PROGRAMA DE EDUCACIÓN PARA EL DESARROLLO Y LA CONSERVACIÓN

ESCUELA DE POSGRADO

Functional trait approach to assess the ecological processes of drought tolerance and water use efficiency in silvopastoral systems in Rivas Department, Nicaragua

Proyecto de tesis sometido a consideración de la Escuela de Posgrado, Programa de Educación para el Desarrollo y la Conservación del Centro Agronómico Tropical de Investigación y Enseñanza como requisito para optar por el grado de:

Magister Scientiae en Manejo y Conservación de Bosques Naturales y Biodiversidad

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Turrialba, Costa Rica, 2011

Esta tesis ha sido aceptada en su presente forma por la División de Educación y la Escuela de Posgrado del CATIE y aprobada por el Comité Consejero del Estudiante como requisito parcial para optar por el grado de:

MAGISTER SCIENTIAE EN MANEJO Y CONSERVACIÓN DE BOSQUES TROPICALES Y BIODIVERSIDAD
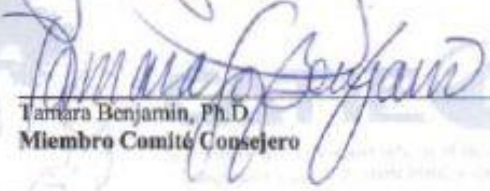
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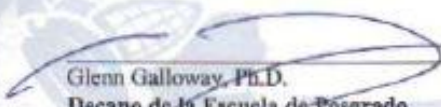
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DEDICATION

To my parents, for teaching me that education leads to true freedom.

… and my three brothers, who challenged me to become a stronger woman every day.

Family is bliss.

ACKNOLEDGMENTS

BIOGRAPHY

The author was born in the Caribbean island of Puerto Rico on June 1, 1982. She studied in the University of Puerto Rico (UPR) at Humacao in the Wildlife Management Biology program and conducted research through the Mona Island Project at the CREST-CATEC (Center for Applied Tropical Ecology and Conservation) of the UPR in Rio Piedras. She moved to Costa Rica in September 2005 to start a more practical approach to biology at the Universidad Latina in San José, where she graduated in Biological Sciences with an emphasis on Ecology and Sustainable Development. In 2009 she began the Master's program in Forest Management and Conservation of Biodiversity at the Tropical Agricultural Research and Higher Education Center (CATIE) and in 2010 started her thesis with the GAMMA group under the project FUNCITree. She has participated in various research experiences including monitoring, laboratory and field work in dry forests, mangroves, and humid forests, in the Caribbean and Central America. Her main areas of interest and experience are ethnobotany, invasive species, forest ecology, agroecology, restoration, wildlife management and conservation.

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ABSTRACT

Olivero Lora, S. 2011. Functional trait approach to assess the ecological processes of drought tolerance and water use efficiency in silvopastoral systems of Rivas Department, Nicaragua. M. Sc. Thesis, Turrialba, Costa Rica, CATIE 74 pp.

Key words: agroforestry, drought tolerance, ecosystems properties, functional ecology, isolated trees, silvopasture, tropical dry forest

From March to August 2010 six species of isolated trees were characterized in silvopastoral systems of Rivas, Nicaragua, according to their ability to withstand drought events. In the pending menace of climate change, the predictions foresee the intensification of drought events in these drylands. In pasture dominated landscapes; the provisioning of services such as drought resistance by local tree species, becomes particularly important. To assess drought tolerant or resistance traits, a functional ecology approach was used to evaluate how trees strategies vary, and the synergies and trade-offs between the traits. The purpose of was to evaluate the potential of functional ecology as an alternative to respond to specific management needs aimed at guaranteeing the provision of ecosystem services in semiarid agroecosystems of Rivas, to be able to predict or improve the functional capacity of agroecosystems to support climate variability, and more specifically, the contribution of the species to assure biomass production through the year. For the physiological and functional approach, a total of 20 traits were assessed and measured to characterize six isolated tree species (*Albizia saman*, *Guazuma ulmifolia*, *Coccoloba caracasana*, *Tabebuia rosea*, *Crescentia alata*, *Enterolobium cyclocarpum*). We aimed to find axes that indicated different drought tolerance strategies. Principal components analysis showed a clear separation of species based on the traditional classifications of avoidance-tolerance vs. conservative-acquisitive axes of specialization. We found in the first PCS axis to be an indicator of drought tolerance and avoidance strategies, dominated by canopy traits. The second PCA axis reflected the individual resource capture and identified as a conservative and acquisitive strategies with traits related to leaf size and toughness. Our finding suggest not only that there are specific

traits associated with responses to climatic stress, but also that this traits manifested in species provide different effects to drought mitigation by preventing understory water loss. We measured actual evaporation under the different canopies trees in relation to the differentiation of the ability of the species to conserve humidity during the end of the drought period. Pasture cover estimation were also made as to relate the drought tolerance service provisioning with the effect of the tree actual pasture production at the end of the dry period and after the first rains. We recommend the species *G. ulmifolia* and *C. alata* to improve provisioning of ecosystem services of drought resistance and pasture production as they prove to have well defined different drought responses, prevent a significant amount of evapotranspiration under their canopies during the dry season, and allow enough light transmission to reach the understory to guarantee pasture production.

RESÚMEN

De marzo a agosto de 2010 se caracterizaron especies aisladas en potreros en sistemas silvopastoriles de Rivas, Nicaragua, de acuerdo a su habilidad para soportar eventos de sequía. Ante la amenaza del cambio climático, las predicciones prevén la intensificación de eventos de sequía en estas tierras secas. Por lo que en este paisaje dominado por pasturas, el aprovisionamiento de servicios como la resistencia y resiliencia a eventos de sequía por especies locales de árboles, se vuelve particularmente importante. Para la evaluación de este reto, un enfoque funcional ha sido utilizado para evaluar como las estrategias de los árboles varían, así como las sinergias e intercambios entre los rasgos. El propósito de este trabajo fue evaluar el potencial de la ecología funcional como una alternativa para responder a necesidades especificas de manejo dirigidas a garantizar el aprovisionamiento de servicios ecosistémicos en agroecosistemas áridos de Rivas, poder predecir o mejorar la capacidad funcional de agroecosistemas para soportar el cambio climático, y de forma más específica, la contribución de las especies para asegurar la producción de biomasa a través del año. Para el enfoque fisiológico y funcional, un total de 20 rasgos fueron evaluados y medidos para caracterizar seis especies de árboles aislados en potreros (*Albizia saman*, *Guazuma ulmifolia*, *Coccoloba caracasana*, *Tabebuia rosea*, *Crescentia alata*, *Enterolobium cyclocarpum*). Apuntamos hacia la búsqueda de ejes de especialización que indicaran diferentes estrategias de tolerancia a sequías. El análisis de componentes principales mostró una clara separación de especies basada en las clasificaciones tradicionales de tolerancia-evasión vs. un eje relacionado a uso de recursos (conservador-adquisitivas). El primer eje es un indicador de estrategias de evasión y tolerancia a sequías, dominado por rasgos de copa. El segundo eje del ACP refleja la captación de recursos de las especies y lo identificamos con estrategias conservativas y adquisitivas con rasgos relacionados tamaño y dureza de hoja. Nuestros resultados sugieren no solo que hay rasgos específicos asociados a las respuestas de estrés climático, si no también que estos rasgos manifestados en las especies proveen diferentes efectos para la mitigación de sequía a través de la prevención de pérdida de agua bajo la copa. Medimos evaporación real bajo las diferentes copas de los árboles en relación a la habilidad de las especies para conservar humedad durante el final de la época seca. Estimaciones de

cobertura de pasto bajo la copa fueron también llevadas a cabo para relacionar el aprovisionamiento del servicio de tolerancia a sequía con el efecto del árbol en la producción de pasto al final de la época lluviosa y después de las primeras lluvias. Se recomiendan las especies *G. ulmifolia* y *C. alata* para mejorar el aprovisionamiento de servicios ecosistémicos de tolerancia a sequía, conservación de agua y producción de pasto. Estas especies han mostrado tener respuestas a sequía bien definidas, previenen una cantidad significativa de evapotranspiración bajo sus copas durante la época seca, y permiten suficiente transmisión de luz a través de la copa para permitir el crecimiento de pasto.

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LIST OF UNITS, ABBREVIATIONS AND ACRONYMS

ANOVA: Analysis of variance

DBH: diameter at breast height

EP: Ecosystem processes

ES: Ecosystem services

INETER: Nicaraguan Institute of Territorial Studies

IPCC: Intergovernmental Panel on Climate Change

LA: Laminar area

LDMC: Leaf dry matter content

LT: Leaf thickness

MANOVA: Multivariate analysis of variance

PFG: Plant functional group

RGR: Relative growth rate

SLA: Specific leaf area

SPS: Silvopastoral system

TS: Tensile strength

WD: Wood density

WMO: World Meteorological Organization

1   INTRODUCTION

Drylands, ecosystems characterized by a lack of water, cover about 40% of the Earth's surface (M.E.A. 2005). Tropical dry forests are one of the ecosystems most affected by human activities such as cattle ranching, hunting, extension of the agriculture frontier, deforestation, and invasion of exotic grasses (Primack et al. 2001). The Central American drylands, mainly characterized by having a long dry season, are affected by severe drought. Their degraded conditions have compromised the natural capacity of the ecosystems to overcome drought disturbances. In Nicaragua alone, an estimated 13 million hectares are deforested (Pomareda 1998), leaving agrolandscapes mostly dominated by a pattern of pastures or annually cultivated lands that maintain some tree cover in the form of scattered trees, small patches of secondary forest, scrubland, live feces, and riparian forests (Harvey et al. 2005). The Department of Rivas is no exception, with a landscape that has been extensively modified as a result of agricultural and cattle-ranching practices.

The ecological simplification and degradation of drylands such as Rivas, already highly vulnerable to changes in rainfall, have increased their vulnerability particularly because changes in vegetation and a decrease in the capacity of ecosystems to store and regulate water flow (Carpenter et al. 2006). As a consequence of this habitat modification, drylands are losing their resilience to externally driven changes such as climate change (MEA 2005). For this reason it is important to understand the physiological mechanisms that facilitate plant survival under suboptimal conditions that are expected to dominate in the future (Chapin 1991).

Modification of habitats and management practices that reduce species diversity and functional composition tend to have greater impacts on ecosystem processes (Tilman et al. 1997), and thus, on ecosystem services (ES). Silvopastoral systems, a form of land use that incorporates trees and shrubs into pastures and livestock production, have recently been given attention for their provision of multiple ES. A particularly important ecosystem service in Rivas is drought tolerance to mitigate the adverse effects of climate variations predicted for this area.

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Modern agrosilvicultural systems need to be designed based on the knowledge of the relationships between plant species traits and their capacity to provide specific functions through ecosystem processes. The enhancement of functional biodiversity in agroecosystems is a key ecological strategy to bring sustainability to production, as such we need to develop agroecological technologies and systems that provide the multifunctionality needed (Altieri 1999) in order to assess the impending global threats and challenges. This study evaluates the potential of functional ecology as an alternative to respond to specific management needs aimed at guaranteeing the provision of specific functions of interest in semiarid agroecosystems of Rivas, Nicaragua.

1.1 RESEARCH OBJECTIVES

1.1.1 General objective

Identify how tree species functional traits respond in order to maximize the provisioning of critical functions such as drought resistance and water use efficiency in silvopastoral systems.

1.1.2 Specific objectives

Determine the value, range, and abundance of specific functional traits associated with isolated tree species in pastures and use them to group the species into drought tolerance functional groups.

Test the relationship between plant functional groups and understory water stress beneath the crowns.

Use the correlation matrix between hard and soft traits to improve functional classification and predict how a larger group of silvopastoral species might be classified.

1.2 General hypothesis

Dominant trees of silvopastoral systems of Rivas can be classified into drought tolerance functional groups based on species specific trait measures.

Trees of different drought tolerance functional types will likewise lead to differences in measures of understory evapotranspiration.

2 LITERATURE REVIEW

2.1 Central American agrolandscapes and anthropogenic pressure

In Central America, native forests have been reduced by approximately 40% over the last four decades (FAO 2006), and in Nicaragua alone, the expansion in livestock production has resulted in the deforestation of 31% of the national territory (Pomadera 1998; Sánchez et al. 2004). The Central American drylands are severely affected by drought and their degraded conditions have compromised the natural capacity of the ecosystems to overcome drought disturbances. The department of Rivas, located in the southwestern part of Nicaragua, embodies a landscape that has reduced its arboreal coverage to small forest remnants, narrow riparian forests, small "charrales" (vegetation cover dominated by shrubs of approx. 5 m high), isolated trees and live fences (Sánchez et al. 2004). In short, pastures in Rivas are largely degraded as a result of over-exploitation and unsustainable land use, and therefore the landscape is severely fragmented.

The ecological simplification and degradation of drylands, regions that are already highly vulnerable to changes in rainfall, increases vulnerability to climatic variation due to changes in vegetation that decrease the capacity of ecosystems to store and regulate water flow (Carpenter et al. 2006). As a consequence of this habitat modification, drylands are losing their resilience to externally driven changes like climate change (MEA 2005). Impending global climate change will alter the fitness of most terrestrial habitats for plant growth; as such it is important to understand the physiological mechanisms that enable plant survival under suboptimal conditions (Chapin 1991). Semi-arid areas are very sensitive to changes in precipitation, and so, plant survival and vegetation productivity can be affected (Hulme 2005).

2.2 Silvopastoral systems and their services

Silvopastoral systems are land use systems where the trees or shrubs are combined with livestock and pasture production in the same land unit (Nair 1993). Ecosystem services (ES) are defined as "the benefits people obtain from ecosystems", and include provisioning services such as food and water; regulating services floods, drought, land degradation, and

disease; supporting services such as soil formation and nutrient cycling; and cultural services such as recreational, spiritual, religious and other nonmaterial benefits (MEA 2005). In agricultural systems, biodiversity performs ecosystem services beyond production of food, fiber, fuel, and income. Some clear examples that occur in SPS are recycling of nutrients, control of local microclimate, regulation of local hydrological processes, regulation of the abundance of undesirable organisms, and detoxification of noxious chemicals (Altieri 1999).

Recent studies have highlighted the relationship between biodiversity and the provisioning of ecosystem services. Many of these past studies have used taxonomic measures of biodiversity for these evaluation, however, classifying species according to their taxonomy presents strong limitations when looking for ecological answers to questions of what drives ecosystem services (Cornelissen et al. 2003). More recent studies have instead focused on measures of functional diversity. This growing focus on plant traits and function not only suggests that traits are responses to environmental conditions, but also that these same traits can exert a significant impact on ecosystem processes (Figure 1).

In the semiarid landscape of Nicaragua, an ecosystem service of particular importance is drought tolerance. This ecosystem service is important to decrease the adverse effects of drought events through the reduction in precipitation and an increase in the drying trends predicted by climatic regional climate change models for Central America (Rauscher et al. 2008). The resistance to drought in silvopastoral systems is a function of species composition and more specifically on the functional traits of the species found in that system. Previous studies have shown that the capacity to endure these adverse events is intrinsically related to the species richness and composition of plant communities (DeClerck et al. 2006). However, the agricultural simplification of ecosystems increases their vulnerability (Carpenter et al. 2006) through the loss of functional diversity (Flynn et al. 2009), including response diversity (La liberté et al. 2010).
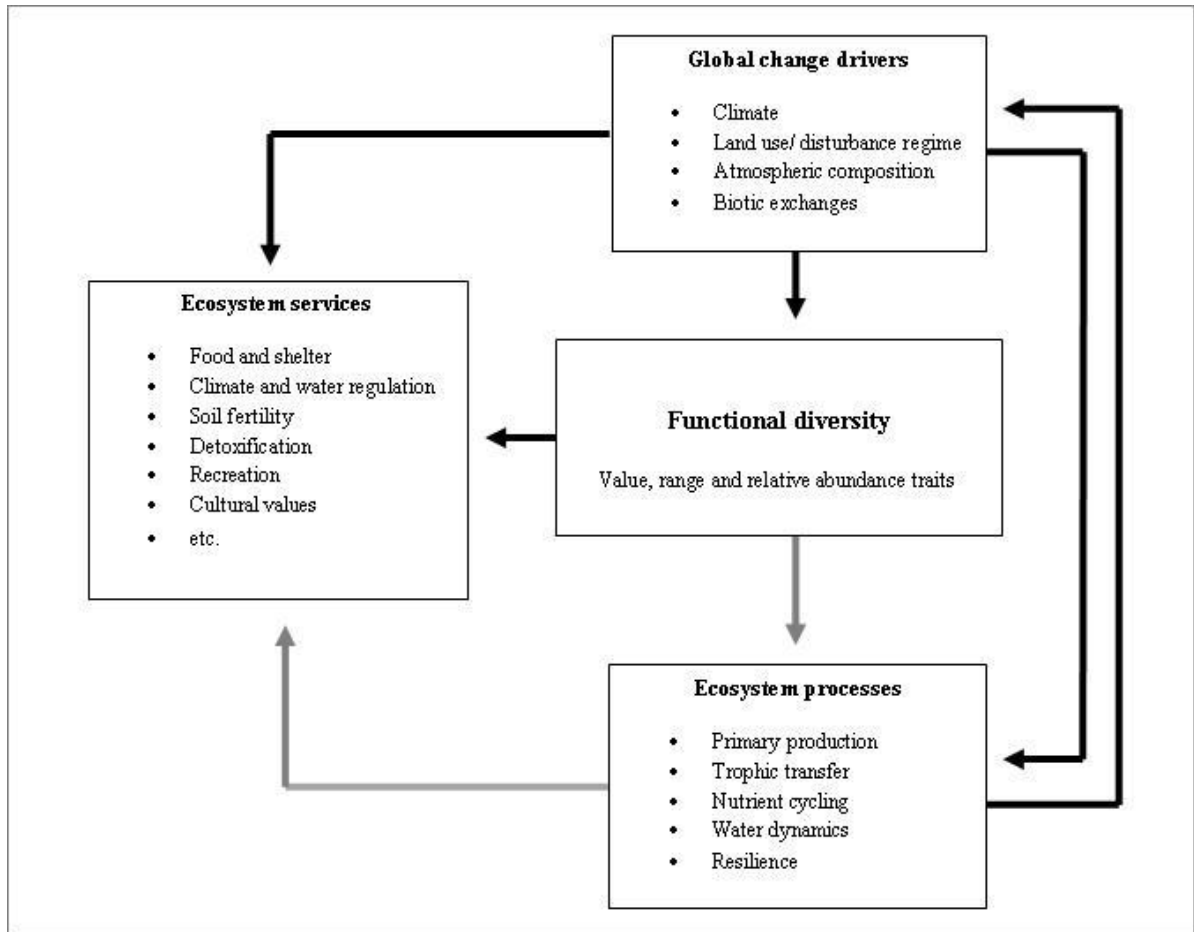
Figure 1. This figure shows that functional diversity is not only a response variable modified by global factors, but that it also has a modifying effect. The grey arrows show the main relations addressed in this study. Modified from Diaz et al. (2006).

It has been suggested that modern agrosilvicultural systems need to be designed based on the knowledge of the relationships between plant species traits and their capacity to provide specific functions through ecosystem processes. The enhancement of functional biodiversity in agroecosystems is a key ecological strategy to increase productivity and sustainability in production, and so, we need to develop agroecological technologies and systems that provide multifunctionality (Altieri 1999). The question remains whether principles of functional diversity and trait combinations of the species retained, can be used to meet these social, economical and environmental challenges.

2.3 Functional ecology: Why functional traits in SPS?

The modification of habitats and management practices that reduce species diversity and functional composition tend to have greater impacts on ecosystem processes (Tilman et al. 1997). It is clear that we need to urgently understand the impacts of climatic and land use changes and formulate predictors of these impacts, and that we are in a position where in most cases we have no detailed knowledge of the ecosystems processes of interest (Diaz et al. 2004). But now there is evidence that the predictions of these effects can be found in the form of single or sets of co-occurring traits (Diaz et al. 2004).

Studying how species and their traits are expressed both at the species and community level allows us to relate biodiversity to ecosystem processes and services of interest. Individual traits can be measured at the species level, including how these traits vary in time and space, or these traits can be scaled up to the community level using different functional diversity measures of functional diversity (FD) which refers to trait distributions and diversity (Díaz & Cabido 2001; Tilman 2001; Lavorel et al. 2008).

A trait is defined as any morphological, physiological or phenological feature that can be measured at the individual level without reference to the environment or any other level of organization (Violle et al. 2007); a functional trait will be a characteristic relevant in terms of its response to the environment and its effects on ecosystem functioning (Diaz & Cabido 2001). In relation with its environment, a trait can be can be classified as a response trait (trait that varies in response to changes in environmental conditions) or as an effect trait (trait that reflects the effects of the plant on environmental conditions, communities or ecosystem properties) (Violle et al. 2007). The assessment of how biotic communities can provide services to the ecosystem is based on the precise measurement of these community traits, which contribute directly to ecosystem functioning (Flynn et al. 2009).

The determination of the interaction among biodiversity changes, ecosystem processes, and abiotic factors still consists of a big challenge (Loreau et al. 2001). An important step towards unraveling these relationships and broadening our comprehension of ecosystem processes is the interpretation of the functional diversity or the distribution of traits

within a community (Lavorel et. al. 2008). Important recent advances have been made in describing the relationship between species diversity and ecosystem processes through the identification of functionally important species and their classification by groups or types.

Functional groups were first defined as a set of species showing either similar responses to the environment or similar effects on major ecosystem processes (Gitay & Noble 1997). A set of species with similar ecological effects may be classified into functional effect groups based on the traits that determine these effects (Hooper et al. 2002; Lavorel & Garnier 2002; Laliberté et al. 2010), and the same can be applied to responses. By grouping and classifying tree species according to their traits in drought resistant functional types we should find useful alternatives for management in drought prone regions.

Even though the ideal tree in terms of drought resistance in a particular landscape does not exist, there are a lot of trees that have important traits and are more tolerant than others (Coder 1999). Plant attributes are related to environmental conditions in a way that they can be used to evaluate the species tolerance to stress (Pugnaire & Valladares 2007). An example of drought related trait would be the wood density or the biomass allocation of the deep roots of a tree species (Markesteijn 2010). Through the study of plant traits we would like to be able to predict, or improve the functional capacity of dryland agroecosystems to withstand climatic variation, and more specifically, the contribution that these species can make in ensuring stable biomass production throughout the year. In order to understand and predict plant species responses to climatic change predicted scenarios, we need insight on the mechanisms of drought tolerance (Poorter & Markersteijn 2007, Markerteijn & Poorter 2009).

2.4 Relation between functional traits and severe drought events

Plants that evade drought are found in regions with a well defined dry season (Kramer & Kozlowski 1979). The fluctuation in the quantity and distribution of precipitation within and across seasons characterizes these drought environments (Swindale & Bidinger 1981). But in order to comprehend how drought affects trees, we have to learn how these factors affect physiological processes (Kramer & Kozlowski 1979). According to Chapin (1991),

environmental stress parameters fluctuate to levels of sub-optimal conditions for plant growth, and so plants have to continuously respond to new combinations of stress.

In their long evolutive process, plants have been able to adapt to temperature and humidity assuming different physical forms, dimensions and physiological attributes that allowed them to cope with climate (Smith 1996). Plants respond to changes in resource availability at different scales. Holbrook et al. (1995) mentions three levels: (a) structure – features that remain relatively constant throughout the life of a plant, (b) physiology – parameters that influence diurnal patterns of water use and gas exchange, and (c) phenology – seasonal patterns of meristem activity. For this study, we considered these levels in which plants have adapted to drought.

For the understanding of ecophysiological behavior and plant responses, the desirable scale to study is the individual because of its integration of activities and processes and the contribution to fundamentally important features such as survival, growth and reproductive success (Meinzer 2003). In order to comprehend why trees grow and respond in different ways to different environments and under different cultural treatments, we need to understand the nature of the physiological processes and how they are affected by the environment (Kramer & Kozlowski 1979). The identification of functional strategies to cope with environmental changes is one way of studying the responses to environmental stress by plants. And when it comes to drought tolerance there are basically two strategies for species to adapt to drought: (a) tolerating drought stress, and (b) delaying drought stress (Markerteijn & Poorter 2009).

There is a wide variety of traits that have influence on the ability of a plant to respond to variations in water availability including rooting depth and root morphology, stomatal response, leaf physiology, leaf phenology, and hydraulic architecture (Mitchell et al. 2008). In plants that tolerate drought, there are important physiological trade-offs between plant growth and water use efficiency. For example, a low allocation of energy to root growth causes plants to have more negative water potentials than deep-rooted species (Padilla et al. 2009). Santiago et al. (2004) found that deciduous tree species in dry sites show greater dominance of short-lived leaves with relative high maximum photosynthetic rates, which suggests a strategy of maximizing photosynthesis when water is available and a minimization to water loss and

respiration costs during periods with no rain. These can be considered as drought avoiders, and low wood density is correlated with these characteristics, which permits storage of water in the stems. This strategy can be contrasted with evergreen species with long-lived leaves of low photosynthetic potential and high wood density, which can be considered drought resisters (Markesteijn & Poorter 2009). Nevertheless, individual traits should not be considered in isolation, because pairs of traits are often correlated, an important part of trait research addresses interrelations among different traits (Westoby & Wright 2006) to ensure the equilibrium of the community.

Plant height represents the distance (in meters) between the superior limit of the main photosynthetic tissues of a plant and the soil level (Cornelissen et al. 2003). This trait is associated with the plant competitive vigor, fecundity and regeneration time after a disturbance (Cornelissen et al. 2003, Kunzmann & Knevel 2005). Plant height tends to be correlated allometrically with the root depth (Cornelissen et al. 2003) which can be a good indicator of a tree strategy for water acquisition, and thus, its strategy for coping with water unavailability due to drought disturbance. Canopy height differentiates from tree height because the former consists of the shortest distance between the highest photosynthetic tissue and the base of the canopy (Weiher et al. 1999; Kunzmann 2005). There are important trade-offs between canopy height and tolerance or avoidance of environmental stress (Kunzmann 2005). In relation to drought tolerance for example, canopy height tends to be correlated with other important size traits such as rooting depth and leaf size (Cornelissen et al. 2003, Kunzmann & Knevel 2005). And the height of the lowest living branch is an important attribute of the tree architecture and defines the height at which prolonged lateral growth is possible (King 1998). These are all important effect traits for describing the tree canopy, which is related to the amount of light transmitted to the understory species.

Leaf phenology primarily consists of the number of months per year that the canopy is green (Cornelissen et al. 2003). Deciduous species, like most of the ones found at the study site, evade loss of important foliar resources through the reabsorption and shedding of leaves before the dry season (Cornelissen et al. 2003; Pugnaire & Chapin 1992; Kazakou et al. 2007). This temporal leaf shedding during drought periods, also prevents water loss (Haase et al.

2000; Ackerly 2004). The seasonal variation in the tree water status seems to be the key determinant of phenology (Bochert 1994).

Leaf size and its interspecific variation is important in terms of leaf energy and water balance since its has been connected with climatic variation and heat stress, cold stress, drought stress and high radiation stress tend to select for smaller leaves (Kunzmann 2005). Another important aspect of leaf size is that it is linked to ecological strategy with respect to environmental nutrient stress and disturbances with climatic zone, and also to allometric factors such as plant size, twig size anatomy and architecture (Cornelissen et al. 2003; Kunzmann 2005).

Specific leaf area (the projected area of a fresh leaf divided by its dry mass) values that are low tend to correlate with relatively high investments in leaf defenses (particularly structural) and a long leaf life span (Cornelissen et al. 2003; Kunzmann 2005). Species in rich environments tend to have a higher SLA than those associated with resource stressed areas (Cornelissen et al. 2003). This is a soft trait, which is easy to measure and is positively correlated with Relative Growth Rate (RGR), and tends to decrease with abiotic stress (Cornelissen et al. 1996; Lambers et al. 1998; Reich et al. 1998; Antúnez et al. 2001; Galmes et al. 2005; Kunzmann 2005; Wright et al. 2005; Ordoñez et al. 2009, Padilla et al. 2009). Relative growth rate has been defined as the increase of biomass per time and per unit of mass already present in the plant (Poorter & Garnier 1999), and it has been found to change in response to drought events (Fernández & Reynolds 2000; Galmés et al. 2005). SLA is also correlated positively to mass-based maximum photosynthetic rate (Cornelissen et al. 2003; Kunzmann 2005). Lower values of SLA tend to correspond to long leaf lifespan and investments on high leaf structural investment.

The leaf dry matter content (dry weight of a leaf divided by its fresh water saturated mass) is another important trait since it relates to the average density of leaf tissues and tends to correlate negatively with the relative potential growth rates and positively with leaf lifespan (Cornelissen et. al. 2003, Kunzmann 2005). Leaves with high content of dry matter tend to be relatively strong, and it is assumed that they are more resistant to physical hazards such as heat or water stress (Cornelissen et al. 2003; Kunzmann 2005). On the other hand, species with low

values of LDMC tend to be associated with productive or highly disturbed environments (Cornelissen et al. 2003; Al Haj Khaled et al. 2005; Vile et al. 2005). Relative water content gives us an estimate of the hydraulic status of a plant, and is easier to measure than water potential (Pugnaire 2009). Physical strength in leaves is related to protection against abiotic (e.g. wind) and biotic factors (e.g. herbivory) and contributes to longer lifespan (Cornelissen et al. 2003).

Studies show that wood density is a trait that works as a good predictor of minimum (midday) leaf water potential and total daily transpiration, as both decrease linearly with increasing wood density for all individuals and species (Bucci et. al. 2004). There are also leaf properties associated with wood density like stomatal conductance, specific leaf area, and osmotic potential at the turgor loss point, all of which also have been found to decrease linearly with increased wood density (Bucci et al. 2004). Mitchell et al. (2008) found that wood density was closely associated with the species ability to withstand more negative water potentials during summer. It has also been mentioned that as wood density increases, there is more resistance to embolism (Bucci et al. 2004). On the other hand, a dense bark provides the structural strength that a plants needs to stand firm and the durability that it needs to live for a sufficiently long period of time (Cornelissen et al. 2003). The stem density is related to relative growth rate (RGR), and higher RGR yields lower SSD. It also is related to physical damage produced by abiotic factors, high defenses with high values of SSD (Cornelissen et al. 2003). The twigs with high dry matter content are expected to dry out relatively fast during the dry season (Cornelissen et al. 2003).

3 REFERENCES

Ackerley, D. 2004. Functional strategies of Chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs 74:25-44

Al Haj Khaled, R.; Duru, M.; Theau, J.P.; Plantureux, S.; Cruz, P. 2005. Variation in leaf traits trough seasons and N-availability levels and its consequences for ranking grassland species. Journal of Vegetation Science 16:391-398

Altieri, M.A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74:19-31

Antúnez, I.; Retamosa, E.C.; Villar, R. 2001. Relative growth rate in phylogenetically related deciduous and evergreen woody species. Oecologia 128:172-180

Bochert, R.1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecological Society of America 75(5): 1437-1449

Bucci, S.J.; Goldstein, G.; Meinzer, F.C.; Scholz; Franco, A.C.; Bustamante, M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiology 24:891-899

Carpenter, S.R.; Bennett, E.M.; Peterson, G.D. 2006. Scenarios for ecosystem services: an overview. Ecology and Society 11(1) Available at: http://www.ecologyandsociety.org/vol11/iss1/art29/

Chapin, F.S. 1991. Integrated responses of plants to stress. A centralized system of physiological responses. BioScience 41:29-36

Coder, K.D. 1999. Tree selection for drought resistance. The University of Georgia, Warnell School of Forest Resources, Athens GA. 4p. Available at: http://www.utextension.utk.edu/publications/spfiles/sp570.pdf

Cornelissen, J.H.C.; Castro Diez, P.; Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology 84:755-765

_____; Lavorel, S.; Garnier, E.; Díaz, S.; Buchmann, N.; Gurvich, D.E.; Reich, P.B.; ter Steege, H.; Morgan, H.D.; van der Heijden, M.G.A.; Pausas, J.G.; Poorter, H. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335-380

Diaz, S.; Cabido, W. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution, 16 (11):646-655

_____; Hodgson, J.G.; Thompson, K.; Cabido, M.; Cornelissen, J.H.C.; Jalili, A.; Montserrat-Martí, G.; Grime, J.P.; Zarrinkamar, F.; Asri, Y.; Band, S.R.; Basconcelo, S.; Castro-Díez, P.; Funes, G.; Hamzehee, B.; Khoshnevi, M.; Pérez-Harguindeguy, N.; Pérez-Rontomé, M.C.; Shirvany, F.A.; Vendramini, F.; Yazdani, S.; Abbas-Azimi, R.; Bogaard, A.; Boustani, S.; Charles, M.; Dehghan, M.; de Torres-Espuny, L.; Falczuk, V.; Guerrero-Campo, J.; Hynd, A.; Jones, G.; Kowsary, E.; Kazemi-Saeed, F.; Maestro- Martínez, M.; Romo-Díez, A.; Shaw, S.; Siavash, B.; Villar-Salvador, P.; Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295-304

FAO (Food and Agriculture Organization of the United Nations). 2006. Cattle ranching and deforestation. Livestock Policy Brief No. 03. New York: United Nations. Available at: http://193.43.36.103/ag/againfo/resources/en/pubs_sap.html

Flynn, D.F.; Gogol-Prokurat, M.; Nogeire, T.; Molinari, N; Trautman, B.; Simpson, N.; Mayfield, M.; DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22-33

Galmés, J.; Cifre, J.; Medrano, H.; Flexas, J. 2005. Modulation of relative growth rate and its components by water stress in Mediterranean species with different growth forms. Oecologia 145:21-31

Gitay, H.; Noble, I.R. 1997. What are functional types and how should we seek them? In: Smith T.M.; Shugart, H.H.; Woodward F.I. (eds.). Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge pp. 3-19

Haase, P.; Pugnaire, F.I.; Clarck, S.C.; Incoll, L.D. 2000. Photosynthetic rate and canopy development in the drought-deciduous shrub *Anthyllis cytisoides* L. Journal of Arid Environments 46:79-91

Holbrook, K.M.; Whitbeck, J.L.; Mooney, H.A. 1995. Drought responses of neotropical dry forest trees. Pages: 243-276 In: Bullock, S.H.; Moone, H.A.; Medina, E. (eds.) 1995. Seasonally Dry Tropical Forests. Cambridge University Press, Great Britain 450p.

Hulme P.E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 42:784-794

Harvey, C.; Alpizar F.; Chacon M.; Madrigal, R. 2005. Assessing linkages between agriculture and biodiversity in Central America: Historical overview and future perspectives. The Nature Conservancy, San Jose, Costa Rica. 162p.

Hooper, D.U.; Solan, M.; Symstad, A.J.; Díaz, S.; Gessner, M.O.; Buchmann, N.; Degrange V.; Grime, P.; Hulot, F.; Mermillot-Blondin, F.; Roy, J.; Spehn, E.; van Peer, L. 2002. Species diversity, functional diversity, and ecosystem functioning. In: Loreau, M.; Naeem, S.; Inchausti, P. (eds.). 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives Oxford University Press, Oxford, pp. 195-208

InfoStat. 2007. Manual del Usuario. Grupo InfoStat, FCA, Universidad Nacional de Córdoba. Primera edición, Editorial Brujas. Argentina, 314 p.

Kazakou, E.; Garnier, E.; Navas, M.L.; Roumet, C.; Collin, C.; Laurent, G. 2007. Components of nutrient residence time and the leaf economics spectrum in species from Mediterranean old-fields differing in successional status. Functional Ecology 21:235-245

King, D.A. 1998. Influence of leaf size on tree architecture: first branch height and crown dimensions in tropical rain forest trees. Trees 12:438-445

Kramer, P.J.; Kozlowski. 1979. Physiology of woody plants. Academic Press, New York

Kunzmann, D. 2005. Leaf traits. In: Knevel, I. C.; Bekker, M.; Kunzmann, D.; Stadler, M.; Thompson, K. 2005.The LEDA Traitbase: Collecting and Measuring Standards of Life-history Traits of the Northwest European Flora.

Lambers, H.; Chapin, F. S.; Pons, T. L. 1998. Plant Physiological Ecology. Springer-Verlag, New York. 610 p.

Lavorel, S.; Grigulis, K.; Mclntyre, S.; Williams, N.S.G.; Garden, D.; Dorrough, J.; Berman, S.; Quétier, F.; Thébault, A.; Bonis, A. 2008. Assessing functional diversity in the field – methodology matters! Functional Ecology 22:134-147

_____; Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545-556

Laliberté, E.L.; Wells, J.A.; DeClerck F.; Metcalfe, J.D.; Catterall, C.P.; Queiroz, C.; Aubin, I.; Bonser, S.P.; Ding, Y.; Fraterringo, J.M.; McNamara, S.; Morgan, J.W.; Sánchez Merlos, D.; Vesk, P.A.; Mafield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology letters 13:76-86

Loreau, L.; Naeem, S.; Inchausti, P.; Bengtsson J.; Grime, J.P.; Hector, A.; Hooper, D.U.; Huston, M.A.; Raffaelli, D.; Schmid, B.; Tilman, D.; Wardle, D.A. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294(5543):804-808

Markesteijn, L.; Poorter, L. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. Journal of Ecology 97(2):311-325

_____; 2010. Drought tolerance of tropical trees; Functional Traits, Trade-offs and Species Distribution. PhD thesis, Wageningen, Neatherlands. Wageningen University, 204p.

Meinzer, F.C. 2003. Functional convergence in plant responses to the environment. Oecologia 134:1-11

Millennium Ecosystem Assessment (MEA). 2005. Ecosystems and human well-being: current state and trends. Island Press, Washington, D.C., USA, 948p.

Mitchell, P.; Veneklaas, E.; Lambers, H.;Burgess S. 2008. Using multiple trait associations to define hydraulic functional types in plant communities of south-western Australia. Oecología 158(3):385-397

Nair, P.K.R. 1993. An Introduction to Agroforestry. Kluwer Academic Publishers. The Netherlands. 543p.

Ordoñez, J.C.; van Bodegom, P.M.; Witte, J. M.; Wright, I.J., Reich, P.B.; Aerts, R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. Global Ecology and Biogeography, 18:137-149.

Padilla, F. M.; Miranda, J.D.; Jorquera, M.J.; Pugraire, F.I. 2009. Variability in amount and frequency of wáter supply affects roots but not growth of arid shrubs. Plant Ecology.

Pomareda, C. 1998. Situación y perspectiva de la ganadería e industrias afines en Centroamérica. En: Taller regional sobre desafíos y oportunidades de la ganadería e industrias afines en Centroamérica. Consejo agropecuario centroamericano/ proyecto RUTA-Banco Mundial. Guatemala.

Poorter, H.; Garnier, E. 1999. Ecological significance of inherent variation in relative growth rate and its components. Handbook of functional plant ecology (Eds F. I. Pugnaire and Valladares) Marcel Deker, Inc., New York, pp. 81-120.

_____; Markesteijn, L. 2007. Seedling Traits Determine Drought Tolerance of Tropical Tree Species. Biotropica 40(3):321-331

Primack, R.; Rozzi, R.; Feisinger, P; Massardo, F. (eds.) 2001. Fundamentos de Conservación Biológica: perspectivas latinoamericanas. Fondo de Cultura Económica, D.F., México

Pugnaire, F.I.; Chapin, F.S. III.1992. Environmental and physiological factors governing nutrient resorption effiency in barley. Oecologia 90:120-126.

_____; Valladares, F. (eds.). 2000. Functional Plant Ecology (2nd ed.) CRC Press, Boca Ratón. FL. USA. 724 p.

_____. 2009. Functional Diversity: An ecological framework for sustainable and adaptable agro-forestry systems in landscapes of semi-arid and arid ecoregions. FUNCiTREE Project report.

Santiago, L.S.; Kitajima, K.; Wright, S.J.; Mulkey, S.S. 2004. Coordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest. Oecologia 139:495-502

Swindale, L.D. & Bidinger, F.R. 1981.The human consequences of drought and crop research priorities for their alleviation. In: Pleg, L.G.; Aspinal, D. (Eds.), The Physiology and Biochemistry of Drought Resistance in Plants. New York, Academic Press, USA, pp.1-13.

Rauscher, S.A.; Giorgi, F.; Diffenbaugh, N.S.; Seth, A. 2008. Extension and Intensification of the Meso-American mid-sumer drought in the twenty-first century. Climate Dynamics 31:551-571

Reich, P.B.; Tjolker, M.G.; Vanderklein, D.W.; Bushena, C. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species growth in high and low light. Functional Ecology 12:327-338

Sánchez, D.M; López, M.; Medina, A.; Gómez, R.; Harvey, C.E.; Vilchez, S.; Hernández, B.; López, F.; Joya, M.; Sinclair, F.L.; Kunth, S. 2004. Importancia Ecológica y socioeconómica de la cobertura arbórea de un paisaje fragmentado de bosque seco de Belén Rivas, Nicaragua. En publicación: Revista Encuentro No. 68. UCA, Universidad Centroamericana, Managua, Nicaragua. 14p.

Smith, R.L. 1996. Ecology and Field Biology. (5ta ed.) Addison-Wesley Educational Publishers, Inc. U.S.A., 740 p.

Tilman, D.; Knops, J.; Wedin, D.; Reich, P.; Ritchie, M.; Siemann, E. 1997. The influence of Functional Diversity and Composition on Ecosystem Processes. Science 277(5330):1300-1302

Violle, C.; Navas, M.L.; Vile, D.; Kazafou, E.; Fortunel, C.; Hummel, I.; Garnier, E. 2007. Let the concept of trait be functional! Oikos 116:882-892

Vile, D.; Garnier, E.; Shipley, B.; Laurent, G.; Navas, M.L.; Roumet, C.; Lavorel, S.; Díaz, S.; Hodgson, J.G.; Lloret, F.; Midgley, G.F.; Poorter, H.; Rutherford, M.C.; Wilson, P.J.; Wright, I.J. 2005. Specific leaf area and dry matter content estimate thickness in laminar leaves. Annals of Botany 96:1129-1136

Weiher, E.; Van der Werf, A.; Thompson, K.; Roderick, M.; Garnier, E.; Eriksson, O. 1999. Challenging Theophrastus: A common core list of plant traits for Functional Ecology. Journal of Vegetation Science 10:609-620

Westoby, M.; Wright, J. 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21(5):261-268.

4 ARTICLE I

Functional characterization of six tree species according to drought tolerance and water relations on silvopastoral systems in Rivas, Nicaragua

Abstract

It has been suggested that modern agrosilvicultural systems need to be designed based on the knowledge of the relationship between plant species traits and their capacity to provide specific function through ecosystem processes. The purpose of this study was to evaluate the potential of functional ecology as an alternative method to respond to specific management needs and the provision of ecosystem services in semiarid agroecosystems. Through studying plant traits, we hope to improve the functional capacity of agroecosystems to support climate variability and maintain human livelihoods. We considered associations between morphological, physiological, and phenological plant traits relating to drought tolerance and water use efficiency of six species commonly found in pastures of Rivas, Nicaragua. We selected a total of 20 plant, leaf and stem traits measured for six species (*Albizia saman*, *Guazuma ulmifolia*, *Coccoloba caracasana*, *Tabebuia rosea*, *Crescentia alata*, and *Enterolobium cyclocarpum*). We used mixed generalized linear models and principal components analysis to identify trait suites, tradeoffs between traits and to classify species according to specific drought response strategies. We identified four major trait associations in the species we studied. The first primary axis distinguished drought response strategies and was associated with the tradeoffs between drought avoidance and drought tolerance. The dominant traits associated with this axis differed in canopy density, leaf area index, leaf phenology, and leaf thickness. The second important axis consisted of traits related to resource acquisition such as leaf area, leaf tensile strength, wood density, and specific leaf area. Species with the greatest drought avoidance characteristics was *T. rosea*, while *C.caracasana* was more tolerant.

4.1 INTRODUCTION

Nicaragua's agricultural landscapes are dominated by a matrix of pastures or cultivated lands that maintain some tree cover in the form of scattered trees, small patches of secondary forest, scrubland, live fences and riparian forests (Harvey et al. 2006). In Rivas, the landscape has been extensively modified as a result of extensive agricultural and cattle-ranching practices since the colonial era. This has aggravated the lack of resilience to externally driven changes like climate change (MEA 2005). The recent work of Laliberté et al. (2010) made it evident that intensified management of ecosystems for resource extraction purposes can increase the vulnerability to disturbances. Their study comprised a meta-analysis across different sites and ecoregions, where Rivas was one of the sites that showed the greatest loss of resilience, through the loss of response diversity, as land-use intensity increased.

Since global change is expected to alter the conditions for plant growth in most terrestrial habitats, it is important to understand the physiological mechanisms that enable and determine plant survival under suboptimal conditions (Chapin 1991). The consequent past, present, and future loss of functional diversity in these areas threatens the capacity of these human dominated landscapes to provide ecosystem services (Flynn et al. 2009). Ecosystem services (ES) are defined as "the benefits people obtain from ecosystems", and include provisioning services such as food and water; regulating services floods, drought, land degradation, and disease; supporting services such as soil formation and nutrient cycling; and cultural services such as recreational, spiritual, religious and other nonmaterial benefits (MEA 2005). In pasture-dominated landscapes the assurance of provisioning of services, such as drought resistance by local arboreal species, becomes particularly important. Substantial drying trends are predicted to occur in dry regions of Central America (Neeling et al. 2006), and according to the IPCC (2005); semiarid areas such as Rivas are expected to have modifications in precipitation regimens, increments in evapotranspiration, and a rise in the frequency and duration of drought events as a function of global climate change. As such, it is important to understand the response diversity encompassed by the species pool in Rivas, and the impacts that these species have on the provisioning of ES.

The theoretical body of functional ecology proposes that plant attributes are related to environmental conditions so that they could be used to assess a species tolerance to stress

(Pugnaire & Valladares 2007); water stress is no exception. Functional ecology proposes that the functional characteristics of any species are more important than its taxonomic identity. Because of this, species with distinct evolutionary histories can be grouped based on shared trait characteristics. Based on this observation, we can functionally characterize individuals of different species and they can be grouped according to their attributes forming plant functional groups (PFG's). The notion of plant functional groups or plant functional types (PFTs) is founded on the notion that functional traits can be grouped according to their responses to environment conditions and disturbances, or based on their effect on ecosystem functions, or both (Lavorel & Garnier 2002). So we can aim to identify the attributes that differentiate species into groups of alternative responses and effects on ecosystems, and agroecosystems as well.

Modern sustainable agrosilvicultural systems need to be designed based on the knowledge of the already mentioned relationship between plant species traits and their capacity to provide specific functions through ecosystem processes. Based on this assumption, increasing effect and response functional biodiversity in agroecosystems is a promising approach to increase the sustainability of production systems. And in this line of thought, by providing more variety or diversity of responses to stress we can improve the resilience of productive systems, and by identifying the species with a clear effect on the ecosystem process of interest for producers, we can improve the provisioning of functions of interest (Laliberté et al. 2010). As such, we need to aim at the development of agroecological methodologies and systems that are multifunctional (Altieri 1999) in order to meet the challenges of production and adaptability. The question remains whether principles of functional diversity and customized trait combinations of species assemblages, can be used to meet these challenges, and whether people want to implement these technocratic fixes.

In this study we identified plant trait tradeoffs to detect different axes of differentiation for functional classification and grouping of tree species in silvopastroral systems. To do so, we selected traits that are known to be important in terms of plant responses to drought and plant effects on ecosystem processes (in this case, bellow crown herbaceous layer). Our specific objectives were: (a) to characterize species according to selected traits and to determine the relationship between functional traits, (b) to use these relationships to

characterize species-specific water use strategy and tolerance to drought, and finally, (c) to identify potential functional response groups among the species.

4.2 MATERIALS AND METHODS

4.2.1 Study area

The study area is located in the southeastern portion of Nicaragua, on the isthmus bounded by the Pacific Ocean to the west and Lake Nicaragua to the East. This vegetation is classified as a Tropical Dry Forest life zone according to Holdridge (1978). Elevation in this area oscillates between 100 to 200 m.a.s.l. and the annual mean precipitation is approximately 1400 mm with an average temperature oscillating around 27 °C. The mean relative humidity is 78%, and the average wind velocity is 3.2 m/sec (INETER 2005). The site is subject to a marked dry season during the months of November to April that puts severe production limitations on farmers, and a wet season from April to November. Soils are predominated by vertisols with high shrink swell capacity, and very high clay content.

Livestock production in Rivas is extensive and dual purpose (milk and meat) on small to medium sized farms that are managed and owned by landowners (Lopez et al. 2004). The dominant silvopastoral systems of the region are isolated trees in pastures and live fences. Sanchez et al. (2004) reports an average of up to 16.2 trees ha^{-1} pastures dominated by very few species. The most abundant tree species found in pastures are (in descending order): *Cordia alliodora*, *Guazuma ulmifolia*, *Tabebuia rosea*, *Byrsonima crassifolia*, *Gliricidia sepium*, and *Cordia dentata* (López et al. 2004a; Sánchez et al. 2004). The producers of Rivas have a wide knowledge of these tree species and the uses they provide, including fodder and fruit production for livestock, firewood, timber and medicine (Joya et al. 2004).
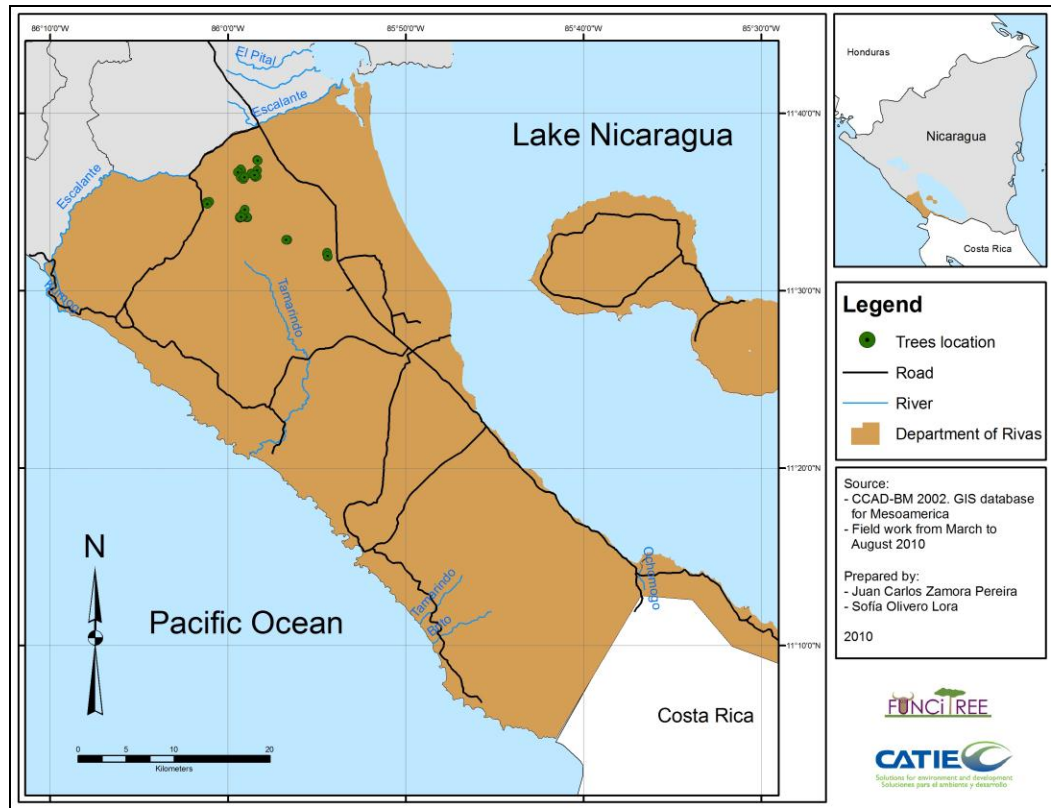
Figure 2. Study area map in Nicaragua and general location of selected individuals in Rivas Department.

4.2.2 Species selection

More than 150 species of trees are found within the Rivas areas (Sanchez et al. 2005). In order to select six species from distinct functional groups for this study, we performed a cluster analysis with the trait values derived from regional floras and stored in the FUNCiTree species trait database (Flynn et al. 2009; Sánchez et al. 2005). We focused primarily on traits that are known to have an effect on species response to drought, and that have an effect on "understory" productivity. Here we used understory to describe the conditions below the crown of an individual tree. We used total tree height, spinescence, foliar area, leaf phenology, wood density, and nutrient uptake strategy as the species traits for this cluster. Spinescence was poorly represented and was eventually excluded from the analysis. We evaluated the distinct clusters produced by the dendrogram and excluded rare species, or those that had missing trait data. We divided the remaining 48 species into five clusters and selected six species with the most differences as possible from the top, middle, and lower clusters targeting

two species per group to later test whether within group variation would be less than between group variation with field data. In the first group were A*lbizia saman*, *Guazuma ulmifolia* and *Crescentia alata* on the extremes of a second group, and *Tabebuia rosea* and *Coccoloba caracasana* in a third group. *Enterolobium cyclocarpum* which was completely separated from the five groups and this separation was driven mainly by tree height. For the other two groups, consisting of four species each, we did not find enough repetitions in the field in order to include them in the study.

Working with isolated trees in pastures for trait research is advantageous because it permits measurements of individuals, free of the influence of neighbors (as compared to research in high density forest systems). Cornelissen et al. (2003) suggest that traits should be measured on "robust, well grown plants, located in well-lit environments, preferable totally unshaded". The six species evaluated in this study (Table 2) are among the most common in the silvopastoral systems of Rivas, Nicaragua. All species are deciduous, except for *C. caracasana* which is evergreen. As they are common in the area, they offer a greater chance of impacting major ecosystem processes of interest (Diaz et al. 2004).

Table 1. Species selected for the study, their common name and respective family.

Common name	Specie	Family
Genízaro	*Albizia saman*	Fabaceae
Guácimo	*Guazuma ulmifolia*	Sterculiaceae
Papalón/Papaturro	*Coccoloba caracasana*	Polygonaceae
Roble	*Tabebuia rosea*	Bignoniaceae
Jícaro	*Crescentia alata*	Bignoniaceae
Guanacaste	*Enterolobium cyclocarpum*	Fabaceae

With the six species selected, we then identified six individuals from each species in the field using the following criteria: (a) healthy adults (medium to large sized) trees with foliage exposed to the sun, (b) isolated from neighboring trees by at least 10 m from crown edge to crown edge, (c) located at least 20 m from any adjacent water body, (d) not located on

a hillside, (e) established pastures (3> years), (f) farmer's permission to work on their farm, and (g) within a vertisol soil type.

4.2.3 Traits selection

The focus of our trait work is on traits related to drought tolerance and water use efficiency. As previously mentioned, there are three primary levels at which trees respond to changes in resources availability: structural, physiological, and phenological (Holbrook et. al. 1995). We selected traits (Table 2) that would permit us to take into consideration these three response types. Other trait selection criteria used were: 1) the relevance with our research objectives, 2) the practicality of collecting and measuring each trait, and 3) their ability to define trade-offs between "hard" based on field measures, and "soft" traits derived from the literature. Another driving factor in the traits selection was our desire to determine whether soft traits can serve as reasonable surrogates for the hard traits, which were measured here.

The traits selected are mainly leaf traits (ten), plus eight whole plant characteristics and three stem traits. Even though root traits are known to be related with water uptake and plant water stress strategies, they were not considered in this study because of the complexity of their measurements. The roots of the subset of the individuals studied here will be the focus of a root-based study in 2011.

Table 2. List of all variables used in this study, abbreviation, description, unit of measure, level of definition (I=individual, SP=specie,) and the source of data used.

Trait	Description	Unit	Level	Source
Whole plant				
TH	Tree height	m	I	Measurements, Literature
CH	Canopy height	m	I	Measurements
HLB	Height to the lowest branch	m	I	Measurements
C-D	Canopy diameter	m	I	Measurements
CD	Canopy density	%	I	Measurements
CS	Canopy shape	m/m	I	
DBH	Diameter breast height	dm	I	Measurements
PH	Crown phenology		SP	Literature
Leaf traits				
LA	Leaf area	mm^2	I	Measurements
SLA	Specific Leaf Area	mm^2mg^{-1}	I	Measurements
LDMC	Leaf Dry Matter Content	$mg\ g^{-1}$	I	Measurements
LRWC	Leaf relative water content	%	I	Measurements
LAI	Leaf Area Index	-	I	Measurements
DIFN	Transmitted light	%	I	Measurements
PL	Petiole length	mm	I	Measurements
TS	Leaf tensile strength	Nmm^{-1}	I	Measurements
LT	Leaf thickness	mm	I	Measurements
LN	Leaflet number	-	SP	Measurements
Stem traits				
TDMC	Twig dry matter content	$mg\ g^{-1}$	I	Measurements
TRWC	Twig relative water content	%	I	Measurements
WD	Wood density	$mg\ mm^{-3}$	P	Literature

4.2.4 Traits measurements

We used the standardized protocols by described by Cornelissen et al. (2003) for most of the trait measures. We made adaptations to some trait measures in relation to the specific research objectives and other available protocols. Below we briefly describe the traits measurements specifications.

Diameter at Breast Height, Tree Height, Canopy Height, Height to the lowest branch, and Canopy Diameter

Whole plant traits were recorded for each individual in the study. We recorded diameter at breast height (1.3 meters) using a diameter tape and measured tree height and height to the lowest branch for each individual with a clinometer. Canopy height consisted of tree height minus the height to the lowest branch. These were measured as characteristics for the individuals related to the age and general physiognomy of the tree, and in order to control some of the intraspecific variation, rather than species traits.

Canopy shape

We calculated the ratio between canopy diameter and canopy height, which served as a descriptor of canopy shape where a value of 1 is considered as a circular crown, <1 an oblong crown, and >1 a wide crown.

Canopy density

We measured canopy density using a standard Cajansus, LIS, convex spherical densiometer (Forestry Suppliers Inc., USA) with four measures taken in each of the cardinal point directions, giving the percent canopy closure to the nearest percentage point. We used the average of the four measurements as an indicator of the individual tree's canopy density during the dry season (CD1) and the transitional season (CD2).

Leaf Area Index and Transmitted Light

We made measurements of leaf area index (LAI) and transmitted light using a LI-COR LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, Nebraska). This instrument uses a fisheye optical sensor to determine canopy structure from measures of solar radiation.

To determine the LAI of individual trees during the dry season a cover was placed over the fisheye sensor that limits the field of view to a forth (25%) of the crown. We first measured in open space, followed by measurements beneath the canopy facing each cardinal direction to account for 100% of tree crown cover. One repetition of the procedure was done and the average of leaf area index and percentage of transmitted light for each tree was automatically computed by the instrument as an average of all measurements. Measures were made on cloudy days, during dusk, or shortly before and after sunset to avoid direct contact with the sun.

Leaf Area and Specific Leaf Area

For the evaluation of leaf area and specific leaf area (SLA), we followed the Cornelissen et al. (2003) protocol. We randomly collected four leaves from the six individuals per species ensuring that each leaf was fully illuminated and with the least of herbivory damage as possible. The leaves were then sealed in plastic bags, and transported to the lab in an ice chest to be processed. In some cases we were not able to immediately scan the leaves, in which we kept them a maximum of 48 hours in the refrigerator until it was possible to measure. For compound leaves with numerous leaflets, we pressed the samples and scanned them as soon as possible. The leaves were scanned using an Epson Stylus TX210 with 600 dpi resolution. We divided the leaves into smaller sections for species with leaves too big for the scanner, and summed the values of the leaflets. Leaf area was determined using Leaf Area Measurement Program Software (Unit of Comparative Plant Ecology, University of Sheffield, 2003) and included the leaf petiole. We oven dried the leaf samples at 60 °C for at least 72 hours to determine SLA (Leaf Area/Dry weight).We weighed each dried leaf and calculated the SLA as the average of four leaves per individual plant.

Leaf Dry Matter Content

We used the same procedure as for the SLA to collect the samples. We attempted several methods for rehydrating the leaves (Cornelissen et al. 2003; Garnier et al. 2001), but field conditions and significant distance from the field sites to the lab had different effects on the leaf conditions particularly for pinnately compound leaves. In the end, we cut the leaves and immediately weighed them. We placed their petioles in sealed plastic water containers and transported them in an ice chest back to the lab. We left the samples in a darkened box

overnight to achieve full rehydration. Then we gently dried and weighed each leaf before placing them in a paper bag to dry them at 60 $^{\circ}$C for a minimum of 76 hours, before reweighing them.

Leaf relative water content

Leaf relative water content is the water fraction stored in a leaf in comparison to the quantity of water stored when saturated. As with other leaf traits, this was measured for four leaves per individual. We measured the samples in the field to obtain their fresh weight before rehydrating them to obtain their turgid weight. The leaves were oven dried for 72 hour at 60°C, and reweighed. This trait differentiates from LDMC since it is an average estimation of the water content instead of the dry matter content. The following equation was used (González & González-Vilez 2001):

$$ RWC = \frac{fresh\ weight - dry\ weight}{saturaded\ weight - dry\ weight} \times 100 $$

Tensile strength

To measure leaf tensile strength, we cut a 1 cm wide fragment of fresh leaf using scissors. With species whose leaves were smaller than 1 cm, we used a smaller width. We put the sections, which excluded the mid-vein or other prominent veins, in a tearing apparatus and gradually applied increasing tension until the leaf snapped. We recorded the tension at the moment of fracture in g/cm^2, converted the value to Newtons (1kg = 10N), and divided the total force by the width of the leaf. This is the same method described by Hendry and Greme (1993) in the Cornelissen et al. (2003) protocol.

Petiole length, Leaflet number, and Leaf Thickness

We collected four leaves from each individual and used vernier calipers to measure petiole length, leaflet number and leaf thickness in the field. We counted the number of leaflets of compound leaves and gave a value of one to simple leaves. Leaf thickness was measured with calipers to the nearest 0.01 mm excluding the midvein.

Twig dry matter content and Twig relative water content

For twig dry matter content and twig relative water content we randomly collected two 20 cm segments of terminal twigs from each individual. We recorded the fresh weight of the sample and placed it in a plastic bag to be transported back to the lab in an ice chest. We placed the thickest end of the twig in water at 3 to 4 cm of depth in a sealed dark container for 24 hours. We then removed dried, and weighed (saturated weight) each sample before placing in an oven at 60°C for 72 hours and reweighing the twig to get dry weight. The oven dry mass of a terminal twig divided by its fresh water saturated mass is TDMC expressed in mg g^{-1}.

Stem specific density and Phenology

The stem specific density (SSD) is the oven dried mass of a section of the main stem of a plant divided by the volume of the same section when it is still fresh, expressed in mg mm^{-3}. This trait was obtained from literature (Flynn et al. 2009; Sánchez et al. 2005). In the case of crown phenology, we used the information already recorded in the literature (Table 3), and was visually confirmed in the field. We calculated this as the number of dry season months that the plant has leaves divided by the total number of months during the dry season.

Table 3. Crown phenology for each species throughout the year, grey cells represent the months with leaves and the white cells the months without leaves. Data obtained from Flora de Nicaragua (Steven, 2001) and Árboles de Centroamérica (Cordero & Boshier 2003).

Species	PH	Months											
		J	F	M	A	M	J	J	A	S	O	N	D
Enterolobium cyclocarpum	0.6	▓			▓	▓	▓	▓	▓	▓	▓	▓	▓
Albizia saman	0.4				▓	▓	▓	▓	▓	▓	▓	▓	▓
Crescentia alata	0.6	▓	▓	▓		▓	▓	▓	▓	▓	▓	▓	▓
Guazuma ulmifolia	0.6	▓	▓		▓	▓	▓	▓	▓	▓	▓	▓	▓
Tabebuia rosea	0.2					▓	▓	▓	▓	▓	▓	▓	▓
Coccoloba caracasana	1.00	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓

4.2.5 Statistical analysis

We ran descriptive statistics (mean, standard deviation, standard error, coefficient of variation, minimum and maximum) for all variables. All variables needed to be standardized because of the differences in variables and because of the heterogeneity of the variance of the

different traits. A cluster analysis using Pearson correlation with Ward linkage was used to portray the relations between traits and a general Pearson analysis matrix to determine the directions and relevance of these associations with a 95% confidence interval. An analysis of variance using mixed models was used to compare trait differences among species and a standardized Fisher least significant difference (LSD) test. We proceeded to do a Principal Components Analysis (PCA) to analyze the multivariate traits associations, to explore the data and determine which variables are important in explaining information using biplot graphs (Gabriel, 1971) and eigenvectors to show the linear relations within the matrix. A final cluster analysis was done by species to illustrate the functional response groups found. The statistical analyses were performed using *INFOSTAT statistical software package*.

4.3 RESULTS

4.3.1 Traits relationships

General statistics are presented below to describe the basic features of the data and observe the general tendencies of the trait distribution for all species together (Table 4). The variable with the highest coefficient of variance was number of leaflets (198.76%) explained mainly because the trait compares simple and compound leaves. This is followed by leaf area (71.6%), and petiole length (71.0%). Nearly all remaining variables (TH, HLB, CH, C-D, CS, WD, PH, DIFN, SLA, CD1, CD2, LT, TS, LN, and TDMC) exhibited coefficients of variation (CV) below 50% indicating lower dispersion in their values, with the exception of DBH (60.46%) and LAI (54.25%). The lowest CV values that indicate more homogeneity are for LRWC and TRWC, with a 5.94% and 6.64% of variation respectively, followed by leaf dry matter content (10.71%).

Table 4. Mean standard deviation, specific error, coefficient of variation, minimum and maximum values for measured variables.

Variable	n	Mean	± S.E.	CV	Min	Max
Diameter at breast height (cm)	36	91.30	9.2	60.46	31.25	239.30
Tree height (m)	36	14.16	0.65	27.66	7.55	22.29
Height to the lowest branch (m)	36	2.57	0.14	33.31	1.15	5.26
Canopy height (m)	36	11.59	0.62	32.16	5.45	20.48
Canopy diameter (m)	36	17.12	1.11	39.00	10.05	38.90
Canopy shape (m/m)	36	1.51	0.06	24.99	0.82	2.25
Wood density (g/cm^2)	36	0.52	0.02	19.68	0.42	0.71
Phenology (months)	36	0.57	0.04	43.43	0.20	1.00
Leaf area index	36	1.44	0.13	54.25	0.22	3.37
Transmitted light (%)	36	0.37	0.03	49.24	0.08	0.84
Leaf area (mm^2)	36	21901.86	2613.42	71.59	1526.76	51374.03
Specific leaf area (mm^2 mg^{-2})	36	8.50	0.45	31.63	5.78	16.83
Canopy density 1 (%)	36	83.04	2.28	16.49	36.75	97.80
Canopy density 2 (%)	36	84.44	2.08	14.75	43.58	97.40
Petiole length (mm)	36	6.13	0.73	70.96	1.26	17.96
Leaf thickness (mm)	36	0.04	1.50E-03	21.06	0.03	0.05
Tensile strength (N mm^{-1})	36	0.79	0.06	48.57	0.26	1.54
Leaflet number	36	175.83	58.25	198.76	1.00	942.00
Leaf dry matter content (mg g^{-1})	36	387.93	6.92	10.71	250.46	490.20
Leaf relative water content (%)	36	0.91	0.01	5.94	0.77	1.00
Twig dry matter content (mg g^{-1})	36	440.76	16.77	22.82	279.18	746.88
Twig relative water content (%)	36	0.91	0.06	6.64	0.76	0.99

The variables that showed positive Pearson correlations with the significant values correlation coefficients ($r > 0.60$, $p < 0.0001$) were CH/TH, C-D/TH, C-D/CH, DBH/PH, DBH/LAI, PH/CD1, LAI/CD1, LAI/CD2, LAI/LT, LT/CD1, and LT/CD2 (see Appendix 1). It is important to highlight the correlations between phenology and canopy density (CD1) during the dry season ($r = 0.62$, $p < 0.0001$) because the complementarities among the leaf phenology patterns are reflected in both traits. Also, a slightly weaker but expected positive correlation was found between petiole length and transmitted light ($r = 0.56$, $p = 0.0003$), which suggest that the longer the petiole of the leaf a higher amount of light reaches the understory.

Several variables showed negative correlations at r values > 0.6 and $p < 0.001$. These include DBH/DIFN, PH/PL, WD/LT, DIFN/CD1, DIFN/CD2, DIFN/LT, PL/CD1, PL/CD2, LT/ PL, and finally TDMC/CD1. Petiole length (PL) was negatively correlated to phenology (PH) ($r = -0.73$, $p <0.001$) and canopy density 1 and 2 ($r = -0.64$, $p < 0.001$; $r + -0.65$, $p < 0.001$), and showed a weaker but significant correlation with Leaf Area Index ($r = -0.49$, $p=0.0022$). This indicates that the longer the petiole, the greater the amount of transmitted light passing through, the lower the density of the canopy (observe leaves differences in Appendix 3). Another important negative relation is between leaf area and wood density ($r = -0.59$, $p = 0.0002$).

4.3.2 Functional traits by species

Results from the mixed-model ANOVA for differences between species for each trait are shown in Table 5. All 19 measured traits showed significant differences between species ($p<0.05$). At Table 5 we can observe that the greatest canopy height value corresponds to *A. saman* (14 m ±1.27) and the lowest to *C. alata* (7 m ±1.27) with significant differences between the two. The height to the lowest branch was highest for *T. rosea* (3 m ±0.03) and *C. caracasana* with the lowest (2 m ±0.3). The highest mean canopy diameter (27.03m ±3.18) was found for *A. saman*. Consistent with this, we observed that the trait canopy shape was also greater for this species (1.84 ±0.15), indicating a crown that is wider than tall. The lowest value for canopy shape was for *T. rosea* (1.04 ±0.08) with a rounder crown.

Table 5. Mean values by species according to the selected variance model with standard error for measured traits(highest values in bold). LSD Fisher test in small letters (P<=0.05).

Trait	*A. saman*	*E. cyclocarpum*	*C. caracasana*	*G. ulmifolia*	*C. alata*	*T. rosea*	F	p
Canopy diameter	**27.03 ±3.18 a**	20.33 ±1.04 a	15.35 ±1.93 b	14.23 ±2.13 b	13.47 ±0.92 b	12.33 ±0.57 b	12.93	<0.0001
Canopy density 1	90.39 ±2.01 ab	86.85 ±2.28 bc	**94.65 ±1.74 a**	85.15 ±2.42 bc	80.85 ±2.85 c	60.34 ±7.11 d	7.74	0.0002
Canopy density 2	91.51 ±1.08 a	87.43 ±2.67 ab	**92.5 ±1.76 a**	87.78 ±3.58 ab	83.14 ±1.85 b	64.25 ±7.03 c	10.22	<0.0001
Canopy height	**14.92 ±1.27 a**	13.86 ±1.27 ab	10.24 ±1.27 cd	10.49 ±1.27 bcd	7.92 ±1.27 d	12.13 ±1.27 abc	4.4	0.0052
Diameter at breast height	102.92 ±14.48 ab	63.48 ±5.22 c	**185.68 ±20.45 a**	81.88 ±17.75 bc	60.73 ±4.79 c	53.12 ±8.04 c	9.5	<0.0001
Height to the lowest branch	2.55 ±0.3 abc	3.08 ±0.3 ab	1.9 ±0.3 c	2.39 ±0.3 bc	2.12 ±0.3 c	**3.37 ±0.3 a**	3.52	0.0151
Canopy shape	**1.84 ±0.15 a**	1.52 ±0.11 ab	1.50 ±0.11 ab	1.38 ±0.10 b	1.75 ±0.14 a	1.04 ±0.08 c	7.59	0.0002
Leaf area index	2.00 ±0.15 a	1.30 ±0.29 bc	**2.46 ±0.29 a**	1.35 ±0.18 b	0.91 ±0.03 c	0.62 ±0.11 d	18.54	<0.0001
Leaf dry matter content	405.29 ±7.67 a	377.63 ±25.84 ab	373.07 ±11.87 b	365.33 ±9.81 b	**418.24 ±13.99 a**	388.03 ±21.01 ab	3.33	0.0194
Leaf area	29590.14 ±3327.13 ab	33249.57 ±3852.43 ab	24589.8 ±2636.32 b	4098.89 ±277.18 c	1719.09 ±92.96 d	**38163.65 ±4581.39 a**	67.32	<0.0001
Leaf relative water content	0.89 ±0.02 ab	0.89 ±0.02 b	**0.94 ±0.01 ab**	0.87 ±0.03 b	0.91 ±0.02 ab	**0.94 ±0.01 a**	2.73	0.0424
Leaf thickness	**0.05 ±0.0015 a**	0.04 ±0.0015 b	**0.05 ±0.0015 a**	**0.05 ±0.0015 a**	0.03 ±0.0015 c	0.03 ±0.0015 c	40.88	<0.0001
Petiole length	5.41 ±0.18 c	6.24 ±0.14 b	2.88 ±0.25 d	1.41 ±0.05 e	6.21 ±0.32 b	**14.67 ±0.79 a**	361.3	<0.0001
Specific leaf area	7.35 ±0.44 b	10.18 ±0.99 a	6.96 ±0.39 b	**12.29 ±1.57 a**	7.26 ±0.43 b	6.95 ±0.38 b	4.04	0.0080
Twig dry matter content	418.40 ±22.01 a	407.26 ±8.48 a	346.65 ±17.47 a	439.63 ±39.81 a	491.27 ±18.64 a	**541.35 ±66.08 a**	7.42	0.0002
Tree height	**17.47 ±1.24 a**	16.94 ±1.24 a	12.14 ±1.24 bc	12.88 ±1.24 bc	10.04 ±1.24 c	15.49 ±1.24 ab	5.66	0.0013
Twig relative water content	0.91 ±0.02 b	0.96 ±0.01 a	**0.96 ±0.01 a**	0.93 ±0.01 ab	0.82 ±0.03 c	0.91 ±0.02 b	5.61	0.0013
Tensile strength	0.87 ±0.14 bc	0.47 ±0.06 de	1.1 ±0.13 ab	0.35 ±0.01 e	0.7 ±0.1 cd	**1.23 ±0.01 a**	1445.2	<0.0001
Transmitted light	0.19 ±0.03 a	0.39 ±0.05 ab	0.18 ±0.03 b	0.36 ±0.04 b	0.47 ±0.05 c	**0.61 ±0.05 c**	14.69	<0.0001

AIC and BIC as model selection criteria.

Another interesting individual characteristic was the diameter at breast height, which was highest in *C. caracasana* (185.68cm ±20.45and showed the highest variation for this trait and was different than the other species according to the LSD test. But this particular species was characterized for having multiple trunks, and so the values were higher. *A. saman* also had values of over 1m in diameter (102.92cm ±14.48) which indicates a selection of large mature trees in comparison. If we compare *A. saman* to the DBH of *E. cyclocarpium* (63.48cm ±5.22) we can see this more clearly since the former usually has wider trunks.

The highest values of canopy density and leaf area index during the dry season correspond to *C. caracasana* (94% ±1.74 and 2.46 ±0.29), which was expected for an evergreen species. The lowest canopy density values were observed for *T. rosea* (60% ±7.11) and leaf area index (0.62 ±0.11). The LSD Fisher showed significant differences for *C. caracasana* and *T. rosea* and for canopy density (p = 0.02) and leaf area index (p < 0.001).

In the case of leaf area the highest value was for *T. rosea* (38,163.65mm^2 ±4581.39) and we found significant differences among this species and *G. ulmifolia* (4098.89mm^2 ±277.18) and *C. alata* (1719.09mm^2 ±92.96). Nonetheless, we should mention that in the case of larger leaves, they had to be cut into pieces in order to scan them and with each scan additional error could have been introduced through the scanning process. We found differences among our species without problems, mainly because of the strong differences among leaf morphology as can be seen in Figure 3.

The petiole length was recorded as an indication of the amount of light that percolates the canopy. The actual amount of transmitted light through the canopy was also recorded. In both cases, *T. rosea* was the species with superior values with a 14 mm ±0.79 of petiole length and 61% ±0.05 transmitted light.

In the case of leaf thickness we have one group consisting of *A. saman*, *C. caracasana* and *G. ulmifolia* with mean values of 0.05mm ±0.0015. The former two leaves have more coriaceous surfaces, while *G. ulmifolia* surface contains a high density of pubescence on both sides. Another trait related to leaf structure and defenses is tensile strength, which was greatest

for *T. rosea* (1.23Nmm^{-1} ±0.01) in contrast to *G. ulmifolia* (0.35 Nmm^{-1} ±0.03). For *C. alata*, we have highest values of leaf dry matter content with 418.24 mg g^{-1} ±13.99.

For leaf relative water content the highest values coincided with the evergreen *C. caracasana* (0.94% ±0.01) and the most drought deciduous *T. rosea* (0.94% ±0.01). This is an interesting relation between two species who seem to have very different strategies. The measurements where conducted during the wet season so they imply water retention during abiotic conditions of no interest to the objectives of these studies and were eliminated from the species principal components and cluster analysis.

a) Albizia saman

b) Enterolobium cyclocarpum

c) Coccoloba caracasana

d) Tabebuia rosea

e) Crescentia alata

f) Guazuma ulmifolia

Figure 3. Images of scanned leaves belonging to the species considered in this study. Important to note they are not at original size scale.

In Figure 4, the first two principal component axes accounted for 55.7% of the total variation in trait values across the species. As was expected *T. rosea* (deciduous) and *C. caracasana* (evergreen) seem to be the species that showed the highest differentiation along the first axis. The traits largely associated to these differences are canopy density, leaf thickness, twig dry matter content, percentage of transmitted light, petiole length, leaf area index and leaf phenology (Table 5). In this PCA we can observe the variation among individuals of the same species. For example, *T. rosea* seemed to have more interspecific variation among the individuals, while in the case of *C. alata* and *G. ulmifolia* we have more defined groups. The other three species (*E. cyclocarpum, A. saman* and *C. caracasana*) have less interspecific differences in trait values, but they do overlap among this first axis.
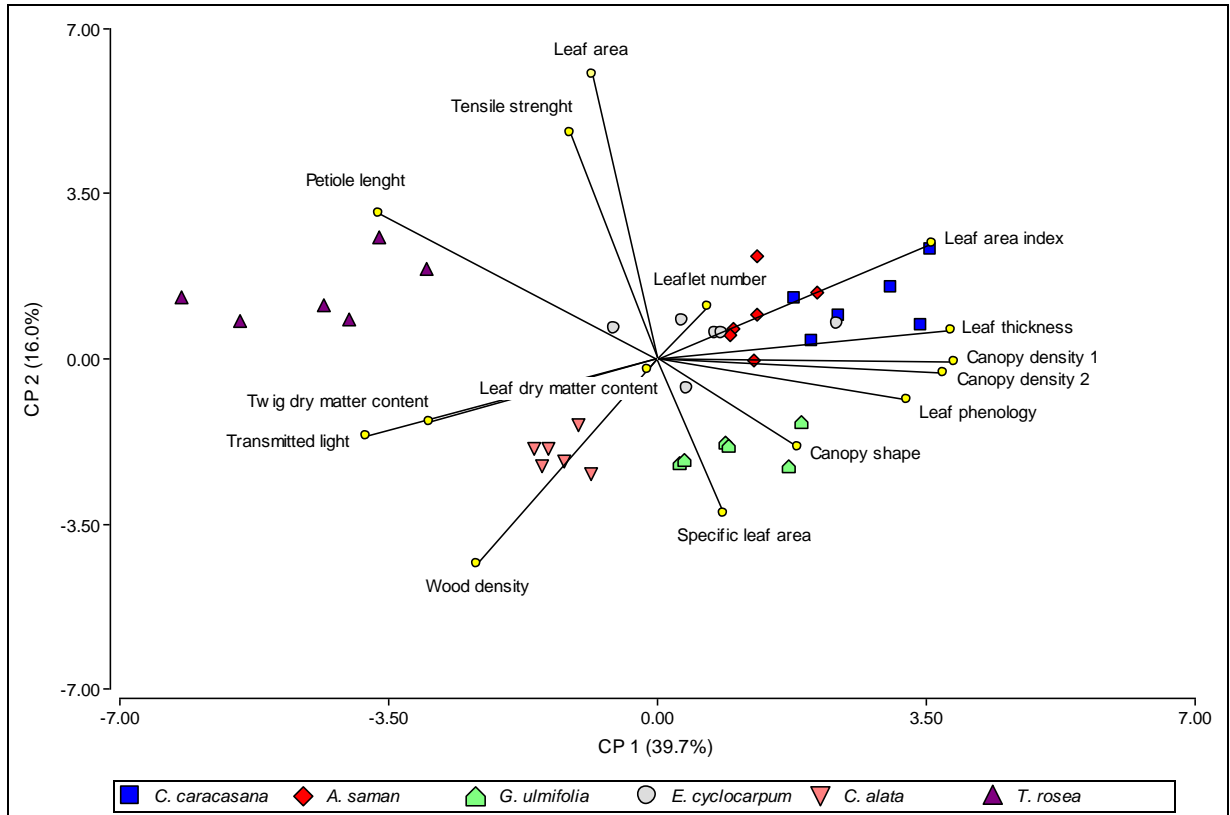
Figure 4. Principal components analysis for all traits that showed significant differences according to species.

This analysis defines species according to those that have dense canopies with thick leaves and low twig matter content on one extreme of the first PCA axis, and "thin" highly deciduous canopies with softer leaves and twig dry matter content on the other extreme of the

first axis. The first, right side group of traits is associated with a tolerance strategy, while the second group as an avoidance strategy. We can appreciate interesting relations among the traits, petiole length, which is inversely related to canopy density and leaf area index (r = - 0.49, p = 0.0022), but positively associated to the percentage of transmitted light through the canopy. The greater the length of the petiole, the greater the amount of light coming through the canopy (r = 0.56, p = 0.0003).

The second axis of the principle components analysis accounts for 16% of the total variance and shows less intraspecific variation among the species, which might suggest that associated traits are less susceptible and might reduce plasticity. The species that are differentiated along this axis include *C. alata* on one side, *C. caracasana* and *T. rosea*. Differences are caused mainly by leaf area and wood density and to a lower extent by leaf tensile strength and specific leaf area (Table 6). Species with rapid growth and large leaves are found on one extreme of the axis, and slow, high wood density species on the opposite side.

Table 6. Eigenvector scores of plant traits in three main PCA axes, ordered according to the absolute magnitude in PCA 1. Highest values are shown in bold. In parenthesis the variance accounted for each axis.

Variables	CP 1 (38%)	CP 2 (16%)	CP 3 (14%)
Canopy shape	0.17	-0.17	-0.18
Wood density	-0.22	**-0.41**	-0.33
Phenology	0.30	-0.08	-0.05
Leaf area index	**0.33**	0.23	-0.13
Transmitted light	**-0.35**	-0.15	0.13
Leaf area	-0.08	**0.56**	0.22
Leaflet number	0.06	0.10	**0.47**
Specific leaf area	0.08	-0.31	**0.46**
Canopy density 1	**0.36**	-0.01	-0.08
Canopy density 2	**0.35**	-0.03	-0.13
Petiole length	**-0.34**	0.29	-0.04
Leaf thickness	**0.36**	0.05	0.09
Tensile strength	-0.11	**0.45**	-0.36
Leaf dry matter content	-0.01	-0.02	**-0.41**
Twig dry matter content	-0.28	-0.13	0.00

In Figure 5, we can observe that the third axis of specialization, which accounted for 17% of the total variance, was primarily defined by specific leaf area and leaf dry matter content, followed by tensile strength. This PCA axis is related to leaf investments as we have higher values of specific leaf area on one side, suggesting lower investments on leaf defenses. While on the other side we have leaves with higher percentages of dry matter content that account for stronger leaves with a longer lifespan, and thus, a higher tensile strength. We can observe that *G. ulmifolia* and *E. cyclocarpum* seem to invert fewer resources in leaf structural defenses, and that *C. alata* and *A. saman* seem to have the larger investments in leaf defenses.
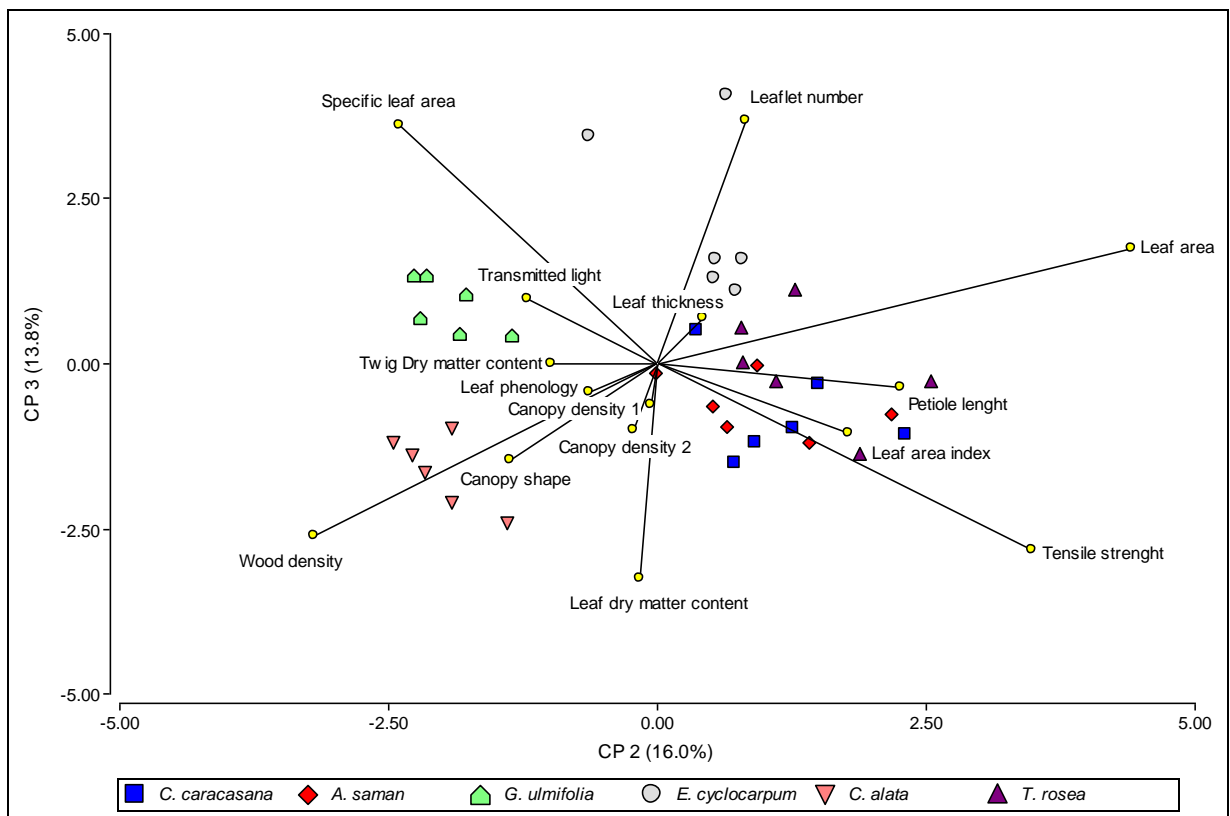
Figure 5. Principal components analysis showing axis 2 and 3.

4.3.3 *Functional response groups*

A cluster analysis was conducted to group and illustrate the differences among strategies. And so, using a Euclidean distance and Ward linkage we constructed a dendrogram that showed four groups (Figure 6). A MANOVA and Hotteling test based on the traits of the species of each group showed significant differences among the four (F=102.98, P < 0.0001).

This cluster analysis allows us to group the species according to drought adaptation strategies in a more visible way. The first group was associated with an acquisitive drought avoidance strategy and was represented by *T. rosea*. The second was represented only by *C. alata* and was defined as having a more conservative and drought avoidance strategy. In the third group we had *E. cyclocarpum* and *G. ulmifolia*, with more tolerant characteristics, but particularly characterized by lower investments on leaf defenses. The fourth and last group was represented by *A. saman* and *C. caracasana*, with a strategy with a drought tolerance strategy.
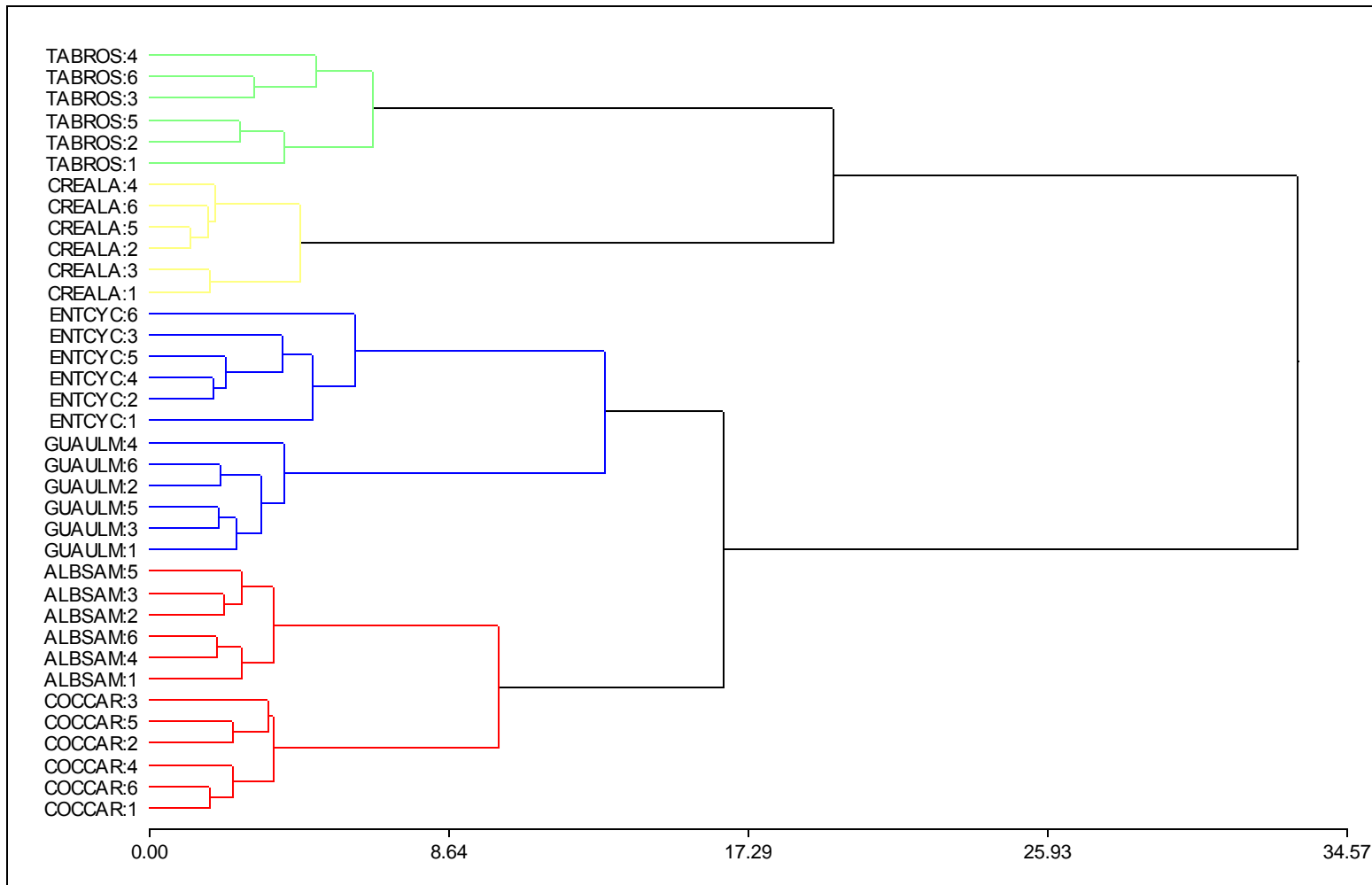
Figure 6. Cluster analysis for all individuals using the measured traits using Euclidean distance and Ward linkage, cophenetic correlation 0.702 (TABROS=T. rosea, CREALA=C.alata, ENTCYC=E.cyclocarpum, GUAULM=G.ulmifolia, ALBSAM=A. saman, COCCAR=C. caracasana).

4.4 DISCUSSION

In the Central American region, the occurrence of extreme warm maximum and minimum temperatures has increased (Aguilar et al. 2005), and the predictions propose drying trends, especially along dry regions (Neeling et al. 2006). We agree with Markesteijn and Poorter (2009) in that the assessment of how species will respond to changes in water availability predicted by climate change scenarios, an understanding of the adaption of species to drought is needed. And that species can be differentiated according to their strategies to cope with different stress conditions.

The response diversity that Laliberte et al. (2010) mention as crucial for ecosystem renewal and organization, is important in coping with environmental stress. The variability of responses to disturbances provides an increment in resilience, and so, we need to consider this diversity of responses in the design of silvopastoral systems. Since drought avoiders and drought tolerance species have different benefits in terms of ecosystem and productive functions, a form of coping with the adversity of drought disturbances is in fact the selection of species with a broad range of strategies as possible. To propose a particular arrangement of species in these productive systems, two things need to be taken into account. The first is to comprehend what functional specific or general effects they have on the system that we are interested in. Then secondly, we can select species that provide those functions, but represent multiple strategies to cope with water stress in order to provide the ecosystem service of drought resistance by maintaining the response diversity.

Recent findings suggest that there might be a limited number of physiological solutions to a given problem when it comes to plant adaptations to the environment (Meinzer 2003). To calibrate the whole set of water use strategies of a community of multiple species, the description of the specific hydrological function of an individual species is needed (Mitchell et al. 2008). But since the precise measurement of these strategies is usually complex and requires the use of hard to measure traits, there is a need to find relatively easy ways to assess species specific strategies. By finding a number of morphological and physiological traits that we can rely on to assess ecological processes; we can fill gaps on management practices in

agroecosystems in terms of provisioning of services. One of the most significant features of our data is that the principal components analysis first axis, which accounted for 40% of the total variation along the measured traits, defined the known basic avoidance-tolerance strategies with clear set of traits. Tolerating drought stress and delaying (or avoiding) drought stress are the most common strategies for species adaptation to drought (Markesteijn and Poorter 2009). The traits related to the distinction of these strategies were leaf area index, canopy density, petiole length, and leaf thickness.

Associations between easy or hard to measure traits has been put forward as a promising way to connect plant traits with major ecosystem processes (Hodgson et al. 1999; Lavorel & Garnier 2002; Diaz et al. 2004), our finding support this and is particularly shown in the canopy density relations to leaf area index, as well to the phenology associations to this both traits. The relations and trade-offs among traits mentioned throughout this work that determine how individual species work by describing ways of resource acquisition and response to the environment will enhance understanding of their roles and performance in an ecosystem (Meinzer 2003). By this line of though, we propose that these characteristic traits that allow us to infer on the provision of the ecosystems services such as drought regulations and resilience by the inclusion of species with stronger strategies to withstand climatic variation. Also, that the most noteworthy difference found among species was between *T. rosea* and *C. caracasana*, and that the variation among the species was mainly driven by canopy descriptive traits, as shown by axis one of the PCA.

If the plant strategy is to be deciduous during the dry season to avoid drought, the traits related to the description of the leaf (leaf thickness, leaf dry matter content, or relative water content) lose some of their relevance it terms of a drought adaptation strategy. We have drought avoidant species like *T. rosea* that sheds its leaves for four months, *A. saman* that sheds its leaves for four months, and on the other hand, we have *E. cyclocarpum*, *C. alata* and *G. ulmifolia*, all of which lose their leaves for only two months. However, it is very important to acknowledge that even if it gives information about the proportion of months with leaves, it does not specify the distribution of those months throughout the dry season. For example, *C. alata* spends two months without leaves at the end of the dry season (April and May), while *G. ulmifolia* spends two months during the middle of the season (February and March) without

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leaves. In terms of water availability, the most critical time for all the components of these silvopastoral systems is at the very end of the dry season.

Leaf area index and canopy density were measured during specific months at the end of the dry season (LAI and CD1), and quickly after the first rains (CD 2). This has to be considered when talking about drought strategies because the leaf shedding patterns across species vary throughout the dry season. This is why we found that by considering the different gradients of shedding patterns among deciduous species we can portrait more accurately the patterns among species. This is why we relied on leaf phenology as a proportion of the reported months that different species lose (or not) their leaves during the dry season. This is an easy-to-measure trait that had strong results in our finding, especially because it seems to have a correcting effect for the lack leaf area index and canopy density measurements repetitions during the entire drought period. We removed the transmitted light trait, and the behavior of the traits was consistent which also supports the affirmation that with an overstory cover measurement such as leaf area index or canopy density, combined with a phenology trait might be enough to assure a tolerance-avoidance strategy axis under the studied conditions.

In the case of *T. rosea*, the canopy density values seem relatively high during the dry season. A reason might be the influences of flowers on the measurements during the month of March where the tree is flowering, although ANOVA test did not show significant differences among measurements from different months. Another interesting characteristic of *T. rosea* canopy is the variation in the canopy shape. As it assimilates a more round shape in comparison with other species, usually the crown is highly asymmetrical.

The petiole length is a trait that shows negative correlations to those corresponding to canopy density and a positive relation to transmitted light. This might imply that petiole length may work as a simple "soft" trait that provides important information about transmitted light across the canopy. This trait in combination with the discussed traits of canopy density and phenology might be enough in order to identify drought avoidance-tolerance strategies. The canopy shape turns out to be a very descriptive trait and it incorporates the differences in canopy height and diameter to bring a more realistic way to picture the canopy form.

Leaf dry matter content is widely used as an indicator of plant resource use strategies in plant functional trait analysis (Vaieretti te al. 2007). For *C. alata*, we have highest values of leaf dry matter content with 418.24 mg g^{-1} ±13.99, and high values of average density of the leaf tissues indicates high investments on leaf defenses and a longer leaf lifespan. The possible reason might be that a partial rehydration procedure was used as recommended by most protocols (Cornelissen et al. 2003; Garnier 2001; Vaieretti 2007) instead of a full rehydration for twenty four hours which has been described as the safest way to measure the trait. On the other hand, Vaieretti et al. (2007), in comparing many studies across unrelated databases, found that differences in the measurement protocol might be less important than the differences among seasons, years, or the quality of the local habitat. This could be tested by conducting direct measurements in a bigger array of species in different land use conditions and augmenting the amount of rehydration hours.

Twigs with high dry matter content values are expected to dry out quickly during the dry season (Cornelissen et al. 2003), and so is no surprise that species with high values of TDMC such as *T. rosea*, have stronger avoidance characteristics than the rest. There are not many studies that take this trait into account, but it an easy to measure trait that presents a positive correlation with and avoidance strategy. Another more evident, but not less important advantage of this trait is that it can be measured during drought season events, regardless of de deciduousness of the different species.

Also important is that SLA is related with relative growth rate which also decreases with abiotic stress (Cornelissen et al. 1996; Lambers et al. 1998; Reich et al. 1998; Antúnez et al. 2001; Galmes et al. 2005; Kunzmann 2005; Wright et al. 2005; Ordoñez et al. 2009, Padilla et al. 2009). Our findings did not coincide with other studies that found strong correlations among wood density and specific leaf area (Bucci et al. 2004) in our case there was no significant correlation among the two, and the traits defined different axes of specialization in our analysis. For tensile strength, the high values associated with the acquisitive strategy indicate protection against abiotic stress (Cornelissen et al. 2003). There seems to be a positive relation between this trait and leaf area in our study, however we were not able to find other mentions of this relationship in the literature.

Another trait of importance is wood density which is not always accessible to measure in the field, but has very interesting relations water stress in trees. According to Bucci et al. (2004) findings, high wood density seems to be related to shallow root systems, and inversely, a low wood density value with a tendency to tap water from deeper soils layers with high soil available data. Also, that more density provides higher resistance to embolism, less sapwood water storage capacity and water transport efficiency. And we coincide with this study in that variation in wood density is a good predictor related to water transport properties and avoidance of turgor loss.

There is intraspecific variation among species that seems to be more marked in some traits than others. This variation could be explained by a sampling error. A good example is *E. cyclocarpum*, the most plastic of all species when considering the traits associated with tolerance-avoidance strategies, due to its investments in leaf defenses. On the other hand, on the axis of specialization in our principal components analysis concerning resources acquisition, the plasticity seems very subtle for all species. This study of six trees species is found to be more detailed, showing more particularities of each species than usual multiple species functional grouping approaches. Because of this, the general strategies are harder to identify than particular strategies of species. Because of the repetitions, we have another level of distribution of traits than those found in numerous species functional analysis. However, in this study we used individuals that were completely isolated, and because of this, the reduction of direct intra or interspecific competition which reduced a lot of noise from the analysis.

A previous study of functional grouping of tree species according to phenology and water storage of stems (among other factors), was completed by Borchet (1994) in the tropical lowland forest of Guanacaste in Costa Rica. They found strong correlations among phenology, seasonal changes in water status and the water capacity of the trees to store water and that the trees clustered into a number of functional types based on this correlations. According to Borchet's classification, *E. cyclocarpum* was considered as a lightwood tree with high stem water storage, and *G. ulmifolia* as well as *T. rosea* as softwood trees that rehydrate and leaf out during drought. In the case of *E. cyclocarpum*, the species appears to have lower values of wood density, which agrees with the lightwood classification. For our other two species not included in the Guanacaste study, we found that both had similar relatively low values of

wood density, they both leaf out during the drought. It is important to mention that in this study, seasonal shedding of leaves was used as a categorical value in a scale from 0 to 3 where: 0-none, 1- few (<20%), 2-many (20-80%), and 3 abundant (>80%). While in our study we used a temporal scale on the amount of time during the water shortage distress that the actual shedding occurred and gave it a proportional value from 0 to 1, where 0 was shedding during all six months of stress, and 1 was presence of leaves during the entire seasonal drought.

Our four functional groups were selected according to this and other important soft traits. We identified *T. rosea* as an acquisitive-drought avoidant species, *C. alata* as a more conservative-drought avoidant species, *A. saman* and *C. caracasana* as acquisitive-drought tolerant species. The species *E. cyclocarpum* and *G. ulmifolia*, seemed to be grouped together as species that have low investments in leaf defenses. Our principal components analysis showed that *E. cyclocarpum* and *A. saman* had some overlapping along the different axes and that in the first axis of specialization (avoidance-tolerance) and the second axis (acquisitive-conservative), *G. ulmifolia* is well differentiated form the rest of the species as a conservative-drought tolerant.

4.5 CONCLUSIONS

We conclude that there are specific trait associations that better define trees strategies to water limitations in silvopastoral systems. There are a variety of trait combinations for this determination. For example, combining canopy density traits and leaf phenology traits are important for discriminating between drought tolerance and avoidance. These trait recommendations are applicable to the broad array of species present in SPS. A good example would be identifying if these response attributes were overlapping to functional effects on understory moisture stress conditions can lead into an improved classification of species and a more efficient selection of response-effect traits. This classification could provide the grounds to apply to bigger set of species and the proposition of alternative multifunctional design in agroforestry systems.

We also support that response diversity is crucial for ecosystem renewal and organization is important in coping with environmental stress. The variability of responses to disturbances provides an increment in resilience, and so, we need to consider this diversity of responses in the design of silvopastoral systems. So in terms of their response effects, we recommend the use of species *G. ulmifolia* and *C. alata*, because they show different well defined strategies to cope with water stress according to our findings, and second, because they show less plasticity along the traits that define those strategies.

Leaf physiology and phenology remain are strong predictors of drought responses, and so, there is no doubt that they should be fairly represented when organizing the set of traits to address this ecological process. Leaf area index, canopy density and phenology provide important axes of differentiation among drought resistance strategies as it was confirmed by the PCA analysis. Also, traits that are known to have very strong relationships with the relative growth rate are very useful to understand acquisition strategies among different species. The set of traits that provided better results were wood density, leaf area and tensile strength.

It is also important to take into account the traits that were measured and are strongly related to access to deep water. Traits such as rooting length, depth and distribution can give information about water uptake, water sources and water strategies to cope with water. Even though we can make rough inferences with trade-offs, to achieve that ideal combination of traits that allow us to understand how species cope with water stress, root traits should be taken into consideration. Further investigation of ecological processes is still needed in other to continue the efforts to relate functional diversity to a process and then an ecosystem service of interest in order to provide enough technological ground for further management and silvopastoral designing.

Comparative studies of species responses to the environment, such as this one, have to take into account multiple scales and information on plant size, allometry and biophysical tissue properties to allow the observed responses and behavior to be normalized. The use of

standardized measurement protocols and selection of variables is important to incorporate as many scales as possible and for the facilitation of meta-analyses with data obtained from this kind of studies.

For future work that cannot have so much detail, or that targets a big amount of species, the relations among the traits observed here can be taken into account. So traits like canopy density, petiole length, twig dry matter content, leaf area or wood density (among others) can give us information that more hard traits would. And although this study considers only a small amount of three species, we can continue to acknowledge that the general attributes that were known to be more important in terms of drought tolerance strategies are still important enough to accommodate small or large groups of species along a gradient of strategies and specializations. If we relate these traits to the effect they have in ecosystems processes for interest, we have information of value in terms of management of silvopastoral components.

4.6 REFERENCES

Aguilar, E.; Peterson, T.C.; Ramirez Obando, P.; Frutos, R.; Retana, J.A.; Solera, M.; Soley, J.; González García, I.; Araujo, R.M.; Rosa Santos, A.; Valle, V.E.; Brunet, M.; Aguilar, L.; Alvarez, L.; Bautista, M.; Castañón, C.; Herrera, L.; Ruano, E.; Sinay, J.J.; Sánchez, E.; Hernández Oviedo, G.I.; Obed, F.; Salgado, J.E.; Vásquez, J.L.; Baca, M.; Gutiérrez, M.; Centella, C.; Espinosa, J.; Martínez, D.; Olmedo, B.; Ojeda Espinoza, C.E.; Núñez, R.; Haylock, M.; Benavides, H.; Mayorga, R. 2005. Changes in precipitation and temperature extremes in Central America and northern South America, 1961-2003. Journal of Geophysical Research 110: 1-15

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74:19-31

Bochert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecological Society of America 75(5):1437-1449

Bucci, S.J.; Goldstein, G.; Meinzer, F.C.; Scholz; Franco, A.C.; Bustamante, M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiology 24:891-899

Chapin, F. S. 1991. Integrated responses of plants to stress. A centralized system of physiological responses. BioScience 41:29-36

Cordero J. & Boshier D.H. 2003. (eds). Arboles de Centroamérica. Un manual para extensionistas. Oxford Forestry Institute (OFI) Oxford University, OXfod, UK; and CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) Turrialba, Costa Rica, 1079 p.

Cornelissen, J. H.C.; Diez, P. C.; Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology 84:755-765

Díaz, S.; Hodgson, J.G. ; Thompson, K.; Cabido, M.; Cornelissen, J.H.C.; Jalili, A.; Montserrat-Martí, G.; Grime, J.P.; Zarrinkamar, F.; Asri, Y.; Band, S.R.; Basconcelo, S.; Castro-Díez, P.; Funes, G.; Hamzehee, B.; Khoshnevi, M.; Pérez-Harguindeguy, N.; Pérez-Rontomé, M.C.; Shirvany, F.A.; Vendramini, F.; Yazdani, S.; Abbas-Azimi, R.; Bogaard, A.; Boustani, S.; Charles, M.; Dehghan, M.; de Torres-Espuny, L.; Falczuk, V.; Guerrero-Campo, J.; Hynd, A.; Jones, G.; Kowsary, E.; Kazemi-Saeed, F.; Maestro- Martínez, M.; Romo-Díez, A.; Shaw, S.; Siavash, B.; Villar-Salvador, P.;

Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295-304

Flynn, D. F; Gogol-Prokurat, M.; Nogeire, T.; Molinari, N.; Trautman, B.; Simpson, N.; Mayfield, M.; DeClerck, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22-33

Gabriel, K. R. 1971. The biplot graphic display of matrices with application to principal component aalysis. Biometrika 58:453-467

Garnier, E.; Shipley, B.; Roumet, C.; Laurent, G. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. Functional Ecology 15:688-695

González, L.; González-Vilaz, M. 2001. Determination of Relative Water Content. Pags: 207-212 In: Reigosa Roger, M.J. (ed). 2001. Plant Ecophysiology Techniques. Kluwer Academic Publishers. 452p.

Hasselquist, N.J.; Allen, M.F.; Santiago, L.S. 2010. Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. Oecologia online: http://dx.doi.org/10.1007/s00442-010-1725-y

Harvey, C.; Medina, A.; Sánchez Merlo, D.; Vílchez, S.; Hernández, B.; Saenz, J.; Maes, J.; Casanoves, F; Sinclair, F.L. 2006. Patterns of animal diversity associated with different forms of tree cover retained in agricultural landscapes. Ecological Applications 16: 1986-1999.

Hodgson, J.G.; Wilson, P.J.; Hunt, R.; Grime, J.P.; Thompson, K. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. Oikos 85:282-294

Holdridge, L. 1978. Ecología Basada en Zonas de Vida. IICA. San José, Costa Rica. 216 pág.

Holbrook, N.M.; Whiteck, J.L.; Mooney, H.A. 1995. Drought responses of neotropical dry forest trees. 243-276 en: Bullock, S.H.; Mooney, H.A.; Medina, E. (eds.). 1995. Seasonally Dry Tropical Forests. Cambridge University Press 450 p.

INETER (Instituto Nicaragüense de Estudios Territoriales). 2005. Dirección General de Meteorología. Consulted on January 19, 2010. Managua, NI. Available at: http://www.ineter.gob.ni/Direcciones/meteorologia/index.html

IPCC (Intergovernmental Panel on Climate Change). 2001. Impacts, adaptation and vulnerability. Summary for Policimakers. Cambridge University Press, New York, US. 18p.

Joya, J.; López, M; Gómez, R.; Harvey, C.A. 2004. Conocimiento local sobre el uso y manejo de árboles en fincas ganaderas del municipio de Belén, Rivas. Revista Encuentro 36(68):44-59.

Laliberté, E.L.; Wells, J.A.; DeClerck F.; Metcalfe, J.D.; Catterall, C.P.; Queiroz, C.; Aubin, I.; Bonser, S.P.; Ding, Y.; Fraterringo, J.M.; McNamara, S.; Morgan, J.W.; Sánchez Merlos, D.; Vesk, P.A.; Mafield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology letters 13:76-86

Lavorel, S.; Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545-556

López, M., R. Gómez, C.A. Harvey, and C. Villanueva. 2004. Caracterización del componente arbóreo en los sistemas ganaderos de Rivas, Nicaragua. Revista Encuentro 36(68):114-133.

Loreau, L.; Naeem, S.; Inchausti, P.; Bengtsson J.; Grime, J.P.; Hector, A.; Hooper, D.U.; Huston, M.A.; Raffaelli, D.; Schmid, B.; Tilman, D.; Wardle, D.A. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294(5543):804-808

Markesteijn, L.; Poorter, L. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. Journal of Ecology 97(2):311-325

_____. 2010. Drought tolerance of tropical tree species; Functional traits, Trade-offs and Species Distribution. Ph.D. Thesis. Wageningen Agricultural University. 204 p.

Meinzer, F.C. 2003. Functional convergence in plant responses to the environment. Oecologia 134(1):1-11

MEA (Millennium Ecosystem Assessment). 2005. Ecosystems and human well-being: current state and trends. Island Press, Washington, D.C., USA.

Mitchell, P.; Veneklaas, E.; Lambers, H.;Burgess S. 2008. Using multiple trait associations to define hydraulic functional types in plant communities of south-western Australia. Oecología 158(3):385-397

Neelin, J.D.; Münnich, M.; Su, H.; Meyerson, J.E.; Holloway, C.E. Tropical drying trends in global warming models and observations. PNAS 103(16):6110-6115

Power, J.S. and Tiffin, P. 2010. Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. Functional Ecology 24(4):927-936

Primack, R.; Rozzi, R.; Feisinger, P; Massardo, F. (eds.) 2001. Fundamentos de Conservación Biológica: perspectivas latinoamericanas. Fondo de Cultura Económica, D.F., México

Pugnaire, F.I. and Valladares, F (eds.).2007. Functional Plant Ecology (2nd ed.) CRC Press, Boca Ratón. FL. USA. 724 p.

Sánchez, D.M; López, M.; Medina, A.; Gómez, R.; Harvey, C.E.; Vilchez, S.; Hernández, B.; López, F.; Joya, M.; Sinclair, F.L.; Kunth, S. 2004. Importancia Ecológica y socioeconómica de la cobertura arbórea de un paisaje fragmentado de bosque seco de Belén Rivas, Nicaragua. Revista Encuentro No. 68. UCA, Universidad Centroamericana, Managua, Nicaragua.

_____.; Harvey, C.; Grijalva, A.; Medina, A.; Vilchez, S.; Hernandez, B. 2005. Diversidad, composición y estructura de la vegetación en un paisaje fragmentado de bosque seco en Rivas, Nicaragua. Recursos Naturales y Ambiente. 45:91-104.

Stevens, W.D.; Ulloa C.; Pool, A.; Montiel, O.M. (eds.) 2001. Flora de Nicaragua. Tomo I, II y III. Missouri Botanical Garden Press. St. Louis, Missouri, 2556p.

Tilman, D.; Knops, J.; Wedin, D.; Reich, P.; Ritchie, M.; Siemann, E. 1997. The influence of Functional Diversity and Composition on Ecosystem Processes. Science 277(5330):1300-1302

Vaieretti, M.V.; Diaz, S.; Vile, D.; Garnier, E. 2007. Two Measurements Methods of Leaf Dry Matter Content Procedure Similar Results in a Broad Range of Species. Annals of Bothany 99:955-958

Yordanov, I.; Velikova, V.; Tsonev, T. 2000. Plant responses to drought, acclimation and stress tolerance: Review. Photosynthetica 38:171-186

APPENDICES

Appendix 1. Pearson correlation matrix for all descriptive variables and traits.

	DBH	TH	HLB	CH	C_D	CS	WD	PH	LAI	DIFN	LA	SLA	CD 1	CD 2	PL	LN	LT	TS	LDMC	LRWC	TDMC	TRWC
DBH	1	0.6135	0.0762	0.3516	0.1673	0.6512	0.0117	2.70E-05	3.50E-08	7.80E-06	0.6895	0.4438	0.0035	0.0085	0.0121	0.1892	0.0009	0.05	0.2664	0.6298	0.0737	0.0482
TH	0.0871	1	0.0538	0	7.50E-06	0.0902	0.004	0.0332	0.4154	0.3821	0.0005	0.7156	0.9817	0.9689	0.133	0.0266	0.519	0.7368	0.2639	0.0927	0.6054	0.1737
HLB	-0.2993	0.3241	1	0.5191	0.6455	0.2306	0.5461	0.0035	0.0806	0.0639	0.0025	0.4143	0.0009	0.0011	0.0117	0.101	0.0492	0.9256	0.0396	0.2868	0.1212	0.199
CH	0.1599	0.9762	0.111	1	6.30E-07	0.1349	0.0041	0.1181	0.2091	0.1792	0.0039	0.8426	0.468	0.5129	0.3134	0.0536	0.261	0.7411	0.4794	0.0417	0.8463	0.2594
C_D	0.2352	0.671	-0.0793	0.7231	1	0.005	0.0078	0.6397	0.0176	0.0057	0.1604	0.7865	0.0067	0.024	0.4326	0.0819	0.0158	0.7503	0.7265	0.01	0.4363	0.4889
CS	0.078	-0.2865	-0.2049	-0.2541	0.4577	1	0.832	0.2117	0.1659	0.0745	0.1427	0.9403	0.008	0.0243	0.0191	0.7403	0.1781	0.2338	0.1684	0.3209	0.1773	0.4317
WD	-0.4158	-0.4676	-0.104	-0.4673	-0.4362	0.0366	1	0.1577	0.0009	0.0018	0.0002	0.4785	0.0253	0.0592	0.2052	0.0046	1.70E-05	0.7965	0.1081	0.6834	0.0077	2.00E-06
PH	0.6397	-0.3559	-0.4742	-0.2652	-0.0807	0.2133	-0.2405	1	0.0004	0.0012	0.0662	0.726	4.90E-05	0.0005	4.00E-07	0.8811	0.0006	0.4649	0.3556	0.8846	0.0016	0.1778
LAI	0.772	0.14	-0.2951	0.2145	0.3935	0.236	-0.5299	0.5589	1	0	0.7879	0.6532	4.80E-06	1.40E-05	0.0022	0.784	1.30E-06	0.4171	0.7403	0.4838	0.0018	0.0625
DIFN	-0.67	-0.1502	0.3121	-0.2289	-0.4515	-0.3009	0.5013	-0.5172	-0.935	1	0.835	0.8464	9.10E-08	3.30E-07	0.0003	0.9363	2.10E-07	0.9067	0.9485	0.4139	0.0024	0.2287
LA	0.0689	0.5531	0.4885	0.4688	0.239	-0.2492	-0.5866	-0.3095	0.0465	0.036	1	0.2097	0.218	0.2351	0.0007	0.0314	0.6088	0.0058	0.4009	0.1943	0.7915	0.0104
SLA	-0.1317	0.0629	0.1403	0.0343	0.0468	-0.0129	-0.122	0.0605	-0.0775	0.0334	-0.2142	1	0.824	0.6287	0.0217	0.1164	0.0488	0.0001	0.1173	0.0702	0.9557	0.3139
CD 1	0.4746	0.004	-0.5274	0.1249	0.4437	0.4349	-0.3723	0.6231	0.6811	-0.7571	-0.2104	0.0384	1	5.50E-09	2.60E-05	0.3769	8.60E-06	0.1976	0.8201	0.0812	0.0001	0.2665
CD 2	0.432	-0.0067	-0.5228	0.1127	0.3754	0.3748	-0.3174	0.5528	0.6566	-0.7353	-0.203	0.0834	0.7983	1	1.70E-05	0.4285	4.00E-06	0.1987	0.0824	0.0731	0.0017	0.4112
PL	-0.4138	0.2553	0.4156	0.1729	-0.1349	-0.3888	0.2163	-0.7315	-0.4947	0.5642	0.5413	-0.3814	-0.6398	-0.651	1	0.9708	2.10E-07	0.0026	0.3619	0.1572	0.0063	0.3384
LN	-0.2239	0.3694	0.2778	0.3244	0.2939	0.0572	-0.4621	0.0258	-0.0473	0.0138	0.3593	0.2663	0.1518	0.1362	0.0063	1	0.5819	0.0277	0.5902	0.2839	0.3441	0.0664
LT	0.5298	0.1111	-0.3302	0.1924	0.3995	0.2295	-0.6516	0.5464	0.7084	-0.7428	-0.0883	0.3308	0.6677	0.6854	-0.7434	0.0949	1	0.3965	0.8479	0.1176	0.0016	0.008
TS	0.3291	0.058	0.0161	0.057	-0.0549	-0.2035	-0.0445	-0.1258	0.1395	0.0202	0.4507	-0.6047	-0.2198	-0.2193	0.4872	-0.367	-0.1457	1	0.2273	0.0374	0.6928	0.6389
LDMC	-0.1902	-0.1912	-0.3446	-0.1217	0.0604	0.2346	0.2723	-0.1586	-0.0572	-0.0111	-0.1444	-0.2657	0.0393	0.2934	0.1565	-0.0928	-0.0331	0.2063	1	0.6992	0.8503	0.0161
LRWC	0.0831	-0.2844	0.1825	-0.3413	-0.424	-0.1702	0.0704	0.0251	-0.1205	0.1405	0.2214	-0.3053	-0.2946	-0.3023	0.2408	-0.1836	-0.2655	0.3482	-0.0667	1	0.6935	0.9852
TDMC	-0.3017	0.0891	0.263	0.0335	-0.1339	-0.2299	0.4369	-0.5083	-0.5012	0.4896	-0.0456	-0.0096	-0.6127	-0.505	0.4466	-0.1624	-0.5078	0.0682	-0.0326	0.068	1	0.0036
TRWC	0.3316	0.2318	0.2192	0.193	0.1191	-0.1352	-0.7003	0.2297	0.3136	-0.2057	0.4217	0.1727	0.1902	0.1413	-0.1643	0.3093	0.435	0.0809	-0.3983	-0.0032	-0.4726	1

5 ARTICLE 2

Tree canopy traits and understory water stress reduction in silvopastoral systems of Rivas, Nicaragua

Abstract

Nicaragua's agrolandscapes are primarily dominated by pastures and annually cultivated lands that retain some tree cover in the form of scattered trees, small patches of secondary forest, scrublands, live fences, and riparian forests (Harvey et al. 2006). In Rivas, the landscape has been extensively modified as a result of agricultural and cattle-ranching practices. In this study we explore the hypothesis that different tree effect traits will lead to different understory conditions with implications for both pasture productivity, and animal well-being – two functions of importance for cattle farmers and contribution to drought resistance. In order to explore this relationship, we evaluated understory conditions through measurements of evaporation and changes in understory cover and composition beneath six common tree species (*Albizia saman*, *Guazuma ulmifolia*, *Coccoloba caracasana*, *Tabebuia rosea*, *Crescentia alata*, *Enterolobium cyclocarpum*). Based on these results we have proposed a classification system based on various response and effect traits that overlap between their responses to climatic variability and their effect on understory water stress conditions. Using an existing database consisting of 139 species, we applied the findings from our six species experiment to group all species within the database into three functional groups using three available functional traits (wood density, laminar unit and phenology) that are known to be related to drought stress.

5.1 INTRODUCTION

Silvopastoral systems are a management option for livestock production that integrates perennial woody plants (trees or shrubs) with traditional pasture production components (both pasture and livestock), typically designed to improve the system's sustainability, productivity, and conservation values (Pezo e Ibrahim 1998). Silvopastoral systems provide a variety of ecosystems services compared to traditional systems: soil fertility maintenance, erosion reduction, nutrient cycling, nitrogen fixation, carbon sequestration, conservation of biodiversity in fragmented landscapes, among others (Beer et al. 2003). One ecosystem service of particular importance in the dryland systems of Rivas however, is the resistance and resilience to drought. The extended dry season experienced in the Rivas landscape places tremendous pressure on cattle farmers to stockpile fodder reserves, use irrigation, or explore the role of integrating trees in pasture to stabilize production throughout the year. Trees in pastures can make multiple contributions towards this goal including reducing the heat stress of livestock, providing a source of dry season fodder through evergreen tree species, and/or reducing below canopy evapotranspiration permitting greater retention of palatable grasses into the dry season (Pezo & Ibrahim 1996).

Recent studies have highlighted the relationship between biodiversity and the provisioning of ecosystem services. Many of these past studies have used taxonomic measures of biodiversity for these evaluations; however, classifying species according to their taxonomy presents strong limitations when looking for ecological answers to questions as to what drives ecosystem services (Cornelissen et al. 2003). More recent studies have instead focused on measures of functional diversity. This growing focus on plant traits and function not only suggests that traits are indicators of responses to environmental conditions, but also that these same traits can also indicate significant impact on ecosystem processes. The traits that explain how a species responds to disturbances and environmental variation are called response traits, whereas those that have an effect on ecosystem properties are called effect traits. For a drought prone region like Rivas, the traits that interest us are those that allow us to identify different responses to drought and direct effect on the reduction of evapotranspiration under the canopy to guarantee pasture productivity and animal well being during stress.

A trait is defined as "any morphological, physiological or phenological feature that can be measured at the individual level without reference to the environment or any other level of organization and; a functional trait will be any trait that has an impact on fitness indirectly via its effect on growth, reproduction or survival" (Violle et al. 2007). Individual traits can be measured at the species level, including how these traits vary in time and space, or these traits can be measured at the community level using different measures of functional diversity which refer to trait distributions and diversity (Díaz & Cabido 2001; Lavorel et al. 2008). As such, understanding the functional diversity of vegetation is important to unraveling the relationship between environmental change, community composition and ecosystem processes (Lavorel et al. 2008). The assessment of how biotic communities can provide services to the ecosystems is based on the precise measurement of these traits, which contribute directly to ecosystem functioning (Flynn et al. 2009). Studying how species and their traits are expressed both at the species and community level allows us to relate biodiversity to ecosystems processes and services of interest.

Modification of habitats and management practices that reduce species diversity and functional composition tend to have greater impacts on ecosystem processes (Tilman et al. 1997). It is clear that we need to urgently understand the impacts of climatic and land use changes and formulate predictors of these impacts, and that we are in a position where in most cases we have no detailed knowledge of the ecosystems processes of interest (Diaz et al. 2004). The importance of the study of plant traits and functional classifications is that they permit us to predict species responses to environmental variation, and to understand the impacts these species have on ecosystem services of interest to farmers in the region. For example, this knowledge can help us to improve the functional resilience of trees in dryland agroecosystems, and more specifically, the contribution that these species make in ensuring stable biomass production throughout the year. For example, farmers interviewed by Mosquera (2010) identified shade for livestock and drought resistance as two important ecosystem services in this landscape. In order to understand and predict plant species responses to climatic change we need insight on the mechanisms of the process of drought tolerance (Poorter & Markersteijn 2007).

Though major advances have been made in describing the relationship between species diversity and ecosystem processes through the identification of functionally important species, and in revealing underlying mechanisms (Loreau 2001), to determine how biodiversity dynamics, ecosystem processes, and abiotic factors interact comprises a big challenge. To assess this challenge, we follow the framework proposed by Lavorel & Garnier (2002), which evaluated ecosystem functioning by searching for functional linkages and trade-offs among traits related to one or several processes (Figure 7). We look to find the overlapping of response and effect traits that allows us to relate species to the processes and ecosystems services of interest. The identification of this multiple purpose traits can be used to scale up to a bigger number of species in order to group them according to their functionality. Plant functional groups (PFG's) or plant functional types (PFT's) is a concept that embodies that functional traits can be grouped according to their responses to the environment or their effect on ecosystem functions, or both (Lavorel & Garnier 2002). Functional effect groups based on complementary resource use provide a method to test for effects of functional diversity on ecosystem level resource use and productivity (Hooper et al. 2002).
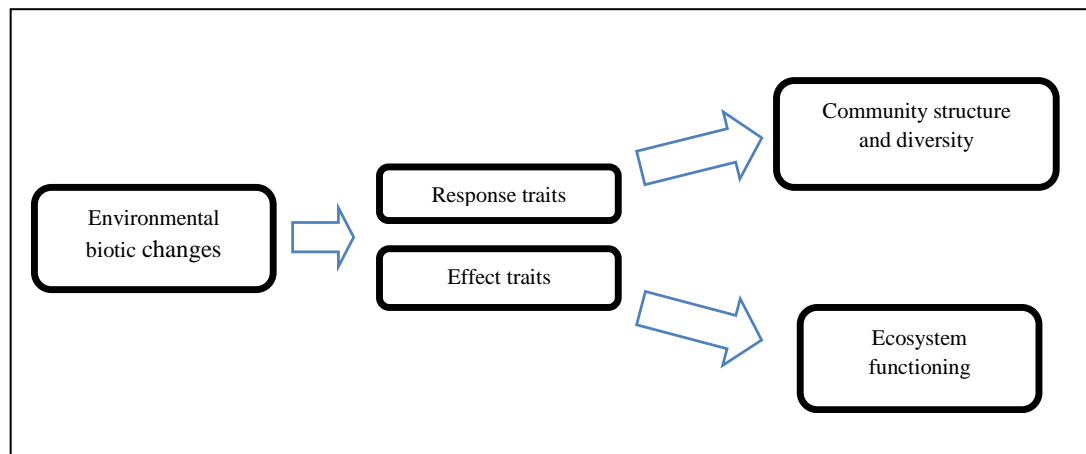

Figure 7. Framework proposed by Lavorel & Garnier (2002) which articulates environmental responses and ecosystems through the overlapping between relevant traits.

In the previous chapter we identified traits associated with different drought response groups. Here, we continue along these lines but focus on identifying which set of traits will provide a functional effect on understory conditions. The determination of the overlap between this two properties, drought tolerance, and modification of understory conditions, will give us a more productive functional classification useful for management and design

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practices in silvopastoral systems in relation to the pending threat of climatic change. By identifying key "soft" (easy to measure traits), or literature based traits that have important effects on understory conditions, we then can extrapolate this to propose a larger species classification of species. One of the difficulties involved in trait based studies in tropical forests is the difficulties in measuring traits of importance (time, energy and funding). By identifying key soft, or literature based traits, and understanding their relationship to field based traits measures we hope to provide a means of extrapolating measures from a subset of individuals to the community. To do this we selected six species that represent a broad range in response strategies to drought, took detailed measures on more than a dozen traits during the 2010 dry season and transition to wet season and we evaluated the effects of these traits in ecosystem processes of interest. The finding of coexisting links between soft and hard traits functions will be used as a way to connect plant traits with ecosystem processes (Lavorel & Garnier 2002; Diaz et al. 2004). Our hypothesis relies in that different effect traits eventually lead to different understory conditions of importance to cattle farmers and are tied to resistance to drought. We tested the relationship between functional effect groups and potential evapotranspiration beneath their crowns. As such this study addressed the overlapping of traits associated with a response process and (response to drought) and an effect process (understory stress conditions).

5.2 MATERIALS AND METHODS

5.2.1 Study area

The study area is located in southwestern Nicaragua near the town of Rivas. The landscape is classified as Tropical Dry Forest life zone according to Holdridge (1978). Elevation in this area oscillates between 100 to 200 m. and the annual mean precipitation is approximately 1400 mm. The mean annual temperature is 27°C, with a mean relative humidity of 78%, and an average wind velocity of 3.2 m/sec (INETER 2005). This site is subject to a marked dry season during the months of November to April and a wet season from April to November that puts severe production limitations on farmers. The soils are alluvial in nature, have very high clay content (vertisols) and high shrink-swell capacity forming deep cracks during the dry season.

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Table 7. List of all variables used in this study, abbreviation, description, unit of measure, level of definition (I=individual, SP=specie) and the source of data used.

Trait	Description	Unit	Level	Source
Whole plant				
TH	Tree height	m	I	Measurements, Literature
CH	Canopy height	m	I	Measurements
HLB	Height to the lowest branch	m	I	Measurements
C_D	Canopy diameter	m	I	Measurements
CD	Canopy density	%	I	Measurements
CS	Canopy shape	m	I	
DBH	Diameter breast height	dm	I	Measurements
PH	Crown phenology		SP	Literature
Leaf traits				
LA	Leaf area	mm^2	I	Measurements
SLA	Specific Leaf Area	m^2kg^{-1}	I	Measurements
LDMC	Leaf Dry Matter Content	$mg\ g^{-1}$	I	Measurements
LRWC	Leaf relative water content	%	I	Measurements
LAI	Leaf Area Index	-	I	Measurements
DIFN	Transmitted light	%	I	Measurements
PL	Petiole length	mm	I	Measurements
TS	Leaf tensile strength	Nmm^{-1}	I	Measurements
LT	Leaf thickness	mm	I	Measurements
LN	Leaflet number	-	SP	Measurements
Stem traits				
TDMC	Twig dry matter content	$mg\ g^{-1}$	I	Measurements
TRWC	Twig relative water content	%	I	Measurements
WD	Wood density	$mg\ mm^{-3}$	P	Lierature

5.2.2 Selected traits

Traits were classified into functional effect groups. Traits descriptions and measurement are detailed in Chapter 4. Some traits that were used are considered to be more plastic and vary over time and some are more specific to species. The objective was not to test the differences among traits. The previous table (Table 7) summarizes all traits examined in this study in relation to understory conditions.

5.2.3   Measurements descriptions

Actual evaporation is defined as the "quantity of water evaporated from an open water surface or from the ground" (WMO 1992). In order to measure actual evaporation, four small leveled evaporation pans were beneath the tree crowns, and another four pans were placed outside of the tree canopy. For their placement we measured the distance from the trunk to the canopy perimeter at one cardinal point, divided that distance by half and proceeded to install the evaporation pans (Figure 8). From the canopy perimeter we used the same distance and placed the evaporation pans outside of the trees influence as a control measurement. The evaporation pans were covered with a metal grid in order to avert significant water loss due to litterfall or animals (birds, cows, dogs, etc.). The pans were filled with 500mL of water and left during dry days for a period of approximately 24 hours. The remaining volume of water was measured in a graduated cylinder to determine the difference in volume as a measure actual evaporation under and outside the individual tree canopies.

The difference between the measurements outside and under the canopy was considered as the potential for reduced evaporation by the tree and served as our statistical unit. For this design we made six repetitions for each of the six species. The advantage of this measure over other understory measures is that it is independent of other measurements of understory drought stress such as soil water content or plant water content, which can be significantly influenced by soil condition, or the composition of the understory (rice straw, improved pasture grasses, or naturalized pastures).
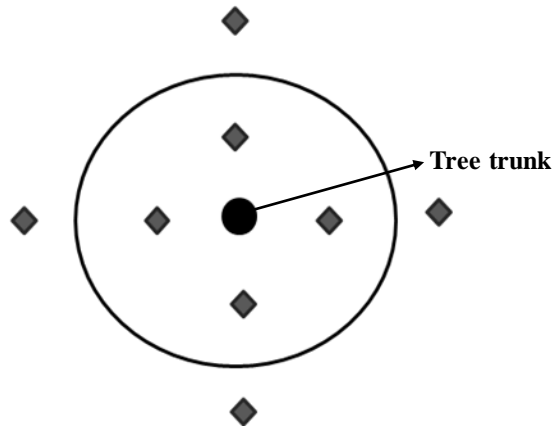
Figure 8.Simulation of measurements for evaporation location under and outside the tree canopy.

Second, we measured the understory community composition by placing four square 0.5 m x 0.5 m quadrats beneath, and outside of the canopy crown. We measured average percent cover measurements under the canopy to estimate the effect of the tree canopy on available pasture for cattle consumption. We placed the quadrats 10 cm to the left of our evaporations pans and estimated the approximate relative cover in five categories: soil, weeds, grasses, legumes, and crops (mainly rice).

Measurements for evaporation and pasture were not necessarily done on the same days. For evaporation, we recorded data from the last three and more critical months of the dry season (22 of March to 20 of May), and the same with measurements of understory composition (26 of March to 21 of May). And for the measurement of understory composition during that transitional change from dry to rainy season, we took measurements as rapidly as we could during the month of June, after the first rains, when all the understory changes were occurring (7 to the 24th).

These measurements were also used to identify specific effect traits, and based on the previous identification of response traits to drought disturbances and water stress (Chapter 4), we used the response-effect correspondence approach to predict the functions of particular species (Figure 9).
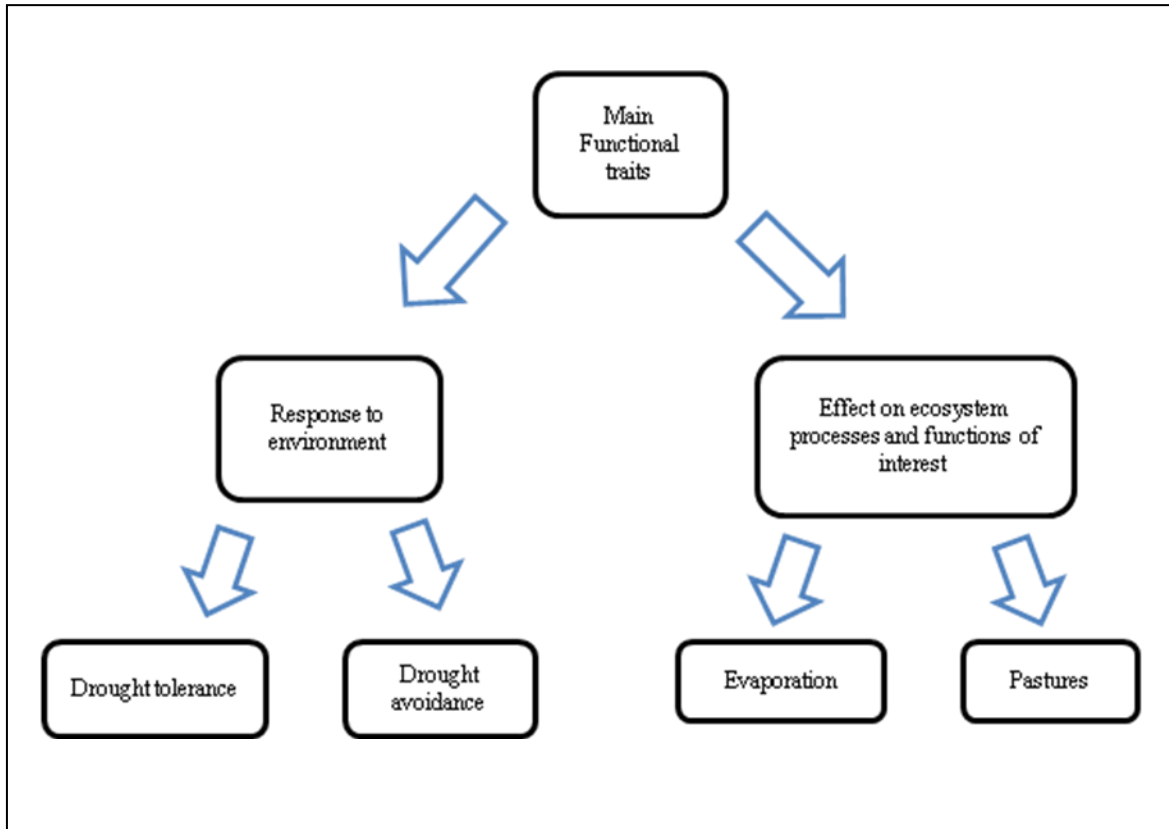
Figure 9. Shows the scheme of the analysis of response traits according to drought events and effect traits according to evaporation reduction and pasture productivity (Based on Lavorel & Garnier 2002).

5.2.4 Statistical analysis

To assure the differences in trait values according to each species we conducted a completely randomized analysis of variance (ANOVA). We ran an LSD Fisher test to determine whether there were significant differences among species, as well as for differences inside and outside of the tree canopy. The evaporation values inside the canopy were subtracted from the outside values to obtain the amount of actual water conserved beneath the trees relative to the amount lost under open sky. We used a square root transformation for the data followed by a Pearson correlation analysis to identify traits associated with evaporation measures. With species that showed a significant correlation we proceeded to conduct linear regression analysis to explore their effect in the understory evaporation prevention values with milliliters of water conserved as the dependent variable and each trait as the regressor. We

also conducted a multiple regression analysis to see if we could identify a particular group of attributes to predict the understory changes.

After identifying the traits that showed the highest relationship to understory conditions, we used an existing database consisting of three soft traits recorded from literature for a total of 142 species, and we ran a Cluster analysis in order to determine whether our previous findings could be applied to a larger set of silvopastoral species. The three variables used for this cluster where phenology (as a Dummy variable), wood density and laminar area. These traits were selected because they were related to the traits that showed more relation to our functions of interest. For example, leaf area is related to leaf characteristics that define some strategies of resource acquisitions as well as its effect on the amount of light that passes through to the understory (Cornelissen et al. 2003). Leaf phenology is one of the most important variables in terms of responses to disturbances and effects on ecosystem processes (Cornelissen et al. 2003, Powers & Tiffin 2010), and since it was categorical, we assigned a value of 1 to evergreen and 0 to deciduous. Since the leaf phenology was a binary variable, we used Gower distance, and Ward linkage for a cluster analysis that allowed us to divide species into groups. We then used a MANOVA with Hotteling test to determine whether the groups where statistically different. Finally, we used cross tabulation to determine which group was associated with the leaf phenology trait. The statistical analyses were performed using *INFOSTAT statistical software package*.

5.3 RESULTS

5.3.1 *Evaporation and Pastures*

As it can be observed in Figure 10, the largest amount of water that was retained under was found under the canopy of *C. caracasana*. A difference of nearly 145 mL of water was the result of the influence from maintaining an evergreen crown during the dry season. The reduced evaporation data consisted on average of water recorded in the evaporation pans outside the canopy, minus the amount of water recorded in the evaporation pans under the canopy. *T. rosea* showed the lowest values of water maintained with only 13.26 mL of water retained under its highly deciduous canopy. The rest of the species, *E. cyclocarpum*, *G.*

ulmifolia, *C. alata* and *A. saman* had middle values that did not maintained a high amount of water, but not too small either.
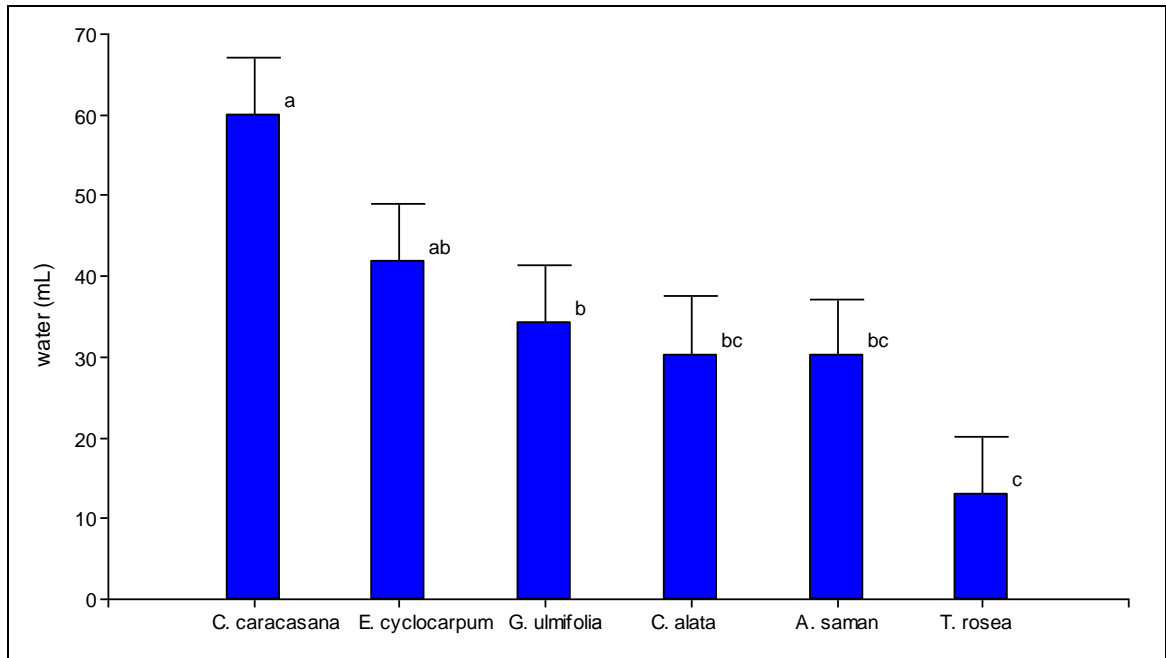

Figure 10.Values of the difference in milliliters of water retained (evaporation out – evaporation in) by species, with standard error and LSD Fisher letters showing differences (p<0.05).

In Figure 11 we can appreciate the differences of pasture productivity, taking into account measurements during the dry season and after the first rains as cover percentage. Under the canopy of *C. alata* we found the highest percentages of pasture cover during the dry season and after the first rains with an average of 19% (±0.06), followed by *G. ulmifolia* with a 17% (±0.05). The following values of pasture were found under *E. cyclocarpum* (9% ±0.05) and *A. saman* (9% ±0.05).

In Figure 12 we can observe that a dense canopy prevents evaporation but allows poor pasture production (*C. caracasana*), and that a low density deciduous canopy has increased evaporation, which prevents pasture production (*T. rosea*). For the middle species, *C. alata* and *G. ulmifolia* have the highest percentages of pasture production.
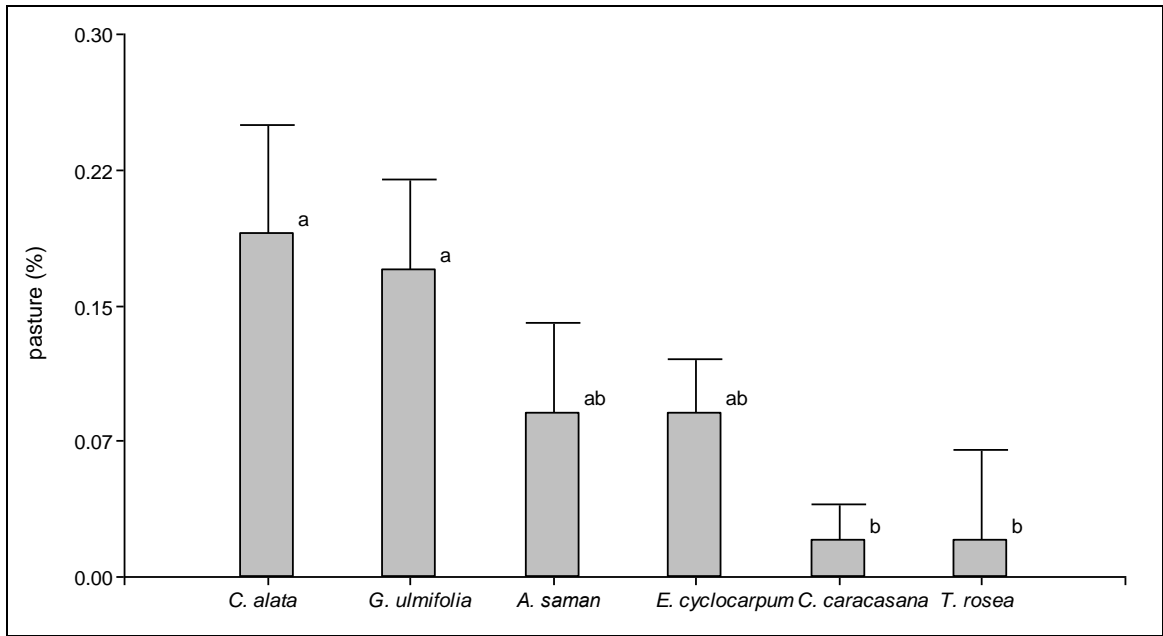
Figure 11. Histogram showing means values of pasture production under different species canopy during the dry season with their respective standard error and LSD Fisher test in letters.
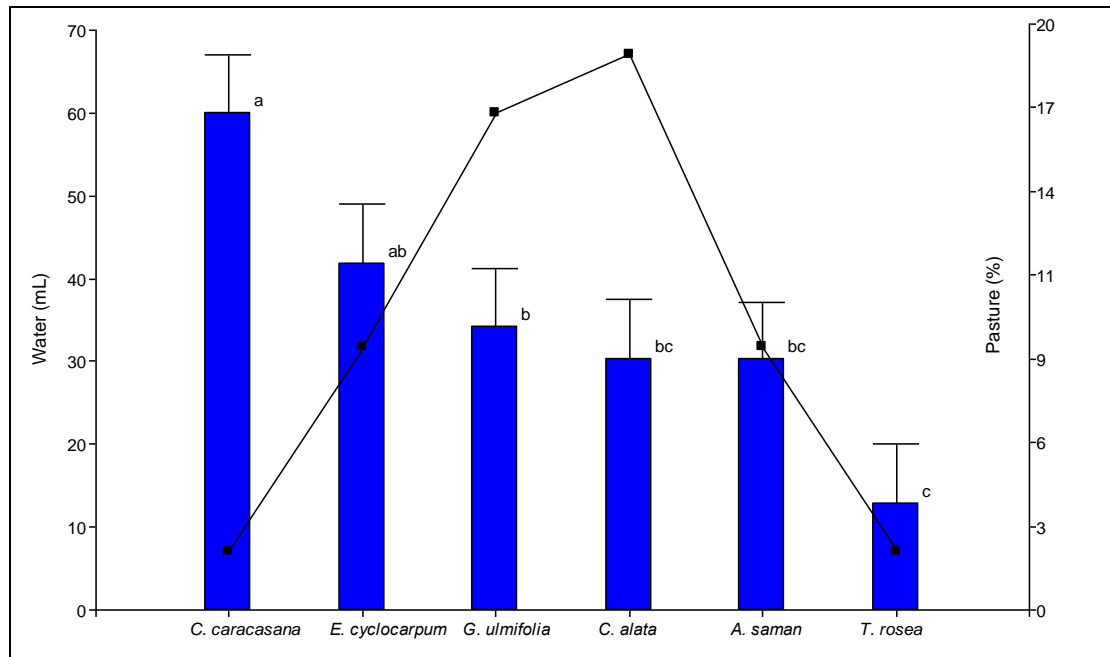

Figure 12. This figure resumes the evaporation prevented under the canopy mean values of our different species in millimeters, and the percentage of pasture cover found under these same canopies.

5.3.2 Overlapping of traits

Results from Pearson correlation analysis showed a significant negative correlation among evaporation and pastures (r=-0.41, p=0.0129). When the amounts of evaporation prevented where higher, less pasture was found under the canopy. Even though we are looking for trees that prevent understory water stress, it seems that in the dry season it is important to guarantee light transmission in order to have a good production of pastures under the canopy.

Only nine of the field measured traits were correlated with evaporation values during the dry season. Correlation values were low, but significant (Table 7). The highest variation in water retained was explained by canopy phenology which explained 30% of the variation, followed by petiole length and leaf area index. A stepwise multiple linear regression analysis was done for these variables in an attempt to identify which traits had a direct effect on understory dynamics but because all variables are autocorrelated a smaller group of variables could not be identified.

Table 8. Linear regression and p values for traits correlated to difference of evaporation inside and outside the canopy (the amount of water conserved by the effect of overstory).

Trait	r^2	p
Phenology	**0.30**	0.0009
Leaf area index	**0.20**	0.0077
Transmitted light	0.16	0.0176
Canopy density 1	**0.19**	0.0094
Petiole length	**0.21**	0.0065
Leaf thickness	**0.19**	0.0096
Twig dry matter content	0.14	0.0288

Wood density seems to be mildly correlated to evaporation (r=0.14, p=0.0283), but is also a trait that is related to the size of the tree. We were unable to find any strong correlations between the proportion of pasture production beneath the tree crown and the traits of the tree species. We did find significant negative correlations between tree leaf relative water content (r=-0.42, p=0.05) and the proportion of cover during the dry season. Also negative relations were found for pasture cover after the first rains (transition) and tree height (r=-0.42; p=0.0104), canopy height (r=-0.38, p=0.0232), and leaf area (r^2=-0.44, p=0.0069).

5.3.3 Extrapolation to a bigger data set

As an exploratory exercise, we used a database with literature based functional traits and classified them in functional groups based on the traits that showed a closer relation to our response-effect correspondence traits (Figure 13). For the 142 species database we identified three groups in the cluster analysis with a cophenetic correlation of 0.928, using the three variables related to this study (laminar area, wood density, leaf phenology). Ideally, we will include more traits, but we found that these are the ones that show a stronger connection with our results. The MANOVA done to differentiate these three groups was significant (p<0.0001) and the Hotteling test showed differences for both laminar area and wood density variables in the three groups. The cross tabulation for leaf phenology showed significant differences (p<0.0001) among the three groups. The first group was characterized with evergreen species with low values of laminar area, and higher values of wood density. The second group has deciduous species with high values of leaf area. And the third group consists of species with high wood density and low leaf area.
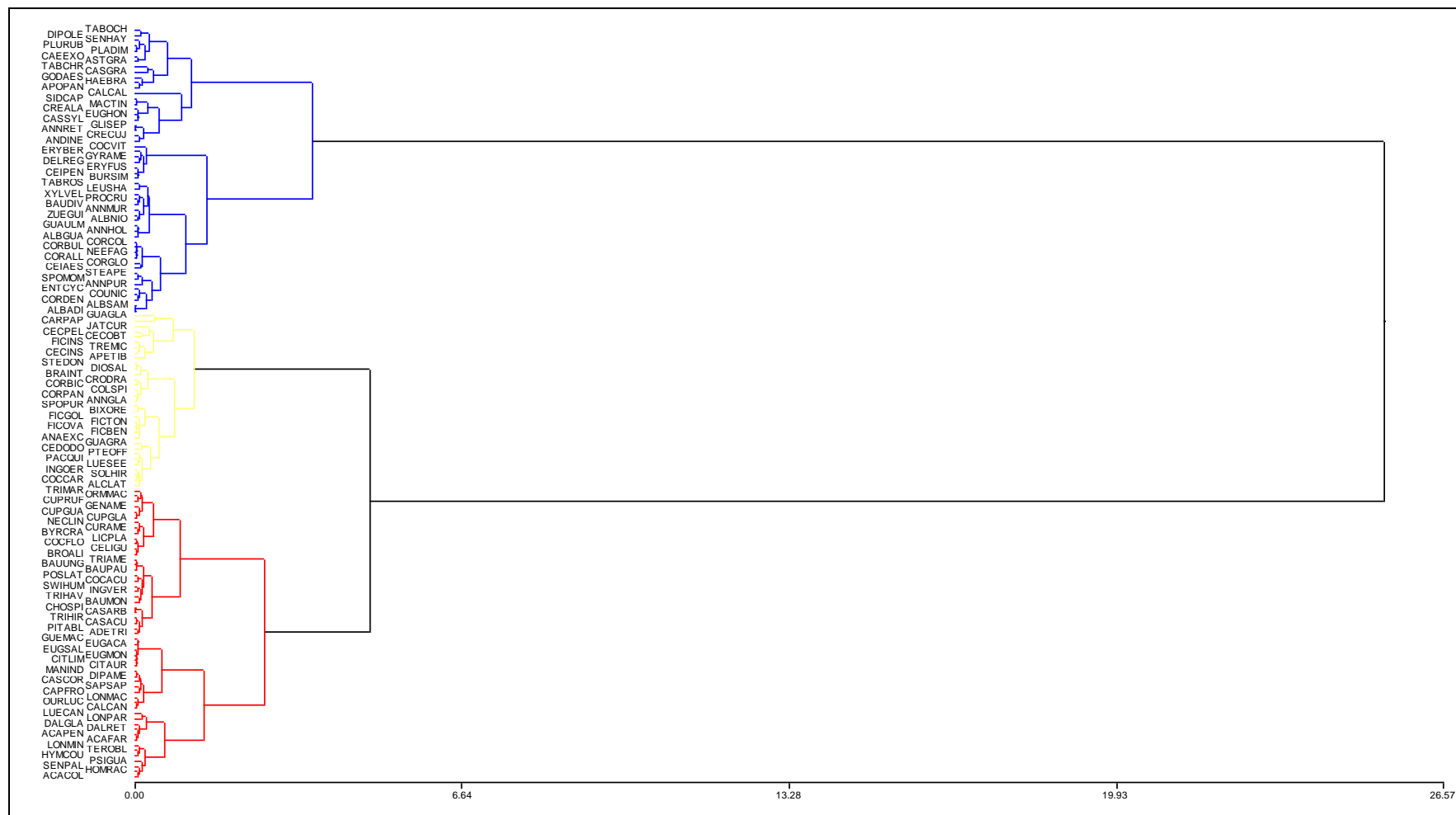
Figure 13. Cluster analysis for 142 species divided in three functional groups:1) drought tolerant conservative species (red); 2) drought avoiders (blue); 3) drought tolerant acquisitive (yellow).

5.4 DISCUSSION

Our results support that simple evaporation measures can be done to comprehend the ecosystem process of understory water stress. The species that suggests the most benefits in terms of evapotranspiration reduction are *G. ulmifolia* and *C. alata*. The importance of these two species shows that while providing enough shade to prevent extreme understory desiccation, they are also able to provide enough light transmission to allow pasture growth. Also, they reduce competition for water resources with adjacent understory vegetation during dry season by limiting photosynthesis through the partial or complete loss of leaves as suppose to an evergreen species such as *C. caracasana*. When we look at the effects on evaporation, we can distinguish that phenology is a very important trait. Tree height, height to the lowest branch and canopy height were all traits that were expected to determine the amount of light that was transmitted to the understory. However, the ratio between canopy height and canopy diameter the trait provided a more accurate description of the canopy shape, and its effect on understory conditions.

The resilience of an ecosystem depends on two factors in terms of functional ecology: (1) functional redundancy – that is the number of species that contribute in a similar way to an ecosystem function, and (2) response diversity – the functional similarity of species to respond to disturbances (Laliberté et al., 2010). By following this line of thought, we can say that augmenting or prioritizing the response diversity and the functional redundancy provided by different species in terms of one (or more) ecosystem functions of interest, we are able to increase the resilience to disturbances such as severe drought in arid and semi arid regions. In the previous chapter we made a classification among the species in this study that allowed us to determine which species had definite strategies for drought avoidance. In the experiments conducted here, we made a quantified approach of the contribution of the same species to understory conditions links to services of interest. By doing this, we propose a set of traits based on the response-effect correspondence across our studied species. Several effect traits that have been correlated to evaporation values strongly overlap with those responses to drought stress. The traits that are correlated to evaporation values (effect traits) and that strongly overlap with those involved in the responses of the species to drought (response traits) are phenology, diameter at breast height, and leaf area index. These are also traits

strongly related to plant strategies to cope with water stress (tolerance-avoidance). We suggest that this functional convergence is an indication of traits that allow us to infer on the provision of the ecosystems services such as drought regulations and resilience.

According to Lavorel & Garnier (2002), "harder" traits (physiological) are more commonly used for effect groups, and "softer" traits (morphological and behavioral) for response grouping. But in our study, we propose that "soft" traits can be used to assess responses and effects for particular functions of interest. The mentioned traits can be used in order to make a larger classification of species in terms of drought responses and effects on humidity conservation. By identifying functional groups and a set of species that have similar responses to the ecosystem processes we can improve the resilience of ecosystem services of interest (Carpenter 2006). As proposed in Violle (2007), the integrations of functions among organization levels need to be made explicit when scaling-up to the levels of populations, communities and ecosystems.

Some of the principal limitations for the adoption of silvopastoral systems mentioned by different authors are the lack of capital for establishment, labor demand, scarce availability of seed, and lack of knowledge of the producers about SPS (Alonzo 2001; Dagang and Nair 2003). As such, for the establishment and design of SPS, the selection of species that provide multiple services is a way of assuring earnings after their adoption. The species contribution to the services is very important. In terms of multifunctionality, our study suggests that the species that provides the largest amount of known services that are of importance to farmers (drought tolerance, minimizing evaporation, pastures conservation, etc.) are *G. ulmifolia* and *C. alata*.

Farmer knowledge influences the decisions for tree management to assure pasture and livestock production. It has been reported that farmers select the trees that provide shade for animals or because the trees help maintain the humidity of the pastures during the dry season (Joya et al., 2004). Two very important species that provide forage during the dry season are *A. saman* (leaves, flowers and seedpod), *G. ulmifolia* (leaves, flower and fruit), and the less studied species *C. alata* (leaves, flower and fruit). Another good source of wood is *T. rosea* with its symmetrical long shaft, and it also provides a source of medicine. The most noticeable

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species from a multi-functional point of view is *A. saman* since it provides multiple services (wood, medicine, live fences).

5.5   CONCLUSIONS

According to our results, the species that we recommend are *G. ulmifolia* and *C. alata*. These species showed clear different strategies to cope with drought stress, and this difference in responses provides that functional diversity that allows a system to be more resilient to climate variation. And also, these species provide a reduction in potential evapotranspiration under their canopy during the most critical times, and allows pastures to receive enough light to grow. There are specific traits that showed a functional convergence between responses and effects in the ecological processes of interest, and because of this, allow us to infer in the provision of ecosystem services of critical importance in the study area.

Isolated tree individuals provide an advantage for the development of experiments that assess the effect of the tree in a particular ecosystem process. And for a functional assessment of trees according to specific ecosystems processes, silvopastoral systems provide an advantage in the design of experiments since it reduces a considerable amount of intra and interspecific competition. In conclusion, we suggest that the functional ecology approach can be used to identify ecosystem processes and functions of importance in silvopastoral systems. Simple independent studies such as this one fill the void of studies that actually try to relate traits to ecosystems processes. And by determining these interactions, we can predict species specific functions in ecosystems services of interest.

5.6 REFERENCES

Alonzo, Y.M.; Ibrahim, M; Gómez, M.; Prins, K. 2001. Potencial y limitaciones para la adopción de sistemas silvopastoriles para la producción de leche en Cayo Belice. Agroforestería en las Américas. 8(30):24-27

Cornelissen, J. H. C.; Diez, P. C.; Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology 84:755-765

Beer, J.; Harvey, C.; Ibrahim, M.; Harmand, J. M.; Somarriba, E. y Jiménez, F. 2003. Servicios Ambientales de los Sistemas Agroforestales. Agroforestería de las Américas 10(37-38): 80-87 Only Abstract.

Dagang, A.B.K.; Nair, P.K.R. 2003. Silvopastoral research and adoption in Central America recent findings and recommendations for future directions. Agroforestry Systems. 59:149-155

Díaz, S.; Cabido, W. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16(11):646-655

————; Hodgson, J.G. ; Thompson, K. ; Cabido, M. ; Cornelissen, J.H.C. ; Jalili, A. ; Montserrat-Martí, G. ; Grime, J.P. ; Zarrinkamar, F. ; Asri, Y. ; Band, S.R. ; Basconcelo, S. ; Castro-Díez, P. ; Funes, G. ; Hamzehee, B. ; Khoshnevi, M. ; Pérez-Harguindeguy, N. ; Pérez-Rontomé, M.C. ; Shirvany, F.A. ; Vendramini, F. ; Yazdani, S. ; Abbas-Azimi, R. ; Bogaard, A. ; Boustani, S. ; Charles, M. ; Dehghan, M. ; de Torres-Espuny, L. ; Falczuk, V. ; Guerrero-Campo, J. ; Hynd, A. ; Jones, G. ; Kowsary, E. ; Kazemi-Saeed, F. ; Maestro- Martínez, M. ; Romo-Díez, A. ; Shaw, S. ; Siavash, B. ; Villar-Salvador, P. & Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295-304

Flynn, D.F.; Gogol-Prokurat, M.; Nogeire, T.; Molinari, N; Trautman, B.; Simpson, N.; Mayfield, M.; DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22-33

Harvey, C.; Medina, A.; Sánchez Merlo, D.; Vílchez, S.; Hernández, B.; Saenz, J.; Maes, J.; Casanoves, F; Sinclair, F.L. 2006. Patterns of animal diversity associated with different forms of tree cover retained in agricultural landscapes. Ecological Applications 16:1986-1999

Hooper, D.U.; Solan, M.; Symstad, A.J.; Díaz, S.; Gessner, M.O.; Buchmann, N.; Degrange V.; Grime, P.; Hulot, F.; Mermillot-Blondin, F.; Roy, J.; Spehn, E.; van Peer, L. 2002. Species diversity, functional diversity, and ecosystem functioning. In: Loreau, M.; Naeem, S.; Inchausti, P. (eds.). Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, pp.195-208

Joya, J., M. López, R. Gómez, and C.A. Harvey. 2004. Conocimiento local sobre el uso y manejo de árboles en fincas ganaderas del municipio de Belén, Rivas. Encuentro, 36(68):44-59

Lavorel, S.; Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plants to traits: revisiting the Holy Grail. Functional Ecology 16:545-556

_____; Grigulis, K.; Mcntyre, S.; Williams, N.S.G.; Garden, D.; Dorrough, J.; Berman, S.; Quétier, F.; Thébault, A.; Bonis, A. 2008. Assessing functional diversity in the field – methodology matters! Functional Ecology 22:134-147

Laliberté, E.L.; Wells, J.A.; DeClerck, F.; Metcalfe, J.D.; Catterall, C.P.; Queiroz, C.; Aubin, I.; Bonser, S.P.; Ding, Y.; Fraterringo, J.M.; McNamara, S.; Morgan, J.W.; Sánchez Merlos, D.; Vesk, P.A.; Mafield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology letters 13:76-86

Loreau, L.; Naeem, S.; Inchausti, P.; Bengtsson J.; Grime, J.P.; Hector, A.; Hooper, D.U.; Huston, M.A.; Raffaelli, D.; Schmid, B.; Tilman, D.; Wardle, D.A. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294(5543):804-808

Mosquera, D. 2010. Conocimiento local sobre bienes y servicios de especies arbóreas y arbustivas en sistemas de producción ganadera de Rivas, Nicaragua.

Pezo, D; Ibrahim, M. 1998. Sistemas silvopastoriles. (2da ed.) CATIE (Centro Agronómico Tropical de Investigación y Enseñanza). Turrialba. CR. 258p.

Primack, R.; Rozzi, R.; Feisinger, P; Massardo, F. (eds.) 2001. Fundamentos de Conservación Biológica: perspectivas latinoamericanas. Fondo de Cultura Económica, D.F., México

Poorter, L.; Markesteijn, L. 2007. Seedling Traits Determine Drought Tolerance of Tropical Tree Species. Biotropica 40(3):321-331

Power, J.S. and Tiffin, P. 2010. Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. Functional Ecology 24(4):927-936

Violle, C.; Navas, M.L.; Vile, D.; Kazafou, E.; Fortunel, C.; Hummel, I.; Garnier, E. 2007. Let the concept of trait be functional! Oikos 116:882-892

World Meteorological Organization (WMO). 1992. International Meteorological Vocabulary (2nd ed.) WMO-No. 182, Geneva. 784p.