paraserianthes falcataria* was recorded near to the tree trunk (0.5 m) in agroforestry and no crop situations. Lateral extent of fine roots depended on species. In *A. nepalensis* and *P. falcataria* fine roots were limited to within 1 m of the tree trunk compared to 1.5 m from the tree trunk in *C. reticulata* and *P. cerasoides*.

Cover of *Medicago sativa* did not affect the lateral extension of coarse roots of *Pinus radiata* compared to no understory in a subhumid climate (Gautam et al. 2003).

A decreasing gradient in fine root biomass, with distance from near the tree trunk to open grass areas, was also found by Sierra and Nygren (2006) in *Gliricidia sepium* in a silvopastoral system with *Dichanthium aristatum. D. aristatum* presented an opposite gradient with the higher fine root biomass density in open areas. Komiyama et al. (2000) also found that the root density of *Ceriops tagal* decreased exponentially with an increasing distance from the tree trunk. Rao et al. (1992) found a high soil volume exploration of *Cassia siamea* and *Leucaena leucocephala* in Kenya, reaching 2 m in depth and 9 m in lateral spread. Similar results were described by Govindarajan et al. (1996) in *L. leucocephala* in hedges, whose fine roots spread across half of a maize alley. Schaller et al. (2003) found that the extension of lateral roots in young *E. deglupta* trees was restricted in association with competitive grasses such as *B. brizantha* and *P. maximum* compared to *S. officinarum*.

5.4.2. Fine root length density

Total fine root length density was greatly increased between sampling periods (265%). Similar to biomass increment, increase in total root length growth (530 vs 170%, respectively) was attributed more to tree root rather than grass root development. However, these results suggested that increase in total fine root biomass can be due to age. Water availability may affect fine roots. Ericsson et al. (1996) argued that fine roots experience changes in water availability more quickly in top soil than in the deep soil. A decrease in soil water availability, to water stress level, promoted carbon allocation to roots so increasing root:shoot ratio (Ericsson et al. 1996). The beginning of the rainy season also increased the root length; however, additional rains slightly reduced root length (Govindarajan et al. 1996).

Total and tree grass fine root length was affected by neither grass nor tree components in both sampling periods. However, *P. saman* produced more roots in *H. rufa* in the wet season (2004) than the other tree species. This behaviour should not have been caused by differences in tree roots, because *P. saman* had similar root length to other species. The effect of understory vegetation was also shown by Gautam et al (2003) where clonal trees of *Pinus radiata* had 65% more root length in the no-understory than in the lucerne treatment. The cause of this behaviour might be lower crown cover (shade) in *P. saman* than *D. retusa* and *D. robinoides* (Andrade et al. 2007c). Most of the root length was due to grasses (73 and 54%, for 2004 and 2005 sampling periods, respectively); however, its contribution dropped between the periods due to an increase of tree root caused by an active tree root development. Zhiping et al. (2004) found that a higher fine root length of *Pennisetum purpureum* cv. Mott compared to *Axonopus scoparius* cv. imperial contributed to a superior acquisition of nitrogen, phosphorus, potassium and calcium from soil. According to Schaller et al. (2003), fine roots of *Eucalyptus deglupta* were more superficial in the more competitive grass treatments.

Root length, similar to biomass, displayed an exponential decrease with increasing soil depth. On average, 66% of root length was located in the first 20 cm soil. Püttsepp et al. (2006) found a similar vertical distribution of fine root length in Norway spruce (*Picea abies* (L.) Karst.) in Sweden. The majority of length in the <1 mm root fraction (59 - 64% of total at 1m depth) was found in the top humus horizon H1. A similar trend was observed for the < 2 mm diameter class. Fine root length density of *Eucalyptus globulus* (Labill.) declined with increasing depth. Root length density was still increasing after 14 months growth even though most of the soil profile had been explored (O'Grady et al. 2005). According to Bowen (1985), in most forest ecosystems root abundances are sufficiently high for optimal water uptake in the upper 30 cm of soil, contrasting with root deficiencies and ineffective water use in deeper layers. Easthman and Rose (1988) found that the root length density of *Eucalyptus grandis* growing in pasture dominated by *Setaria sphacelata* was greater in the upper 0.1 m, decreasing with depth. Eighty-three percent of the roots sampled occurred in the upper 0.3 m of the soil profile.

In the current research, an apparent reduction of water availability caused a reallocation of root length in the soil profile, increasing the bulk of root length in top 20 cm, rising from 60% in wet (2004) to 72% in early wet season (2005). This change in root allocation was seen in the proportion of roots in 20-40 and 40-60 depth which dropped from 26 and 14% in wet season to 20 and 8% in early wet season, respectively. A decrease in rainfall between the wet season of 2004 and that of 2005 (237 vs 166 mm month^{-1}, for the three previous months respectively) may have promoted the root production in the first 20 cm. Ericsson et al. (1996) argued that fine roots in top soil will experience changes in water availability more quickly than in the deep soil.

It seems reallocation of roots (as measured by length) was possibly caused by the effect of the first light rains after a long period of dry. In spite of the pattern of grass root length through the soil profile being similar in both sampling periods, the contribution of grass roots dramatically dropped in all horizons with decrease of available water. This suggested that the reallocation of carbon for roots was operating in tree root systems. Gautam et al. (2003) found similar results where there was no difference with depth in the number of tips of *Pinus radiata* at an early stage of fine root initiation as soil moisture and temperature was similar for both depths. However, the effect of depth on fine root elongation was primarily related to soil moisture content (Gautam et al. 2003).

Although the total and grass fine root length was similar between under and intermediate canopy sampling positions in both periods, tree root length was slightly higher at the under canopy position. The difference in tree root length was more perceptible in wet season (2004) than early wet season (2005). The first light rains in early wet season may have caused an increase in water availability in intermediate positions (edge of the tree crown), which promoted of the fine root production in this zone. According to Gautam et al. (2003), the fine root tip initiation of *Pinus radiata* was strongly influenced by soil moisture content. Govindarajan et al. (1996) found a similar response when fine root of *Leucaena leucocephala,* in an agroforestry system with maize, increased when the rains began (Govindarajan et al. 1996). Higher radiation in open and intermediate canopy areas would promote root production; an increase in active leaf area may conduce to improve the rate of photosynthesis providing more assimilates to roots. Improved light conditions are generally associated with a shift in carbon allocation towards roots (Ericsson et al. 1996). In the same way, Edwards et al. (2004) argued that the root activities of temperate grasses are reduced by shading.

It seems that differences in fine root length through transects from tree to open areas is more marked in young trees. According to O'Grady et al. (2005), the fine root length density of *Eucalyptus globulus* (Labill.) declined with distance from the tree. However, after 14 months, distance from tree became less important as roots occupied the inter-rows (3 m of width). The thinnest roots (diameter < 1 mm) were the largest contributors to length.

5.4.3. Tree - grass competitiveness

The tree competitive ability, in terms of its relative proportion of root length with respect to grass species, has been influenced by climatic conditions, mainly water availability. This ability was not affected by components (tree and grass) in wet season, contrasting with increased tree competitive ability of *P. saman* in *B. brizantha* systems when the rains have started. Fine root of tree species (*Leucaena leucocephala* and *Pinus radiata*) were greatly influenced by water regime (Govindarajan et al. 1996, Gautam et al. 2003).

Tree species had longer and thinner fine roots than grass species. The evaluated trees tended to have higher root competitive capacity in deeper layers and close to tree trunk. This result suggested a degree of niche separation in tree-grass interface, where trees are more competitive in deeper soil layers close to their trunk, whereas, grasses were growing better further away from the tree stem, where there was less shade. Trees tended to have thicker fine roots at superficial soil layers. These results agree with those found by Singh et al. (2000) who argued that the proportion of very fine roots (<0.5 mm) of tree species increased with depth in mixed forest of *Eucalyptus camaldulensis* and *Acacia nilotica*.

5.4.4. Soil nitrogen and its relationship with fine root length

Despite there being no statistical differences in total soil nitrogen, the non-significant differences of means among tree treatments and control plots suggested a moderate nitrogen accumulation due to effect of trees. These nitrogen accumulation rates are higher than other studies. Silvopastoral systems with deep-rooted grass species and nitrogen-fixing tree species can increase nutrient cycling, improving animal production as suggested by Fisher et al. (1994). May and Attiwill (2003) estimated a nitrogen fixation rate of 40 kg N ha^{-1} year^{-1} by *Acacia dealbata* in the top 10 cm of soil through five years in Australia. Forrester (2004) reported a mean rate of nitrogen fixation between 51 and 86 kg ha^{-1} year^{-1} for *Acacia mearnsii* in mixtures with *Eucalyptus globulus* and in monoculture plantations. The foregoing studies estimated nitrogen fixation in top 5 or 10 cm and, considering the same depth of soil, results from the current work broadly agree with values given in the literature.

Total root biomass and length were correlated to the soil nitrogen concentration. Nevertheless, the development of root systems in *B. brizantha* based systems is more closely correlated to soil nitrogen content than that in *H. rufa* systems. Although all evaluated tree species are nitrogen fixing species (Salazar et al. 2000, Durr 2001, Parker 2003, Barrett and Parker 2006), the soil N concentration was better correlated to total than to tree root length.

In relation to N – tree and grass root relationships, it seemed that fine roots of grasses were having a higher impact in N accumulation (Andrade et al. 2007a), than tree roots, through increases in organic matter. This higher organic matter accumulation may have been caused by root mortality as a consequence of a high defoliation by grazing. It seems that additional factors, such as water availability, were affecting root development. Wilcox et al. (2004) found that inorganic nitrogen was not the primary limiting factor to fine root growth. Differences in surface soil nitrogen levels did not affect the fine root growth dynamics in four Mojave desert shrubs (*Ambrosia dumosa*, *Ephedra nevadensis*, *Larrea tridentata*, and *Lycium pallidum).* These findings agreed with other studies. Lee and Jose (2003) did not find significant effect of N fertilization on fine root production in either cottonwood (*Populus deltoids* Marsh.) or loblolly pine stands (*Pinus taeda* L.). Specific root length, specific root area, mean root diameter and frequency of fine roots of perennial grasses were not affected significantly by nitrogen supply. Species from infertile sites responded to low nitrogen supply with a significant increase in root hair length and root hair density (Boot and Mensink 1990). However, a limitation in soil N availability can affect carbon allocation. Ericsson et al. (1996) argued that a decreased soil N availability increased the carbon allocation to roots in plants. It is logical to expect that shortage of any mineral nutrient, N, P or S, would give rise to an increased root:shoot ratio (Ericsson et al. 1996). In agroforestry systems with coffee in wet tropics of Costa Rica, van Kanten et al. (2003) found stimulation of fine root growth from fertilisation.

5.5. CONCLUSIONS

Tree and grass roots seem to be affected by environmental factors such as soil water availability. Tree fine roots explored deeper layers in soil looking for water and nutrient, giving a higher competitive ability which enhances the probabilities of establishment success in grassland areas.

Higher transmitted radiation, due to lower crown area, in *P. saman* caused an improved root activity in periods with water availability. The introduction of improved and drought tolerant grass species, such as *B. brizantha*, enhances the root development of whole systems increasing the coexistence of components in region with seasonal water deficits. The nitrogen fixating ability of these native timber tree species is another advantage when silvopastoral systems are being designed. The results suggested that one of the strategies to establish native timber trees in grasslands would be to plant trees in improved grasses or to introduce improved grasses in silvopastoral systems. Another strategy might be to prepare the soil before the establishment of silvopastoral systems in un-improved grasslands.

The bulk of the fine roots in these tree-grass associations occurred in the top soil. A degree of niche separation was evident, because grass species had a higher competitive ability in upper horizons further away from trees, while trees dominated deeper soil layers closer to their trunks. The establishment and management of tree-grass mixtures should take advantage of this type of niche separation in root exploration. However, a temporal separation of soil volume for root exploration may also improve the survival and growth of trees. This separation could be attained by planting trees well before grasses are sown or establishing grasses in strips leaving space for tree roots to develop.

An apparent reallocation of roots, increasing the proportion in the top soil, was seen when there was a decrease in soil moisture. This reallocation is driven by roots looking for water in top layers. Depth is not the only factor that affects root profiles; other environmental factors, such as water availability, also determinate root exploration and distribution. The knowledge of how root systems respond to environment conditions, mainly water status of soil, can provide management tools for increasing the successful and adoption of silvopastoral systems in dry regions.

The high variability of samples in root studies made it difficult to obtain statistical differences between treatments (as is often observed in root studies in this field). It is recommended in this type of research, that the number of core samples be increased to incease the level of statistical support.

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CHAPTER VI

6. WATER USE AND RADIATION TRANSMISSION IN SILVOPASTORAL SYSTEMS WITH NATIVE TIMBER TREE SPECIES IN THE DRY ZONE OF COSTA RICA

Hernán J. Andrade[10]; Phillipe Vaast[2]; Robert Brook[3]; Muhammad Ibrahim[2]; Fergus Sinclair[3]; Francisco Jiménez[4]

Summary

Water use and radiation transmission between trees and grass species are key issues in the design and management of silvopastoral systems in dry conditions. Niche separation and benefits of trees on microclimatic conditions, resulting in improved total water use, have been reported but hydrological and physiological factors are still poorly understood. To evaluate water and radiation interactions, three indigenous tree species (*Pithecellobium saman*, *Diphysa robinioides* and *Dalbergia retusa*) were planted in an improved (*Brachiaria brizantha*) and a naturalised pasture (dominated by *Hyparrhenhia rufa*) on a farm in the seasonally dry lowlands of Cañas, Costa Rica. The following parameters were studied: the tree canopy cover, transmission of photosynthetically active radiation (PARt) through tree canopy, tree and grass water use by sap flow and simplified water balance methods and leaf water potential of the interacting species. The PARt varied between 46.6 and 68.0% for *D. robinioides* and *P. saman*, respectively. Grass species did not affect the sap flow velocity of *D. retusa* and *D. robinioides*; whereas *P. saman* presented higher sap flow velocity in association with *B. brizantha* compared with *H. rufa*. Tree species did not affect the

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[10] PhD Candidate, CATIE-University of Wales (Bangor): handrade@catie.ac.cr (Author for correspondence)

[2] Department of Agriculture and Agroforestry, CATIE. Emails:mibrahim@catie.ac.cr; pvaast@catie.ac.cr

[3] School of the Enviroment and Natural Resources, University of Wales (Bangor). Emails: r.m.brook@bangor.ac.uk; f.l.sinclair@bangor.ac.uk.

[4] Department of Natural Resources and Environment, CATIE. Email: fjimenez@catie.ac.cr.

water use of grasses. These young trees used less water than grasses (on average, 0.11 vs 1.2 mm day^{-1}, respectively), showing the importance of adequate selection of grass species in these dry conditions. *D. robinioides* and *D. retusa* were found to be adapted species to drought conditions, showing plasticity in regulating water according to soil and climatic conditions. These results indicated a possible coexistence of these tree and grass species in silvopastoral systems, to increase their efficiency of resource use.

6.1. INTRODUCTION

In spite of the advantages of maintaining trees on grasslands, Central American livestock producers tend not to adopt silvopastoral systems and technologies (Dagang and Nair 2003). One of the most important reasons for this lack of adoption may be the perception of strong competition between plant components (Ruhigwa et al. 1992, Govindarajan et al. 1996). There are also strong limitations for the implementation of these systems in arid and semiarid conditions, due to the lack of water availability in some seasons (Droppelmann et al. 2000). However, these systems are currently receiving more critical evaluation as potential alternatives to fully clearing land for pasture or for rehabilitation of degraded land.

The complementarities in sharing resources between tree and crop may be the key for the success of the agroforestry systems. One of the ways to achieve these complementarities is through a differentiation in spatial niche, when for example, deep-rooted tree species could utilise resources outside the reach of the roots of annual crops (Anderson and Sinclair 1993, Emmerman and Dawson 1996, Breman and Kessler 1997, Lehmann et al. 1998, Ong and Leakey 1999, Gyenge et al. 2002). The benefits of tree presence in terms of water regulation for grass species mainly in arid and semiarid conditions have been documented. The addition of trees to a conventional cropping system may increase the water-use of the system directly, through the utilisation of rainfall which cannot be used by the crop alone, or in the case of steeply sloping areas, through reduction of the amount of water lost via runoff (Young 1989).

In the subhumid tropics, the suitability of this system has depended on the complementary and competitive relationships between trees and grass for limited resources, principally water (McIntyre et al. 1997). Trees in an agricultural system influenced the hydrological cycle by affecting rainfall interception, runoff, evapotranspiration and water uptake from the soil profile (Cajas et al. 1999, Gyenge et al. 2002, Otieno et al. 2005, Cernusak et al. 2006, van Kanten and Vaast 2006). Alterations of the water balance by tree species in tree-crop systems were mainly attributed to changes in microclimatic conditions such as the incoming radiation, windspeed, air temperature and air humidity (Tournebize 1994). As a general rule, these changes reduced the grass evaporative demand under a tree canopy and could improve the water status of the grass, especially during the dry season (Belsky et al. 1993). These results imply that the improvement of grass water status may compensate for the effect of a lower incoming radiation level in silvopastoral systems. Still, water competition may be more detrimental than benefits provided by the associated tree such as improvement of soil fertility (Smith et al. 1997).

Despite an increasing number of studies on water interactions in agroforestry systems, hydrological and biological factors determining the success or failure of agroforestry systems are still poorly understood. However, traditional agroforestry systems under arid and semi-arid conditions provided evidence of their feasibility in water-limited environments of north-west India (Ong et al. 2000).

The main objective of this study was to examine the radiation and water interactions between native timber trees and contrasting grass species in the seasonal dry area of Costa Rica. The effects of trees on incoming radiation were measured by Sunscan (a linear array of PAR sensors) and canopy cover was estimated by hemispherical photography, tree water use was recorded using sap flow techniques, tree and grass evapotranspiration by simplified water balance and the water status of tree and grass species through measuring of their leaf water potential.

6.2. MATERIALS AND METHODS

6.2.1. Description of experimental site

This study was carried out on the farm Hacienda La Pacifica, Cañas, Costa Rica. Details of location, soil and landscape characteristics, and establishment of the trial are given in materials and method section in chapter IV. The climatic conditions in the study zone contrast strongly between seasons (rainy and dry; Figure 1). The rainy season extends from mid-May to the beginning of November; while December to April is the dry season. However, three seasons were considered for this study according to the mean rainfall and reference evapotranspiration (ETo): rainy, transition and dry seasons. The rainy season (May to October) is characterised by the the highest rainfall but with the lowest ETo, while the dry season is characterised by low monthly rainfall (282 vs 8 mm month^{-1}, respectively) and much higher ETo values than that of the the rainy season (3 vs 7 mm day^{-1}, respectively). The transition season presents low rainfall but has intermediate ETo values (Figure 1).

6.2.2. Establishment of the experiments

6.2.2.1. General experiment

A randomized complete block experimental design with three replications was used. The treatments had a factorial structure with a split plot design where two grass species (*Hyparrhenia rufa* dominated or newly established *Brachiaria brizantha*) formed the main plots with four randomized treatments (*Pithecellobium saman*, *Diphysa robinioides, Dalbergia retusa* and no-tree control) in the subplots.

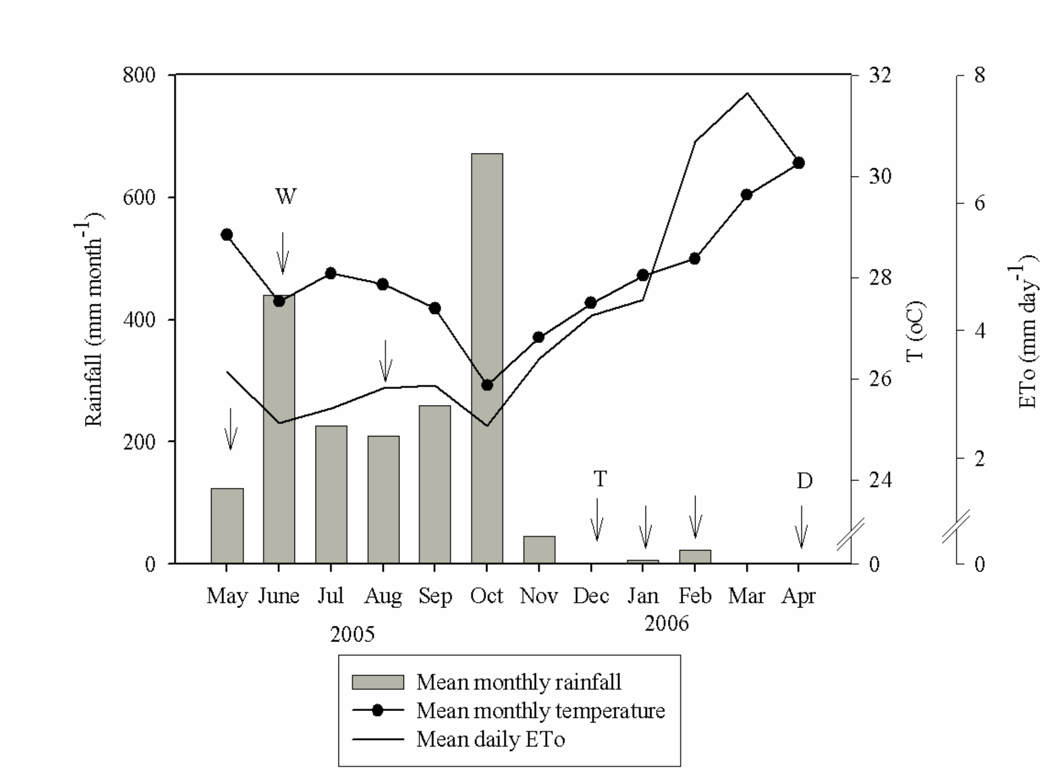

Figure 1. Climatic conditions in the sampling periods in the dry tropics of Costa Rica (Cañas, Guanacaste, 2005-2006). ETo by FAO-Penman-Monteith method (Allen et al. 1998). Arrows indicate periods of sap flow monitoring; W: wet, T: transition and D: dry seasons.

6.2.2.2. Tree – grass competition control trial

This study was carried out using the same general experiment. However, this factorial trial is composed of three factors: grass species in the main plots, tree species in the subplots and grass competition control (no grass and grass competition) in the sub-subplot.

The sub-subplots (2 m in diameter) were isolated from the surrounding plots to prevent invasion by external roots, and lateral movement of water. To achieve this, a vertical thick plastic sheet was installed as a barrier in each sampling plot down to 50 cm below the soil surface and protruding at least 5 cm aboveground. In the no-grass plots, grass was eliminated by repeated sprays of glyphosate herbicide and a plastic sheet with small perforations covered the soil inside the plastic barriers. The perforations were allowing rapid penetration of rainwater but minimizing soil evaporation.

6.2.3. Sap flow study

6.2.3.1. Monitoring of tree sapflow

This experiment was carried out in the main plots of *B. brizantha* and *H. rufa* in the first block of the general trial. This was due to restrictions in the number of gauges and the maximum distance between trees and a central point (30 m). Eighteen trees, 42 months old, from the three evaluated species with diameters at sensor height (around 1 m above ground level) ranging from 2.1 and 12.6 cm were selected to conduct these studies. This range is representative of the trees in the subplots. Three individual trees were selected by species for each grass cover. The sapflow gauges, composed of two ”Granier” probes (the upper heated and the lower reference), were installed during at least five consecutive days per sampling period which represented all climatic seasons in the study zone. All trees were located at a maximum distance of 30 m from a central point due to cable length restrictions.

The gauges were placed on the main trunk of each monitored tree and covered by a solar isolator (aluminium weather and radiation sheet), a plastic bottle and, finally, a plastic sheet to protect against radiation, rain and insects. The gauges were inserted into the conducting xylem or sapwood after removing a piece of cortex (around 1 x 1 cm) to measure the differential temperature between the upper heated probe and the lower reference probe (Granier 1987, Smith and Allen 1996).

Sap flow was monitored by the heat dissipation method (Granier 1985, 1987, Lu et al. 2004, Roupsard et al. 2006) with 20 mm-long radial probes supplied by CIRAD in Vanuatu (Roupsard et al. 2006). Each set of probes (heated and control probes) was connected to a data-logger (CR10X and AM 16/32 Multiplexer located in an enclosure ENC 10/12, Campbell Scientific, Shepshed, UK), which read at 15 second intervals and stored 15 minute averages. Each heated probe was connected to a 138 mA DC potentiometer, powered by a 12 V / 60 A h^{-1} car battery connected to a 20 Watt Solar Panel, MSX20). The battery was changed when the voltage was below 11.8 V. The datalogger, multiplexer and car battery were always protected inside a heavy duty metal box. Sapflow was monitored during seven contrasting sampling periods: 4 – 10th May, 22 - 29th June, 18 – 25th August, 13-18th December 2005 and 25 – 29th January, 30th January – 2nd February and 5 – 11th April 2006.

6.2.3.2. Calibration of the sap flow probes

Calibration process was carried out in a greenhouse to avoid water gain from rainfall. Three individuals per tree species (*Pithecelobium saman, Dalbergia retusa* and *Diphysa robinioides*) were each planted in 20 L plastic pots. Where the probes were installed, trees had a stem diameter greater than 2.0 cm at 10 cm height. Pots were watered beyond field capacity and left until drainage had ceased. The pots were covered by two plastic bags to avoid soil water loss and hence to allow the fine monitoring of tree water via sap flow. The pots were periodically weighed with a portable digital balance (70 kg x 5 g) every 110 to 265 min, depending on climatic conditions and tree transpiration rate. The difference between consecutive weighings was considered to be the real water loss by transpiration. Pots were also weighed immediately before sunset (around 18:00 h) and before dawn (around 06:00) to calculate night transpiration.

After 17 days of monitoring, all pots were re-watered and a second set of calibration was carried out for five additional days. Excess water was allowed to drain from the pots for 18 h before the onset of the monitoring. Microclimatic variables were recorded around five times a day (07:00, 09:00, 12:00, 15:00 and 18:00 h) in the greenhouse. Soil moisture of the pots was estimated at the end of the experiment using the gravimetrical method. Soil moisture in pots throughout the whole experiment was estimated, based on the final soil moisture and dry soil mass.

At the end of this calibration trial, all plants were cut to estimate the relative conductive area of stems (cross sectional area of the conducting sap wood). Each plant was cut and put into a solution of tryphan blue for around 5 minutes to stain the conducting tissue; the inferior disk (1 cm of height) was cut to evaluate the coloration of upper face of each disk. The stem was again put into the same solution to repeat the process. All disks were visually evaluated and scanned to estimate the proportion of conductive area referred to as the blue tissues. Leaf area was also estimated in all plants at the beginning of the calibration.

The empirical equation developed by Granier (1985, 1987) for estimating sap flow velocity (u) is based on differential temperature between probes (K):

$$\mathrm{K} = \left[\frac{\Delta T_o - \Delta T_i}{\Delta T_i}\right] \qquad \text{Equation 6.1}$$

Where;

K: Sap flow index (dimensionless)

ΔT_o and ΔT_i: Daily maximum and current temperature difference between the two sensors of the probe (^{o}C), respectively

$$\upsilon = \alpha K^{\beta} \qquad \text{Equation 6.2}$$

Where;

υ: Sap flow velocity (m s^{-1})

α and β: Parameters of the model (1.19×10^{-4} and 1.231, respectively for the Granier's empirical equation)
K: Sap flow index (dimensionless)

The average K was calculated for the same period between two consecutive weighings. The sap flow by gravimetrical sampling of water loss was calculated thus:

$$\upsilon = \frac{Wl}{As \times t \times 100} \qquad \text{Equation 6.3}$$

U : Sap flow velocity (m s^{-1})
Wl : Water loss (cm^3 = g), differential weight between two consecutive measures
As : Cross sectional area of the conducting sap wood (cm^2)
t : Time elapsed (s)

The gravimetrically determined sap flow velocity was correlated with the K value in each sampling period. Linear models with and without logarithmic transformation were tested to identify the best fit equation based on the highest R^2 and adjusted R^2 and the lowest root square mean error (RSME) and the sum of squared predicted residual (PRESS), also bearing in mind the biological logic of the model. A general equation using dummy variables to identify each tree species was tested to evaluate the statistical differences between intercepts and slopes from all equations. The best fit equation developed by this calibration was compared with models developed by Granier (1985, 1987) and Roupsard et al. (2006). Real sap flow velocity (RSFV; gravimetrically) was correlated with K. Four regression equations were tested: linear, logarithmic, exponential and power. These equations refer to relationships between RSFV and K, with and without base-10 logarithmic transformations. Equations for all species and for each species were developed.

6.2.4. Variables recorded

6.2.4.1. Climatic conditions

The climatic variables during the period of the field research were collected from an automatic climatic station close to the study site. This station recorded data of rainfall (mm), temperature (^{o}C), relative humidity (%), wind speed (m s^{-1}) and global radiation (W m^{-2}) every 15 minutes. This information was sent by a telemetry communication system (Adcon Telemetry) to a central computer to be stored in the software addVANTAGE.

6.2.4.1.1. Vapour pressure deficit

Vapour pressure deficit (VPD) was calculated using the climatic information following the procedure recommended by Allen et al. (1998) from the FAO Penman-Monteith equation:

$$VPD = e_a - e_d \qquad \text{Equation 6.4}$$

Where;
VPD : vapor pressure deficit (kPa)
e_a : air saturation vapor pressure (kPa)
e_d : vapor pressure at air temperature (kPa)

$$e_a = 0.6108 * \exp\left[\frac{17.27 * T}{T + 237.3}\right] \qquad \text{Equation 6.5}$$

Where;
e_a : air saturation vapor pressure (kPa)
T : air temperature (^{o}C)

$$ed = \frac{ea * RH}{100}$$ Equation 6.6

Where;
e_d : vapor pressure at air temperature (kPa)
RH : relative air humidity (%)

6.2.4.1.2. Reference evapotranspiration

Reference evapotranspiration (ETo) was calculated every 15 minutes during the sap flow studies and on a daily basis during all other periods of this research. ETo (mm) was estimated with the FAO Penman-Monteith equation (Allen et al. 1998) using an adaptation of two Excel spreadsheets developed by the FAO (Food and Agriculture Organisation) for a daily and hourly time step. The inputs for the estimations in both periods were: wind speed at 2 m height (u2), temperature (T), relative humidity (RH) and global radiation (W m^{-2}).

6.2.4.1.3. Air water potential

The air water potential was calculated based on air relative humidity and temperature at the specific times, using the following equation:

$$\psi = \frac{RT}{V_w} * Ln(RH)$$ Equation 6.7

Where;
R : gas constant (0.0082 L MPa/mol degree)
T : temperature (^oK)
V_w : partial molar volume of liquid water (55 mole/l)
RH : relative humidity of the air (fraction)

6.2.4.2. Tree canopy cover, leaf area index and transmission of radiation to grasses

The study of tree canopy and radiation behavior was carried out in the general experiment. Tree canopy cover was characterized by measuring the crown dimensions of individual trees and via hemispherical photography.

6.2.4.3. Projected crown area

The projected crown area (m^2) was measured to estimate the tree cover in each subplot. Two perpendicular diameters (N-S and E-W) of the projected crown were measured in all 36 central trees by subplot to calculate the crown area as a circle whose diameter is the average of two perpendicular diameters. The proportional tree cover was estimated as the sum of all individual tree projected crown area divided by the total area of the central trees (360 m^2 due to a tree density of 1000 trees ha^{-1}).

6.2.4.4. Hemispherical photography

Hemispherical photographs were taken in three contrasting climatic periods (rainy season 2004, transition period 2005 and dry season 2006) using a digital camera, Nikon Coolpix 4500 with a maximum resolution of 5 Megapixels and a fish eye lens. All photographs were taken supporting the camera on an 85 cm-height wood base to capture all vegetation above this horizontal level with a resolution of 300 dpi. The photographs were taken using a standard configuration (default) immediately before sunset (around 18:00 h) and before dawn (around 06:00) when the sun's radiation did not reach the camera's lens. Between 10 and 30 photographs were taken in each sub-plot equally divided between under canopy and intermediate canopy (0.5 and 1.0 m away from tree trunk). The number of photographs depended on the canopy variability in each sub-subplot, more photographs being taken in a subplot with high variability.

The hemispherical photographs were analyzed using the software Gap Light Analyser version 2.0 (GLA; Frazer et al. 1999). This software computes canopy and site openness, effective leaf area index, sunfleck-frequency distribution and daily duration, and the amount of above- and below-canopy (transmitted) direct, diffuse, and total solar radiation incident on a horizontal or arbitrarily inclined receiving surface. Tree canopy cover (TC) percentage was calculated as the complement of canopy openness (CO; TC (%) = 100 – CO (%)). Tree canopy cover estimations by GLA analysis were compared against the tree cover estimated by measuring tree projected crown area.

The estimations of the radiation variables require the inclusion of geographical location and the slope of the terrain. The radiation configuration includes the solar constant (1367 W m^{-2}); the cloudiness index (also known as Kt) was 0.5, indicating that half of the extraterrestrial radiation would reach the ground as total solar radiation over the specified period. A spectral fraction of 0.5 was also assumed (because PAR is considered to be 50% of global solar radiation) and the beam fraction which is the ratio of direct (beam) to total (global) spectral radiation incident was set as 0.5 (Frazer et al. 1999).

6.2.4.4.1. Calibration of hemispherical photography (GLA outputs)

Nine trees, three for each species, were destructively sampled to calibrate the GLA method. Hemispherical photographs were taken before and after cutting these trees. Between 13 and 16 hemispherical photographs (depending on the tree size) were taken at each sampling time every 0.5 m away from the tree in each compass direction (north, south, east and west). The sampling points were marked with stakes pushed into the ground. Trees were separated by components (stem, branches and leaves). A sub-sample of around 200 g of fresh leaves was weighted to calculate dry matter content. Total leaf area of each tree was calculated based on the leaf biomass and specific leaf area (SLA), which was estimated taking 24, 78 and 111 leaves for *D. retusa*, *D. robinioides* and *P. saman*, respectively. The leaves were scanned in three or four sets, according to their size, using a conventional scanner, Canon LIDE-20. Images were saved as TIFF files with a resolution of 400 dpi in 8-bit format. Leaf area by set was estimated using the Lafore software (Lehsten 2005). All leaves from each set were oven dried (65 ^{o}C until constant weight was obtained) and weighed. Specific leaf area (cm^2 g^{-1}) was then calculated by dividing leaf area (cm^2) by dry weight (g).

Leaf area index of each sampled tree was calculated by dividing total leaf area (m^2) by projected crown area (m^2). The LAI was calculated by GLA for the LAI 4 ring, which is the effective leaf area index integrated over the zenith angles 0 to 60^{o} (Stenberg et al. 1994). LAI by destructive sampling was correlated to LAI output by GLA to determine a calibration equation.

6.2.4.5. Transmitted photosynthetically active radiation measured by Sunscan

Transmission of photosynthetically active radiation (PAR) to grasses was calculated during the second month of the dry season (January 2005) using a 1 m long Sunscan probe (a linear array of PAR sensors) line Delta-T Devices, Cambridge, UK). All measurements were carried out between 11:00 and 13:00 during completely sunny periods (without clouds intercepting solar radiation). The incident PAR was measured by taking around 20 instantaneous readings in each position with respect to the canopy; the instrument calculated the average of these 20 measurements. PAR transmission was calculated as the portion of PAR under canopy and intermediate canopy positions with respect to incident PAR over the tree crown, which was assumed to equal the PAR incident in open areas (in the middle of tree lines, 4 m away from the trees). The following equation was used:

$$PARt = \frac{PARo}{PARg} * 100 \qquad \text{Equation 6.8}$$

Where;

PARt : Transmitted PAR (%)

PARo and PARg : PAR above and below tree canopy (µmol m^{-2} s^{-1})

6.2.4.6. Canopy light extinction coefficient (k)

The canopy light extinction coefficient (k) was estimated based on PARt estimated with the Sunscan and the corrected LAI estimated through hemispherical photography. Both variables were recorded in the same period, the second month of the dry season (January 2005). The Beer's law equation was used to estimate k:

$$PARt = e^{-k*LAI} \qquad \text{Equation 6.9}$$

$$k = -\frac{Ln(PAR_t)}{LAI} \qquad \text{Equation 6.10}$$

Where;

k : Canopy light extinction coefficient

PARt : Transmitted PAR (fraction)

LAI : Leaf area index

6.2.4.7. Water use

6.2.4.7.1. Sap flow of tree species

The sap flow velocity (SFV, cm h^{-1}) was estimated using the equation generated by the calibration trial. The water use of individual trees was estimated as the product of sap flow velocity and the conductive cross-sectional sap-wood area (As, cm^2). The water use of the whole subplot (stand level) was estimated by multiplying the SFV of each tree by the basal tree area of the subplot, using the following equation (BA, m^2):

$$WU = SFV * BA * (1m/100cm) * 1000(l/m^3) * (1ha/10000m^2) * 24(h/day)$$

Equation 6.11

Where;
WU : Water use of the stand (transpiration; mm day^{-1})
SFV : Sap flow velocity (cm h^{-1})
BA : Basal area of the stand (m^2)

6.2.4.7.2. Water use in trees growing in pots in a greenhouse

Water use of the trees growing in pots was estimated by sap flow measurements every 15 minutes. Sap flow velocity and water use by individual trees were estimated following the same procedure with the equation developed in the calibration process. Air temperature and relative humidity were recorded five times a day (6:00, 9:00. 12:00. 15:00 and 18:00 h) during the whole trial period using a portable-digital thermohygrometer. Soil volumetric moisture at the end of the trial was calculated by weighing the moist soil and taking a sub-sample to obtain moisture content gravimetrically in the laboratory (drying at 65^{o}C for 48h) and multiplying by its bulk density. Mean volumetric soil moisture for the whole measurement period was estimated by soil moist weight minus the dry weight and subtracting plant biomass and weight of plastic bags and pots.

6.2.4.7.3. Water use in tree – grass competition control trial

An event approach was selected to estimate water use of each sub-subplot. Periods with low rainfall were selected to estimate the water use of plants in the top 60 cm of soil depth. The volumetric soil moisture was estimated by taking samples for gravimetrical estimation of moisture at three soil depths (0-20, 20-40 and 40-60 cm). The samples were collected, using an engine auger of 5 cm diameter, and stored in a plastic, hermetically sealed receptacle until analysis in the laboratory. Gravimetric moisture content of each sample was obtained by the difference between the humid and dry weights (60 °C to constant weight). Soil volumetric moisture was estimated based on gravimetric moisture and bulk density, which was estimated by the cylinder method according to the following equation:

$$\theta = \frac{Ww}{Wds} \times bd \times 100 \qquad \text{Equation 6.12}$$

Where;

θ : Soil volumetric moisture (%)
Ww : Weight of water (g)
Wds : Weight of dry soil (g)
bd : Bulk density (g cm^{-3})

The water availability in each sampling period was estimated by the following equation:

$$WA = \frac{CM - PWP}{100} xSd \qquad \text{Equation 6.13}$$

Where;

WA:	Water availability (mm)
CM:	Current moisture (%, volumetric moisture)
PWP:	Permanent wilting point (%, volumetric moisture)
Sd:	Soil depth (mm)

Field capacity and permanent wilting point were estimated in the CATIE soil laboratory by applying a pressure of 33 kPa and 1.5 MPa to undisturbed soil samples. The water use in each sub-plot was estimated using the following equation:

$$WU = \Delta WC + R \quad \text{Equation 6.14}$$

Where;

WU : Water use of the system (mm)

ΔWC : Change in volumetric water content in the soil between two consecutive samplings (mm)

R: Rainfall (mm)

6.2.4.8. Water use efficiency

Water use efficiency of tree species (*P. saman*, *D. retusa* and *D. robinioides*) growing in both contrasting grass species (*B. brizantha* and *H. rufa*) was estimated by dividing the aboveground biomass accumulation at 51 months old (Andrade et al. 2007a) by the tree transpiration. In contrast, the water use efficiency for grass species was estimated by dividing their mean annual dry mater production (Andrade et al. 2007a) by their evapotranspiration when they were growing in the absence of trees.

6.2.4.9. Leaf water potential

The water status of plant species in these silvopastoral systems was estimated by measuring the leaf water potential in contrasting climatic seasons: rainy, transition and dry. Water leaf potential of green leaves from each individual tree was estimated with a pressure chamber (Scholander et al. 1965) with a maximum operating pressure of 40 bars (4 MPa). The chamber was connected to a cylinder of pressurised air; which was regularly recharged from a bigger cylinder.

Each leaf was excised from the plant and immediately inserted into the lid of the chamber, then increasing pressure to the chamber at a constant rate of around 0.1 MPa every 5 s, until a drop of water emerged from the petiole. In the case of tree species, entire leaves were cut at the base of petiole and placed in the chamber leaving the end of the petiole outside the chamber via the circular rubber seal. In the case of grass species, the leaf was cut transversally removing a piece of the leaf lamina from both sides of the central nerve to allow the entrance of the central nerve through the flat rubber seal of the chamber. The measurements were registered when a water drop emerged from the central nerve.

6.2.5. Statistical analyses

The sampled variables from the general experiment and the grass-tree competition trial were analysed using an experimental design of randomized complete blocks with split split plots and split split split factorial arrangements, respectively. The tests were carried out using the procedure PROC GLM of SAS (SAS 1988). Means were compared using the least square means (LSMEANS) procedure of SAS. The effect of components (grass and tree species) on sap flow study was analysed using "t" test through the PROC TTEST of SAS (SAS 1988). In this case, the statistical comparison of means was carried between couples of levels in each factor. In the case of the tree factor, which had three levels (three species), the analysis was developed comparing pairs of levels. All regression procedures were developed using the PROC REG in SAS.

6.3. RESULTS

6.3.1. Calibration of hemispherical photographs

There was a good correlation between leaf area index (LAI) in ring 4 (0 to 60^o of azimuth) of the hemispherical photographs and the measured LAI as determined destructively for the trees used in the calibration procedure (R = 0.94; Table 1). The linear equation developed provided the most accurate method of estimating LAI non-destructively (Figure 2). In contrast, the relationship between tree cover area and canopy cover was lower (R = 0.83; Table 1).

Table 1. Correlation coefficients (R) between measured LAI (destructive sampling) and LAI estimated by GLA.

	Gap Light Analyzer variables					
Variables from destructive sampling	**LAI4**	**LAI5**	**Log(LAI4)**	**Log(LAI5)**	**Canopen (%)**	**Log (canopen)**
LAIR	0.94 (0.0002)	0.94 (0.0002)	0.74 (0.0241)	0.72 (0.0293)	0.80 (0.0153)	0.64 (0.0658)
Log(LAIR)	0.92 (0.0005)	0.91 (0.0006)	0.81 (0.0082)	0.77 (0.0144)	0.83 (0.0054)	0.72 (0.0274)
Acanopy (m^2)	0.63 (0.0706)	0.64 (0.0650)	0.66 (0.0549)	0.67 (0.0484)	0.75 (0.0189)	0.66 (0.0527)
Log(Acanopy)	0.73 (0.0268)	0.74 (0.0238)	0.79 (0.0117)	0.82 (0.0070)	0.83 (0.0056)	0.79 (0.0112)

Numbers in parenthesis correspond to probability (P) level. LAIR: Measured leaf area index from nine trees destructively sampled; Acanopy: Vertically projected crown area; LAI4: Effective leaf area index integrated over the zenith angles 0 to 60^o (Stenberg et al. 1994); LAI5: effective leaf area index integrated over the zenith angle 0 to 75^o (Welles and Norman 1991); Canopen: Tree canopy open – sky fraction without tree canopy cover; Log: Base-10 Logarithm.

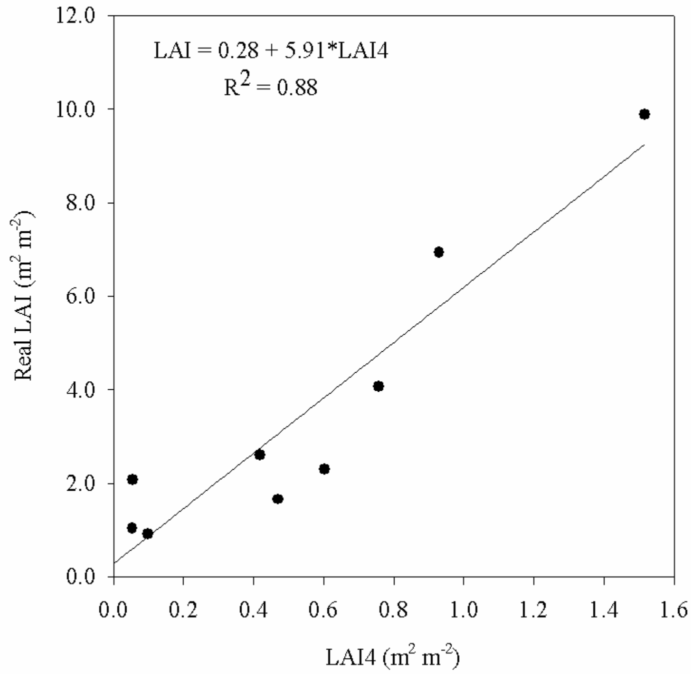

Figure 2. Equations for estimating leaf area index based on Gap Light Analyzer estimations. Measured LAI: Leaf area index for destructively sampled trees; LAI4: Effective leaf area index integrated over the zenith angles 0 to 60° from GLA (Stenberg et al. 1994).

6.3.2. Tree canopy cover

Tree canopy cover (TC) was greatest overall during the transition season 2005; whereas, the effect of the dry season resulted in a decline of the TC due to defoliation of trees (Figure 3). There was a tree x grass interaction ($P<0.01$; Table 2) in all seasons. *P. saman* always had the lowest tree cover in both grass treatments (Figure 3). *H. rufa* did not affect TC in the three studied seasons (Figure 3). In contrast, in *B. brizantha* plots during rainy season 2005 and dry season 2006, *D. robinioides* had higher TC than *D. retusa;* whereas, it was the opposite result in the transition season (27.0±0.8 vs 25.0± 0.7, 32.2±0.9 vs 35.6±1.4, 28.3±0.7 vs 27.9±1.4 % for *D. robinioides* and *D. retusa* in rainy, transition and dry seasons, respectively; Figure 3). On average, *D. robinioides* had the highest percentage tree cover, followed by *D.*

retusa then *P. saman* (P<0.01; 30.6±0.4 vs 27.8±0.5 vs 9.7±0.1, respectively; Figure 3).

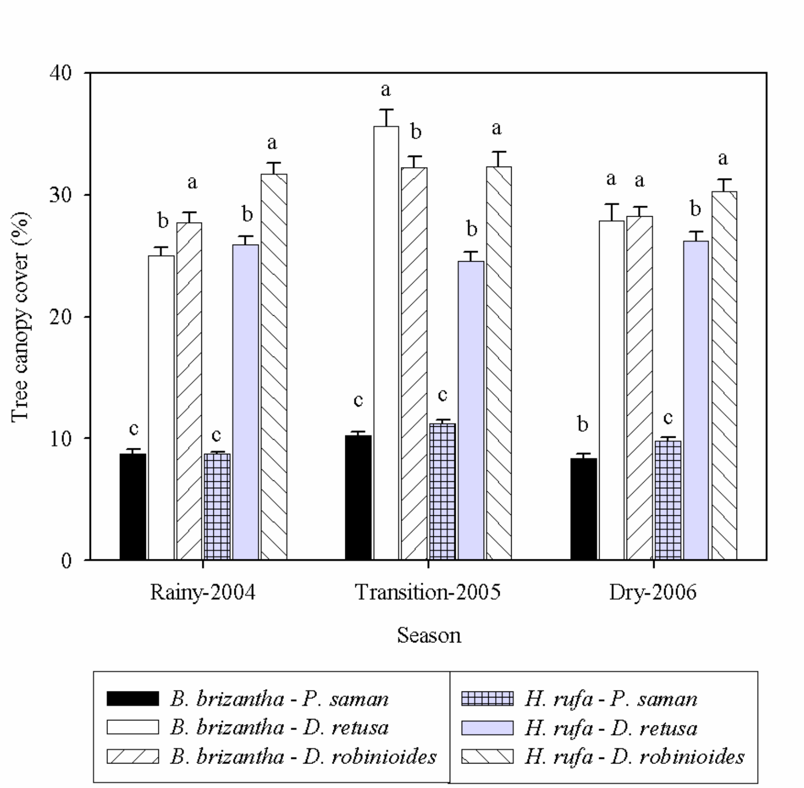

Figure 3. Tree canopy cover (percentage of plot covered by vertically projected canopy area) of three native timber species in three contrasting seasons in silvopastoral systems in the dry tropics of Costa Rica. Different letters mean statistical differences among tree species in each grass species (P < 0.05). Error bars indicate standard error of means.

6.3.3. Transmission of photosynthetically active radiation (PAR)

6.3.3.1. Hemispherical photographs

PARt through tree canopies was slightly different between seasons. Rainy season 2004 had the highest PARt, followed by dry season 2005 then transition season 2005 (51, 46 and 42%, respectively; Figure 4a). A strong correlation between tree cover and PARt (R=-0.91; P<0.01) was found. However, a tree x grass interaction was also found for all seasons (P<0.05; Table 2). *P. saman* had the highest PARt in all evaluated seasons followed by *D. retusa*, which was significantly higher than that of *D. robinioides* (62.9 vs 47.1 vs 32.2%, respectively; Figure 4a). Nevertheless, in the transition season 2005, the PARt of *D. retusa* and *D. robinioides* were similar (P>0.05) with *B. brizantha* and so were the PARt of *P. saman* and *D. retusa* with *H. rufa* (P>0.05).

Table 2. P values tabulated for tree cover, leaf area index (LAI), transmitted photosynthetically active radiation (PARt) of six silvopastoral associations during three sampling seasons (rainy 2004, transition 2005 and dry 2005) in Cañas, Costa Rica.

	Rainy 2004			**Transition 2005**			**Dry 2006**		
Source	**Tree cover (%)**	**LAI**	**PARt (%)**	**Tree cover (%)**	**LAI**	**PARt (%)**	**Tree cover (%)**	**LAI**	**PARt (%)**
Block	0.1107	0.0859	0.1348	0.1990	0.2382	0.2408	0.3280	0.2573	0.1328
Grass (G)	0.3924	0.1065	0.4400	0.4163	0.7781	0.9769	0.8521	0.5334	0.2967
Tree (T)	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
G x T	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.0296	0.0083	0.0374
Position (P)		<.0001	<.0001		<.0001	0.0078		<.0001	0.0002
T x P		0.0004	0.0130		0.2787	0.9696		0.0703	0.2284
G x P		0.0009	0.1476		0.4902	0.7501		0.3640	0.3214
G x T x P		0.0007	0.5520		0.8897	0.3614		0.6179	0.7762

During the rainy season 2004 and dry season 2006, PARt of *P. saman* was statistically higher than that of *D. retusa* and *D. robinioides* (66, 50 and 53%; P < 0.05; Figure 4a). However, in the transition season 2005, the PARt of *D. retusa* and *D. robinioides* were similar (33.4 ± 2.5 vs 33.4 ± 1.9 %, P>0.05; Figure 4a) with *B. brizantha* and, also, the PARt of *P. saman* and *D. retusa* were similar with *H. rufa* (50.6 ± 2.2 vs 50.7 ± 2.2%; P>0.05; Figure 4a).

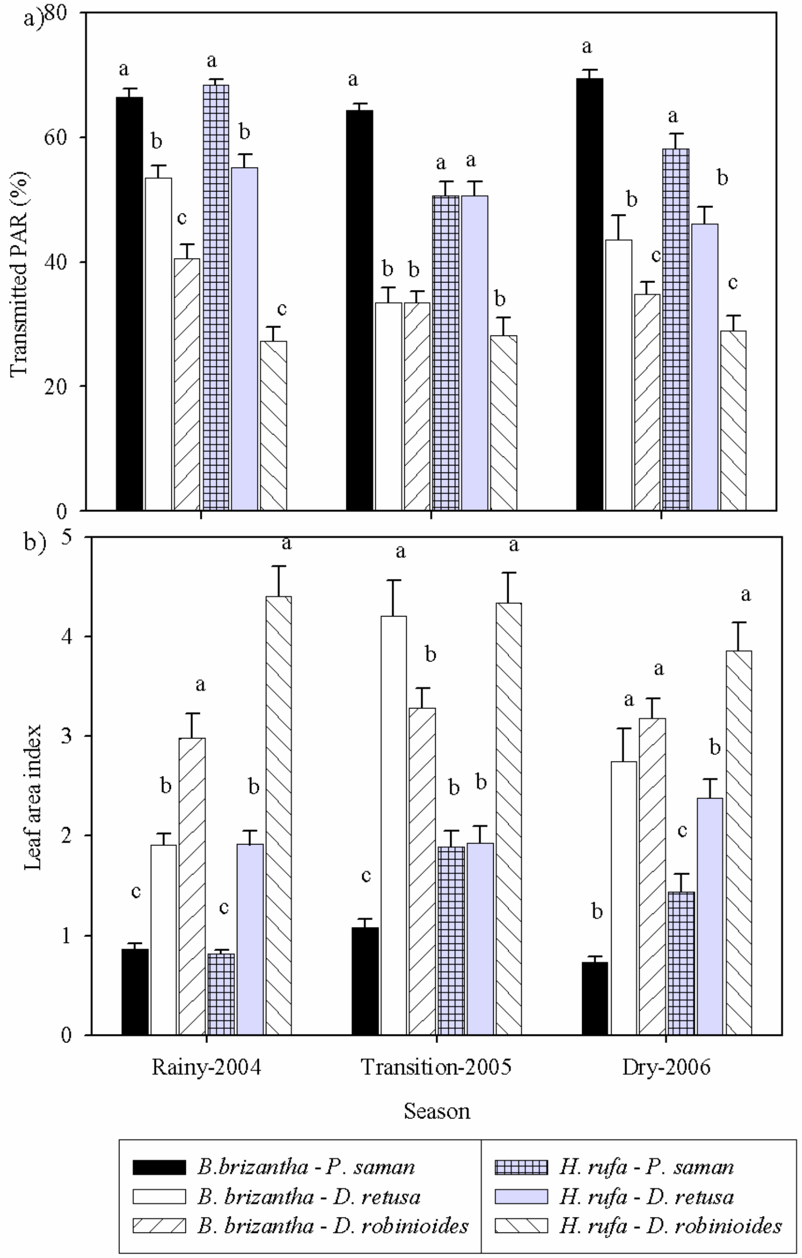

Figure 4. a) Transmitted PAR and b) leaf area index estimated by hemispherical photography in three contrasting seasons of six silvopastoral associations in the dry tropics of Costa Rica. Different letters indicate statistical differences among tree species in each grass species (P < 0.05). Error bars indicate standard error of mean.

6.3.3.2. Sunscan measurements

The estimation of PARt with the Sunscan gave similar results to those from hemispherical photography. There was an acceptable relationship between PARt estimated by hemispherical photographs and by Sunscan (R=0.75) directly under canopy and at intermediate canopy sampling positions. Tree species displayed statistical differences in PARt (P<0.01) in both sampling positions (under and intermediate canopy). On average, the PARt at the intermediate canopy positions were 80% higher than directly under canopy positions (Figure 5). There was a tree x grass interaction (P<0.05). *P. saman* had the highest PARt in comparison to that of *D. retusa* and *D. robinioides* (68.0, 47.9 and 46.6%, respectively; Figure 5).

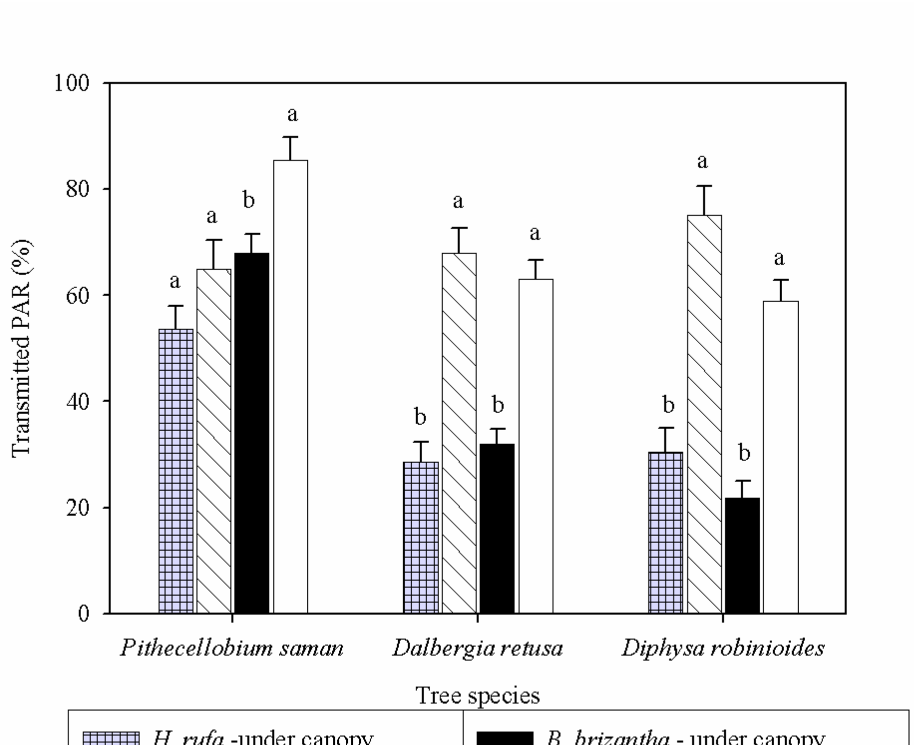

Figure 5. Transmitted photosynthetically active radiation (measuring by sunscan) of native timber tree species in silvopastoral systems in the dry tropics of Costa Rica.

6.3.4. Tree leaf area index (LAI)

There was a grass x tree interaction for tree leaf area index (LAI) during all three sampling periods ($P<0.01$; Figure 4b). In all silvopastoral associations and either in both rainy and dry seasons, *P. saman* presented the lowest LAI compared to *D. retusa* and *D. robinioides* (Figure 4b). However, in the transition season there was a slightly different effect for both grasses. With *B. brizantha*, *D. retusa* had a significantly highest LAI in comparison to *D. robinioides* and *P. saman* ($P<0.01$; 4.2±0.4 vs 3.3±0.2 vs 1.1±0.1, respectively; Figure 4b). In contrast, with *H. rufa*, the general tendency was for *P. saman* and *D. retusa* to have the lowest LAI in comparison to *D. robinioides* ($P<0.05$; 1.9±0.2 vs 1.9±0.2 vs 4.3±0.3, respectively; Figure 4b).

Tree species had lower LAI in the dry season in comparison to the transition season, except for *D. retusa*, whose LAI increased in 23% with *H. rufa* (Figure 4b). During the dry season, *B. brizantha* reduced LAI by 3, 33 and 35 % for *D. robinioides*, *P. saman* and *D. retusa*, respectively compared to those in the transition season. LAI of *D. robinioides* and *P. saman* were also reduced during the dry seasons when associated with *H. rufa* by 11 and 24%, respectively (Figure 4b).

6.3.5. Canopy light extinction coefficient (*k*)

Values of k were not affected by grass species. Values of k for *D. retusa* and *D. robinioides* were similar (0.24±0.04 vs 0.25±0.07, respectively); contrasting with *P. saman* for which PARt was reduced to a higher extent (0.31±0.05).

6.3.6. Water use

6.3.6.1. Calibration of sap flow gauges

A strong correlation was found between the relative temperature differences from the paired needles of sap flow sensors and gravimetric transpiration of trees in pots (Figure 6). This demonstrated that it is possible to estimate sap flow velocity of trees sampled in field based on temperature differential of sap flow gauges (Figure 6; Table 3). It was also found that just one model could be used to estimate sap flow velocity as the slopes of regression equation for the three species were similar ($0.20<P<0.61$ for comparison of pairs of equations; Table 4). The intercept of the regression line of *P. saman* was also similar to that of *D. retusa* and *D. robinioides* ($P=0.20$ and $P=0.38$, respectively, Table 4). In contrast, a statistical difference between intercepts for *D. retusa* and *D. robinioides* was found ($P=0.03$, Table 4). Estimations of sap flow velocity derived from the present equation were more similar to that from Grainer's (1985, 1987) equation (Figure 7) than that from Roupsard et al. (2006) due to presence of lower residuals. On the other hand, the model developed by Roupsard et al. (2006), using the same sensors seemed to overestimate the sap flow velocity by up to three to four times.

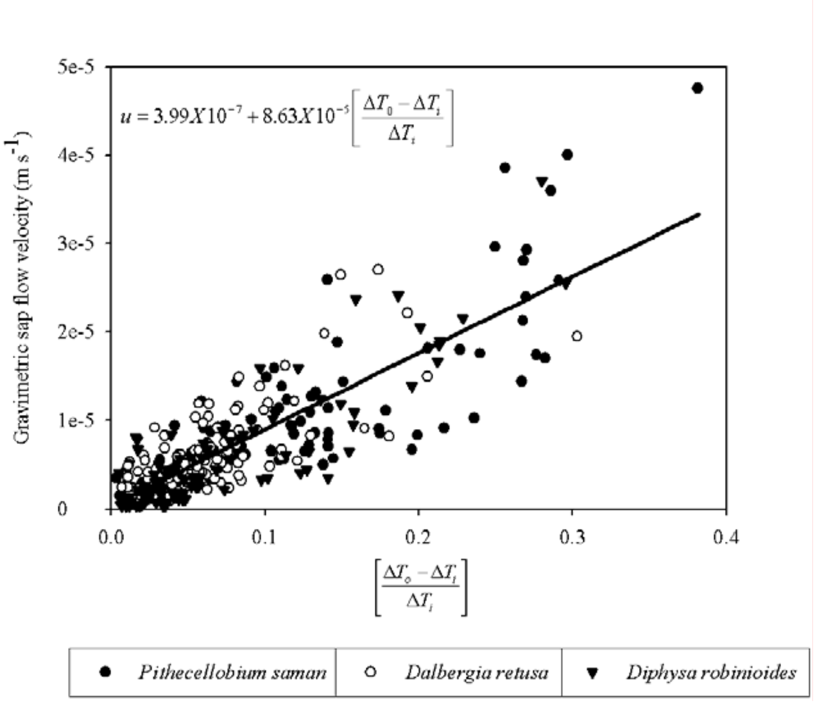

Figure 6. Calibration of Granier`s sap flow gauges using gravimetric method for three native timber tree species in greenhouse conditions. u: sap flow velocity (m s^{-1}) ; $\left[\frac{\Delta T_o - \Delta T_i}{\Delta T_i}\right]$ is the relative differential temperature between paired gauges (dimensionless).

Table 3. Comparison of four tested models for estimating sap flow velocity of three native timber species growing in silvopastoral systems in the dry tropics of Costa Rica.

Model	**RMSE**	**R^2**	**PRESS**
$u = 3.99X10^{-7} + 8.63X10^{-5}\left[\frac{\Delta T_0 - \Delta T_i}{\Delta T_i}\right]$	3.99 X 10^{-6}	0.70	5.0 X 10^{-9}
$u = 2.34X10^{-5} + 1.28X10^{-5}\ Log\left[\frac{\Delta T_0 - \Delta T_i}{\Delta T_i}\right]$	5.23 X 10^{-6}	0.48	8.6 X 10^{-9}
$u = 2.20X10^{-6} * 10^{4.37\left[\frac{\Delta T_0 - \Delta T_i}{\Delta T_i}\right]}$	0.28	0.55	24.4
$u = 4.94X10^{-5}\left[\frac{\Delta T_0 - \Delta T_i}{\Delta T_i}\right]^{0.801}$	0.271	0.57	23.2

u: Sap flow velocity (m s^{-1}); ΔTo and ΔTi: maximum (no flow) and current temperature differences between two gauges; RMSE: Root of mean square error; PRESS: Sum of predicted residual squares.

Table 4. Comparison of models to estimate sap flow velocity of three native timber species growing in silvopastoral systems in the dry tropics of Costa Rica.

Variable		**Parameter estimated**	**Standard error**	**P value**
Intercept	*P. saman* vs *D. retusa*	1.2×10^{-6}	9.1×10^{-7}	0.20
	P. saman vs *D. robinioides*	-7.8×10^{-7}	8.9×10^{-7}	0.38
	D. retusa vs *D. robinioides*	2.0×10^{-6}	9.1×10^{-7}	0.03
Slope	*P. saman* vs *D. retusa*	-9.7×10^{-6}	9.4×10^{-6}	0.30
	P. saman vs *D. robinioides*	4.0×10^{-6}	7.9×10^{-6}	0.61
	D. retusa vs *D. robinioides*	1.4×10^{-5}	7.9×10^{-5}	0.20

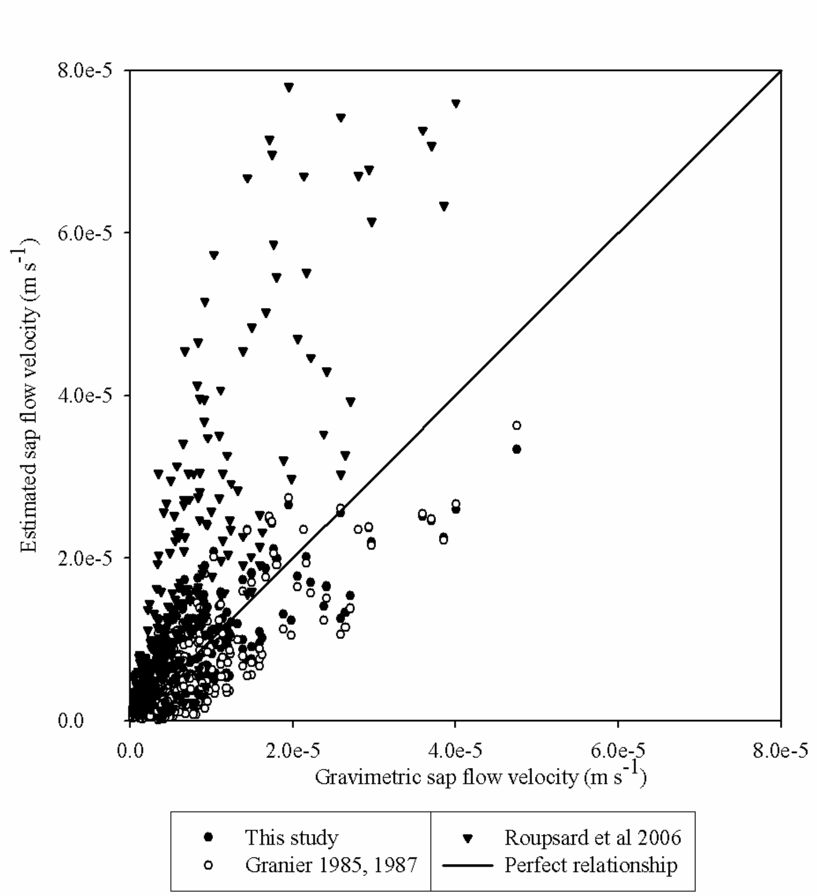

Figure 7. Relationship between estimated and measured (gravimetrically) sap flow velocity with the equation developed (this study) and Granier (1985) and Roupsard et al. (2005) models.

6.3.6.2. Tree water use

6.3.6.2.1. Diurnal trends in sap flow velocity

On average, tree sap flow velocity was considerably higher in the rainy season than in the transition and dry seasons; by 40 and 44%, respectively. Transpiration occurred between 6 and 18 h during all three seasons; typical diurnal distributions of sap flow velocity in wet and transition seasons with a peak in sap flow velocity close to midday (Figure 8). During the dry seasons, a less pronounced peak at midday was observed, especially for *D. retusa* in *H. rufa* where the sap flow velocity was apparently reduced at this time. The differences in tree sap flow velocities were higher in the dry season than in wet and transition seasons (Figure 8). As expected, VPD (vapour pressure deficit) was the lowest during the rainy season; however, this climatic factor had a higher influence on tree sap flow velocity during transition and dry seasons (Figure 8). *D. retusa* was the tree species most affected by water deficit in the dry season; its sap flow velocity was reduced by 65% compared to the value during the rainy season. Small decreases were also observed for *D. robinioides* and especially for *P. saman* (by 12% and 2%, respectively).

6.3.6.2.2. Integrated tree water use

No significant effect of grass species was found ($P>0.05$) in mean sap flow velocity (Table 5). Irrespective of the grass species, *P. saman* had a significantly higher sap velocity than *D. retusa* and *D. robinioides* ($P<0.01$; 4.2±0.3 vs 2.8±0.2 vs 2.5±0.2 cm h^{-1}; Table 5); no significant difference was found between the last two species ($P>0.05$). Despite the lack of significant effect of grass species on sap flow velocity, *P. saman* used more water by unit area of conductive sapwood when associated with *B. brizantha* than with *H. rufa*.

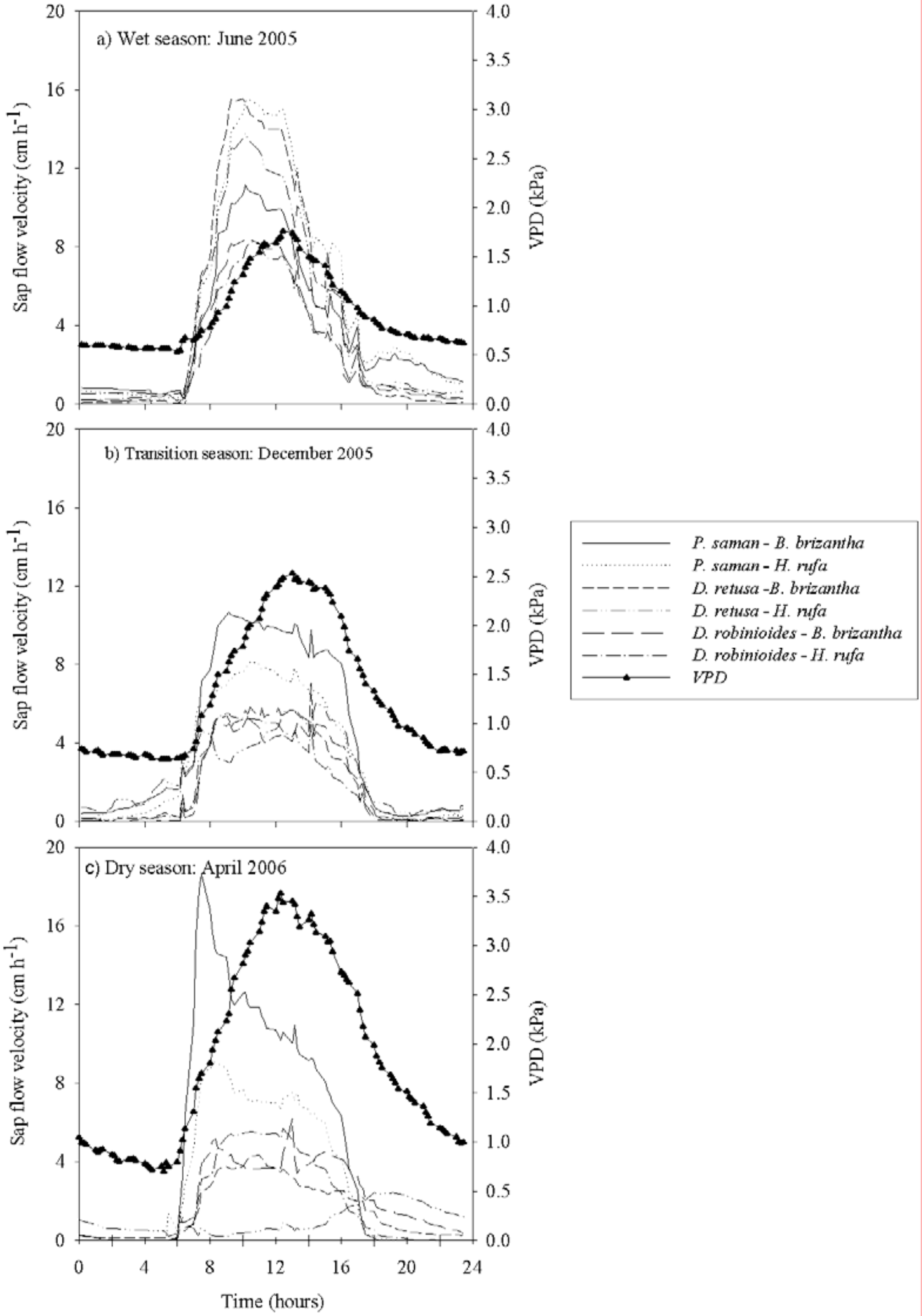

Figure 8. Variation of sap flow velocity of trees and vapour pressure deficit (VPD) during the day in six silvopastoral associations in three contrasting seasons in the dry tropics of Costa Rica

Table 5. Integrated (in an annual basis) sap flow velocity and water use of native timber tree species in silvopastoral systems in the dry tropics of Costa Rica.

Tree species	**Grass species**	**Sap flow velocity ($cm\ h^{-1}$)**		**Water use**			
				ml h^{-1} $tree^{-1}$		**mm day^{-1}**	
		Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
P. saman	*B. brizantha*	4.6	0.50	45.3	10.0	0.05	0.01
	H. rufa	3.9	0.36	128.3	32.2	0.10	0.01
D. retusa	*B. brizantha*	2.8	0.28	42.6	4.8	0.10	0.01
	H. rufa	2.8	0.28	44.6	3.8	0.03	0.00
D. robinioides	*B. brizantha*	2.7	0.27	96.7	18.3	0.20	0.02
	H. rufa	2.2	0.21	53.8	8.2	0.20	0.02

When scaled up to water use per tree per hour or per day, an interaction was found between tree x grass in individual water use. Grass species did not affect the water use by *D. retusa* individuals ($P>0.05$). On the other hand, trees of *P. saman* presented a higher transpiration associated with *H. rufa* than with *B. brizantha* (128.3±32.2 vs 45.3±10.0 ml h^{-1} $tree^{-1}$; Table 5), contrasting with the opposite result for *D. robinioides* (53.8±8.2 vs 96.7±18.3 vs ml h^{-1} $tree^{-1}$; Table 5).

A tree x grass interaction was also found for water use at stand level. *P. saman* used more water with *H. rufa* than with *B. brizantha* ($P<0.01$; 0.10±0.01 vs 0.05±0.01 mm day^{-1}; Table 5). Water use at stand level for *D. retusa* was significantly higher with *B. brizantha* than with *H. rufa* ($P<0.05$; 0.10±0.01 vs 0.03±0.001 mm day^{-1}; Table 5). Grasses did not affect stand water use of *D. robinioides* ($P>0.05$).

6.3.6.2.3. Effect of season on sap flow

- **Wet season**

The sap flow velocity and individual transpiration of all three tree species in the rainy season were not statistically affected by grass species ($P>0.05$; Figure 8). The water use at stand level for *P. saman* and *D. retusa* were affected by associated grass species ($P<0.05$). Stands of *P. saman* used more water associated with *H. rufa* than that with *B. brizantha* (0.07±0.01 vs 0.03±0.00 mm day^{-1}); contrasting to the higher transpiration of *D. retusa* associated with *B. brizantha* (0.03±0.00 vs 0.11±0.01 vs mm day^{-1}).

- **Transition season**

As in the wet season, individual tree transpiration in the transition season was not significantly affected by any of the grasses (P>0.05); still, sap flow velocity of *D. retusa* was higher with *B. brizantha* than with *H. rufa* (4.24±0.61 vs 3.78±0.26 cm h^{-1}; Figure 8). The transpiration at stand level had an opposite pattern compared with the wet season. *P. saman* transpired more with *H. rufa* than associated with *B. brizantha* (0.15±0.01 vs 0.06±0 mm day^{-1}; Figure 9); whereas *D. retusa* used more water with *B. brizantha* (0.14±0.01 vs 0.08±0 mm day^{-1}; Figure 9).

- **Dry season**

Neither sap flow velocity of *D. retusa* nor that of *D. robinioides* were affected by grass species (P>0.05) during the dry season. *P. saman* had a higher sap flow velocity with *B. brizantha* than with *H. rufa* (P<0.05; 5.0±0.6 vs 3.1±0.2 cm h^{-1}; Figure 8). Individual tree water use was not affected by grass species in this season (P>0.05). However, the stand water use of *P. saman* and *D. retusa* were significantly affected by grass species. Stand water use of *P. saman* was higher in *H. rufa* association than in *B. brizantha*, contrasting with the opposite result in *D. retusa* (P<0.05; 0.13±0.01 vs 0.07±0.01 and 0.02±0.01 vs 0.08±0.01 mm day^{-1}, respectively; Figure 9).

6.3.6.2.4. Stand water use

D. robinioides had the highest stand water use, irrespective of grass treatment, for all seasons (Figure 9). A tree x grass interaction was observed for *P. saman* and *D. robinioides*. *B. brizantha* increased the stand water use of *D. retusa* and decreased the stand water use of *P. saman* (Figure 9). The integrated water use of the *D. robinioides* was low, around 5% of reference evapotranspiration in the study zone (0.20 vs 4.3

mm day^{-1}, for transpiration and ETo, respectively) with a canopy cover of around 30%.

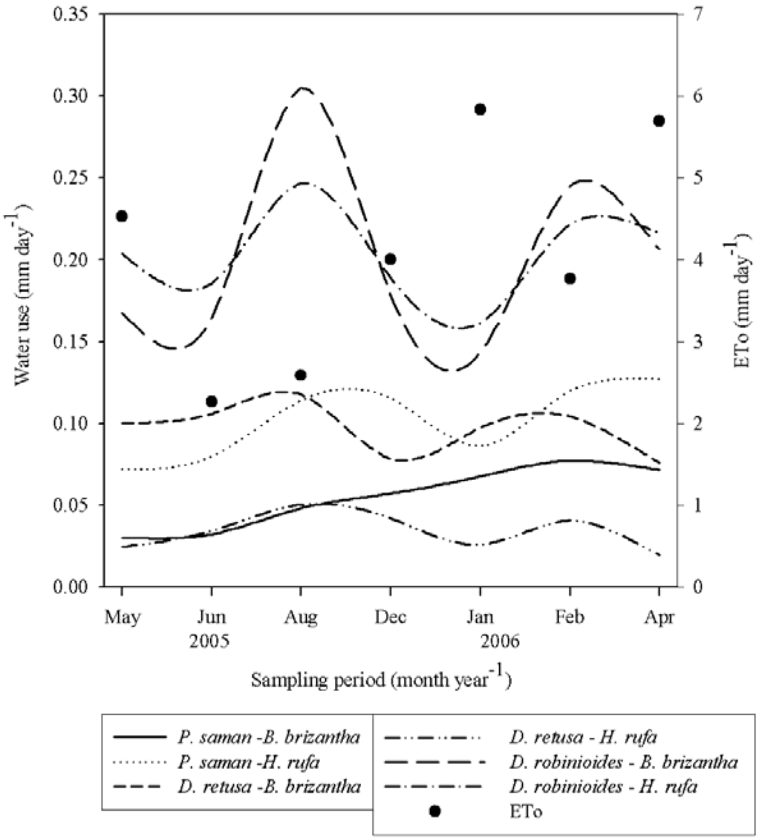

Figure 9. Summary of dynamics of water use at stand level of native timber tree species growing in silvopastoral associations in the dry tropics of Costa Rica

6.3.6.2.5. Water use per leaf area

The water use by leaf area unit was markedly different in the three tree species ($P<0.01$); it was higher for *P. saman* than for the other two timber tree species ($P<0.01$; Figure 10). Water use by unit leaf area for *D. robinioides* was significantly higher than that of *D. retusa*. Grass species did not affect the water use by unit of leaf area of *D. robinioides* and *D. retusa* ($P>0.05$; Figure 10). Although the effects were not statistically different, the mean water use of *P. saman* in *B. brizantha* was slightly higher than in *H. rufa*; whereas, *B. brizantha* caused a higher water use in *D. robinioides* in comparison than that in *H. rufa*. In contrast, *D. retusa* used the same water by unit of leaf area with both grass species.

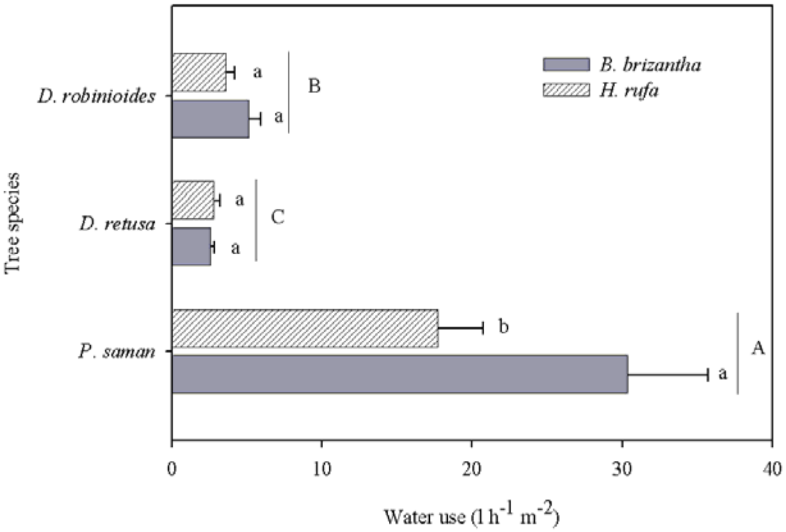

Figure 10. Integrated tree water use by leaf area in silvopastoral systems in the dry tropics of Costa Rica. Different lowercase letters indicate statistical differences between grass species for the same tree species ($P<0.05$). Different uppercase letters indicate significant differences between tree species ($P<0.05$).

6.3.6.3. Relationship between water use and climatic conditions

The climatic conditions recorded every 15 minutes during the day (vapour pressure deficit – VPD- and reference evapotranspiration -ETo), usually regarded as the principal drivers of plant transpiration, had a moderate influence on transpiration at the individual tree level and whole stand level ($0.28<R<0.67$; Table 6). Transpiration was better explained by ETo than by VPD (Table 6). Water use of *P. saman* was more dependent upon climatic conditions than *D. retusa* and *D. robinioides*. However, grass species did not have any influence on the relationships between tree transpiration and VPD or ETo. The relationships between tree transpiration and climatic conditions were similar for all seasons.

Table 6. Relationship between water use of native timber tree species and climatic conditions in silvopastoral systems in the dry tropics of Costa Rica.

Interacting species		**Water use**	**Climatic variable**	
Tree	**Grass**		**VPD (kPa)**	**ETo (mm day^{-1})**
P. saman	*B. brizantha*	Fs	0.42	0.54
		Fsa	0.48	0.59
		Wu	0.54	0.67
	H. rufa	Fs	0.30	0.40
		Fsa	0.47	0.54
		Wu	0.54	0.67
D. retusa	*B. brizantha*	Fs	0.43	0.53
		Fsa	0.52	0.55
		Wu	0.49	0.59
	H. rufa	Fs	0.29	0.41
		Fsa	0.30	0.30
		Wu	0.29	0.41
D. robinioides	*B. brizantha*	Fs	0.32	0.43
		Fsa	0.46	0.48
		Wu	0.40	0.55
	H. rufa	Fs	0.40	0.55
		Fsa	0.45	0.54
		Wu	0.48	0.63

Pearson correlation coefficients. All Pearson coefficients were significant (P<0.01). Fs: sap flow by individual tree (ml h^{-1} $tree^{-1}$); Fsa: transpiration by unit leaf area (ml h^{-1} cm^{-2}); Wu: tree water use at stand level (mm day^{-1}).

6.3.6.4. Tree water use in pots in the greenhouse

In greenhouse conditions and high soil water availability, *D. retusa* had the significantly highest (P<0.01) transpiration by unit of leaf area, followed by *D. robinioides*, which was statistically higher than *P. saman* (p<0.01; 1.89±0.03 vs 0.57±0.01 vs 0.32±0.01, respectively; Figure 11). Changes in individual tree transpiration of *D. robinioides* and *P. saman* throughout the whole experiment were low; contrasting with *D. retusa* whose transpiration was highly variable during the trial (Figure 11).

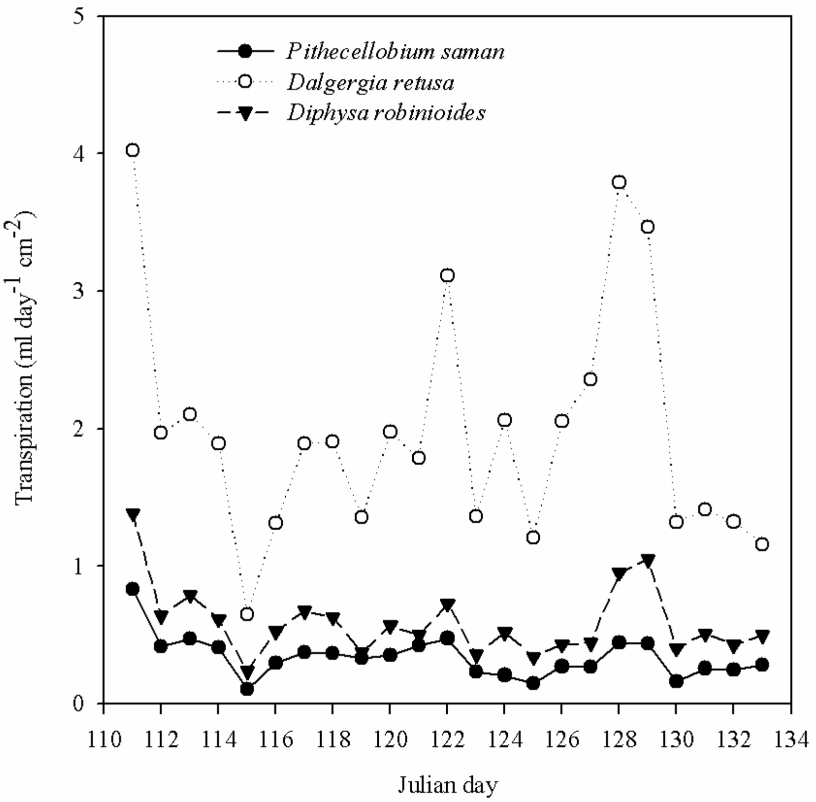

Figure 11. Mean daily tree transpiration per leaf area of three timber tree species growing in pots in a greenhouse.

A poor correlation was found between tree transpiration by unit of leaf area and VPD and soil moisture (0.26<R<0.46 and -0.29<R<-0.03, respectively; Figure 12). However, transpiration was positively affected by VPD with the higher influence in *P. saman* than in the other two tree species.

6.3.6.5. Water use of trees and grasses by the simplified water balance approach

The evapotranspiration of *H. rufa* and *B. brizantha* growing without trees was statistically similar over all of the seasons (P>0.05). However, slightly higher grass evapotranspiration was observed in *H. rufa* compared to *B. brizantha* (2.0±0.49 vs 2.9±0.61 and 0.3±0.03 vs 0.43±0.03 mm day^{-1} in periods with low and high ETo, respectively; Figure 13). An inverse correlation between water use and ETo for both grasses was found.

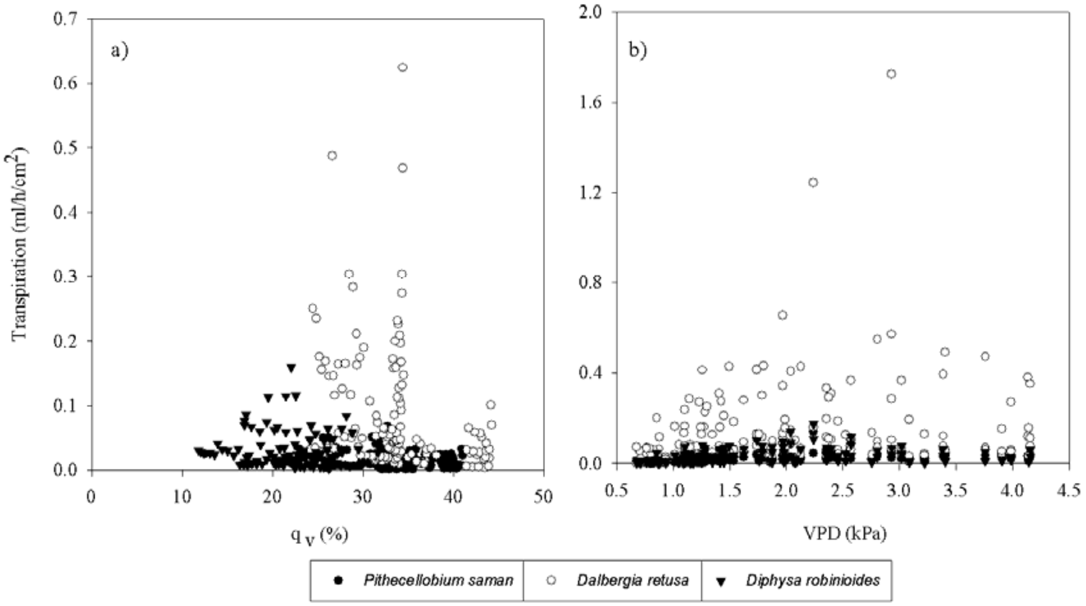

Figure 12. Relationship between tree transpiration per leaf area and a) soil volumetric moisture and b) vapour pressure deficit (VPD) in three timber species growing in pots in greenhouse conditions.

There were no significant differences in water use at individual tree level between tree species in periods with medium and high ETo (P>0.05); in contrast to a statistical difference in tree water use between *P. saman* and *D. robinioides*, which had the highest and the lowest values, respectively in the low ETo period (P<0.05; Figure

14a). Tree transpiration by unit of leaf area exhibited the same behaviour (Figure 14b).

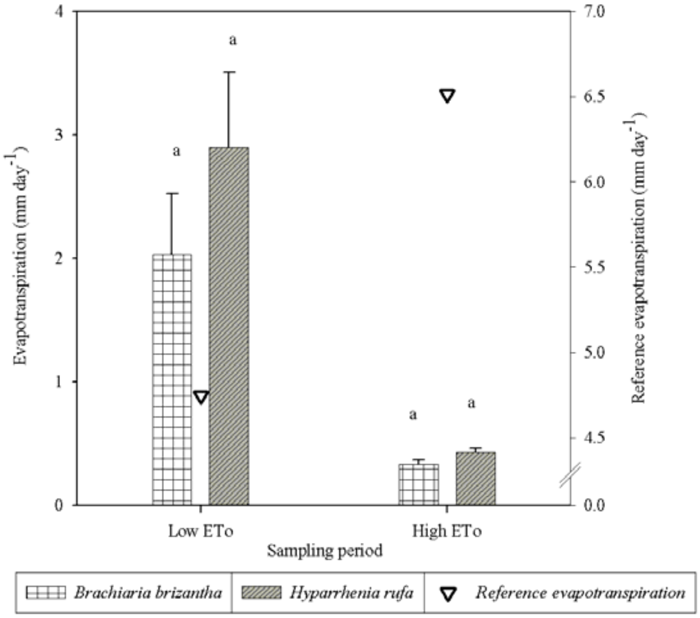

Figure 13. Mean daily evapotranspiration by grass species in no-tree control in the dry tropics of Costa Rica in the soil depth 0-60 cm. Similar letters in the same period mean no significant differences between grass species ($P<0.05$) according to “t” test.

Grass and trees species and grass-free control treatments did not statistically affect the water use of the whole systems ($P>0.05$). However, a trend could be observed with increasing total water use in absence of grass around trees (1.1±0.2 vs 1.2±0.2 vs 1.4±0.2 mm day^{-1} for *B. brizantha*, *H. rufa* and grass-free plots, respectively; Figure 15). In spite of the fact that there were no statistical differences among tree species, *P. saman* tended to use more water than *D. retusa* and *D. robinioides* (1.5±0.2 vs 1.2±0.2 vs 1.0±0.2 for *P. saman*, *D. retusa* and *D. robinioides*, respectively; Figure 15).

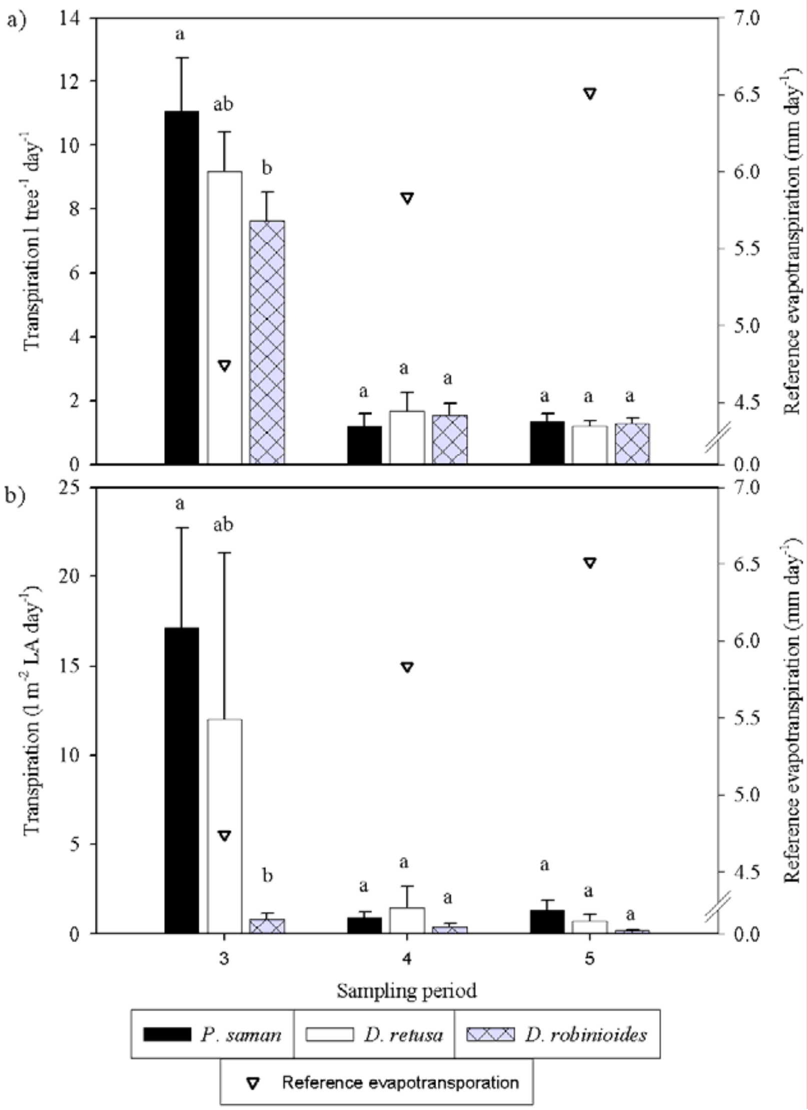

Figure 14. Mean daily transpiration of tree species in grass-free treatments in the dry tropics of Costa Rica in the soil depth 0-60 cm. a) At individual level, b) Transpiration per leaf area. Similar letters in the same period indicate no significant differences between grass species (P<0.05).

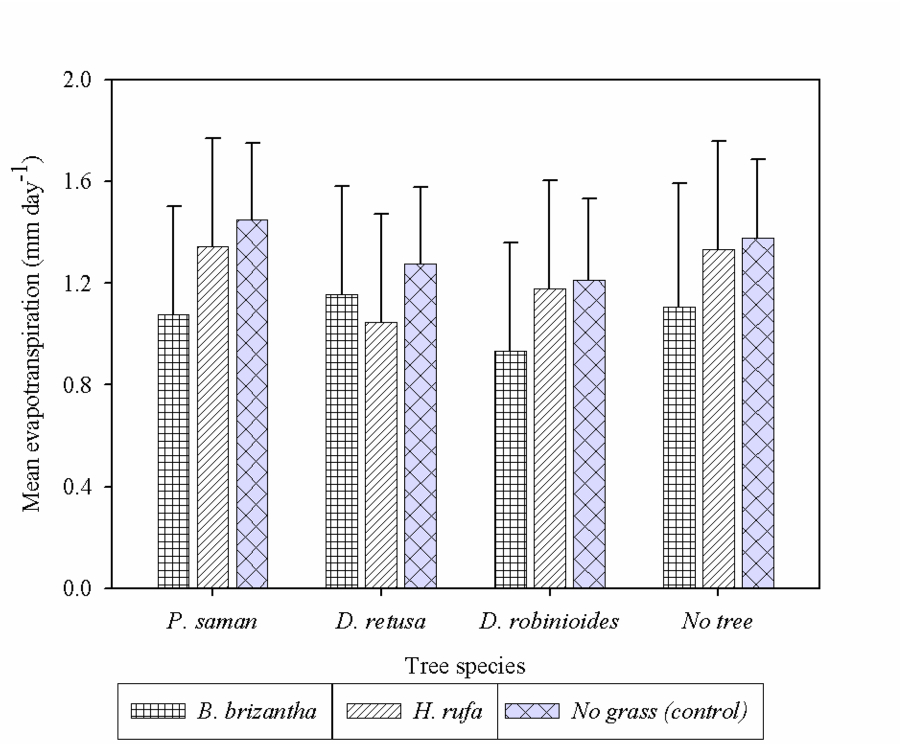

Figure 15. Mean daily evapotranspiration in six silvopastoral association in the dry tropics of Costa Rica in the soil depth 0-60 cm. Error bars correspond to standard error.

6.3.7. Water use efficiency

Grass species growing without trees had higher water use efficiency than tree species associated with grasses (on average, 2.5 vs 2.3 g DM kg^{-1} H_2O, respectively; Table 7). However, the water use by grass species was considered as evapotranspiration; in contrast, for tree species it was considered as transpiration. As for transpiration at stand level, a tree-grass interaction was found. *D. retusa* had higher water use efficiency associated with *H. rufa*; whereas *P. saman* water use efficiency was higher with *B. brizantha* (Table 7). *D. robinioides* was not affected by grass species (Table 7). The water use efficiency of *B. brizantha* was around three times higher than that of *H. rufa* (Table 7).

Table 7. Water use efficiency of trees growing in silvopastoral systems and water use efficiency of grasses growing in no-tree plots.

	Tree water use efficiency (g DM kg^{-1} H_2O)[1]		
	Grass species		Mean
Tree species	***B. brizantha***	***H. rufa***	
P. saman	2.6	1.7	2.2
D. retusa	2.3	4.8	3.6
D. robinioides	1.1	1.1	1.1

	Grass water use efficiency[2]
	No-tree plots
B. brizantha	3.7
H. rufa	1.2

[1]: Based on tree transpiration; [2]: based on grass evapotranpiration.

6.3.8. Leaf water potential

6.3.8.1. Grass leaf water potential

Statistical differences were found for leaf water potential (LWP) of grasses between seasons ($P<0.01$). LWP of grasses was significantly lower in the dry season compared to transition and rainy seasons ($P<0.01$); but no differences between the last two seasons were found. LWP of *H. rufa* was always lower than that of *B. brizantha* (-2.6±0.09 vs -2.1±0.08 MPa, respectively; $P<0.01$; Figure 16). However, tree species did not affect the LWP of either grass species (Figure 16).

No correlation was found between LWP and soil moisture ($0.11<R<0.14$; $0.37<P<0.50$). In contrast, air water potential had a strong relationship with LWP ($0.53<R<0.59$; $P<0.01$; Figure 17). The effect of soil and environment on LWP of grasses was similar for both grass species.

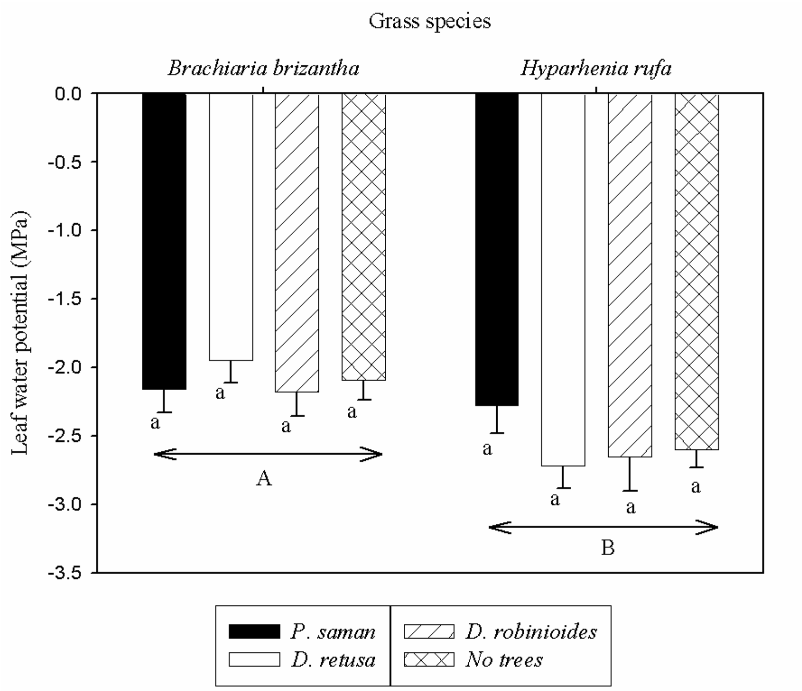

Figure 16. Mean leaf water potential during all three seasons of *B. brizantha* and *H. rufa* growing in silvopastoral systems and without trees in the dry tropics of Costa Rica. Different lowercase letters indicate statistical differences among tree species ($P<0.05$). Different uppercase letters indicate statistical differences between grass species ($P<0.01$).

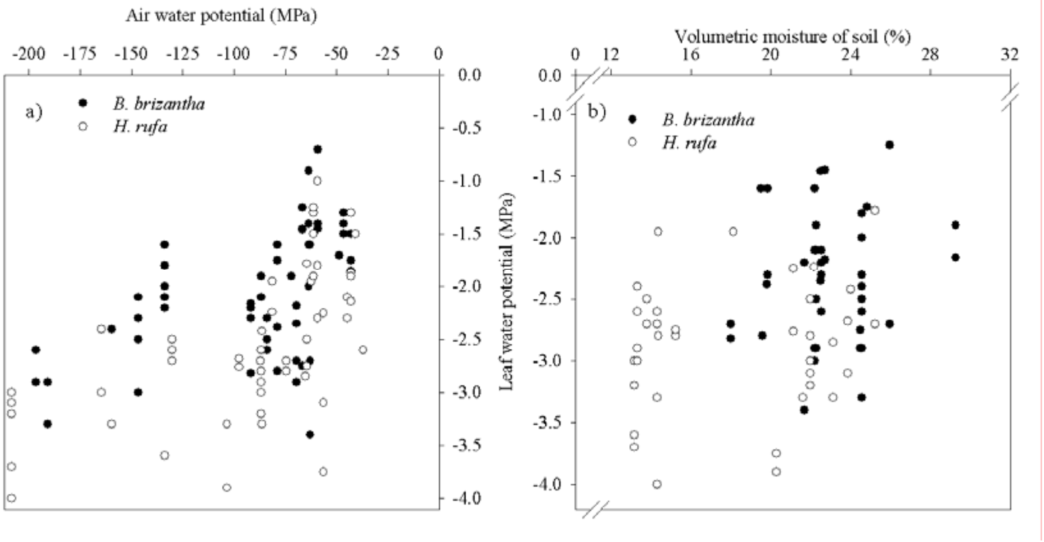

Figure 17. Relationships between leaf water potential of grasses and a) air water potential and b) soil moisture in silvopastoral systems with native timber tree species in the dry tropics of Costa Rica.

6.3.8.2. Tree leaf water potential

LWP of tree species was not affected by grass species (P>0.05), whereas there was an effect of seasons on LWP. During the rainy season, *P. saman* had a significantly lower LWP than *D. retusa* and *D. robinioides* (P<0.05; -2.7±0.2 vs -1.9±0.2 vs -1.5±0.2 MPa, respectively; Figure 18). When water was becoming less available, the LWPs were more similar between tree species. In the transition season, LWP of *D. robinioides* tended to increase (lower tension) becoming significantly higher than that of *P. saman* and *D. retusa* (-1.3±0.1 vs -2.9±0.2 vs -2.6±0.2 MPa, respectively; Figure 18).

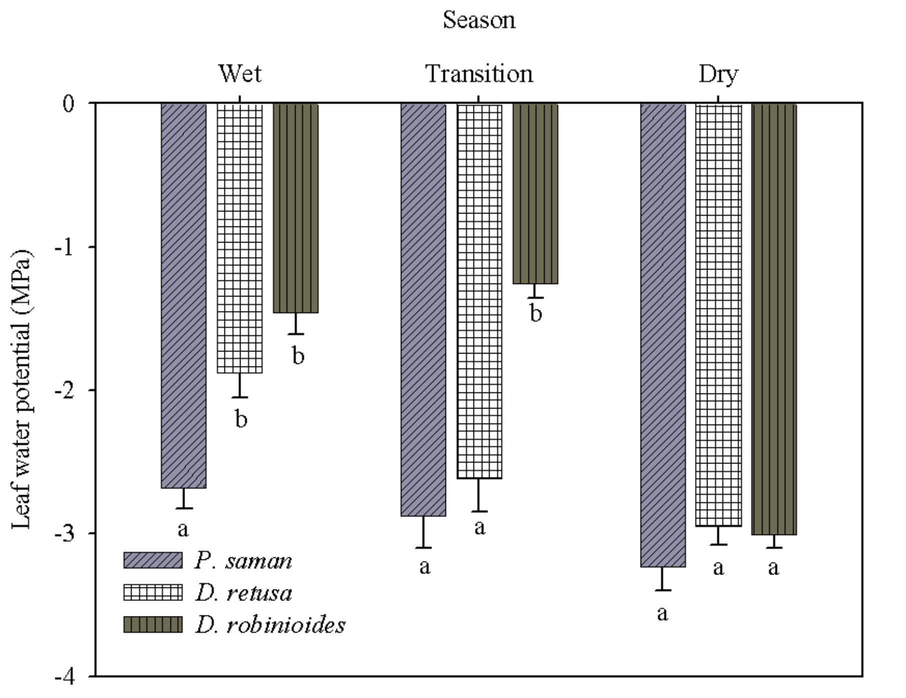

Figure 18. Mean leaf water potential of tree species in three contrasting seasons growing in silvopastoral systems in the dry tropics of Costa Rica. Error bars indicate standard error.

On average, *P. saman* had the most negative LWP compared with *D. retusa* and *D. robinioides* (-3.0±0.10 vs -2.6±0.12 vs -2.1±0.13 MPa, respectively). *P. saman* tended to have the lowest LWP, mainly in the season with high water availability

(Figure 18); whereas, *D. robinioides* presented the highest LWP overall ($P<0.05$; Figure 18).

Neither grass nor tree species statistically affected LWP of trees ($P>0.05$; $P>0.05$, respectively) in the dry season. Similarly, no interaction was found in the tree-grass associations ($P>0.05$) and the grass-free control did not affect tree LWP ($P>0.05$). As for grass species, no correlation was found between tree LWP and soil moisture or air water potential ($-0.2<R<0.46$ and $-0.24<R<-0.24$, respectively; Figure 19). Neither leaf nor air water potential could explain tree transpiration as demonstrated by the poor correlations between these variables ($-0.36<R<0.28$ and $-0.16<R<0.35$, for leaf and air respectively; Figure 20).

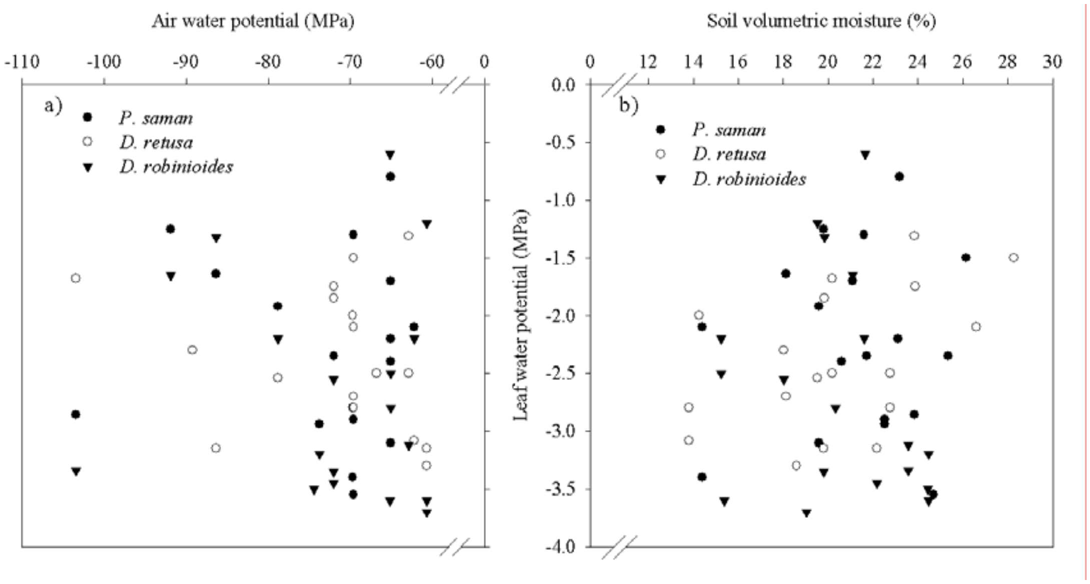

Figure 19. Relationships between water leaf potential of trees and a) air water potential and b) soil moisture in silvopastoral systems with contrasting grass species in the dry tropics of Costa Rica.

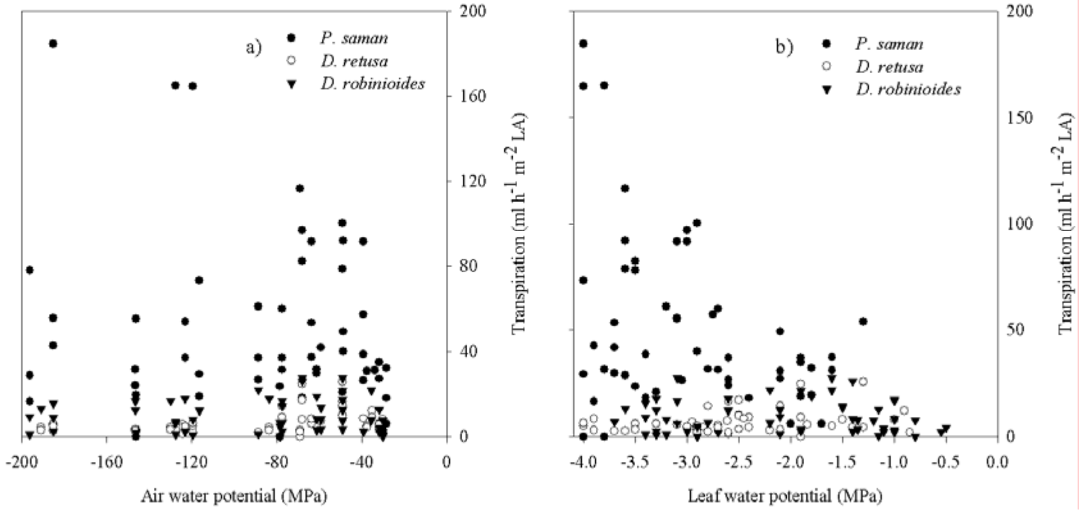

Figure 20. Relationship between tree transpiration per leaf area and a) air water potential and b) leaf water potential growing in silvopastoral systems with contrasting grass species in the dry tropics of Costa Rica

6.4. DISCUSSION

6.4.1. Tree canopy cover

The maximum tree canopy cover was found in the transition season because this is the end of a long period of leaf production (wet season). These tree species reduced their crown area by losing leaves between January to April (Durr 2001, Jiménez et al. 2002) as a strategy to save water in drought conditions. The higher tree cover in the transition season of *D. retusa* may indicate its rapid canopy expansion with increasing soil water availability and higher photosynthetically active radiation. *P. saman* always had the lowest canopy cover allowing more non-shaded areas for grass growth. *H. rufa* had no effect on tree canopy cover, contrasting with the significant effect of *B. brizantha* on tree cover of *D. retusa* and *D. robinioides*.

6.4.2. Transmission of PAR

Transmission of radiation through the tree canopy to grass species is a key characteristic for designing silvopastoral systems. *P. saman* allowed the highest PARt to grasses compared to *D. retusa* and *D. robinioides* (68.0, 47.9 and 46.6%, respectively). Kotzen (2003) found a mean transmitted radiation of 45% in six native tree species (*Acacia gerrardii, A. raddiana, A. tortilis, Pistacia atlantica, Tamarix aphylla* and *Ziziphus spina-christi*) in the desert of Negev (Israel). An important tree characteristic in terms of radiation interactions is the light extinction coefficient (*k*), which determines the PARt by a given LAI. *P. saman* presented the highest k value followed by *D. robinioides* and *D. retusa* (0.31, 0.25 and 0.24, respectively). High values of *k* are caused by the horizontal leaves or more regular arrangement in space (Wang and Miller 1987, Jones 1992). *P. saman* and *D. retusa* have similar proportion of gaps in their crowns; however, the former tree species has the bigger, thicker and more horizontal leaves. This implies that at the same leaf area, *P. saman* intercept more radiation than the other two tree species.

The differences in tree crown projected area and PARt between tree species did not affect the grass dry matter production (Andrade et al. 2007a; Chapter IV). Other studies in silvopastoral systems have found that, until light attenuation reached 30-40%, it did not commonly affect grass production under tree canopies. Bergez et al. (1997) found that interception up to 30% of radiation by *Acer pseudoplatanus*, *Larix x eurolepis* and *Fraxinus excelsior* did not significantly affect the annual carrying capacity of a ryegrass (*Lolium perenne*) pasture in UK. Diaz (2003) found that tree cover between 12 and 40% did not significantly affect the dry matter production of natural grassland in the arid Chaco.

6.4.3. Sap flow calibration

This experiment demonstrated that the calibration of sap flow gauges on potted plants is an important procedure for obtaining accurate estimates of transpiration in the field (Smith and Allen 1996, Lundblad et al. 2001, Wilson et al. 2001, Fernández et al. 2006, Roupsard et al. 2006); however, this is generally a difficult task (Lu et al. 2004). The Granier system is rather empirical, as it does not measure sap flow as such. Our calibration results were consistent for our three species; however, they did not match some other published values (Roupsard et al. 2006). But, our estimates are close to those using Granier's equation (Granier 1985, 1987) for gauges built with other materials (Roupsard personal communication).

6.4.4. Influence of climate conditions on tree transpiration

Tree transpiration was higher, as expected, in well-watered conditions. Similar results were presented by Van Kanten and Vaast (2006) who found a higher transpiration in the rainy season than in dry season for coffee (*Coffea arabica* L.) and associated trees (*Eucalyptus deglupta*, *Terminalia ivorensis* and *Erythrina poeppigiana*) in a tropical humid zone of Costa Rica (3500 mm year^{-1}). Tognetti et al. (1998) found a strong effect of severe drought in whole-plant transpiration of *Quercus ilex* in the Mediterranean. During the rainy season, tree transpiration followed the curve of VPD. In contrast, during the dry season, the climatic conditions (VPD and ETo) did not explain tree transpiration to a large extent. Soil water deficit did not affect sap flow of *P. saman* and *D. robinioides*; in contrast to a strong reduction in *D. retusa.* This implies that *D. retusa* may rapidly decrease its stomatal conductance and canopy resistance to save water (Margolis and Ryan 1997). The stomata aperture seems to be regulated by climatic conditions in well-watered conditions; contrasting with dry season where soil moisture may be the key factor in the control of stomatal conductance and transpiration (Sadras and Milroy 1996, Gao et al. 2002, Coll et al. 2004, Otieno et al. 2005, Sinclair et al. 2005, Romero and Botía 2006).

6.4.5. Tree transpiration per leaf area

P. saman displayed the highest water use by unit leaf area compared to *D. robinioides* and *D. retusa*. Large differences in transpiration per unit leaf area can be expected in tropical tree species such as *Dalbergia retusa, Pachira quinata, Platymiscium pinnatum, Swietenia macrophylla* and *Tectona grandis* (Cernusak et al. 2006); which might be caused by their canopy structure and leaf area and shape (Domingo et al. 1996, Cajas et al. 1999). Species with open canopies allow more airflow inside the canopies, increasing the water use. This contrasts with closed canopies which create a barrier to airflow, which is a strategy to decrease water loss. Romero and Botía (2006) found differences in water status, which was related to transpiration, in *Prunus dulcis* between seasons in a semiarid region. Transpiration per unit of leaf area was not affected by grass species. Although slow growing, *P. saman* can eventually reach a large size, and these results indicate that it could be competitive for water in such circumstances. The canopy aperture and leaf properties seem to be the responsible for this characteristic.

6.4.6. Tree-grass water interactions

Grass species did not affect the sap flow velocity of *D. retusa* and *D. robinioides* in any of the seasons, showing that both grass species (*Brachiaria brizantha* and *Hyparhenia rufa*) had similar water competitiveness. Gyenge et al. (2002) found that pines and grasses probably did not compete for soil water during the dry period, due to the grasses using surface soil layers while pines explored deeper layers. It can be explained by a similar grass fine root proportion with *B. brizantha* and *H. rufa* (56 and 50%, respectively; Andrade et al. 2007b). In contrast, *P. saman* used more water in *B. brizantha* than in *H. rufa* implying a higher competition for water by the last species, which is commonly used in this zone. Coll et al. (2004) also found a reduced growth in beech (*Fagus silvatica*) seedlings due to grass competition, which reduced the soil water availability. This was perhaps unexpected, in that *B. brizantha* is the more productive of the two grass species and thus might be expected to be more competitive for water and *P. saman* produced more fine roots when associated with *B. brizantha* (Andrade et al. 2007b). Gyenge et al. (2002) found a higher evapotranspiration in silvopastoral systems of *Pinus ponderosa* with *Stipa speciosa* and *Festuca pallescens* than in grass growing in open areas (706 vs 647 mm year^{-1}) in the Argentinian Patagonia.

On an annual basis, grass species affected the water use of tree species in different ways. Grasses did not affect the water use of *D. robinioides*, which is the biggest tree species. *P. saman* used more water when it was growing with *B. brizantha*. This tree x grass interaction in water use could not be explained by tree or total (tree plus grass) fine root length density because grass did not affect these variables (Andrade et al. 2007b). Changes in LAI seem to be the responsible for the interaction in water use between tree and grass species. The higher transpiration of *P. saman* has potentially great importance in the management of water interactions in these systems because silvopastoral systems with this species would consume much more water than with the other tree species at similar tree density and size.

Despite lack of statistical differences in water use between grass species, *H. ru*fa had an unexpectedly slightly higher water use than *B. brizantha*, which also had a higher relative fine root density (Andrade et al. 2007b). Trees did not affect grass water use which disagrees with many other studies where trees modified soil moisture due to density, distribution, and microclimatic conditions. Dulormne et al. (2004) found that the evapotranspiration from the grass *Dichanthium aristatum* was always lower in silvopastoral systems than in grass, but only in a subhumid tropical region. Roberts et al. (2005) found that the cumulative difference between broadleaved beech woodland

and grassland in UK was small but evaporation from grassland was 3% higher than that from the woodland. This suggested that either tree component was relatively less competitive for water or that the grasses were less subject to conditions leading to high evapotranspiration such as lower radiation or cooler temperatures during the dry season. In water-deficit seasons, the trees in the silvopastoral systems contributed to the conservation of water in the upper layers, because of their litter deposition and protection against radiation (Marlats et al. 1999).

Grasses had considerably higher water use efficiency than tree species. This is in spite of water use of trees being considered as transpiration. The differences in water use efficiency between grass and tree species is mainly explained by their photosynthetical processes. This agrees with Black and Ong (2000) who argued that water use efficiency of tropical C_4 cereals were often more than double those for C_3 species in equivalent conditions.

6.4.7. Total evapotranspiration in silvopastoral systems

Tree transpiration at stand level was significantly different between tree species. *D. robinioides* used more water than *P. saman* and *D. retusa* (0.20, 0.07 and 0.06 mm day^{-1}, respectively). However, a tree x grass interaction was found for different grass species in the total water use at stand level in *P. saman* and *D. retusa*; which can be attributed to the same pattern in tree growth rather individual water transpiration (Andrade et al. 2007a). The water use efficiency showed a similar tree-grass interaction compared to that found for tree transpiration at stand level. However, the total transpiration of *D. robinioides* was quite low compared to the reference evapotranspiration (0.20 vs 4.1 mm day^{-1}), which could be attributed to the young tree age and low crown area. Evapotranspiration of grass species were similar (1.1 and 1.2 mm day^{-1}, for *B. brizantha* and *H. rufa*, respectively); however, the water use efficiency of *B. brizantha* was three times greater than that of *H. rufa*. This implies that the evapotranspiration from grass species is the most important component in the total water use of these silvopastoral systems.

Tree-grass water use is in approximate accord with the findings of Roupsard et al. (2006) who found that the evapotranspiration of a *Cocus nucifera* L. (coconut) stand with a LAI of around 3 and 75% of canopy cover in a tropical site (Vanuatu, South Pacific), was around 68% of the evapotranspiration of the grass understorey (1.8 and 2.6 mm day^{-1}, respectively). On the other hand, these results contrast highly with those from Yepez et al. (2003) who found that 15% of total evapotranspiration of the tree-grass natural ecosystems in Arizona (343 mm year^{-1}) can be attributed to understory transpiration and 70% for tree transpiration with a LAI of 1.6. The differences between both studies might be explained by the very low and very erratic distribution of rainfall in Arizona. This implies that the surface soil has a water deficit most of the year in contrast with possibly higher soil moisture at deeper layers, which can be taken by the deeper roots of tree vegetation.

6.4.8. Effects of tree leaf phenology on water and radiation interactions

The maximum LAI was found in the transition season (after rainy season) where there is potential high soil water availability produced by previous rains together with high incident PAR. The large variation in LAI between seasons suggested a high loss of leaf area in the dry season (Jiménez et al. 2002, Cordero and Boshier 2003). In their natural habitats, *D. robinioides* starts defoliating later than *P. saman* and *D. retusa* (Cordero and Boshier 2003). This small difference in leaf phenology may cause the interaction tree x grass and the differences between seasons. *D. retusa* increased its LAI in the same period in systems with *H. rufa*; whereas, this species reduced its LAI when associated with *B. brizantha* (Andrade et al. 2007a; Chapter IV). This suggested that *H. rufa* was not having a strong competitive effect on *D. retusa*. Do et al. (2005) found that the environmental conditions predicted 50% of canopy fullness (leaf flush or leaf fall peaks) of *Acacia tortilis* in the dry tropics of Senegal. On other hand, Fort et al. (1998) found leaf shedding (30% loss in leaf area) in *Betula pendula* under severe drought in a greenhouse.

The defoliation of all tree species in the late dry season resulted in changes in water and radiation interactions. Differences in PAR transmission between seasons are attributed to loss of leaves of these species; they have a deciduos nature in their natural habitat (January to April; Durr 2001, Jiménez et al. 2002). This reduction can be explained by Beer´s law, which considers a light coefficient extinction that depends on inclination of leaves and arrangement of tree canopy (Wang and Miller 1987, Jones 1992). Significant reduction of transpiration by leaf area is a sign of drought conditions, which promoted the defoliation. At the same time, the defoliation caused an obvious reduction in tree water use at individual and stand level.

6.4.9. Leaf water potential

The interacting species displayed differences in leaf water potential in well-watered seasons, implying differences in adaptation to drought between interacting species. *D. robinioides* and *D. retusa* were better adapted to dry conditions than *P. saman* as they decreased their leaf water potential when the soil is became drier. It seems that *P. saman* did not regulate its leaf water potential as it did not change in any of the seasons and its transpiration by unit leaf area was always the highest. Similar results were presented by Otieno et al. (2005) in leaf water potential of *Acacia tortilis* and *A. xanthophloea* that had the lowest leaf water potential in very low soil water content. Roy and Berger (1983) found a relatively good agreement between leaf water potential and transpiration of *Dactylis glomerata* at low or zero rates; whereas at high transpiration rates, the correlation was lower. *D. retusa* and *D. robinioides* seemed to have mechanisms for increase their leaf water potential when water is available looking for a potential increase in photosynthesis rate. This mechanism may be a reduction of stomatal conductance. Intrinsic control of stomatal aperture may be induced by soil water availability in these two species. Zhang and Cregg (2005) found an effect of climatic conditions on leaf water potential of *Pinus ponderosa.* Romero and Botía (2006) found a close relationship between leaf water potential and vapour pressure deficit in well watered conditions in *Prunus dulcis* in comparison to no relationship in severe drought. Garnier and Berger (1987) showed that leaf water potential and the air vapour pressure deficit explained 49% of the stomatal conductance variance in peach trees.

Grasses decreased their leaf water potential during dry periods. However, *H. rufa*, whose leaf water potential was lower than that of *B. brizantha*, seemed to be more adapted to arid and semiarid conditions using better water regulation or by using less water for transpiration. However, *B. brizantha* used less water to produce more dry matter. As found for water use of grasses, tree species did not affect the leaf water status of grasses. This contrasts with Gyenge et al. (2002) who found better water status in grasses (*Stipa speciosa* and *Festuca pallescens)* growing under high tree canopy cover compared to those in the open before and after the driest month.

6.4.10. Considerations for research on water and radiation interactions in agroforestry systems

Hemispherical photography with its respective calibration showed a high accuracy in characterizing tree canopy and estimation of transmission of photosynthetically active radiation (Bellow and Nair 2003). This method estimated leaf area index with higher accuracy than using the Sunscan PAR sensors. However, hemispherical photographs are not convenient for estimating crown dimensions such as Brown et al. (2000) found a using Hemiphot analysis, other software to analyse hemispherical photographs.

Sap flow monitoring showed higher accuracy than the method of simplified water balance for estimating tree transpiration. Nevertheless, research at leaf level, using a porometer or infrared gas analyzer, should be implemented to complement of whole-plant studies such as sap flow monitoring. Grass water use, which was the most important component of evapotranspiration at system level, needs to be evaluated with higher accuracy. Efforts should be made to formulate approaches for estimating water use in a more efficient way. Leaf water potential proved to be a good tool for evaluating the water status in tree and grass species.

6.5. CONCLUSIONS AND IMPLICATIONS

Transmission of radiation through the tree canopy, a key characteristic for designing silvopastoral systems, depends on a set of tree variables which includes the light coefficient extinction factor and the leaf area index. The leaf area index is given by the structure and gaps within tree crowns in the system. In this study, the differences in transmission were better correlated to tree density and crown area rather the light extinction coefficient. *P. saman* presented an open canopy; however, their leaves intercept more light than that of *D. retusa* and *D. robinioides*. In terms of tree canopy area and light occlusion, *D. robinioides* allowed the transfer of less radiation to the understorey grasses. These results imply that lower tree density should be used to establish *D. robinioides* while *D. retusa* and *P. saman*, which had similar transmission of incident radiation to the herbaceous stratum, can initially be planted at a higher density.

This experiment demonstrated that the calibration of sap flow gauges on potted plants is an important step for obtaining accurate estimates of transpiration in the field especially with the Granier system, which is rather empirical as it does not measure sap flow as such. The equations developed for estimating sap flow velocity in this research were similar to the equations for the three tree species, individually. In examining drivers of transpiration, tree transpiration in the well watered season followed the behaviour of vapour pressure deficit; whereas, the dry season caused a depression of tree transpiration. One reason for this was the loss of leaves in the dry season. The evaluation of water use of tree species in agroforestry systems needs to be based upon on sap flow velocity rather in individual or stand water use, as the last two variables are dependent on tree density and size.

That both grass species (*Brachiaria brizantha* and *Hyparrhenia rufa*) did not affect the sap flow velocity of *D. retusa* and *D. robinioides* in any of the seasons showed that these species had similar water competitiveness. In contrast, *P. saman* used more water with *B. brizantha* than with *H. rufa*, implying a higher water competition of *H. rufa* a grass species commonly used in the zone. This was perhaps unexpected, in that *B. brizantha* is the more productive of the two grass species and so might be expected to be more competitive for water. *B. brizantha* seems to use water more efficiently than *H. rufa*. *P. saman* presented the highest water use by unit leaf area, which implies that this species uses more water than *D. retusa* and *D. robinioides* if it achieves a similar leaf area. Although slow growing, *P. saman* can eventually reach a large size, and these results indicated that it could be competitive for water in such circumstances. The canopy aperture and leaf properties seem to be the responsible for this characteristic. Tree transpiration in this dry zone was shown to be a minor component of water use in these silvopastoral systems with low tree densities and young trees. Water use of grass species appeared to be the most important component in water balance in silvopastoral systems with relative low tree cover. This needs more research effort in order to evaluate the impact of grass species in whole water use of silvopastoral systems. Research at leaf level, using a porometer or infrared gas analyzer, needs to be implemented to complement of whole-plant studies, such as sap flow monitoring.

The management or design of silvopastoral systems in regions with seasonal drought must consider the ability and response of tree species to dry conditions. Water availability in some seasons is one of the strong limitations for the implementation of agroforestry systems in arid and semiarid conditions (Ruhigwa et al. 1992, Govindarajan et al. 1996, Droppelmann et al. 2000). The three evaluated tree species, indigenous to dry areas, adapt to drought through leaf shedding and apparently reduced stomata conductance to save water in dry periods. However, *D. robinioides* and *D. retusa* are plastic species, changing their water status and retention of water as a function of soil water availability. In dry areas, the tree behaviour in water partitioning is more relevant than light interactions; however, a balance for the water and radiation relationship needs to be found to develop cohabitable tree-grass systems. This research suggested that *B. brizantha*, a drought tolerant species, used the same amount of water as *H. rufa* indicating that it will be useful in silvopastoral systems in areas with seasonal drought.

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CHAPTER VII

7. GENERAL DISCUSSION AND CONCLUSIONS

7.1. GENERAL DISCUSSION

7.1.1. Performance of silvopastoral systems in the dry tropics

Native timber trees in these silvopastoral systems grew similarly to those in pure or mixed plantations in the same zone (0.6-0.8 vs 0.4-1.2 m year^{-1} in height and 0.8-1.3 vs 0.6-2.3 cm year^{-1} in diameter at breast height, respectively; Herrera and Lanuza 1995, Ugalde 1997, Fonseca et al. 2000, Fonseca et al. 2002, Gutiérrez and Fonseca 2002, Piotto et al. 2004; Chapter IV). These results show slight effect of grass species in early tree growth; however, this effect disappears where trees are taller as for *Diphysa robinioides*.

As expected, the improved grass species (*Brachiaria brizantha*) had a significantly higher production than the naturalised grass species (*Hyparrhenia rufa*; 14.7 vs 5.3 DM ha^{-1} year^{-1}; Chapter IV). This demonstrated why farmers are changing from naturalised to improved pasture, mainly with *Brachiaria* species, in the study zone (Esquivel et al. 2003, Holmann et al. 2004). *B. brizantha* demonstrated greater drought and shade tolerance than *H. rufa* (Chapter IV). Some authors argue the advantages of *B. brizantha* in terms of dry matter production in silvopastoral associations in a range of climatic conditions (Bustamante et al. 1998, Andrade et al. 2004, Esquivel et al. In prep).

There was an interaction between grass and tree species with respect to tree growth which is of significance for establishing compatible silvopastoral mixtures with native tree species. It seems that the effect of grass species is dependent on tree size and cover. *D. robinioides*, the tallest species, was not affected by grass species. *B. brizantha* decreased the rate of growth of *P. saman*, the smallest species, whereas, *D. retusa* grew better with *B. brizantha*. This may indicate that there is a critical tree size or rate of tree growth for successful inclusion in silvopastoral systems. Once a higher size has been reached; the competition of aggressive grasses was less important (Schaller et al. 2003). Other studies show the effect of grass species in early growth of trees; e.g. natural regeneration of native tress in pastures was not affected by grass species in a study conducted in Muy Muy, Nicaragua (Esquivel 2005).

In this study, dry matter production of *H. rufa* pastures decreased with increased tree cover but with *B. brizantha* pastures there was no effect of tree cover on grass dry matter production (Chapter IV). The effect of trees on grass production varies with respect to the distance from woody plants and according to grass species. Wilson (1998) found no effect of distance from trees on the grass yield for *Acacia stenophylla* and *Albizia lebbeck*; whereas there was reduced grass production for *Eucalyptus argophloia*, and a higher yield at the stem base in *Leucaena diversifolia* (Wilson 1998). Sharrow (1991) noted that biomass yields of pasture were lower under the canopy of *Pseudotsuga menziessi* (Douglas –fir) trees and yield increased as distance from the tree to open pasture increased. This response was associated with the loss of under story vegetation due to the intense competition with trees for moisture, nutrients and light.

7.1.2. Determinants of water use in silvopastoral systems

7.1.2.1. Interacting species

Climatic conditions (vapour pressure deficit –VPD- and reference evapotranspiration –ETo) are the driving forces of tree transpiration in well-watered soil conditions

(Chapter VI). When soil became drier, trees tended to manage their transpiration by physiological controls such as stomatal aperture. *D. robinioides* always presented the highest water use at stand level followed by *D. retusa* and *P. saman* (0.20, 0.07 and 0.06 mm day^{-1}, respectively; Chapter VI). However, the transpiration of *D. robinioides*, the tallest tree species, was not affected by grass species contrasting with the effect on *P. saman* and *D. robinioides*. *P. saman* used more water when associated with *B. brizantha* whereas transpiration of *D. retusa* was higher in the *H. rufa* association (Chapter VI). *P. saman* displayed the highest water use by unit leaf area in comparison to *D. robinioides* and *D. retusa* (Chapter VI). Large differences in transpiration by unit leaf area can be expected in tropical tree species (Cernusak et al. 2006); these differences might be caused by their canopy structure and leaf area and shape (Domingo et al. 1996, Cajas et al. 1999). Species with an open canopy such as *P. saman* and *D. retusa* allow the entrance of airflow inside the canopy decreasing leaf boundary layer resistance and thus increasing water use, contrasting with a more closed canopy which creates a barrier to airflow, as strategy to decrease water loss.

D. robinioides and *D. retusa* seemed to be better adapted to dry conditions than *P. saman* due to their decreased their leaf water potential as the soil became drier. It seems that *P. saman* did not change its leaf water potential and soi it had the highest transpiration rate by unit leaf area (Chapter VI). This phenomenon may indicate that *P. saman* is a water spender. The decrease in leaf water potential by *D. robinioides* and *D. retusa* could have been associated with a decrease in soil water potential when soil was drier. This in turn can be attributed to stomata closure, which is the major control point of plant water relations (Lambers et al. 1998).

The grass evapotranspiration was similar for *B. brizantha* and *H. rufa* (1.1 and 1.2 mm day^{-1}, respectively; Chapter VI). These rates were not affected by tree species (Chapter VI). According to these results, water use of grasses is more important than that of trees (Chapter VI). The total water use in these silvopastoral systems is not necessarily the sum total of water use by each component in monocultures (Brown and Stott 1984). Contrasting results were found regarding the portion of water use attributed to herbage component. Roupsard et al. (2006) found that the evapotranspiration of a *Cocus nucifera* L. stand was around 68% of the evapotranspiration of the grass understory (1.8 and 2.6 mm day^{-1}, respectively); whereas Yepez et al. (2003) found that 15% of total evapotranspiration of the tree-grass natural ecosystems in Arizona (343 mm year^{-1}) can be attributed to understory transpiration contrasting with 70% for tree transpiration in the same system. Both grass species (*B. brizantha* and *H. rufa*) seemed to be adapted to dry regions as they decreased their leaf water potential during dry period (Chapter VI). However, *H. rufa*, whose leaf water potential was lower than that of *B. brizantha*, seems to be better adapted to arid and semiarid conditions, more efficiently regulating water or using less water for transpiration (Chapter VI).

7.1.2.2. Leaf distribution: phenology, shade and radiation

The maximum tree cover and leaf area index was found in transition season, the period with high soil water availability and radiation (Chapter VI). All evaluated tree species lost their leaves in dry season (between January and April; Durr 2001, Jiménez et al. 2002) in order to control their transpiration more efficiently. Reduction in leaf area index in tree species caused significant reductions in PARt and water use at individual and stand level. *Pithecellobium saman* always presented the lowest crown cover and highest transmission of photosynthetically radiation (PARt) followed by *Dalbergia retusa* and *Diphysa robinioides* (9.7 vs 27.8 vs 30.6 % of tree cover and 68.0, 47.9 and 46.6% of PARt for *P. saman*, *D. retusa* and *D. robinioides*, respectively; Chapters IV and VI). However, in silvopastoral systems with low density or trees in patches, such as the evaluated associations, there are two ecological components: an open herbaceous layer dominated by annual species, and an area affected by the tree canopy which includes an herbaceous stratum (Gonzalez

Bernaldez et al. 1969). *P. saman* allowed more radiation under its canopy for grass growth (Chapter VI).

However, *D. retusa* rapidly changed its tree cover through leaf production in well-watered conditions (Chapter VI). Contrasting with the PARt, the light extinction coefficient (k) of *P. saman* was the highest compared to *D. robinioides* and *D. retusa* (0.31, 0.25 and 0.24, respectively; Chapter VI). The differences are attributed to canopy architecture and leaf angle (Wang and Miller 1987, Jones 1992, Ozier-Lafontaine et al. 1998); *P. saman* and *D. retusa* have similar proportion of gaps in crown; however, the former tree species has the bigger, thicker and more horizontal leaves. Significant reductions in leaf area of tree species lead to substantial decrease in water use at individual and stand level (Chapter VI).

7.1.2.3. Fine roots distribution

The fine root length has primordial importance in water interactions and nutrient diffusion from soil (Marschner 1997), mainly in mixed systems such as agroforestry. Fine root length of grasses and trees was not affected by associated component (Chapter V). However, competition for belowground resources is inevitable (Ong and Leakey 1999). In contrast, other studies have found effects of components on fine roots in silvopastoral systems (Bowen 1985, Easthman and Rose 1988, Gautam et al. 2003, O'Grady et al. 2005, Püttsepp et al. 2006). As expected, the tree fine roots tended to be more abundant than that of grass species in deeper layers and in under canopy positions. A type of niche separation could be seen here, with higher root competitiveness of trees in deeper soil layers close to their trunks (Ong et al. 1989, Ong and Black 1994, Ong and Leakey 1999), whereas, grasses were more successful further away from the tree stem, where there was less shade (Chapter V). Similar results have been reported by Singh et al. (2000) in mixed forest of *Eucalyptus* *camaldulensis* and *Acacia nilotica*. Fine tree roots have affected the soil water availability to a higher degree in deeper layers (Marlats et al. 1999).

The ideal vertical root distribution in agroforestry systems which implies the occupation of more or less separated soil layers for each component may reduce overall root competition improving the utilisation of soil resources (Schroth 1999). In these young silvopastoral systems in dry tropics, most of the fine roots were located in the first 20 cm soil (66%; Chapter V) decreasing exponentially with depth. Similar results to these were found by Bowen (1985), Easthman and Rose (1988), O'Grady et al. (2005) and Püttsepp et al. (2006). This separation of root exploration could induce to a potential hydraulic lift from trees. Trees might take water from deeper soil layers and distribute it on the soil surface to be used by other species (Emmerman and Dawson 1996, Dagang and Nair 2001). This process occurs primarily at night, when stomata are closed and the plant is at equilibrium with root water potential (Lambers et al. 1998).

Total fine root length was very dynamic between the two sampling periods (wet seasons 2004 and 2005) with a high increase (265%), which was attributed more to tree root growth rather than grass production (530 vs 170%, respectively; Chapter V). This increase in fine roots may have been a result of age; however, it seems that tree fine roots quickly response to changes in water availability. The results of this research suggested that drought caused a deeper soil exploration, contrasting with a promotion of fine root production in first 20 cm soil with initial rains (Chapter V). The root distribution changed dramatically with water soil availability; water stress promoted carbon allocation to roots (Ericsson et al. 1996) but the beginning of the rainy season increased the root length; however, additional rains slightly reduced root length (Govindarajan et al. 1996).

7.1.2.4. Carbon and nitrogen accumulation

The soil organic carbon content in these silvopastoral systems increased at a rate between 2.6 and 7.4 Mg C ha^{-1} year^{-1}. Tree species had the highest impact in the soil organic carbon content in comparison to the grass only effect (2.6 to 7.4 vs -1.4 to 6.2 Mg C ha^{-1} year^{-1}, for trees and grasses, respectively; Chapter IV). *B. brizantha* had a higher impact on soil organic accumulation than *H. rufa*. Changes in soil carbon storage reported by other authors vary highly according to the evaluated systems. Trouve et al. (1994) argued that plantations of *Eucalyptus* and *Pinus* would increase total organic carbon in 9.4 mg C g^{-1} year^{-1} in the Congo in 30 years. Long et al. (1992) found a mean of 0.1 Mg C ha^{-1} year^{-1} in grasslands of Mexico, Kenya and Thailand without fires; whereas, Young (1989) estimated a decrease of total organic carbon of 0.5 Mg C ha^{-1} year^{-1} in 50 years of agricultural use. In contrast, Fassbender et al. (1991) found net accumulation of total organic carbon of 1.7 Mg C ha^{-1} year^{-1} in agroforestry with cocoa in humid tropics of Costa Rica. As for fine roots, the bulk of soil organic carbon was found in 0-20 cm (60.4%; Chapter IV). Changes in soil organic carbon was markedly higher in first 20 cm soil than in 20-40 cm; this is mainly attributed to changes in the light fraction carbon (Chapter IV).

Native timber tree species contributed to increases in the soil nitrogen content. *D. retusa, D. robinioides* and *P. saman* had an impact on soil nitrogen accumulation, increasing it to 294, 286 and 254 kg N ha^{-1} year^{-1} at 60 cm of depth, respectively. These results were higher than those reported in other studies; values between 40 and 86 kg N ha^{-1} year^{-1} were found in *Acacia dealbata* in the top 10 cm of soil through five years in Australia and for *Acacia mearnsii* in mixtures with *Eucalyptus globulus* and in monoculture plantations (May and Attiwill 2003, Forrester 2004). The increment of light fraction carbon and nitrogen was widely attributed to root production and decomposition (Rosell and Galantini 1997, Trujillo et al. 1997, Abril and Bucher 2001). Although the three evaluated tree species are nitrogen fixing species, it seemed that fine roots of grasses were having a higher impact on N accumulation, through increases in soil organic matter (Chapter IV), as total root biomass and length were correlated to the soil nitrogen concentration (Chapter IV). This higher organic matter accumulation might be caused by root mortality as a consequence of a high defoliation by grazing or pruning as suggested by Gregory (1996).

7.2. GENERAL CONCLUSIONS AND IMPLICATIONS FOR DESIGN AND MANAGEMENT OF AGROFORESTRY SYSTEMS

Early tree growth in these systems is a key point in their establishment; the use of aggressive grasses such as *Brachiaria brizantha* can considerably reduce the development of slow growing native trees. The establishment of these land use strategies should involve some management practices, such as weeding around young trees, to enhance their success. The inclusion of *B. brizantha*, a shade tolerant grass species, in silvopastoral systems in the seasonally dry tropics has enormous potential due to its enhanced forage production and low reduction of yield under tree cover. Farmers in this region generally retain lower densities of trees, using mainly isolated trees, mainly of native species, in pastures to reduce competition with grasses; but there is a tendency to produce several stems from the base of the trunk in these species. If the objective is to produce high quality timber, silvicultural management must be required to produce a good bole, necessitating management activities such as pruning and thinning.

The inclusion of improved grasses in silvopastoral systems increases the availability of grass dry matter for animal consumption. This factor may cause a mitigation of the animal damage of trees for feeding, improving the tree growth in these conditions. Even though some native tree species are slow growing, well managed silvopastoral systems may enhance temporary storage of carbon by pastures and the longer term storage of carbon in timber. In soils with low organic matter content, such as degraded soils, carbon sequestration in soils due to silvopastoral practices is more important than the amount of carbon in biomass.

Tree roots responded more rapidly than grass roots to availability of water resources, giving a higher competitive ability for soil exploration and enhancing the probabilities of success of tree establishment in grassland areas. The introduction of improved and drought tolerant grass species, such as *B. brizantha*, enhances the root development of the whole systems improving the coexistence of components in regions with seasonal water deficits. This behaviour may be due to increases in soil porosity due to root exploration and increases in soil organic matter due to root dieback. The nitrogen fixating ability of these native timber tree species is another factor, which can contributes to the success of silvopastoral systems. The results suggested that an appropriate strategy to establish native timber trees in grasslands would be to plant trees in improved grasses or to introduce improved grasses into existing silvopastoral systems. This strategy should include soil preparation and no grazing in the first two years of establishment.

The tree-grass associations evaluated exhibited the highest density of fine roots in the top horizons of the soil. A degree of niche separation was evident, because grass species had higher competitive abilities in upper horizons further away from trees while trees dominated deeper soil layers closer to their trunks. The establishment and management of tree-grass mixtures should take advantage of this type of niche separation in fine root exploration. However, a temporal separation could be considered to improve the proportion of survival and growth of trees. This separation could be achieved by planting trees in a period before grasses are sown or establishing grasses in strips leaving space for rooting of trees.

An apparent reallocation of roots, increasing the proportion in the top soil, was seen when there was a decrease in soil moisture. The knowledge of how root systems respond to environmental conditions, mainly water status of soil, can provide management tools for increasing the successful and adoption of silvopastoral systems in dry regions. However, the high variability of samples in the root studies made it difficult to detect treatment effects in evaluated treatments (as is often observed in root studies in the field). It is recommended in this type of research, that the number of core samples be increased so that conclusions can be made with more certainty.

Transmission of radiation through the tree canopy, a key characteristic for designing silvopastoral systems, depends on a set of tree variables which includes the light coefficient extinction factor and the leaf area index. In this study, the differences in transmission were attributed more to tree density and crown area rather light extinction coefficient. *P. saman* presented an open canopy; however, their leaves intercept more light than that of *D. retusa* and *D. robinioides*. In terms of tree canopy area and light occlusion, *D. robinioides* allows the transfer of less radiation to the understorey grasses. These results imply that lower tree density should be used to establish *D. robinioides* while *D. retusa* and *P. saman*, which have similar transmission of incident radiation to the herbaceous stratum, can initially be planted at a higher density.

Defoliation during the dry season caused a depression of in tree transpiration. *Brachiaria brizantha* and *Hyparrhenia rufa* presented similar water competitiveness when associated with *D. retusa* and *D. robinioides* as they did not affect tree sap flow in any species. In contrast, *P. saman* used more water with *B. brizantha* than with *H. rufa* implying a higher water competitiveness of *H. rufa*, a grass species commonly used in the zone. This was unexpected, as *B. brizantha* is the more productive of the two grass species and thus might be considered to be a more efficient water user.

The management or design of silvopastoral systems in regions with seasonal drought must consider the ability and response of tree species to dry conditions. Water availability in some seasons is one of the limiting factors for the implementation of agroforestry systems in arid and semiarid conditions (Ruhigwa et al. 1992, Govindarajan et al. 1996, Droppelmann et al. 2000). The three evaluated tree species, indigenous to seasonally dry areas, adapted to drought through leaf shedding and apparently reduced stomatal conductance to save water in dry periods. However, *D. robinioides* and *D. retusa* are plastic species, changing their water status and retention of water as a function of soil water availability. In dry areas, the tree behaviour in water partitioning is more relevant than light interactions; however, a balance in the water and radiation relationship needs to be found to develop productive tree-grass systems. This research suggested that *B. brizantha*, a drought tolerant species, used the same amount of water as *H. rufa* indicating its ability to be successful in silvopastoral systems in areas with seasonal drought.

7.3. TESTING THE RESEARCH HYPOTHESES

Several research hypotheses were tested in the three research chapters. In this section, a summary of the assessment of each hypothesis is given:

7.3.1. Chapter IV

- It is accepted that early tree growth was affected by grass species according tree size. There was a tree-grass interaction: tree growth of *D. robinioides* and *P. saman* was higher with *H. rufa* than with *B. brizantha*; whereas, *D. retusa* grew better with *B. brizantha*.
- Dry matter production was higher for *B. brizantha* than for *H. rufa* but tree species did not affect it
- Tree species had similar carbon concentration in biomass overall; however, it was higher in stems. Grass species had similar carbon concentration in belowground biomass contrasting with higher concentration in aboveground biomass of *B. brizantha*. In grass species, belowground biomass had higher carbon concentration than aboveground biomass.

- Soil had the highest carbon storage followed by aboveground biomass of trees and fine roots. Silvopastoral systems with *D. robinioides* had the highest carbon storage
- Ligth fraction of soil organic carbon was partially affected by total fine root biomass

7.3.2. Chapter V

- Fine root biomass and length was different between seasons as a result of active root development. The bulk of fine roots was found in the top 20 cm of soil
- Trees had higher fine root competitiveness when associated with *B. brizantha.* Trees had more fine roots in the deeper layers
- Niche separation was found in fine root exploration between tree and grass species. Trees had higher proportion of fine roots in deeper layers under the tree canopy; whereas, grasses were more dominant in superficial soil layers away from trees
- Trees promoted the accumulation of soil nitrogen. *D. robinioides* and *D. retusa* had a higher soil nitrogen accumulation rate than *P. saman*
- Soil nitrogen was partially correlated with fine root biomass

7.3.3. Chapter VI

- *D. robinioides* had the highest tree canopy cover. This was affected by associated grass species and season
- Leaf area index of *D. robinioides* was the highest and was not affected by grass species. *P. saman* had a higher leaf area index with *B. brizantha*; whereas *D. retusa* had higher with *H. rufa*

- *D. robinioides* had the highest water use with no effect due to grass species. A tree x grass interaction was found for the other two tree species. *D. retusa* used more water with *B. brizantha*; while *P. saman* used more water with *H. rufa*. This was affected by season
- Water use efficiency of grass species was higher than that of trees. *D. retusa* had higher water use efficiency than other tree species. The water use efficiency of *D. robinioides* was not affected by grass species; in contrast, grass species affected in the water use efficiency of the other tree species. *D. retusa* had higher water use efficiency with *H. rufa* with an opposite result for *P. saman*. *B. brizantha* had higher water use efiiciency than *H. rufa*
- Trees lost their leaves in dry seaons. *D. retusa* and *D. robinioides* exhibited changed leaf water potential; whereas, *P. saman* did not. Ability to shed leaves and change leaf water potential are strategies that helped the trees to tolerate dry conditions. *H. rufa* had higher leaf water potential than *B. brizantha*.

7.4. GENERAL RECOMMENDATIONS AND CONSIDERATIONS FOR FUTURE RESEARCH ON WATER AND RADIATION INTERACTIONS IN AGROFORESTRY SYSTEMS

Inclusion of more aggressive and drought tolerant grass species such as *Brachiaria brizantha* might contribute to a higher soil volume of root exploration, increasing the possibilities of success in seasonally dry environments. However, weeding control at early stages is recommended to promote tree growth. The production of native timber tree species in silvopastoral systems needs to consider applying some management activities to improve the timber quality such as pruning and thinning. However, there is a new market emerging, using native woods in the production of handicrafts, where the size and shape of the tree trunk are not important.

The high variability in spatial and temporal pattern of fine roots may be misleading; the number of soil cores should be increased to reduce variability. However, due to the high cost of analysis, some techniques and indicators could be developed to make this task more efficient. Hemispherical photography, with its associated calibration, showed a high level of accuracy in characterizing tree canopies and estimation of transmission of photosynthetically active radiation. This method estimated leaf area index with a higher accuracy than the Sunscan PAR sensors. Radiation interactions in multistrata systems may be studied in an efficient way using hemispherical photography using digital cameras when possible.

The evaluation of water interactions between trees and grasses should be based upon sap flow velocity rather than individual or stand water use, as the two last variables are dependent on tree density and size. Although simplified water balance is one of the most used methods for estimating grass water use in grass species, other methods, using direct estimations of water use, should be developed to increase the accuracy. The impact of grass water use on total water use needs to be investigated in more depth. Sap flow monitoring gave higher accuracy than the use of simplified water balance for estimating tree transpiration. However, sap flow monitoring should be complemented with research at the leaf level, using a porometer or infrared gas analyzer.

7.4. REFERENCES (Chapters I, II, III and VII)

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