

FUNCiTREE

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Cross-site analyses of agroforestry ecological functions in sub-humid and semi-arid regions

Editors
Graciela M. Rusch
Francisco I. Pugnaire

COOPERATION

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Graciela M. Rusch

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CONTACT INFORMATION
Graciela M. Rusch: graciela.rusch@nina.no
Francisco I. Pugnaire: fip@eeza.csic.es

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1 Coping with water shortage

Cristina Armas (EEZA-CSIC), Fernando Casanoves (CATIE), Fabrice DeClerck (CATIE), Joseph S. Diémé (EEZA-CSIC & ISRA), Mayécor Diouf (ISRA), Dioumacor Fall (ISRA), Bocary Kaya (IER), Iván Prieto (EEZA-CSIC), Francisco I. Pugnaire (EEZA-CSIC), Ignacio Querejeta (CEBAS-CSIC), Lester Rocha (NINA), Graciela M. Rusch (NINA), Dalia Sánchez (CATIE) & Harouna Yossi (IER).

1.1 Introduction

Unraveling belowground processes in plant-soil interactions remains one of the greatest challenges in plant ecology. Stable isotopic analyses of xylem water and leaf tissues coupled with data on soil and different water sources provide valuable insights on fundamental ecological processes such as plant water sources and plant water and nutrient use efficiency, to name a few.

In water-limited habitats with heterogeneous conditions and pulsed resource availability, plant responses rely on contrasted water use strategies. However, there is no single strategy to cope with water shortage that results from variability in rainfall distribution patterns. Coexisting plant species may adopt contrasting resource use strategies through differences in key traits that are the result of adaptive processes in evolutionary time.

One of FUNCiTREE's aims was to explore the functional diversity of agro-silvo-pastoral systems in Central America and the Sahel, with respect to functions related to drought tolerance and water use efficiency.

1.2 Methods

We used the stable isotopic composition of xylem water and leaf tissues of agroforestry (AF) species coupled with the isotopic signal of soil and freatic water to gain insights on the water sources used by the different tree species and their efficiency in different seasons. The method of stable isotope analysis is based on the fact that different rates of biophysical and biochemical processes can lead to differences in isotope signature of an element. Thus by studying the isotopic composition of different elements in plant material it is possible to gather useful information on the different physiological processes where this element has been involved. In FUNCiTREE we analyzed the oxygen and hydrogen stable isotope composition of xylem water in stems, soil water (at different depths), well water and rain to obtain information on where the trees took up water (Fig. 1).

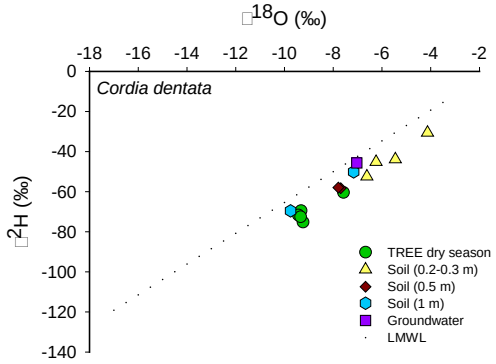


Figure 1: Interpretation of stable isotopic signals to assess water sources. δ^2H and $\delta^{18}O$ values in Cordia dentata xylem water samples, in soil water at different depths, in groundwater at the sites where the trees grew in the dry season, , and the Local Meteoric Water Line (LMWL). The coincidence of the signal in the tree and of the water at 1 m depth indicates that the tree primarily absorbes water from this layer in the soil at this time of the year.

The carbon isotopic composition of leaves gave us information on the integrated value of the intrinsic water use efficiency of a plant during the lifespan of the leaf. This analysis is only valid in C3 species, such as AF tress in this project. We took samples in the wet and rainy seasons on 21 species in each site, Rivas (Nicaragua), Potou (Senegal) and Ségou (Mali), and 6 trees per species following a common protocol.

1.3 Results and discussion

The analysis of $\delta^{2}H$ and $\delta^{18}O$ composition of xylem sap, soil and groundwater, and the composition in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ of dry leaves, revealed high plant functional diversity in all three AF systems. They show that multiple-isotopic analyses of AF trees and water provide a unique way to explore the relationships between water and carbon fluxes in the plant-soil-atmosphere continuum. They also evidence a diversity of water-use and drought coping strategies in AF species in seasonally dry areas, thereby revealing a high plant functional diversity in the AF systems studied in FUNCiTREE.

Case-specific study of tree water sources

In Rivas, during the dry season only two species relied on the small quantities of water stored in the surface soil (around 25 cm deep): *Karwinskia calderonii* and *Spondias purpurea*. Both species have a semideciduos habit and drop a considerable portion of foliage during the dry season. Most of the species analyzed obtained water from intermediate soil depths (between 0.5 and 1.0 m depth); e.g., *Byrsonima crassifolia, Cordia alliodora, C. dentata, Guazuma ulmifolia, Simarouba amara, Spondias mombin, Swietenia humilis* and *Tabebuia rosea*, and from deep soils profiles (more than 1 m) e.g., *Albizia niopoides, Ceiba pentandra, Coccoloba caracasana, Enterolobium cyclocarpum, Mangifera indica and Myrospermum frutescens*. None of the species in the AF cases in Rivas obtained the water from the relatively deep groundwater (median depth at 20 m) (Fig. 2).

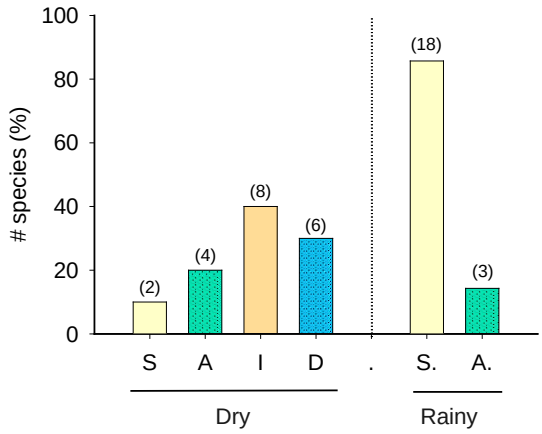


Figure 2: Number of species relying on different water sources in Rivas, Nicaragua. S: Superficial (<0.3 m depth); I: Intermediate (between 0.5 and 1.0 m depth), D: Deep (> 1 m depth) and A: Multiple depths along the soil profile.

The depth of the water source changed during the rainy season. Plant water sources were then rather shallow and most species relied on rain water stored in the first centimetres of soil surface. Soils from these AFs are silty and have quite low infiltration capacity. During the rainy season floods and waterlogging phenomena are not uncommon in some properties (potreros) and in such events some trees can even be uprooted by water. The vertisolic properties of the soil, with very high clay contents and low permeability may also be contributing factors to the relatively low-depth water absortion displayed by the trees in this area in the dry season.

In Potou field site, plant water sources were more diverse and contrasted among seasons. On the dry season, most species relied on water stored in soils at intermediate depths (between 0.5 and 1.0 m depth); e.g., *Acacia seyal, Acacia tortilis, Annona senegalensis, Boscia senegalensis, Combretum glutinosum, Prosopis juliflora, Sclerocarya birrea* and *Balanites aegyptiaca*, and from deep soil (below 1 m deep but above groundwater level); e.g., *Acacia nilotica, Adansonia digitata, Aphania senegalensis, Bauhinia rufescens* and *Celtis integrifolia*. Other species took up water from several different depths along the soil profile; e.g., *Acacia senegal, Neocarya macrophylla, Tamarindus indica* and *Faidherbia albida*. Finally, some species mostly relied on groundwater both in the dry and rainy seasons (e.g. *Ziziphus mauritiana* and *Maytenus senegalensis*) and during the dry season (e.g., *Cordia sinensis* and *Tamarix senegalensis*). Around 65% of the species changed their preferred water source when the rainy season was settled, and obtained the water from shallower soil profiles compared to dry season (from deep to intermediate soil profiles and from intermediate to shallow soils) (Fig. 3).

Water use efficiency (WUE)

Intrinsic Water Use Efficiency (WUE) of all species analysed also differed among seasons, the main water sources used and sites. In Rivas, during the dry season, species specific WUE decreased with increasing depth of the plant water source. On the other hand, tree WUE was generally lower in the rainy season compared to the dry season, but there were no differences in WUE among group of species that accessed different water sources in the soil profile in this season. These results are in agreement with earlier evidence indicanting that the resource use efficiency of plants decreases with resource availability, i.e. when water is readily available (deep in the soil in the dry season, and more in the wet than in the dry season) trees displayed lower WUE.

The most remarkable relationship among WUE and other tree physiological traits was among WUE and leaf N, C:N ratio, leaf dry matter content (LDMC) and photosynthetic efficiency of photosystem II (an overall measure of plant physiological stress). During the dry season plants with higher concentration of N in leaves had higher WUE but this relation changed in sign during the rainy season. An inverse relationship was found for C:N ratio and LDMC.

In Potou, Senegal, species intrinsic WUE was higher in the rainy season than in the dry season which contrasts with the general notion that WUE becomes lower when resource supply increases. Within both the dry and the rainy season there were no differences in WUE among groups of preferred water sources but there were some small differences in WUE among species with different leaf phenology. The species that were most efficient in their water use during the dry season were the deciduous trees and the least efficient ones were the semi-deciduous species. We considered the case of *Faidherbia albida* separately since this is the only rainy season deciduous species in our dataset. In terms of WUE, it behaved in-between a deciduous and an evergreen.

In species with C_3 photosynthetic pathway, the discrimination in ^{18}O in leaves is inversely related to the ratio of atmospheric to leaf intercellular water vapour pressure, and thus, it provides a time-integrated indication of stomatal conductance (gs) and transpiration (E) during the growing season, or in other words, the mechanisms that regulate water loss in the plant (Farquhar et al. 1989, Dawson et al. 2002, Klein et al. 2005). Interestingly, discrimination in ^{18}O in leaves is not related to photosynthetic rate (A), and thus it can help to separate the independent effects of A and gs on WUE. We measured $\delta^{18}O$ in leaves of trees in the AFs from Senegal in the dry season. Results showed a positive relationship between WUE and $\delta^{18}O$ in leaves which we attributed to differences in control of water loss. This means a tight control of plant E and gs rates when soil water was less available for plants, also reflected by the relationship between WUE and stem water potentials; the higher the water potential the lower the WUE of the species. Finally, plants with higher leaf N had lower gs and/or transpired less, likely due to higher amount of photosynthetic enzymes (such as Rubisco) which allow for higher CO_2 fixation at lower gs values.

These results of AF trees and associated processes that affect water and carbon dynamics are important because they may suggest that despite differences in water availability, trees in these areas have the capacity to affect more strongly the processes involved in the water cycle (amount and source of water absorbed and transpired), than the carbon cycle (the amount of atmospheric CO_2 captured) given the low N levels in the soil. This knowledge is important to understand and model bio-geochemical cycles and the changes that may occur with shifts in the climate and the composition of the plant communities.

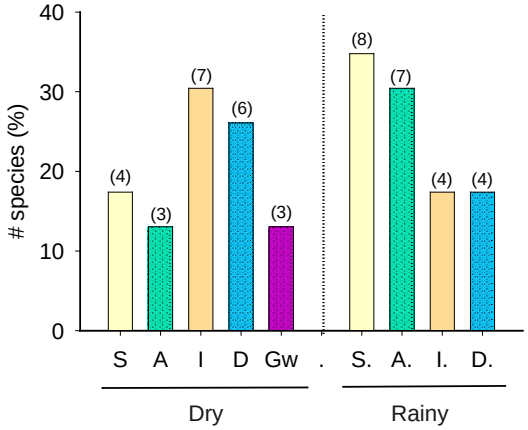


Figure 3: Number of species relying on different water sources in Potou, Senegal. S: Superficial (<0.3 m depth); I: Intermediate (between 0.5 and 1.0 m depth), D: Deep (> 1 m depth) and A: Multiple depths along the soil profile.

Cross-regional comparisons of water sources and water use efficiency

Trees of AFS in Rivas, Nicaragua and Potou, Senegal –where isotope analysis are already available- mainly relied on soil water stored at intermediate (<0.5 m) to deep (1 m or deeper) soil profiles during drought periods. Also, trees changed soil water sources between seasons and, as expected, these sources were usually shallower in the rainy than in the dry season.

Furthermore, the efficiency of water use depended on the source where the trees took up water, with substantial differences between trees in Central America and the Sahel. First, the *time-integrated intrinsic Water Use Efficiency* (WUE) was usually related to the source of water that trees relied on in Nicaragua, but not in the Sahel. In AF sytems in Nicaragua, trees relying on deep, permanent water sources displayed the lowest WUE values, while those which withstand pulsed resource availability (surface soils) displayed the highest WUE. Tree WUE changed also among seasons. In the rainy season plant WUE of Central America species was lower, but in Sahelian species WUE was higher in the rainy than in the dry season.

2 Tree traits and their effect on soil properties

Marcel Hoosbeek (WUR), Roy Remme (WUR), Dioumacor Fall (ISRA), Peter Buurman (WUR), Pere Casals (CTFC), Cristina Armas (CSIC), Mayécor Diouf (ISRA), Ibrahima N'Diaye (IER), Muhammad Ibrahim (CATIE), Bocary Kaya (IER), Andreas Nieuwenhuyse (CATIE), Francisco I. Pugnaire (CSIC), Johanna Romero (CATIE), Graciela M. Rusch (NINA), Dalia Sánchez (CATIE), E. Velthorst (WUR) & Harouna Yossi (IER).

2.1 Introduction

The decline in soil fertility limits agricultural productivity with consequences for food insecurity and rural poverty across the semi-arid and sub-humid tropics where low-input agriculture and husbandry is practised. Thus, AF is increasingly used to restore soil fertility and raise agricultural productivity, since solitary trees in addition to many other services, trees enhance soil characteristics and change the cycling of C and nutrients in their vicinity. Knowledge about the effects of trees on soil nutrient contents and dynamics will improve the theoretical basis for soil and tree management oriented towards improving or maintaining soil fertility in tropical pastures, thereby harmonizing food production systems with environmental and biodiversity preservation.

Plant species influence ecosystem nutrient dynamics through a variety of mechanisms (Craine 2009 and references therein), and trees with different characteristics are expected to have different effects on soil nutrient stocks and cycling (Kumar 2008). Therefore, the success of an agroforestry system depends largely on the tree species and its traits.

2.2 Methods

FUNCiTREE studied the influence of 14 woody species in the Sahel, and 5 species of trees in Central America on a series of soil fertility indicators. In the Region of Louga, Senegal, we studied 11 species of trees (*Acacia senegal, A. tortilis var. raddiana, Faidherbia albida, Celtis integrifolia, Combretum glutinosum, Adansonia digitata, Balanites aegyptiaca, Neocarya macrophylla, Tamarindus indica, Zizyphus mauritiana and Sclerocarya birrea*) and 3 species of shrubs (*Annona senegalensis, Boscia senegalensis and Maytenus senegalensis*). In Rivas, the 5 species were *Guazuma ulmifolia*, *Enterolobium cyclocarpum*, *Albizia saman, Tabebuia rosea* and *Crescentia alata*.

In both areas, we did side-by-side comparisons of soil fertility indicators on paired plots, located under the area of the canopy influence of the tree and in open grassland (Figure 4). This approach was chosen to minimize the confounding effects of climate, topography or soil type between sites on the canopy factor (under tree and open grassland). The possible correlation of species with site characteristics was minimized by selecting paddocks with similar landform and soil characteristics. The indicators of soil fertility were soil pH, carbon and nitrogen stocks, and available phosphorus in addition to some site-specific indicators such as density of mycorrhiza spores in Senegal, and various organic matter fractions, extractable cations, and the natural abundance of ^{13}C in soil organic matter.

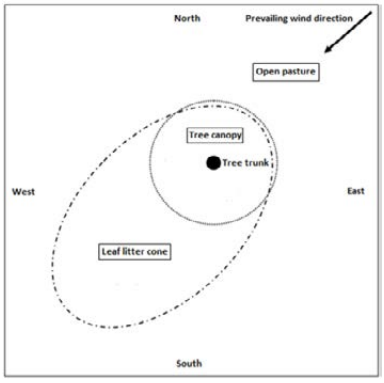


Figure 4: Diagram indicating the location of soil sampling in the Rivas site. Samples were collected under the tree canopy and in a similar area of grassland with no influence of the tree canopy.

In addition, we used stable isotope analysis to gain insights on the sources of nitrogen in the trees. $\delta^{15}N$ was analysed in leaves of 65 species, aprox. 20 species in each site.

2.3 Results and discussion

Case-specifc results

In the Sahel site, species considerably increased electrical conductivity and slightly acidify the soil except in the case of *C. integrifolia* and *A. senegal*. *C. glutinosum, S. birrea, T. indica, B. senegalensis, N. macrophylla* and *B. aegyptiaca* increased soil electrical conductivity more than 200%.

The impacts on soil organic matter were highly significant, particularly in the case of *T. indica, A. raddiana, F. albida, A. senegal* and *N. macrophylla* where the increase in total carbon was higher than 150%. The effect on soil N varied more with the species. Legume species, which are putative nitrogen-fixing trees (*A. raddiana, F. albida* and *A. senegal*) increased total nitrogen substantially (over 150%) only *F. albida* increased the available phosphorus with over 100%. These enhancing effects of *F. albida* corresponded with an above-average net positive effect on the understorey herbaceous biomass production.

Trees had a negative effect on the occurrence of mycorrhizal fungi. In general, the density of fungal spores was lower under tree cover than in the open grassland except for *C. integrifolia, S. birrea and M. senegalensis*. Based on these variables, *F. albida, N. macrophylla, A. raddiana, T. indica* and *A. senegal* were the species that had the most important positive effect on soil fertility.

In Nicaragua, we also observed a significant effect of trees on soil properties. Soil organic C and N, available P and extractable K+ and Ca2+ were higher under the tree canopy than under paired open grassland. Also stable isotope analysis (natural abundance of $\delta^{13}C$ in of soil organic matter) indicated a strong role of trees in soil formation, showing a significant input of tree biomass and debris (signal related to C_3 photosynthetic pathway) under the trees, compared to the open pasture (showing a signal corresponding to C_4 metabolism, characteristic of the grasses in the region). The basal area of trees was positively related with the canopy effect on soil variables, thus suggesting that the age or sizes of the trees are relevant factors associated with the content of soil C and nutrients.

On the other hand, and in contrast to the results obtained in the Sahel site, no specific effects related to the legume species group were detected. Our results indicate that in fertile seasonally dry subtropical pastures, scattered trees have an overall effect on soil fertility, and that the magnitude of the effect depends more on the tree characteristics (i.e. basal area, crown area) than on whether the species is a legume or not.

Additionally, we explored potential differences between species in the effects on soil respiration species using 2 examples, *Guazuma ulmifolia* and *Crescentia alata*. Also these results show a net positive effect of trees on soil C content ($P<0.001$), particularly in the upper soil layers ($P<0.001$). Also, these results confirm the results from the other studies in the project indicating an overall effect of the tree, regardless of the species. The Soil C present in the “free labile” and “occluded” fractions was only lower in the sub-soil ($P<0.001$), but otherwise not affected. The mineral associated C fraction was affected in a similar way as total soil C content.

As in the case of C, soil N content was higher under the trees ($P<0.001$) and lower in the sub-soil ($P<0.001$), but there were some differences between tree species. Total N was higher under the canopy and leaf litter fall zone of Jícaro ($P=0.012$). Soil P content was not affected by tree species or relative location to the trees. Soil respiration, measured as CO_2 efflux at the soil surface, was highest in the leaf litter zone, intermediate in the pasture and lowest under the canopy ($P<0.001$), while average respiration was higher under *G. ulmifolia* ($P=0.013$).

From these results, we inferred that high soil C storage is promoted by the canopy and leaf litter zones of *C. alata* trees. The latter corresponds well with the observed higher respiration rates under *G. ulmifolia*.

Based on the observed effects on the C:P ratios, but not on C:N ratios in *C. alata*, there are some indications of higher uptake of P under *C. alata* and possible limiting role of P in the areas where the species occurs. By looking at the free labile and occluded fractions, the early stages of soil C stabilisation



Photo 1: Soil samples taken under Celtis integrifolia (right) and in an adjacent area of open grassland (left). The darker colour of the soil under the tree indicates higher organic matter content and possibly, more moisture. Photo: G. M. Rusch

processes do not seem to be affected by tree species or location (under the tree vs open grassland), or may be obscured by the rapid turn-over of organic matter and its high spatial variability. However, the most stable mineral associated fraction, which makes up ~ 89% of total soil C, is about one-and-a-half times larger under *C. alata* than under *G. ulmifolia* or the pasture. Carbon sequestration as an ecosystem service may therefore be promoted by the use of Jícaro in silvopastoral systems.

Cross-site comparisons

In all FUNCiTREE sites, the effects of trees on the soil were assessed using paired samples and comparing open grassland with the zone under the influence of well-established trees. In all cases, both in Central America and the Sahel, we have recorded a net positive effect of the trees on soil organic C. These findings are in agreement with many studies in the literature that have assessed the impacts of trees in AF systems and savanna vegetation. With the use of stable isotopes in the Rivas site, our studies give further support of the net contribution of tree litter and other debris into the soil.

On the other hand, tree species in interaction with the physical conditions where they occur appear to differ in terms of the rates of organic matter accumulation and decomposition rates, as shown by the differences among species in the accumulation of stable mineral association fractions and in the amounts of Potentially Mineralizable N fractions shown with the Rivas material. The association of tree characteristics with these critical processes in nutrient and carbon cycles deserves further assessments.

The contribution of trees to soil N also varied with the species both in the Central American and the Sahel site. Legume species are known to provide a very important input of nitrogen for pastures in AF systems, due to their putative N fixation function. Therefore, legume trees are often recommended for AF systems to reduce inputs of chemical fertilizers. They also have the added benefit of improving animal feed, because they usually have high N requirements and high leaf N contents. As expected from earlier studies and the general notion about the role of legume species in soil N enrichment, we found a consistent enhancing effect of legume species (3) on soil N in Potou. However, our data from Nicaragua do not support these findings. Although we found a difference between tree species in the contribution of soil N, this impact was not related to whether the species was a legume or not. One reason for this may be that the level of nodulation of N-fixing symbiotic bacteria is low in the Nicaraguan study sites, which could be a result of the low drainage capacity, and the tendency of water logging and cracking of these soils.

The analysis of stable isotopes ($\delta^{15}N$) samples, indicate a significant differences in N sources between the Sahelian sites and the site in Nicaragua. $\delta^{15}N$ contents in leaves of trees from African AFs were similar but differed from the lower values displayed by trees in Central America AFs. High and positive values of $\delta^{15}N$ (way above zero) (Fig. 5) can be associated with high loads of livestock faeces and urine in the Sahelian sites, but there seems to be little relationship with atmospheric N fixation. In this case, $\delta^{15}N$ should be closer to zero.

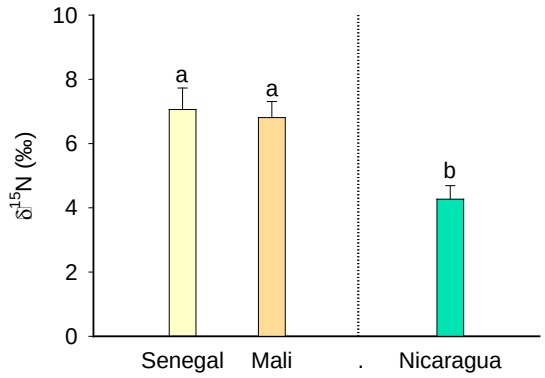


Figure 5: Average stable istope content ($\delta^{15}N$) in the three case study sites.

Based on these results, we conclude that generalizations about the contribution of legumes to soil fertility and in particular soil N content are not possible; and that before recommendations on the introduction of trees in agroforestry systems for soil fertility enhancement are made, a closer assessment of the capacity of the species in the particular biophysical growth condition needs to be conducted.

3 Tree traits and fodder production

Nelson Pérez Almario (CATIE), Vincent Heslein (CIRAD), Darwin Fabian Lombo (CATIE), Muhammad Ibrahim (CATIE), Hubert Guerin (CIRAD), Alexandre Ickowicz (CIRAD), Christina Skarpe (NINA) & Cristóbal Villanueva (CATIE).

3.1 Introduction

Farmers in arid and sub-humid regions traditionally know trees and shrub species with fodder and medicinal value. In areas with strong rainfall seasonality, as in the case of FUNCiTREE cases, woody plants are an alternative forage for cattle feed particularly in the dry season when grasses dry out. The general practice in the dry season in these areas in Nicaragua is extensive grazing (over larger areas without rotation, and based on standing dry grass biomass) with some nutritional supplement. In sub-saharan Africa animal feeding depends mainly on free grazing on rangelands and also in this region, pastoralists also have to deal with fodder shortages during the dry season. During the lean season, trees and shrubs represent the only source of green fodder available on rangelands. FUNCiTREE aimed to identify fodder species and their functional characteristics as animal feed on the specific conditions of Sahelian rangelands with a focus on the Louga area in Senegal. This context is characterized by high anthropogenic pressure and a low biodiversity of the tree layer.

Droughts have prompted investigations to characterize, quantitatively and qualitatively, forage provision by trees and preferences by animals. Exotic species have also been tested. Despite many descriptive and analytical data there has been little effect on the management of forestry and tree species in agro pastoral rangelands. New research stimulated by climatic and demographic changes must integrate socio-economic processes of management of forest stands and the multi-functionality of trees. Within this overall framework, the functional traits related to forage function must express:

- productivity of foliage and reproductive organs
- availability of forage for livestock following sychronicity between phenological cycles and major nutritive needs of animals
- palatability of species
- nutritional value expressed by concentration of digestible nutrients (nitrogen, minerals, fiber)
- capability of re-sprouting after browsing or pruning both in the rainy and dry seasons
- low contents of tannins or other characteristics that deter herbivores
- easy propagation, which is in turn related to the capacity to re-sprout after browsing
- low competition with the pasture

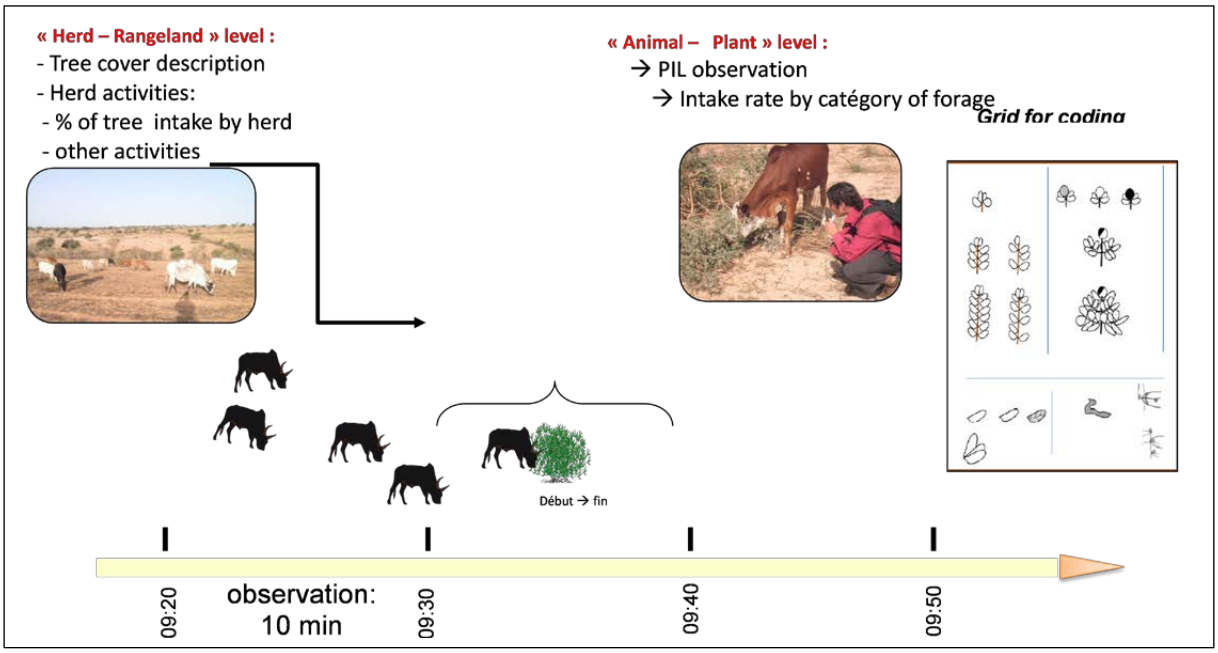
The traits related to these functions are then, those associated with to resource capture and use (productivity), demography (seed production), bud banks (capacity to resprout), chemical composition, morphology (accessibility of forage) and finally, the preference by animals determined by animal browsing behaviour and intake. Much data exist. It must be organized so that they are accessible, located in their agro-climatic and socio-economical environments, taking into account the multi-functionality of species. Furthermore, these criteria are not absolute, but depend on the biodiversity of savannah stands. The use of such data for engineering in land management based on needs and constraints of the users must take into account this diversity between and within species, and consider growth conditions.

3.2 Methods

FUNCiTREE conducted studies to assess the preference by animals of local AF tree species. In Rivas, preference was determined in ten species by cafeteria testing using five cows. The combination of ten species in pairs originated a total of 45 events for each cow, each event lasted three minutes.

In addition to fodder quality, biomass production and regrowth capacity after harvesting or browsing are important traits in trees supporting the fodder production function. Six species common in AFS in Rivas were studied, using six replicates (a total of 36 samples). The selected trees had not been managed with pruning close to the start of the experiment.

In Potou, we analysed the behaviour and the feed preferences of cattle for the available woody species on rangelands. Regular monitoring of cattle herds was done during the dry season and food preferences were determined by direct observation of woody plant intake, and the results compared with biological aspects of consumed species. The observations were conducted in three sections of the agro-ecological gradient ranging from West (Niayes area) to East (Dieri area), during the dry season (April to July). Each survey lasted 1-2 days and were conducted with a frequency between 5 and 20 days. Both herds of cattle, and sheep and goats were observed (Fig. 5).



3.3 Results and discussion

Case-specific assessment of traits and fodder provision functions

Central America

Cows consumed in descending order *Samanea saman*, *Leucaena leucocephala*, *Albizia niopoides*, *Cordia dentata*, *Moringa oleifera*, *Guazuma ulmifolia*, *Gliricidia sepium*, *Brosimum alicastrum*, *Mimosa pigra* y *Acacia farnesiana*. The preference by cows was associated with several whole-tree and leaf traits. The most preferred species are legumes which generally had higher leaf nitrogen content; the leaves are large and soft.

However, some of the least consumed trees were also legumes. The low preference in these cases was due to the presence of thorns and the high concentration of condensed tannins. Many trees with potential to be used as fodder present condensed tannins that can poison livestock if consumption is high. However, poisoning usually occurs when cattle have this only food in the diet and it is difficult that this happens in a pasture where there is a variety of forages.

Preference studies give us guidance on the animal choice, but for the design of silvopastoral systems other attributes such as ease of propagation, resprouting capacity, forage yield, and tolerance to frequent pruning must be considered as well.

The studies on biomass production and regrowth capacity after harvesting (or browsing) showed signigicantly different reponses among tree species. *Cordia dentata* and *Pithecellobium dulce* had the highest production of edible biomass 5,95 $\pm$ 1,43 and 3,20 $\pm$ 1,12 Kg dry matter (DM) / tree respectively; while *Albizia niopoides* showed the lowest yield 0,53 $\pm$ 0,14 Kg DM / tree.

The species differed in re-sprouting capacity as well. In descending order the average production of sprouts per tree was *Pithecellobium dulce* (260,5), *Cordia dentata* (147,83), *Guazuma ulmifolia* (69,0), *Albizia saman* (54,0), *Gliricidia sepium* (24,33), and *Albizia niopoides* (17,33). In terms of functional traits was determined that a lower leaf area seems to be related to a higher reservoir meristems and axial buds which improve the capacity to resprout and productivity, as in the case of *Pithecellobium dulce* (4171,9 mm^2) and *Cordia dentata* (4212,1 mm^2). Both species may have a potential for cattle feeding in the dry season, either under the cut-and-carry system or by cutting and offering the fodder on the ground near the tree. However, the effect of prolonged pruning on the response of *Cordia dentata* and *Pithecellobium dulce* needs to be determined before the species can be proposed as important fodder trees.

One of FUNCiTREE's important objectives has been to explore functional roles of a diversity of native species in the AFS in the study areas. The studies described above have made an important contribution in widening the knowledge about the fodder value of several native woody species that currently occur in paddocks in the area of Belén, Rivas, and seem undervalued, as is the case of *Cordia dentata, Gliricidia sepium, Guazuma ulmifolia, Albizia saman and Albizia nipoides*. Species like *Leucaena leucocephala*, *Cordia dentata*, *Gliricidia sepium*, and *Guazuma ulmifolia* have important advantages as on-farm feed resources. The combined use of the species such as *A. saman* + *C. dentata*; *L. leucocephala* + *C. dentate*; *A. niopoides* + *C. dentata* to supplement the basal diet in the dry season (*Pennisetum purpureum*, molasses and minerals) can improve milk production from 6.5 kg - when based only on grazing of dry grassland and with supplement of manure, molasses and mineral salt - to between 6.7 and 7 kg / cow / day. The best response is due to the associative effect of mixed browse material (at least 2 woody species such as *L. leucocephala* + C. dentate) that enhances nutrient uptake.

In the Sahel

Two shrubs, *Guiera senegalensis* and *Boscia senegalensis* appeared to be the most consumed species; they represented 60% to 100% of the feeding time on woody plants. However, the contribution of woody species in the diet shifted along the Niayes – Dieri gradient. Livestock spent significantly more time in woody species intake in the Dieri area than in the Niayes and intermediate zone.

Differences in foraging behaviour were partially explained by differences in morphological characteristics and phenology stages among the fodder species. Based on estimates on daily intake, biomass of *G. senegalensis* was primarily consumed in the first period of the dry season (April), and became of minor importance from May to July. In this period, *B. senegalensis* was the woody species with highest contribution to the daily intake. The preference of *G. senegalensis* at the start of the dry season corresponded with the period of fruit production in this species. Fruits seem to have been the main feed source in this species. The decline in consumption was associated with a period of leaf production. Our results also indicate phenological differences between the populations of browsed and non-browsed *G. senegalensis*. Changes in the flowering, fructification and leaf production stages were observed between these populations. In the case of *B. senegalensis*, fruits were not consumed, and leaves are the most consumed part of the shrub. One reason for the preference of these two shrubs in this area could also be that the rangelands have undergone a process of degradation of the biological diversity and of the fodder

provision functions, and that only a few easily accessible species remain in considerable amounts. The high medicinal value of *Guiera senegalensis* indicates furthermore that this species may contain high levels of anti-herbivore substances, which could be an explanation for why leaves in this species are barely consumed.

Both *G. senegalensis* and *B. senegalensis* were always consumed if present in the site where the herds foraged. Two other woody species, *Combretum glutinosum* and *Prosopies juliflora* were consumed, but in this case, the animals browsed only on some populations. In the case of these two species differences among populations are apparent, likely associated with the presence of chemical repelents and/or structures in the tree that deter herbivory (such as spines).

Cross-site comparisons

FUNCiTREE has advanced the understanding of the fodder provision function of woodey species in the case study areas. They show the potential of woody species to cover the feed deficit during the dry season, which is associated with the capacity of trees and shrubs to explore deeper soil water resources than the grasses.

FUNCiTREE tree used two different approaches to explore fodder preferences by livestock and relative consumption/intake rates in Central America and in the Sahel, which enabled to illustrate different dimensions of the fodder provisioning function by woody species and the factors that determine consumption. Differences in the socio-economic system, livelihoods and land-use rights also call for a variety of approaches to study these socio-ecological systems. The experience learnt in Central America shows that there are a number of native species, relatively abundant in the farms, that are consumed by livestock if accessible and that appear to tolerate harvests and/or direct browsing through vegetative growth. Other species appear to have high nutriticious value but show lower growth rates. The establishment of fodder banks, and also, promoting the establishment of some of the fodder provision species in the paddocks or in live-fences together with shredding or coppicing (cutting of side branches that are offered to the animals) are practices that can be promoted. These functions provided by different tree species are complementary and the studies highlight the importance of fodder species diversity to fulfill the fodder provision service. This conclusion is also evident from the studies in the Sahel site. They show that the species that are mostly consumed by livestock differ in their phenological development, that different parts of the plant are consumed in the different species, which results in that the important of each species as a fodder resource changes along the dry season. The FUNCiTREE studies also reveal the importance of within species variability in the fodder provision function. In the Sahel study, we found large variation in consumption among populations of the same species, which could indicate within-species differences in the content of substances that deter herbivory and/or an interplay of these characteristics with the physical environment. This knowledge is important for the recommendation to promote the establishment of a species. Within-species variability in consumption has been observed in other rangeland trees, such as in the case of *Geijera parviflora* in Australia wherethe trees appear to vary greatly in palatability. Therefoe, in order to further disentangle the particular traits that impact the food choices of woody plants, more detailed chemical analysis of the consumed trees and shrubs need to be performed in the future. In addition, to strengthen the diagnostic of traits related to the fodder function of these forage species, the results obtained in FUNCITEE must be compared to those from studies in other, more diverse sahelo-sudanian agro-pastoral rangelands.

Other functions beneficial for livestock fulfilled by trees in AF systems

The need of tree diversity in the silvopastoral system is also manifested in the other functions that trees fulfill in the livestock production system in addition to fodder provision. Trees provide shelter and shade for the animals, ameliorating in this way heat stress, but there are differences among functional groups in the provision of this service. Depending on the activity of the cow and the time of day, the animals visit

different functional groups of trees. For instance, cows use trees with less coverage to graze and those with denser canopy coverage for protection.

4 Impact of AF trees on the grass vegetation

Graciela M. Rusch (NINA), Cristina Armas (EEZA - CSIC), Mayécor Diouf (ISRA), Piedad Zapata (CATIE), Dioumacor Fall (ISRA), Fernando Casanoves (CATIE), Joseph S. Diémé (ISRA & EEZA – CSIC), Muhammad Ibrahim (CATIE), Fabrice DeClerk (CATIE), Lisa Furu Baardsen (NINA) & Francisco Pugnaire (EEZA – CSIC).

4.1 Introduction

In savannas, wooded meadows and similar systems with trees in a matrix of herbaceous vegetation, the two tiers, trees and herbaceous plants, interact in several ways. Through indirect effects of trees on soil water, nutrients and light reaching the soil, as well as directly on understory vegetation through competition for resource, trees have a large impact on understorey growth conditions. Understanding how trees affect understorey vegetation is thus critical for planning agroforestry systems since trees and understorey grassland, pasture or crop fulfill different roles. Trees may suppress grass growth through direct competition for water, light, and nutrients but trees may also facilitate grass by directly or indirectly improving environmental conditions for understorey growth.

The knowledge about how tree characteristics affect understorey vegetation is important because different tree traits may considerably affect the outcome of interactions. For instance, differences in tree size (height) will affect the amount of light interception. Also, differences in size between plants strongly imply asymmetric competition. On the other hand, as shown in previous sections, trees contribute significantly to soil formation, and reduce evaporation and temperature, which may favour the understorey species through higher nutrient availability, water retention and lower evapotranspiration demand.

Tree-understorey interactions encompass both competition and facilitation. Current knowledge supports the idea that the relative importance of facilitative and competitive processes is a function of environmental harshness, with higher facilitation effects towards more extreme environments (e.g. drier and/or with higher salinity) while competition predominates in benign conditions. We therefore compared the effects of AF trees on understorey herbaceous vegetation along a gradient of environmental productivity ranging from the Sahel to Central America, and encompassing a range of environmental productivity that included both soil properties and rainfall.

It is important to understand the nature of the the interaction between trees and understorey vegetation in AF systems since this ecological function can cause either positive or negative effects on the understorey, resulting in either synergies or trade-offs between services provided by trees.

4.2 Methods

In Central America and the Sahel, we assessed the effect of trees on the understorey by comparing above-ground net primary productivity (ANPP) of the grassland growing under the canopy of isolated tree species, and the adjacent area of grassland in similar topographic conditions. In both sites, ANPP was assessed by sampling the biomass and calculating the average daily accumulation in a period of 3 months starting at the onset of the rain season; i.e., from May to July in Nicaragua and from July to September in Senegal. When the trial started, 50 x 50 cm metal mesh cages were placed in the field to hinder grazing by large herbivores (Photo 2). A total of 17 tree species (3 in Rivas and 14 in the Sahel) were included in the experiment, with 5 replicates each. Biomass samples were harvested, dried for at least 48 h, and weighted. To assess the net effect of trees on understorey ANPP, we calculated the Relative Interaction Index (RII) following Armas et al. 2004. RII enables the comparison of tree effects by using a standardize scale (from -1 to 1) calculated on differences between paired samples under the tree canopy and open grassland.

A



B



Photo 2: Collection of biomass for grassland productivity assessment. A: Cages to exclude large herbivores established at the start of the rainy season in Potou. B: Biomass collection in Rivas. (Photos: G. M. Rusch)

4.3 Results and discussion

In Nicaragua we found, in general, negative effects of trees on understorey ANPP, particularly at peak production. However, the effect differed among tree species, with some species being associated with minor reductions in ANPP and others in which understorey ANPP was ca 30 % lower than in the adjacent grassland.

In Senegal, on the other hand, almost all tree species were either associated with an increase in ANPP or had a neutral effect.

Trees occurred in very different environments and strong differences appeared to be related to understorey conditions. There were significant differences among sites regarding variables such as understorey species richness and productivity, nutrient availability, pH, soil salinity, and the presence of mycorrhizal fungi. Soil pH was stronghly related to grass species richness, the higher the pH the more species were present. Soil salinity also influenced productivity, and the less salinity, the more species. Grass richness and fungi also depended on water availability (indirectly assessed through tree leaf relative water content), with more species and more fungal spores present with greater availability of water.

We also found that tree attributes were associated with characteristics of understorey vegetation. Trunk diameter and height influenced negatively understorey biomass and cover; taller trees were associated with fewer species in the understorey and trees with dense foliage were associated with less grass productivity and cover in the understorey.

Site productivity explained a large portion (42%) of the net effect of trees (outcome of competition and facilitation effects) on understorey above-ground net primary productivity (ANPP). The effect of trees growing in more productive sites was predominantly negative, resulting in a decrease of ANPP compared to open patches, while the facilitative effects of trees increased with decreasing site productivity. This relationship between the effect of trees and site productivity was monotonic, indicating the absence of thresholds and showing a steady decrease in the importance of facilitation with site productivity. The shape of the function and the degree to which site productivity determined the net effect of trees on understorey ANPP was similar in Nicaragua and Senegal, but site productivity had a stronger explanatory power in Nicaragua than in Senegal (ca 47 % and 26%, respectively). Also, sites in Nicaragua showed overall higher productivity, and hence, there was a trend for competitive effects to predominate among trees in Central American AF systems compared to the Sahel.

Overall, the net effect of trees on understorey ANPP was negatively associated with tree size, as large trees had stronger negative effect on pasture growth than small trees (p=0.0003).

The net effect of trees on grass ANPP (positive or negative depending on site productivity) was unrelated to the tree's net effect on soil C, N and pH, indicating a predominance of direct (tree-grass biological interaction) compared to indirect (through changes in soil properties) effects of the trees on the pasture.

We also observed species-specific responses. For instance, *Celtis integrifolia* in Senegal, showed a considerably negative effect on the understorey that would be expected from the general site productivity. *Celtis integrifolia* occurred in relatively low-producitivity sites, where a predominant facilitative effect would have been expected, but this species showed strong negative effects on its understorey. Allelopathic effects or other attributes of leaves affecting the quality of litter incorporated into the soil could explain such differences, and possibly stronger competition, although we would expect less intensity of competition in more stressful environments.

In contrast, *Faidherbia albida*, also one of the species growing in Senegal, had a net facilititave effect considerably larger than expected from site productivity. *Faidherbia albida* is a species highly valued in AF systems in the Sahel as it promotes an increase in crop yield and pasture growth. This effect could be associated to the "inverted" phenology of the species. It retains foliage during the dry season and shed it during the rain season; therefore most likely below- and above-ground competition is low as other species are not active during its growth period, thus escaping from competition. Since the species drops its foliage at the start of the rainy season, the input of fresh litter implies an important addition of nutrients for crop growth, particularly because *F. albida* is a legume.

Opposite to Nicarauga, most individuals and species studied in Senegal had a net positive effect on understorey ANPP, and there was also a trend of more net facilitative effects than expected from site producitivity.

Trees in tropical agro-pastoral systems fulfil many important functions and both trees and grasses are vital for system productivity. These functions may be in conflict with each other at times, particularly in the most productive sites, where competition prevails. However, facilitation effects were more frequent in less productive sites. In conclusion, and although there are site-specific effects, particularly dependent on site productivity, there are parallelism between Latin American and African AFS, where different tree species have different access to resources and affect understorey productivity in different ways, providing tools for improvement of agro-forestry systems. Generally in AFS, it should be expected that trees will tend to reduce pasture productivity as the amount of resources (water, nutrients) available increase, but, interestingly, trees will promote pasture growth with higher environmental harshness.

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Based on the principles of functional ecology, FUNCiTREE addresses the provision of multiple services of silvopastoral systems (SPS) in semi-arid regions in Africa and Central America. FUNCiTREE aims to provide farmers in the regions with a portfolio of regionally suitable tree species that are capable of providing multiple services. The project integrates theories and concepts from agroforestry and ecological science and will provide a scientifically based model for the design of modernized SPS.

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