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ABSTRACT OF THESIS

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ABSTRACT

This work aimed to contribute to the understanding of tree - grass inter-cropping interactions so that the productivity and sustainability of extensive livestock husbandry can be increased. The work was carried out in the context of a small farm in Oaxaca, Mexico, where increases in productivity are limited by shortage of capital and where the tree component would be used as green manure. It is difficult to investigate the effectiveness of such a system by only using conventional field trials. I constructed a mathematical model to simulate how the main components of the system function under conditions that would not be evaluated in the field. Issues such as how many trees to plant and what tree species combine with grass cattle and environment, can be answered with the model.

The particular features of the model are: 1) It describes an agro-ecosystem where trees perform several biological functions like nitrogen capture for use in the silvopastoral system, 2) It links grass and trees with the animal and 3) Nutrient availability depends mainly on soil organic matter decomposition and mineralisation rather than on external inputs. The present research consisted of 1) constructing the model prototype using data from the literature, 2) conducting field experiments to investigate the actual performance of the silvopastoral system, 3) perform laboratory research and greenhouse experiments complementarily to the field experiments and 4) elaborate on the carbon and nitrogen balance of the silvopastoral experiment, by combining research results and the mathematical model. The field experiment consisted of an array of 13 plots with one of the tree species *Gliricidia sepium*, *Leucaena leucocephala, Delonix regia* and *Lysiloma auritum* in a gradient of plant densities within a *Brachiaria decumbens* paddock. Results showed that the presence of trees in pastures is potentially useful for retaining nitrogen and carbon that would be lost in the grass mono-crop. Trees did not incorporate nitrogen through biological fixation, perhaps because the lack of adequate nodulation and they did not established their rooting systems to a depth beyond the grass roots (> 1.20m) so as to recover leached nutrients. However, trees produced mulch that was rich in nitrogen (3.8%) and whose decomposition rate ensures a slow release to prevent leaching. At the plant density used, the tree population caused no harm to grass as to production and nutritive value. Further increments in tree density in order to improve the potential for nitrogen capture should be evaluated in terms of the reduction of grass production. Several biological attributes of the species were determined, in some cases for the first time: biomass productivity, specific leaf area, nutritive value, phenolic content, root biomass, grass root longevity, root vertical distribution, etc. Such characterisation is useful for the understanding of the system inter-cropping and specially for the parameterisation of the silvopastoral model. Even though the mixtures proved able to survive for the span of the experiment, the sustainability of tree - grass inter-cropping as to the stabilisation of soil fertility requires longer monitoring. Other limiting factors such as phosphorus availability and the management of grazing systems have to be incorporated for an adequate evaluation of the silvopastoral system.

1. Introduction

The content of this chapter derives from a review of relevant literature and my own experience after twelve years working as an agronomist in the public service and in the Laboratory of Ecology, Faculty of Sciences, National University of Mexico.

The investigation of alternative approaches to pasture production has been stressed in international panels such as the Workshop on Conversion of Tropical Forest to Pasture in Latin America, Oaxaca, Mexico, 1988 (Hecht, 1988) and the International Grassland Congress, Nice, France, 1989 (Pearson *et al.*, 1989). At these meetings recommendations were made to facilitate research projects on forest and pasture sustainability, decreasing the access to tropical forest zones, promoting alternative sources of income that substitute for forest clearance, facilitating technology transfer and dissemination of information to the local level, introducing new forage species on cleared lands, agroforestry and other integrated uses encouraging diversity, optimising low input technology and intensifying management of existing pastures, among others.

1.1 Rationale.

In the last decade, there has been a considerable amount of research in the field of sustainable resource management. Governmental and international agencies, universities and research institutes have strongly encouraged many scientific projects on environmentally sustainable social and economic development.

Often, the main reason for this research is concern about global climatic change related to the role of forest management in the restoration of plant cover and the capture of carbon. Another major motivation for assistance programmes is the linkage between poverty and natural resource deterioration, particularly in rural areas of underdeveloped countries. Such deterioration has been caused by the use of ploughing, fertilisers and pesticides without proper technical assistance, or in areas unsuitable for intensive agriculture.

Despite the importance of sustainable development, the amount of money invested and the quantity of publications produced are not satisfactorily reflected in either the farmers' standards of living or in the ecological conditions of agro-ecosystems. One of the main causes of such imbalance can be found in the process of technology transfer. Because research is carried out either on experimental fields - with comparatively good conditions - or on privately owned lands - with particular site

conditions - it is difficult to apply research results to small scale farming systems. This is because environmental variability and the fragmentation of land between tenants produce an agroecological mosaic in which long-term developmental programmes are difficult to introduce. Such variability must be considered in order to achieve a broader adaptability for research results. One way of doing this is to feed simulation models with specific sets of data (parameterised) to evaluate the production system under changing environmental or managerial conditions. Models, as decision support tools, should be made available to managers in charge of regional programmes, in order to facilitate the generation of recommendations for each type of production unit.

Incorporating nitrogen fixing trees into extensive grazing systems could bring advantages such as an additional source of forage during the dry season, a high protein supplement for grass based feeds, nitrogen fixation from the atmosphere, more effective cycling of other nutrients, improvement of soil structure and a better microclimatic environment for grass and animals.

Establishment of silvopastoral demonstration plots, for local farmers to examine and discuss, requires many variables to be controlled and several years for the trees to grow and the system to be profitable. Although this long term, expensive process is indispensable, it is impossible to test every feasible change in the variables, for reasons of cost.

Constructing a mathematical model to simulate how the main components of the system vary under a given management regime would readily allow the profitability of such a system to be predicted under different conditions. Issues such as how many trees to plant in order to overcome soil nutritional deficiencies, how many trees could generate excessive competition with grass for light, water and nutrients, which tree species matches with a given combination of grass, cattle and environment, can be rapidly solved through a suitable model.

1.2 Traditional extensive livestock husbandry in the humid tropics of Mexico.

1.2.1 Description of the system

Extensive livestock husbandry at low stocking rate (one or less than one head per hectare) is one of the main economic activities in the Mexican tropics. As a general rule, the establishment of pastures follows slash and burn and a period of maize cropping, which continues until the soil fertility decreases and consequently weed competition becomes a significant constraint. This process generally takes between one and three years to happen. Another area is then cleared thus starting a new cycle. In the final year of maize cultivation, livestock owners spread vegetative parts or seeds of naturalised grasses on the soil. The productive live period of a new pasture can vary from seven to ten years, but, tropical pastures are sooner or later bound to be abandoned; about 80% of the pastures in the tropics during the past 30 years have been given up (Hecht, 1985). The temporary stability of pastures can be explained in terms of the low productivity of traditional livestock husbandry. Calving interval is approximately 24 months, the age to puberty is around 36 months and the stocking rate of pastures is 1 to 1.5 animals per hectare. These simple parameters suggest a less productive system than would be expected in a climate as favourable as the humid tropics.

Because small scale extensive livestock husbandry (1 to 30 bovine heads grazing on grasslands and crop residues or communal lands) is not a strictly profitable system, it is hard to find suitable alternatives of development. Traditionally, small-scale livestock husbandry plays the role of a strategic cash box, where the farmer deposits occasional surpluses of money, on the grounds of quick access in case of urgency. This is due both to the ease of selling livestock and to its comparatively low risk level. The majority of small farmers' investments are not improvements to the system components (fertilisers, improved grasses, etc.) but are aimed at the reduction of risk (vaccines, medicines, parasiticides, etc.). The environmental consequence of such strategy is the deterioration of soil fertility due to the permanent extraction of nutrients without a proportional return of fertilisers. In fact, typical pastures are energy limited during the dry season and protein limited throughout the year (Butterworth, 1985). The abandonment of an unproductive field results in the

deforestation of a new area and in the vulnerability of the familiar economy to an eventually unfavourable change in climatic or market conditions. An eventual productivity rise should not only aim to increase cash availability, but to transform the system into a profitable one, with an active cash flow and animal feeding and finishing plans driven by market requirements, instead of selling only in case of economic urgency.

1.2.2 Environmental and Socio-economic context

Climate

The most influential factors in Mexican weather are the geographical position of the country between 14°30' and 32°42'N, and its funnel shape, wide in the north and narrow in the south, both coasts raised to more than 2,500 m.a.s.l. by the Sierra Madre mountains. Valle Nacional, which has a climate typical of the Mexican tropics, experiences a high inflow of solar radiation, with 3,000 to 3,200 h yr^{-1} of bright sunshine or 6.7 GJ m^{-2} yr^{-1} (total solar radiation). Maximum temperatures normally occur around April with a mean maximum of 28°C and 39°C absolute maximum. Minimum temperatures (January) are never lower than 20°C.

Relative humidity in spring time is 30 to 50% whereas in summer it can reach more than 70%. Cloudiness in the dryer part of the year (December to May) varies between 20 and 30%, whilst in the rainy season it is more than 60 to 70%. Precipitation is governed by the trade wind inversion point, west from the Azores (Atlantic Ocean), combined with the mountain barriers of Eastern and Juarez Sierra Madre. Moist winds from the Pacific also contribute to the high precipitation regime (3,750 mm yr^{-1}). Between May and November tropical cyclones hit the Gulf of Mexico. The associated winds can exceed 50 to 60 m s^{-1}. Similarly, storms are caused by the presence of the inter-tropical convergence zone arriving in the Pacific in October. Early in winter, north-easterly polar winds, warmed up throughout the Gulf of Mexico, bring heavy rains to the Papaloapan river basin, where Valle Nacional is located (Martyn, 1992). As summer circulation gives way to the winter one, monthly average precipitation decreases, causing a summer drought or *canicula*, right in the middle of the rainy season (Mosiño-Aleman and García, 1974).

Soil

Most of the soils in the Neotropics are Oxisols and Ultisols, which contains low levels of available nutrient reserves, acidity (4.5 to 5.0) and phosphorus deficiency caused by aluminium fixation (Szott *et al*., 1991b). Other constraints commonly associated with these soils are the low cation exchange capacity, susceptibility to erosion and compaction and water stress in the dry season due to a low water holding capacity. Nonetheless, the most widespread constraints in Oxisols-Ultisols are chemical rather than physical, and when these are eliminated the productivity of these Oxisols and Ultisols is among the highest in the world (Sanchez and Salinas, 1981).

The highest bulk of nutrients in tropical forests is in the biomass rather than in the soil. Consequently, a notable increase of nutrients in soil is given after clearing. The volume and permanence of such a level of fertility depends on the rate of decomposition of organic matter which, for some nutrients, can be accelerated by burning in contrast to a long term decomposition carried out by soil micro-organisms and other soil fauna, although their activity gathers speed when soil surface temperature increases (Okigbo and Lal, 1979).

Vegetation.

Tropical Mexico is covered by deciduous forest, disturbed evergreen forest and pastures, the lower strata of the former including the grasses *Bouteloua filiformis*, *B. hirsuta*, *B. curtipendula*, *Opizia stolonifera* and widespread herbaceous legumes as *Setaria* sp., *Crotalaria* sp. and *Calopogonium* sp. In wetter areas there exist *Paspalum notatum*, *P. conjugatum*, *P. minus*, *Axonopus affinis* and *A. compressus* (Butterworth, 1985). Extensive areas of the Papaloapan basin have now been planted with improved species such as *Panicum maximum* (guinea), *Digitaria decumbens* (pangola), *Cynodon dactylon* (Coastcross 1), *Cynodon nlemfuensis* (star), *Andropogon gayanus*, *Brachiaria decumbens* (signal), *Brachiaria mutica* and *B. brizantha* (locally called "Insurgente").

Socio-economic factors

There exists a significant sector within the rural population of tropical America which remains implicitly marginalised from the national programmes of development. The majority of technologies generated by research centres and further commercialised as inputs for agriculture, generally ignore small farmers (campesinos), as they normally do not purchase inputs, do not generate commercial goods and ultimately they are not liable for taxation. The present work is focused on a specific technology with regard mainly to small farms, although its results can be applied to larger farms.

Small farmers are the largest social sector in the rural areas of Mexico. It is important to classify them into types in order to facilitate understanding of the pattern of the adoption of technology. The types of small farmers can be described according to the availability of means of production: land owners, tenants and seasonal labourers. Land owners possess the rights on their usually small fields but they do not have the capital to invest to effectively make the land more productive. This group includes smallholders and communities holding the land in common.

Tenants work a landlord's field in accordance with an agreement on future payment or the division of the crop. This group also includes squatters on private or national property and displaced persons and refugees who occupy land for agriculture on a temporary basis. Because the farmers in this group do not own the land they work, it is unusual for them to consider investing in infrastructure or establishing of improved pastures or planting trees, -at least not before they sort out their agrarian status. Moreover, farmers of this type are not normally eligible for credit from commercial banks nor are they enrolled in farmer unions.

Seasonal labourers remain below the threshold of subsistence as far as their own agricultural production unit is concerned. They must find a way to get external incomes from various sources in order to subsidise their own farm. This group includes small farmers from dry regions, where only one harvest is possible each year and where some members of the family migrate to areas of commercial agriculture or big towns to work as labourers. This group also includes those families whose strategy consists in combining incomes from their own fields and from some of the members of the family who are away on a permanent basis. The big difference

between seasonal labourers and tenants in terms of their chances for transforming their production system is that, after cash, the limiting factor for the former group is labour, whereas for the latter it is land. One important aspect to be considered during the process of technology transfer is that campesino systems are chiefly based on family labour, meaning that the purchase of agricultural inputs may affect the full satisfaction of the family's bare necessities or at least that such inputs arrive but in time and amount out of programme.

Among the groups just mentioned, that with the highest potential for a technological shift is the land owners, for they would not hesitate to invest in their own land for long term projects, and they remain looking after the land during the whole year. It is at this group of small farmers that the silvopastoral system is mainly aimed.

The profile of the farmer this research is aimed to deal with corresponds to those farmers who produce directly the major part of the food for their family but who, additionally, grow some crops to exchange for cash necessary for living expenses. As long as a certain level of risk is not exceeded, this combination of production processes gives economic stability to the whole system.

The main systems interacting in the farm economy in Valle Nacional, Oaxaca state, are maize cultivation, extensive livestock husbandry, rubber (*Hevea brasiliensis*) production, coffee production, mixed orchard and back yard animal husbandry.

In years with a long rainy season, families capitalise by selling rubber and surplus maize, while in dry years they sell a larger amount of maize from the rainy (summer) season harvest and subsequently sow the winter cycle in the lowlands because of the greater water content of the soil, in order to ensure the continued supply of maize throughout the year.

1.2.3 Sustainability

After clearing, burning and sowing grass, all nutrient balances change, routes of exportation are accelerated and the biomass-nutrient to soil-nutrient ratio diminishes drastically, which increases the risk of nutrient losses. Grazing on degraded pastures, extraction of wood for fuel in overexploited hillsides, wind erosion, continuous cropping and bush fires are heavily responsible for decreasing agricultural productivity in third world countries (Sanchez, 1979; Adegbehin *et al.*, 1990). On a global scale, as high temperature reaches the soil surface and heavy storms quickly

saturate soil macropores, release of nitrous oxide to the atmosphere builds up, affecting the volume of stratospheric ozone, which absorbs hazardous ultraviolet radiation (Binkley, 1993).

The use of land recently cleared by burning results in the rapid establishment of an apparently good quality sward, fairly resilient to weed competition and highly productive in terms of biomass per hectare. Soil organic matter from the decay of forest roots makes it possible to sustain, in the long term, suitable growth conditions for pasture, such as delaying Al toxicity and soil acidification and maintenance of satisfactory levels of Ca and Mg (Sanchez, 1979).

The efficiency with which nutrients are mineralised depends largely on the form in which the nutrients are present and the environmental conditions that facilitate these processes. The low C to N ratio of manure alters the balance in which microbes perform naturally, resulting in the acceleration of mineralising processes towards a balance restoration (Bohn *et al*., 1985), which can generate a rapid P release from manure, eventually recoverable by grasses (Powell and Williams, 1993). Decomposition takes place as soon as dung is dropped. During the first week available N and P reach their highest level, while soil acidity rises, possibly because of the rapid release and leaching of cations. After five weeks N contents diminish considerably (both by utilisation for grass growth and by leaching), P availability diminishes as well (immobilisation or intake) and acidity decreases (higher than original levels) since Ca ions are liberated (Omaliko, 1984).

The more intensive the grazing in terms of carrying capacity, the smaller the volume of nutrients in dead leaves, while the amount of nutrients in manure becomes larger. The size of each pool varies depending on the particular nutrient. Animals represent an effective mechanism for the recycling of mobile nutrients as N and K whereas they are a secondary component for P recycling. However, the diminishing of available P due to grazing on degraded pastures leads to the overgrowth of weeds and secondary vegetation (Sanchez, 1979). Most evidence suggests that is feasible to solve the problem by hand clearing, burning the pasture every two or three years and adding S and P yearly, which results in the recovery of grass cover (weed control) and increasing live weight gain (Schubart, 1977).

However, land degradation continues since pasture prevents secondary succession, essential to the restoration of soil productivity, and chemical fertilisation is not used as the grass seems to perform well on poor soils. Consequently, livestock husbandry productivity drops dramatically after five to ten years of grazing the same area (Locker, 1994). Moreover, weeds arise again, treading causes soil compaction and the seed bank for natural succession disappears.

Such problems worsen by lengthening the period of land use, which prevents an effective mechanism for returning nutrients to the soil. Consequently, soil fertility decreases and those species that can grow on poor soils, which have a low fodder value, tend to increase.

1.2.4 Main limiting factors

From the paragraphs above it can be seen that the main limiting factor in livestock husbandry in the humid tropics in Mexico is soil fertility and the mechanism to maintain it in the long term, and keep out of environmentally costly or negative practices, is the development and adoption of low input technology.

1.2.5 Nitrogen balance

Sources of nitrogen

Rainfall: Rain water can be a significant source of nitrogen for the system. In some areas close to urban and industrial settlements, where oxides of nitrogen emissions pollute the atmosphere, nitrate precipitation can reach up to 50 kg ha^{-1} yr^{-1}, but the potential of capturing nitrates from rainfall in rural areas is likely to be negligible. The amount of nitrate effectively taken up by plants depends on the stage of growth (root system size). The nitrogen which is not taken up immediately is likely to be immobilised, carried away by run off or leaching, or returned to the atmosphere by denitrification to nitrous oxide or N_2.

Organic Matter: Pasture establishment means the full and permanent repopulating of soil surface, resulting in the cessation of sheet erosion caused by the impact of rain drops in intense showers. Grass cover produces the constant incorporation of organic matter which promotes the activity of soil fauna and microbes (De las Salas, 1978; Okigbo and Lal, 1979). With regard to the animal component, its linkage with the

productivity of pastures through the recycling of organic matter is unambiguous. Manure increases the availability of nutrients, water holding capacity and cations exchange capacity. Results from a long term trial carried out in the Sahel (Powell and Williams, 1993) show that manure deposition in the less drier lands (>600mm yr^{-1}) can average 3800 kg ha^{-1} yr^{-1} of dry matter (carrying capacity was not presented). Such an amount of manure supplies up to 45 kg N and 5.7 kg P ha^{-1} $year^{-1}$. The most remarkable finding is the effect of urine on sward yield (up to 52% superior to those where cattle were penned outside). An additional explanation for the better performance of directly grazed paddocks (faeces + urine) is that manure from corrals contains only half of the original N, the rest is lost by leaching and volatilisation.

Biologically fixed nitrogen: Specific prokaryotic bacteria like *Rhizobium*, *Bradyrhizobium* and *Frankia* are able to break the triple bond of atmospheric nitrogen thanks to the nitrogenase enzyme, reducing it to the biologically useful ammonium. The aerobic environment needed for this process is found in nodulating tree roots, which also provide the bacteria with carbohydrates (Binkley and Giardina, 1997). It is assumed in the present study that the main purpose of leguminous nitrogen fixing trees in a grazing system is their influence in the recycling of nutrients. The amount of nitrogen that can be incorporated in the agro-ecosystem through biological fixation (BFN) by some tree species was expected to be quite high. *Leucaena leucocephala* at 830 trees ha^{-1} has been reported to fix up to 110 ± 30 kg N ha^{-1} yr^{-1} (Högberg, 1982). This process relies mainly on the abundance of *Rhizobium* strains infecting the roots of the leguminous tree. The root length density (mainly in the upper layer of the soil) is also important, as the root constitutes the potential infection surface. Available mineral N, moisture, pH and salinity in the rhizosphere may constrain BFN severely (Jones and Darah, 1996; Dart, 1994). The *Rhizobium* infection produces nodules (colonies of *Rhizobium*) on the root tips, which develop infection threads within the root hair and new nodules grow up from them (ibid.). Nodules are able to transform free atmospheric nitrogen (N_2) into nitrogen rich organic compounds, namely ureides and amides, which are exported to the root phloem. Plant roots in return, supply sucrose and amino acids to the nodule (Parsons *et al*., 1993). Plant-*Rhizobium* symbiosis exists provided a continuous supply of atmospheric fresh air ventilates the interstitial spaces in rhizosphere soil.

The volume of mineral nitrogen (ammonium and nitrate) available for the tree roots and the presence of organic forms of nitrogen directly assimilable or readily mineralisable are factors which conspicuously determine BFN. It has been well documented that fertile soils or amendments based on mineral sources of nitrogen inhibit nodulation (infection) and nodule growth (Parsons *et al*., 1993). The explanation is that a high availability of substrate nitrogen in plant phloem results in an increment in the partition fraction of photosynthates toward those parts of the plant that are above ground (allowing new tissue to grow and elongate). It has negative effects on *Rhizobium* nodulation in two ways:

- since assimilate supply is diminished, fine root production is reduced and consequently the area available for infection spots is also reduced. It is known that the ratio of crop roots to shoot in fertile soils is smaller than those in poor soils, and
- the reduction in the supply of carbohydrate, constrains the metabolism of the symbiont, causing difficulties for *Rhizobium* reproduction;

it is also possible that a satisfactory plant nutrition status inhibits secretion (exudation) of enzymes necessary to trigger *Rhizobium* infection.

Another fertility related issue is the availability of phosphorus (P): soils lacking P restrict BFN. There is no clear explanation of the role of P in nodulation and N_2 fixation, but it is known that P is crucial in the early stages of growth of Nitrogen fixing trees (Sanginga *et al*., 1995). These authors also mentioned a certain degree of dependence of BFN on mycorrhizae. The higher absorption capacity that mycorrhizae confers to roots is some times even capable of eliminating the P limitation on the N_2 fixing capacity.

Moisture stress constrains nodule growth and functioning, though well adapted species exist, which are capable of maintaining the symbiosis and fixing nitrogen even in the dry season (Sanginga *et al*., 1995). *L. leucocephala* and other nitrogen fixing trees develop a thick protective husk layer around the *Rhizobium* colony. This layer contains a peripheral sheet of suberised and thickened cells, the husk cells also are high in tannins. Both characteristics are presumably protective adaptations against desiccation and the attacks of pests (Dart, 1994).

Soil acidity affects the establishment of the Nitrogen Fixing Tree-*Rhizobium* association. Some researchers reported that NFT species such as *L. leucocephala* do not adapt to acidic soils due to its unsuitability for developing nodules and consequently to fix nitrogen (Ahmad and Ng, 1981). On the other hand, other workers reported that an abundant nodulation was found not to be enough to achieve satisfactory growth for *L. leucocephala* in acidic soils (Halliday and Somasegaran, 1982, quoted by Sanginga *et al*., 1995).

Losses of nitrogen

Leaching: As nitrate is more mobile than ammonium in forest soils, less nitrification is needed to satisfy nitrogen root requirements. Nitrate and ammonium mobility varies according to soil conditions, but nitrate is always from 10 to 100 times faster. It is possible that leaching of nitrate that is not absorbed by roots occur, since forest soils show low anion exchange capacity. Virgin forest with fairly uniform nitrogen cycling will lose less than 1% a year (Binkley, 1993). However, soil with exceptionally high mineralisation rates, like recently cleared areas, can lose a great deal of nitrate to the groundwater.

Denitrification: This only occurs in the absence of oxygen, usually caused by saturation of the soil. The reduction of organic compounds gives the electrons necessary for denitrification of nitrate to nitrite to nitrous oxide to gaseous nitrogen. Readily mineralisable sources of carbon promote higher denitrification levels. Fortunately nitrification and denitrification develop under strictly contrasting atmospheres, namely presence and absence of oxygen respectively, with the result that the latter seldom occurs in measurable amounts (Binkley, 1993). Again, pastures in the humid tropics, where high soil organic matter combines with high temperatures and frequent events of water saturation, are prone to loss of nitrogen by denitrification.

Ammonia volatilisation: Ammonium and urea from decomposing organic matter and urine is reduced to the more volatile NH_4^+ as in ammonium carbonate in low acidity soils. A flooded environment also facilitates such hydrolytic reduction. High temperature, high wind speed and the depth of floodwater accelerate ammonium volatilisation (Jayaweera *et al*., 1991).

Export of nitrogen in livestock: Extensive grazing in the tropics shows an average

productivity of about 100 kg (live weight) ha^{-1} yr^{-1}, which implies the extraction of no more than 2 kg N ha^{-1} yr^{-1}. Experiences in both wet and dry land in the Sahel (Powell and Williams, 1993) agree that with moderate grazing it is possible to maintain the nutrient balance in soil, provided carrying capacity remains at no more than one head ha^{-1}.

Other nutrient losses: Once the rainforest has been cleared, raindrops beat the soil surface directly causing clods to break down, and splash, whose droplets carry small soil particles into the run-off stream, causing sheet erosion (Russell, 1973), which may cause the loss of tonnes of soil per hectare, only in the two first years after slash and burn. The volume of eroded material depends on the slope, the erosivity of the rain or wind events and the erodibility of the soil, as well as on the precedent agricultural practices. In bare soil, important amounts of nutrients are lost in the form of organic matter and minerals from burning since clods rich in organic matter are feeble in wet conditions (*ibid.*).

High temperatures in the soil surface, reached during burning and by direct sunshine, accelerate the volatilisation of nutrients (particularly nitrogen) freed during the decomposition of organic matter. Owing to the absence of restitution of organic matter, soil structure is drastically modified, rendering it less capable of retaining water and facilitating the leaching of soluble elements (N, K, S, Ca and Mg).

1.3 Discussion

Tropical ecosystems are rich in plant biomass, which is considered both the major reservoir of nutrients in the system and the agent of stabilisation of nutrient cycles through the different compartments. Once the woody cover disappears, balance is broken down and a rapid leak of minerals (through leaching, volatilisation and erosion) takes place. Although such imbalance is controlled as pasture is established, net primary production level and fertility are substantially lower. Nevertheless this system seems to be particularly stable, even if no fertilisers are applied. There are two major constraints to tackle in order to attain -or maintain- its sustainability in the long run:

- The growing demand for animal products, given the increase of population, which encourages the increased productivity of the land (otherwise there is overgrazing), and

- The lack of reservoirs of nutrients (e. g. decomposable soil organic matter) and nutrients pumped by deep rooted woody populations, especially in more intensive grazing systems.

Social and economic as well as environmental exigencies require the finding of a way to restore the stabilising role of trees, mainly in slope agriculture and grazed areas (Szott, *et al*., 1991a) and also suggest the incorporation of acidified or naturally acid lands to agriculture (Sanchez and Salinas, 1981). Within this context, silvopastoral systems may become a key component for the recuperation of pasture productivity in the humid tropics.

In 1980 Latin America had a population of 360 million and for the year 2000 a population of 520 million is expected (annual rate of population increase: 2.3%). On the other hand, land dedicated to grass and forage cultivation rose from 1.9 million hectares in 1980 to 2.1 in 1995, although there is unlikely to be any significant increase for the next five years, mainly because the lack of new lands that can be used for grazing or fodder cultivation and because of the spread of environmental policies (FAO, 1990).

Alternatives to confront the growing demand for food should be based on increasing efficiency and productivity of the land rather than an expansion of the land under exploitation. Often, governmental policies encourage farmers to tackle the low productivity of traditional systems through high-input technologies. Many authors have analysed failures of this high-tech approach and agree that these have been designed for farmers who are able to make long-term investments and whose final purpose is marketing. Moreover, most of the high-input technologies have their origin in the exploitation of deep soil flat lands, that can be irrigated. Such classes of land only comprise between 10 and 20 % of the worked lands of Latin-American countries. The rest of land requires technologies that combine low ecological impact, the increase -or maintenance- of productivity and low -or no- inputs. It is in this context that we suggest the introduction of a grass species highly resistant to infertile soils. This strategy must be accompanied by the use of nitrogen fixing trees as a source of fertiliser, since this reduces the need for chemical amendments.

1.4 Objectives

The present work aims to contribute to the understanding of a tree-grass inter-cropping system to make possible to increase the productivity of extensive livestock husbandry in a sustainable manner. In order to achieve this general goal, the following objectives have been established:

1) To compare the annual production and quality of biomass in pastures of *Brachiaria decumbens* as a function of the associated tree species and of distance from trees.

Hypothesis: The productivity of the pasture system can be improved by incorporating tree prunings onto the soil surface, provided the upper-storey canopy remains small.

2) To evaluate root development in grass and trees as a means for the elucidation of the extent of soil exploitation, as well as the actual status of complementarity or competition for nutrients between the two species.

Hypothesis: Most grass and tree roots are concentrated in the top soil layer, but deep roots play an important role on recycling leachates, making the two species complementary.

3) To determine the decomposition rate of mulch from leguminous trees as an indication of their potential as a source of green manure for pasture systems.

Hypothesis: Mulch from leguminous trees is rich in nitrogen and low in fibre, allowing for a rapid decomposition into soil organic matter.

4) To build a mathematical model to make possible the simulation of the effect of the presence and management of trees within grazing pastures, allowing for the testing of different tree species, plant densities and pruning schedules.

This model aims to represent how the silvopastoral agro-ecosystem performs in the particular environmental conditions of Oaxaca State in Mexico, especially when the trees are cultivated specifically for fertiliser rather than timber production.

2. Characterisation of Silvopastoral Systems in the Humid Tropics. A Review.

2.1 The Nitrogen fixing trees-*Brachiaria decumbens* silvopastoral system

Tree-grass inter-cropping has been practised in the tropics under a wide range of conditions and objectives, from isolated trees in pastures (Carvalho, 1997; Harvey *et al*., 1998) to live fences (Alayón *et al*., 1998) to alley cropping (Tournebize and Sinouquet, 1995; Cruz, 1997; Nygren and Cruz, 1998) to full mixture (Catchpoole and Blair, 1990a; Jayasundara *et al*., 1997) to grazing in crops or forest plantations (Chen *et al*., 1978; Rika *et al*., 1981; Murgueitio and Calle, 1998). The particular system relevant to this thesis consists in the use of the trees as a source of fertiliser or green manure for pastures. The principle is the association of improved pastures of *Brachiaria decumbens* with nitrogen fixing trees at densities of 800 to 1500 trees ha^{-1}. The trees are pollarded every four months and leaves and twigs are strewn on the grass. Leaving about 20% of leaves on the tree will help to accelerate re-growth and to maintain some nodules of *Rhizobium* for nitrogen fixation.

2.1.1 Comparative advantages

The use of nitrogen fixing trees in farming systems in the tropics is particularly important for two reasons: the high prices of commercial inorganic fertilisers with respect to the financial resource base of small farmers and the tendency to a reduction in the fallow period, with a concomitant decline in soil productivity (NAS, 1980). The use of nitrogen fixing trees in improved pastures in the tropics has been suggested to fulfil two alternative goals: to complement pasture-based diets, usually on a 'cut-and-carry' basis, or as source of fertiliser (green manure).

The differences between the two options have implications for the speed and efficiency of the turnover of nutrients, the agronomic management of the two species and the labour involved in each alternative. The convenience of the former against the latter in the particular conditions of Mexico is discussed below. Some aspects of both options are described in terms of the limiting factors stressed in Chapter One: finance, soil fertility and technology transfer in a scenario of converting traditional pasture systems into a silvopastoral system.

Finance

Infrastructure: Pruning (for green manuring) instead of carrying (for feeding) would be more readily adopted by farmers who do not have mangers or other facilities for feeding their animals. This is generally the case in small farms in tropical Mexico.

Fertilisation: Cut-and-carry depends on larger additions of fertilisers since the exportation of nutrients accelerates the reduction of soil fertility. Thus this system can only be sustainable in farms with permanent positive cash flow. Again that is not generally the case in the rural areas of Mexico.

Labour: Pruning the whole stand every 4 months is less costly than cutting and carrying on a daily basis. Grazing animals return about 90% of intake N and P in faeces and urine. When animals are enclosed overnight, like in dairy systems, supplementation is usually provided in such enclosures. Moving excreta to the field involves carrying costs and wastage.

Soil Fertility

Productivity: Traditional pastures have low nutritive value (eg 4-8% crude protein) and are very sensitive to water availability, reducing production and fodder quality during the dry season. By replacing traditional with improved pastures, the carrying capacity of soils of low fertility is, in the short term, enhanced, thus reducing the energetic cost of harvesting food by the animal. Improved pastures can offer satisfactory protein levels during most of the rainy season, with no need for diet supplementation such as prunings from fodder trees. In order to maintain high productivity, a strategy of soil fertilisation must be observed. *Brachiaria decumbens*, when adequately managed, produces forage of over 14% crude protein (Vallejos, 1988). Its deep rooting system (>1.5m) prevents the crop from suffering drought stress during dry spells and acts as a safety net against nutrient leaching. Thus enclosures for supplementary feeding of livestock in extensive systems are less necessary.

Efficiency: Pruning for fodder requires shorter cycles in order to optimise the protein level (higher leaf to stem ratio) and must be done on a daily basis so that the rumen microbes get well accustomed to the improved diet and utilise it. When harvesting for green manuring, chemical quality is not crucial since the building and utilisation

of soil organic matter is a long term process. Indeed, a high carbon to nitrogen ratio could, to a certain extent, be desirable because this entails a lower rate of decomposition to synchronise with plant requirements, whereas high rates of release of nutrients in the humid tropics can lead to losses by leaching before the plant roots or soil microbes can take the nutrients.

Resource management: Intensification of grazing systems endangers sustainability because of the accelerated extraction of nutrients. Trees may not be as important as means of incorporating resources into the system (apart from nitrogen) as for nutrient sequestration and as a mean of making them available according to crop demand. They are also important for the replenishment of high quality soil organic matter.

Soil fertility in highly productive pastures should not rely exclusively on tree-grass inter-cropping if the incorporation of nutrients through tree deep rooting or biological fixation are not ensured. However, by adequately managing tree mulch and litter from roots and nodules, the silvopastoral system can reduce the use of chemical fertilisers, help synchronise nutrient release and uptake and act as a carbon and nitrogen sink, reducing losses to the atmosphere.

Technology transfer

Adequacy: Cut-and-carry should result in a more convenient technique to improve dairy systems based on pastures with commercial supplementation, as well as feed lots and dairies of small ruminants in stalls. However, the great majority of Mexican herds feed on extensive pastures.

When cash is more limiting than land (see Chapter One), green manuring with tree prunings can be a more cost effective way of using this resource. Smaller countries or those with relatively larger population density like some islands in the Caribbean face the opposite situation, as land is scarce and expensive and there is no opportunity for extensive grazing systems (Dr. Pekka Nygren, INRA, personal communication).

2.2 Agroecological effects of introducing trees in pastures

The agro-ecological effects of tree-grass inter-cropping, including grass, animal, soil and environment have been described elsewhere (Torres, 1983; Adegbehin *et al*., 1990; Loker, 1994; Serrão *et al*., 1995) for different management options. Here, five

biological processes that are especially important in the silvopastoral system are analysed.

2.2.1 Solar radiation interception

Solar radiation interception causes direct and indirect effects on the pasture. In direct form, it causes the simultaneous alteration of two important resources for the grass, incident photosynthetically active radiation (PAR) and heat. Indirectly, it produces the alteration of moisture in the top soil layer, which is important for the hydraulic balance of the crop and for mineralisation and assimilation of nutrients in soil solution. It has been demonstrated that according to environmental conditions, a relatively scattered upper canopy can favour pasture growth through an improved micro-environment under each individual tree. Grass growth under *Erythrina poeppigiana*, *Gliricidia sepium*, *Pithecoelobium saman* and *Cordia alliodora* cover of up to 50% in Central America shows clear increments in nutritional quality with no reduction on biomass production (Daccarett y Blydenstein, 1968). Incremental shade resulted in higher crude protein levels and lower fibre content, although the latter was less obvious. This can be explained in terms of the fibre rich parts of the tillers, namely culms and stolons, whose length and thickness increases proportionally to daily maximum air temperature (Murtagh *et al*., 1987). Moreover, high irradiance inhibits protein synthesis earlier than carbohydrate synthesis in leaves (Bronstein, 1983). Van Keulen and associates (1989) presented an extensive review of the relation of laminar leaf N concentration and photosynthesis performance in crops; they concluded that there is a linear relation in which increasing CO_2 assimilation rate ensues increments in N concentration in leaf provided the photon flux density is enough to ensure light saturation.

In environments where air temperature is supra-optimal for photosynthesis, grasses subject to lower air temperatures (moderate shade) reduce their photosynthetic rate (Ludlow, 1978 -C_4 grasses-; Johnson and Thornley, 1984 –temperate grasses-; Herrero, 1995 –*Pennisetum clandestinum*-) and consequently reduce leaf turnover. As leaf appearance rate diminishes, nutrient translocation is also reduced, thence maintaining Rubisco (ribulose biphosphate carboxylase oxygenase) and chlorophyll concentration in the same leaf for longer (Ludlow *et al*., 1988). Consequently, the

nutritive value of grass biomass available for grazing remains at its best for longer periods. Despite photosynthetic rate being reduced, light use efficiency (the ratio of absorbed PAR to biomass production) increases as a result of the higher concentration of nitrogen in leaf and the reduction of the respiratory and evapo-transpiration rates of the grass (Toledo and Torres, n.d.). It must be stated that light use efficiency (LUE), as defined above is not strictly a measure of efficiency, which should be dimensionless; it could be referred to as the light conversion coefficient. Murtagh *et al*. (1987) reported the specific respiratory rate for the maintenance of *Pennisetum clandestinum* to grow from 11 mg g^{-1} d^{-1} at 15°C to 37 mg g^{-1} d^{-1} at 30°C, reducing the LUE, as an increase in the consumption of photosynthates for maintaining metabolism occurred. Charles-Edwards (1982) formulated the relationship between the intercepted PAR and biomass production as

$$G = n\, LUE_w\, J - V \qquad (2.1)$$

where the rate of growth of above ground herbage (G) is expressed as a function of the partitioning coefficient for distribution of biomass to tops (*n*), the LUE for photosynthetic accumulation into hole plant biomass (LUE_w), the amount of photon irradiance over a given time interval (J) and the biomass turnover over the interval (V). LUE_w times *n* (i.e. LUE for above ground biomass) can be referred to as the difference of gross rate of canopy photosynthesis and the respiratory rate over the growth interval. The difference between C_3 and C_4 plants being that the former show light saturation at high irradiance; Wilson and Ludlow (1991) stated that as to the LUE concern, the two groups are very similar at low photon irradiance, thus it is more accurate that C_3 can be referred as non sun-adapted, rather than the common viewpoint of the C_4 as non shade-adapted. When scaling to canopy, light response appears to perform linear to changes in photon irradiance both for C_3 and C_4 plants, the difference being the higher slope of the tangent to the light response curve in C_4 canopies. This suggest a lower quantum yield (ie such a slope) at low photon irradiance than expected from the consideration of the leaf light response curve. Perhaps light competition between subsequent layers of the grass canopy becomes crucial when PAR is scarce. Very little reports exist, however, on the response of C_4 grass canopies to low light irradiance conditions (Wilson and Ludlow, 1991).

In Guadeloupe, French Antilles, shade from rows of trees in *Dichantium aristatum* grasslands consistently increased the LUE of the pasture during both the dry and the wet seasons (Cruz, 1997). Shade did not yield more standing grass biomass, but grass production was more efficient in terms of the available solar radiation at the pasture canopy level, probably due to a higher concentration of nitrogen in the laminae. These results suggest that an important fraction of biomass in full sun was senescing tissue and stems, which do not constitute the photosynthetic apparatus.

Cruz (1997) also found that grass growing under shade showed higher metabolic N to structural N ratio and that N uptake rate in the shade was consistently higher than that of the open stand. The ratio of N uptake to biomass production is an indicator of soil N availability (Lemaire and Salette, 1984).

2.2.2 Production of biomass

Reviews indicate that nitrogen fixing trees in alley cropping can produce up to 20 Mg DM ha^{-1} of prunings, containing as much as 358 kg N (Young, 1989; Szott *et al*., 1991b), much larger than the requirements of most crops. Above ground mulch varies in amount and composition between and also within species. The factors affecting such variability are provenance, soil fertility, climate, season, age of prunings and frequency of pollarding (Palm, 1995).

Effect on grass biomass production

Catchpoole and Blair (1990,a) in Sulawesi, Indonesia, found that in spite of the grass production under shade being reduced by 35%, the edible biomass productivity of tree/grass mixtures (*Calliandra calothyrsus*, *Gliricidia sepium* or *Leucaena leucocephala* with *Panicum maximum*) was approximately twice that in pasture alone and 50% higher than tree mono-crop. Ezenwa *et al*. (1995) in Southwest Nigeria found unaltered productivity in grass (*Panicum maximum*) growing near the hedgerow (*Gliricidia sepium* + *Leucaena leucocephala*) or in the middle of the alley but differences were caused by pruning frequency. The more intensive pruning scheme (every three months) produced the highest total foliage production (2.18 Mg ha^{-1} yr^{-1} from trees and 4.36 Mg ha^{-1} yr^{-1} from grass).

Tree biomass production

Gliricidia sepium: *Gliricidia sepium* in alley cropping in an oxic Paleustalf in Ibadan, Nigeria (Yamoah *et al*., 1986) averaged 2.7 Mg DM ha^{-1} per pruning or 1.08 kg DM $tree^{-1}$ yr^{-1}, incorporating 238 kg N ha^{-1} yr^{-1} to the soil. Nygren and Cruz (1998) in Guadeloupe, obtained 1.05 Mg ha^{-1} of *Gliricidia sepium* leaves in six months in a partially pruned alley cropping system of 28 months of establishment, equivalent to 0.88 kg DM $tree^{-1}$ yr^{-1}. These results are in good agreement with the figures on the potential productivity of trees in alley cropping collected by Fernandes *et al*. (1994) from different authors, which can be extrapolated to silvopastures when the trees are pollarded regularly as a source of green manure or fodder. They included results from moderately fertile and infertile soils of the humid and sub-humid tropics. Figure 2.1 shows similar maximum levels of above ground biomass production (1.2 to 1.4 kg DM $tree^{-1}$ yr^{-1}) in zones with a range of precipitation between 2200 and 3000 mm yr^{-1} and a gradient of plant density between 3300 and 6700 trees ha^{-1}.

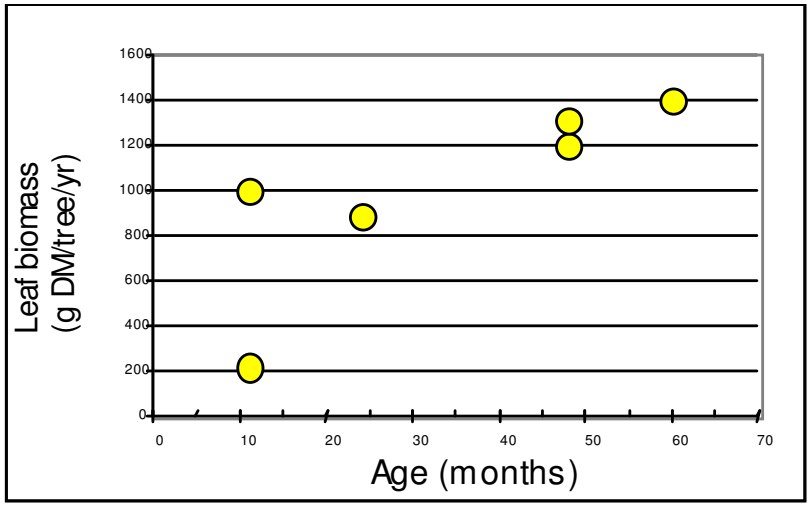


Figure 2.1. Leaf biomass production of *Gliricidia sepium*in alley cropping with respect to plant age. Adapted from Fernandes*et al.* (1994), with data from Fernandes (1990), Kass, *et al.* (1989) and Rosecrance, *et al.* (1992). Data were fitted assuming a leafy:woodyfraction ratio of 1.6:1 g/g(Sanginga, *et al,* 1994).

Variations within stands with the same plant density were associated with age and provenance. Trees achieve higher productivity as they age and the root system broadens to capture water and nutrients. Apparently the trees reach their maximum productivity at approximately four years old. Data in Figure 2.1 were transformed to

kg per tree per year basis and then adjusted for leaf to woody biomass ratio. The use of kg DM tree^{-1} yr^{-1} allows for the comparison of experiments in which different tree density and experimental periods were used.

Leucaena leucocephala: Kitamura (1988) found a similar pattern with *Leucaena leucocephala* - *Pennisetum purpureum* mixtures in the Ryukyu Islands, Japan, with maximum edible tree biomass production of 8000 kg ha^{-1} yr^{-1} and 19700 kg ha^{-1} yr^{-1} of grass forage. *Leucaena leucocephala* prunings contributed 23.8% of nitrogen in associated maize, which corresponded to 9.4% of that released during decomposition in a degraded Alfisol at Ibadan, Nigeria (Mulongoy and van der Meersch, 1988). Since most of the nitrogen in mulch is not new input but recycled nitrogen, it is unlikely that the sole organic amendment will offset nitrogen losses in the exported crop. Nitrogen in mulch is bound to a process of decay (decomposition-mineralisation) before it can be taken up by the accompanying crop roots (Palm, 1995). In Chandigarh, India, associations of *Leucaena leucocephala* 'K8' and *Pennisetum purpureum* (napier NB 21) growing on a hypertermic Ustocrept produced an average of 82 kg N ha^{-1} yr^{-1} in the prunings, corresponding to 167% of that harvested in the grass (Grewal *et al*., 1993). In the same experiment, the agroforestry association lost only 280 kg ha^{-1} whereas the traditional cropping system (*Sesamum indicum-Brassica napus* rotation) lost 2690 kg ha^{-1}.

The protective role of mulching in agroforestry systems must be also considered. Its importance is reflected in the improvement of both the physical and the chemical conditions of soil. Yamoah and co-workers (1986) stressed the primacy of improving the physical properties of soil as the nutrients released by prunings would be of no use if soil conditions do not favour root development.

2.2.3 The dynamics of soil organic matter

Trees in silvopastoral systems in the humid tropics can be considered a permanent source of mulch and litter of better quality than pasture alone. Soil organic matter is produced from the humification of the dead parts of plants and animal faeces. Plant litter includes not only leaves and stems but also roots and the associated micro-organisms attached to those parts (eg *Rhizobium* and mycorrhizae).

Nitrogen in soil organic matter is found as a component of organic compounds, thus its mineralisation rate depends on the decomposition rate of the plant fraction to which it is attached (Cortufo *et al*., 1995; Mulongoy and Gasser, 1993; Thomas and Asakawa, 1993). The overall process of decomposition of plant tissues takes place essentially as a result of the assimilation of carbohydrates –as a source of energy- by soil micro-organisms. Such a process occurs selectively from those compounds with lower molecular weight.

The decomposition rate of the cell contents, chiefly constituted by low molecular weight compounds, is rather fast, particularly in warm environments. Several studies have found that the decomposition rate of this fraction can be represented as a negative exponential function:

$$Y_t = Y_0 \, e^{-kt} \qquad (2.2)$$

with decay constant k between 0.03 and 0.20 week^{-1}. Such values are typical of prunings from leguminous trees in the tropics (Table 2.1). Note that the averages of humid and dry tropics are not different, being the species a more important factor determining the decomposition rate.

Table 2.1. Relative decomposition rate (k weeks^{-1}) of prunings from woody leguminous used as green manure in tropical regions.

Species	k*	Observations	Source
Acioa barteri	0.011	leaves and twigs (humid tropics)	Tian, *et al*. (1992)
Gliricidia sepium	0.192	leaves and twigs (humid tropics)	Tian, *et al*. (1992)
	0.121	leaves (dry tropics)	Mwiinga, *et al*. (1994)
Leucaena leucocephala	0.125	leaves and twigs (humid tropics)	Tian, *et al*. (1992)
	0.103	dry leaves (year average)	Vanlauwe, *et al*. (1995)
	0.099	leaves (dry tropics)	Mwiinga, *et al*. (1994)
Flemingia congesta	0.029	leaves (dry tropics)	Mwiinga, *et al*. (1994)
Sesbania sesban	0.091	leaves (dry tropics)	Mwiinga, *et al*. (1994)
Senna siamea	0.088	dry leaves (year average)	Vanlauwe, *et al*. (1995)
Dactyladenia barteri	0.046	dry leaves (year average)	Vanlauwe, *et al*. (1995)
Erythrina sp.	0.072	ash free biomass (humid tropics)	Palm and Sanchez (1990)
Inga edulis	0.061	ash free biomass (humid tropics)	Palm and Sanchez (1990)
Cajanus cajan	0.067	ash free biomass (humid tropics)	Palm and Sanchez (1990)
Humid tropics average	0.088 (δ= 0.06)		
Dry tropics average	0.085 (δ= 0.04)		

*Rates derived by fitting litter residues to the exponential equation $Yt = Y_0 \, e^{-kt}$ where Yt is the remnant of the original sample Y_0 after a period t.

Compared with prunings, naturally dead material is richer in carbon polymers such as cellulose/hemi-cellulose, as well as lignin and other polyphenolics. Its

decomposition rate can be of one to three orders of magnitude lower than that of the cell contents. Experiments on the mineralisation rate of nitrogen in plant residues of different quality have shown decomposition rate to have a high positive correlation with the cell's soluble fraction (Vanlauwe *et al*., 1997) a and high negative correlation with polyphenolics to nitrogen ratio (Oglesby and Fownes, 1992; Palm and Sanchez, 1991) lignin to nitrogen ratio (Kachaca *et al*., 1993; Melillo *et al*., 1982) and carbon to nitrogen ratio (Vanlauwe *et al*., 1997). These factors are governed by age and plant as well as genotype. Residues from older plant parts contain a higher proportion of nitrogen attached to the cell wall, where carbon to nitrogen ratio is also higher (c 100:1) and consequently, the mineralisation rate is significantly slower (Handayanto *et al*., 1995).

2.2.4 Uptake of nitrogen by deep roots

Uptake of nutrients by deep roots has been demonstrated to have a beneficial effect in some agroforestry systems where tree roots penetrate deeper than crop roots and recover leachates, specially in the humid tropics (van Noordwijk *et al*., 1996b). However, for most leguminous trees the bulk of fine roots occur in the top 30 cm of soil (Jonsson *et al*., 1988). Thus, they are unlikely to form such a safety net, having more a beneficial role in the fixation and subsequent release of nitrogen through pruning, and fine root and nodules litter (Catchpoole and Blair, 1990b). Eastham *et al*. (1990) pointed out that the importance of sub-soil nutrient uptake increases when the top soil dries out. On the other hand, root length densities in the sub-soil would be expected to increase during phases of leaching risk (Budelman, 1988). Incidentally, leaching rates are the highest in perhumid climates, where nutrient pumping is least efficient (Schroth, 1995).

The safety net attribute is restricted to those species that are genetically able to develop deep rooting systems under certain environmental conditions. Hairiah and associates (1992) conducted trials on an ultisol in Lampung, Sumatra and found that *Leucaena* roots did not penetrate to the subsoil and *Gliricidia* only to a limited extent, whereas *Calliandra*, *Pletophorum* and *Erythrina* could form a safety net underneath maize roots (30-50 cm).

Things should be different for some longer living crops as their roots can reach and densely populate the sub-soil, leaving behind shallower rooted species. Root length density (0-30cm) and minirhizotron root counts (1-50cm) in cereal rye (*Secale cereale* L), hairy vetch (*Vicia villosa* Roth) and crimson clover (*Trifolium incarnatum* L.) in Georgia, US, showed a positive correlation with nitrogen uptake. The grass had significantly greater root count than the leguminous cover crops, suggesting more effectiveness in reducing residual and potential leaching of soil nitrate early in the growing season (Sainju *et al*., 1998).

The safety net hypothesis is in contradiction with the observation that most trees have maximum root length density in the top soil. Many common factors in tropical agroforestry systems contribute to that situation: shallow, acidic soils prevent the development of deep roots, fertilisation/mulching makes top soil more attractive to root systems and pollarding promotes root branching in the top soil (Schroth, 1995). The same author suggested a 'seasonal safety net' for the recovery of nutrients during times of absence of crops and high mineralisation rate of soil organic matter. Again, this is not the case with permanent pastures.

2.2.5 Root turnover

Reports on the contribution of tree roots to the nitrogen budget of crops are scarce; yet, it is considered that trees contribute two to four times more nitrogen through roots and nodules turnover than from prunings (Bowen, 1984). Potentially symbiotic roots (diameter < 2mm) have a high turnover rate. Studies with a minirhizotron have shown that a considerable portion of fine roots have a longevity of no more than twenty days (Hooker *et al*., 1995; Forbes *et al*., 1997; Black *et al*., 1997). Such a rapid turnover entails nodule death and organic nitrogen release. However, it is still uncertain to what extent nutrients are released either by exudation or by short lived fine roots. Although high turnover rates may suggest the lack of a nutrient reallocation process prior to the death of root hairs, this fact has not been clearly demonstrated.

Fownes and Anderson (1991) suggested a high renewal rate for Rhizobium based on observations on the proportion of active and senescent nodules. It is likely that the variation in longevity of roots from the same plant is influenced by different

conditions of fertility and soil moisture at a micro-site level; it may denote a trial and error behaviour in roots seeking for the fertile zones in the soil. Humid ecosystems are associated with greater root longevity (Van Noordwijk *et al*, 1996a). In addition, in agroforestry systems involving pruning, a proportion of roots and their attached nodules die after the cutting of their aerial parts (Nygren and Campos, 1995). In both cases, nitrogen in dying nodules is further mineralised and assimilated by crop and tree roots, constituting an additional source of nitrogen in the system.

2.3 Ecological Sustainability

2.3.1 Biogeochemical pathways of C and N

Carbon

Higher plants are the most important contributors of carbon into ecosystems, although some autotrophic algae, cyanophyta and bacteria also play a role in carbon fixation in the soil. Tropical rain forest and tropical pastures do not differ greatly in the rate of carbon fixation. Fisher and associates (1994) measured an annual average of 2.9 Mg C ha^{-1} yr^{-1} sequestrated during nine years in the soil (80 cm) by the tropical grasses *Brachiaria humidicola* and *Andropogon gayanus*. Managed tropical forest carbon sequestration have been estimated in 110 Mg C ha^{-1} in 30 years, equivalent to 3.7 Mg C ha^{-1} yr^{-1} (Jong *et al*., 1995); this suggest a lower rate for non managed forest. Pasture and forest differ, however, in that forests, and specially secondary forests, retain most of the carbon in live tissues, whereas pastures retain very little carbon, transferring the rest to low efficient ruminants or to the soil litter pool. As the food chains go from autotrophic organisms to heterotrophic to decomposer ones, part of the carbon in the food is retained for biosynthesis and the other part is released to the atmosphere as carbon dioxide; the more efficient the organisms, the less carbon dioxide per unit of carbohydrates they release (Killham, 1994).

Carbon turnover can be considered the driving force for carbon and nutrient recycling since decomposers use dead plant tissues as a source of energy and minerals, releasing unused nutrients to the soil solution in a way analogous to the production of urine by ruminants. Recycling of mayor elements in organic tissues (carbon, nitrogen, sulphur and phosphorus) is, in most of the pathway, bound to the

fate of carbon in the herbivoral and detrital food webs. Carbon is also important for biological fixation of nitrogen as most of nitrogen fixers are free-living heterotrophs or symbionts, whose demand for energy is satisfied with the breakdown of carbohydrate molecules in the rhizosphere (Killham, 1994).

Nitrogen

The only important pool of free nitrogen for ecosystems is the atmosphere. No natural forms of inorganic nitrogen can be found in the soil. Only a relatively limited amount of living beings can utilise atmospheric nitrogen directly through biological fixation. The rate of fixation is variable among micro-organisms: symbiotic *Rhizobium* averages 50-200 kg N ha^{-1} yr^{-1} and free-leaving *Pseudomonas* and green-blue algae do not normally fix beyond 75 kg N ha^{-1} yr^{-1} (Elston and Snaydon, 1976). The other important input of nitrogen into ecosystems is industrially fixed nitrogen. However, the more important source of utilisable nitrogen for low input agriculture is the recycling of excreta and residues from plants and animals. Recycled nitrogen is found as nitrate (and to a lesser extent as ammonium) in the soil solution. Most nitrogen in plants, and hence in forage, is returned to the system in the form of urine, litter and manure.

Omitting chemical fertilisation, inputs to the soil solution are organic matter mineralisation, urine, atmospheric pollutants and leaching from above-ground plant parts. Outputs from soil solution are plant uptake, leaching to deeper soil layers, denitrification and volatilisation. The volume of nitrogen being mobilised from plant litter and manure to the soil solution depends on the size of the litter pool, the mineralisation rate of each fraction and the abundance of soil micro-organisms for such a process.

The amount of nitrogen being removed from soil to plant depends on root biomass, the stock available and the uptake rate. The three environmental factors that ultimately govern uptake and mineralisation are hydric regime, air/soil temperature (high soil water content and temperature accelerate process rates) and soil texture (clay particles interfere with the access of microbes to the substrate). The bigger the imbalance between much available nitrogen and low uptake rate, the higher the risk

of losses to the environment. This is, in a rather simplified manner, the cycle of nitrogen in pastures (Figure 2.2).

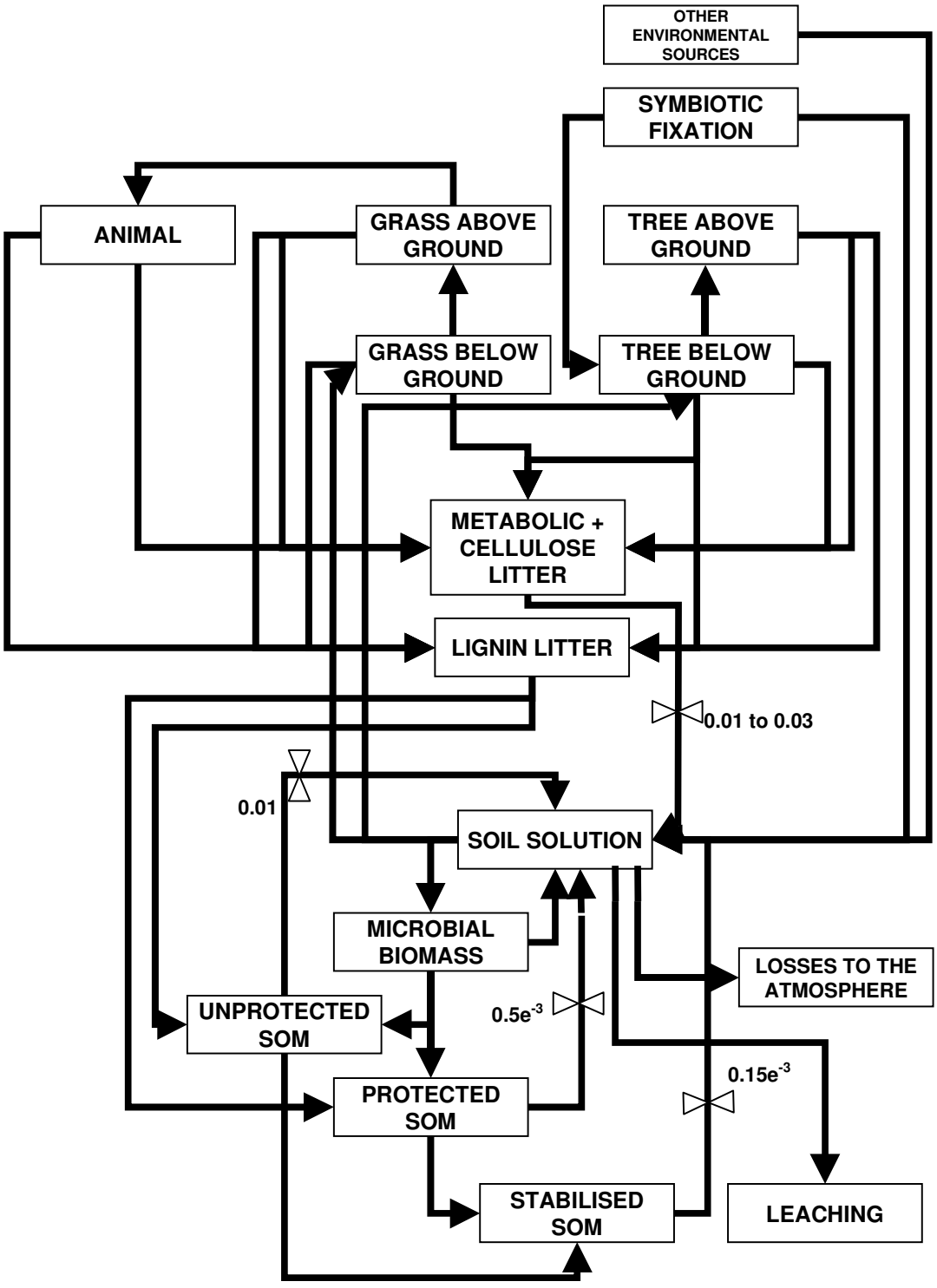


Figure 2.2 Nitrogen cycle in the silvopastoral system (the relative mineralisation rates are in g g^{-1} $days^{-1}$). **SOM** is Soil Organic Matter.

2.3.2 Impact of trees and improved grasses on C and N cycles

Fast growing nitrogen fixing trees can directly affect the carbon cycle in tree-grass associations. Shade limits the growth and ageing of grass, thus less carbon enters the system. On the other hand, the upper canopy increases the efficiency of light interception of the whole system, thus a larger fraction of the carbon in the system is retained as biomass, reducing overall emissions to the atmosphere. Mulch from tree prunings shows lower C:N ratio, this boosts microbial activity (mineralisation).

Improved species of grass like *Brachiaria decumbens* penetrate deeper into the soil profile, reducing leaching of nitrogen. Higher nitrogen concentration in tissues and more biomass per hectare contribute to retain more nitrogen in the biotic component. Associated trees are bound to compete for nutrients with the pasture. However, such competition can be seen as positive in a low input strategy. Fast growing grasses require nitrogen in large quantities, thus trees can reduce the grass growth rate by competing for the available resources, likewise *Erythrina poeppigiana* trees slow down *Coffea arabica* ripening in Costa Rica (Beer, 1988). Nitrogen in tree leaves and fine roots can be made available to the grass rooting system through pruning. Choosing the appropriate species of tree would help to control the decomposition rate according to pasture necessities (Palm, 1995).

2.3.3 The general hypothesis of agroforestry

High input agriculture is hardly feasible in marginal lands, firstly because it is conceived in terms of large investments (intensive use of commercial inputs, terracing, irrigation, etc.) that small farmers can not afford and second, because of the lack of a helpful policy environment (Sanchez, 1994). Sanchez highlighted that the biophysical pitfalls in marginal lands are essentially the result of socio-economic limitations. He also stressed the need for an alternative paradigm for tackling agricultural development in such lands, relying more on “biological processes by adapting germplasm to adverse soil conditions, enhancing soil biological activity and optimising nutrient cycling to minimise external inputs and maximise the efficiency of their use” (Sanchez, 1994, p. 69).

Sanchez (1987) formulated the hypothesis that appropriate agroforestry systems have the potential to maintain soil organic matter and soil physical properties, augment

nitrogen fixation and promote efficient nutrient cycling. Cannell *et al*. (1996) complemented the hypothesis by proposing that agroforestry is operative when trees capture resources from zones which the crop would not otherwise exploit. The presence and management of trees offset the export of nutrients via production, erosion, leaching and volatilisation and also counteract the physical deterioration of the soil due to cropping or grazing. Fernandes *et al*. (1994) and Huxley (1999) elaborated on the role of the trees on:

1) nutrient uptake by deep-rooted species and recycling to the topsoil, allowing capture of nutrients beyond the reach of crop roots, mainly in fertile deep soils (more efficient nutrient cycling);
2) increasing amounts of organic inputs to the soil (from roots and above ground parts), maintaining soil organic matter and thus improving soil structure, nutrient status and reducing soil acidity;
3) increasing nutrient additions to the soil from N fixation and dust or aerosol interceptions by the tree canopy;
4) improving biological activity in the soil and nitrogen mineralisation through tree shade;
5) increasing biomass production by improving light and rainfall capture and utilisation efficiency;
6) providing beneficial shelter to associated crops/grasses.

The applicability of these hypotheses to the particular case of this study, although clear, requires its own perspective. As to the first and second hypotheses, expanded nutrient uptake assumes that crop roots will not reach a deep 'pool' of nutrients (leachates) and that, through the proper selection of the tree species, the agricultural system will gain access to that pool. The deep rooting system of *Brachiaria decumbens* suggests the existence of such a pool, but at the same time undermine the need for deep tree roots. However, trees can contribute to the reduction of nutrient leaching by increasing the amount and quality of soil organic matter and raising soil pH.

Regarding the third hypothesis, the addition of nitrogen from biological fixation supposes that properly inoculated nitrogen fixing trees will fix atmospheric nitrogen. Nitrogen fixation from the atmosphere can also be attributable to *Brachiaria*

decumbens (Boddey and Victoria, 1986), thus increasing the overall potential sustainability of the system. Nevertheless, frequent pruning and mulching can substantially diminish *Rhizobium* activity. With respect to hypotheses 4, 5 and 6, although C_4 grasses show no photo-saturation, they show higher light use efficiency (LUE) under reduced sunlight (Wilson and Ludlow, 1991). The management of the tree canopy in the silvopastoral system targets the balance between supplying enough biomass to the soil and producing a certain amount of shade so as to optimise grass photo-production. Finally, as the grass canopy covers the entire soil surface, reducing the impact of rain drops, thus preventing runoff, the importance of tree canopy for the control of soil erosion is reduced.

2.4 Economic Sustainability

Traditional livestock farming and the silvopastoral systems are both agroforestry systems. The former, however, is less sustainable than the latter. Since traditional extensive livestock husbandry on small farms is neither a strictly profitable system nor an ecologically sustainable one, it can hardly be considered sustainable from the economic point of view either. Its dependence on the natural recovery of soil fertility, involving a large area of fallow, mean that it cannot continue because of the pressure for land and the social concern for the preservation of the forest.

The low degree of control over external influences (weather, epidemics, market) and the irregularity with which the farmer sells an animal suggest that there are more socio-economic benefits in the farmer's rationale than the sole balance of inputs and outputs (Sharma and McGregor, 1991).

I believe that farmers put more value in their livestock because they do not demand permanent labour, allowing for complementary economic activities. However, animals can be sold at any time of the year, which means an insurance policy. Farmers also give high value to expectations (Anderson and Dent, 1976): livestock means some money in an emergency, but apparently it would accumulate if emergencies do not occur. That means that provided one has enough land to raise more animals each year, one can become a bigger rancher.

Huxley (1999) suggested some descriptors to assess (social-)economic sustainability. Although outside the scope of this research, I regard their consideration as important

for the proper understanding of the context in which the silvopastoral system is to be established.

Valuation of services. This is the internalisation of beneficial effects of the system to the environment. By reducing carbon dioxide emissions, prolonging the usefulness of the land, creating niches for fauna and lowering air temperature among other beneficial effects, the silvopastoral system can be considered more sustainable than the traditional one. Methane and nitrous oxide emissions per unit area can be, nonetheless, higher in the silvopastoral than the traditional system.

Level of consumption. The traditional system has a relatively low impact on the consumption patterns of the community. Pork and poultry comprise most of the meat in the farmers diet. Likewise, milk is very seldom seen on their table. Ceremonial or celebration rituals are events commonly associated with the consumption of beef dishes. Selling of live animals can provide cash for purchasing food. Perhaps the impact of the silvopastoral system on consumption can be through the establishment of the grounds for a more intensive system like milk production, thus incorporating dairy products into the diet.

Assessment of gross outputs. As the use of land is intensified, the silvopastoral system would produce more gross output per unit area than the traditional system. This is, however, not an indicator of sustainability *per se*, but gives a description of the economic stability of the systems.

Profitability. Profitability is easier to assess at village level –increase in cash sales-, although prices are variable beyond the influences of supply and demand. On grounds of the increase in the productivity of the land, the silvopastoral system, once adopted for a significant group of farmers, ensures a more numerous herd in the community, thus more investment in medicines and other inputs, but also more sales. However, this system involves more labour per unit area, producing the reduction of pasture lands per farm in order to maintain the labour input unaltered and provided that the farmers' priorities remain the same. Non-cash inputs and rewards make assessment difficult.

2.5 Discussion

Productivity and sustainability in small livestock farms in Mexico face increasing land degradation as a result of the invasion of areas not suitable for agricultural

systems. Socio-economic pitfalls have been shown to be the origin of such land degradation. Scientific efforts are developed in order to reverse land degradation upon the basis of the integral and efficient use of natural resources without using external inputs. The improvement of an existing, even though unsustainable, livestock husbandry system rather that the introduction of an alternative use of the land is preferred on the grounds that the small farmers consider it an important one, as it confers to the cattle owner a relatively higher status. Cattle provide the farmer's family with the financial certainty and self-esteem that are necessary to continue working the land. The introduction of nitrogen fixing trees and improved pastures gives a new shape to the system, responding to the objectives of the farmer but at the same time tackling the two issues defined as limiting factors from the socio-economic point of view: the cost of fertilisers and the adoption of a new technology. Knowledge about tree-grass inter-cropping has not been systematised, and so published results are difficult to compare and no conclusive evidence can be offered with respect to the hypothesis of agroforestry. Nevertheless, findings of increased productivity and the rebuilding of the physical and chemical properties of the soil are encouraging and reveal new possibilities to be studied. Grass growing under the tree canopy benefits, at least during the dry season, from shade and moisture and nutrients released from dead tree roots and litter from trees and tree guests fauna and from leaves and stem flow. The silvopastoral system explores non traditional facets of tree - grass agroforestry. Enhancing grass nitrogen content can offset reduced incident radiation, in some cases maintaining grass photo-production, with the additional reward of tree mulch production. Using prunings as fertiliser rather than animals foodstuff reduces the risk of losses through urine and faeces. Tree roots might not be deeper than grass roots, but they contribute by capturing resources and thus synchronising the recycling according to grass requirements. After pruning, root turnover may release more nutrients than leaves, in addition, root are in contact with soil decomposers whereas above ground mulch is subject to weathering and other possible losses. In contrast to fodder trees, green manuring trees can present a slow decay rate although a minimum of 2% of nitrogen is needed to prevent immobilisation of free nitrogen in soil.

3. General Description of the Work

3.1 General Methodology.

This research comprised three groups of activities that combined to address the objectives proposed. The first group of activities involved field research, embracing experiments and monitoring in a silvopastoral field trial. The second group consists of the experiments and analysis carried out under controlled conditions (growth room and biochemistry laboratory). The third group refers to the development of a computerised model for the simulation of nitrogen and carbon cycling in the silvopastoral system.

The field research was conceived as a mean to capture the integrated functioning of all the components of the system under real environmental conditions. The only biotic component avoided was the animal. I considered it inappropriate to allow grazing in the paddocks due to the rather small size of the trees, as the animals could reduce the survival of the trees with thinner stems. The effect of the animals on the silvopastoral system was partially simulated by the disposal of the grass forage, cut at regular intervals. Returning of organic matter through excretes, selectivity of the grass consumed as well as potential soil compaction due to high stocking rate were ignored in the field work but must be considered when analysing the results.

Carrying out the field work faced some difficulties such as the distance to the road or any safe place for samples and tools, making necessary to carry most of the materials from and to the house, five kilometres distant, throughout the forest, every day. Whereas the route in the dry season was 45 minutes because of the rocky hillside, in the wet season it became 90 minutes or even impassable when the gullies grew. Also, most of the measurements were performed manually, being necessary to train support personnel to achieve consistency and accuracy in consecutive readings; this happened every time a new experiment was set up.

The poor availability of instruments in the field made it difficult to produce detailed physiological measurements on *Brachiaria decumbens*. Experiments on root longevity and responses to change in light environment were carried out back in Edinburgh, where instruments were available, although growth room facilities were necessary. The information derived from these experiments was considered complementary to the field research for the understanding of the processes related to the partitioning of assimilates and the adaptation of the grass to the inter-cropping.

The simulation model was proposed as a mean to conceptualise the different components and their relations in the system, especially those concerning the recycling of nitrogen. Experimentation under controlled conditions, alongside the laboratory analysis, was also necessary for the parameterisation of the mathematical model.

3.2 Plant material

A nursery was established in Vega del Sol, a rural community about 20 km from the experimental site. After a pre-germination treatment with cold water of up to 72 hours in some cases, seed of four species of nitrogen fixing tree were sown in seed beds: *Gliricidia sepium* (Cocoite), *Leucaena leucocephala* (Guaje), *Delonix regia* (Framboyan) and *Lysiloma auritum.* When the seedlings were large enough (about 10 cm), they were transplanted into polythene bags and cared for until they reached the suitable size for planting out.

All the tree seeds were obtained from the Germplasm Bank of the Forest Service, Ministry of Agriculture, Guatemala. Many seeds failed to germinate or become established, so the experimental plan was constrained by the availability of the trees.

Signal grass (*Brachiaria decumbens*) was sown in the same plots as the trees as a result of its performance, which was tested and compared with several other tropical grasses. Among the most promising were *Brachiaria brizantha*, *B. decumbens* and *Andropogon gayanus*. Past experience suggested that *Andropogon* should not be planted in perhumid soils (Udic moisture regime). Market availability of seeds led us to sow *B. decumbens*.

3.2.1 *Brachiaria decumbens*.

Botanical description

Family: Gramineae

Tribe: Paniceae

Species: *Brachiaria decumbens* Stapf.

Synonym: no synonym found.

Vernacular names: Signal grass, palisade grass (these shared with *Urochloa - Brachiaria- brizantha*), chontalpo (Mexico).

Plants perennial. Culms rhizomatous, decumbent. 0.55 – 1 m high, nodes glabrous to sparsely pilose. Blades and leaf sheaths glabrous to pilose; margins scaberulous to spinulose. Branches terminating in a paired, ellipsoid to obovate spikelet, 4-5 mm, distally usually pubescent, that disarticulate above the glumes; spikelets base stipitate. First lemma 5-7-nerved, acute to acuminate. Second lemma acutish, dull and finely longitudinally punctate-striate. Inflorescence a panicle of ribbon-like racemes; anthers 2-3.5 mm long; peduncle pilose below the inflorescence. Rachis of racemes 1-1.7 mm wide, more or less flat. Pedicels glabrous. Lower glumes truncated to rounded, (Veldkamp, 1996). Most cultivated *B. decumbens* varieties are indeed intermediates between *B. decumbens* and its close relative *Urochloa brizantha*. A more detailed description being required to separate the two species (Veldkamp, 1996):

Brachiaria decumbens is stoloniferous. Blades 5-20 cm long. Common axis 1-8 cm long. Racemes 2-7, 1-5 cm long. Upper glume and first lemma membranous, dull.

Urochloa brizantha (formerly *Brachiaria brizantha*) tufts are of culms erect to geniculate at the base. Blades 10-100 cm long. Common axis 3-20 cm long. Racemes 1-16, 4-20 cm long. Spikelets 4-6 cm long, usually glabrous, in one row, rachis more or less crescentic with narrow inrolled wings, approximately 1 mm wide. Upper glume and first lemma chartaceous, somewhat shiny.

Distribution

Brachiaria decumbens is pantropical, with its centre of diversity in the surroundings of Lake Victoria, eastern Africa (Kenya, Rwanda, Burundi, Uganda, Tanzania and Zaire; Keller-Grein *et al*., 1996; Parsons, 1972). It is very likely that the cultivar in the present research work is *Brachiaria decumbens* cv. Basilisk (Signal grass), originated in Uganda, accession 001058 EMBRAPA, Brazil, first evaluated by CSIRO, Queensland.

Habitat

Brachiaria decumbens is a vigorous, trailing grass, which is very similar in characteristics to Para grass (*Brachiaria mutica*) and Pangola grass (*Digitaria decumbens*). The stolons root and branch readily at each node forming a dense mat. Signal grass is adapted to humid, tropical areas of summer rainfall not less than

1,500 mm (800 mm in soils of satisfactory water retention), with a dry season shorter than five months. Nevertheless, it grows well on quick-drying, shallow, hillside soils. It forms an aggressive, high-yielding sward and for this reason it is not easy to maintain legumes in association, especially at high grazing pressures, but tolerates infertile soils, withstands heavy stocking and trampling and responds dramatically to nitrogen amendments (Davidson, 1986; Stür and Shelton, 1991).

Adaptability

Brachiaria grass species, and predominantly *Brachiaria decumbens* cv. Basilisk, are the most widely grown pastures in humid and sub-humid tropics. Some of the attributes that enable them to adapt to low-fertility acid soils are (1) maintenance of root growth at the expense of shoot growth. (2) acquisition and use of both nitrate and ammonium forms of nitrogen (this attribute is not present in *Brachiaria decumbens*). (3) acquisition of nitrogen through associative fixation predominantly by bacteria from at least three species of the genus *Azospirillum*: *A. amazonense*, *A. brasilense* and *A. lipoferum* (Reis *et al*., 1999). Biological nitrogen fixation is particularly important in *Brachiaria decumbens* cultivated in N poor soils. (4) acquisition of phosphorus through an extensive root systems and association with vesicular-arbuscular mycorrhizae and (5) acquisition of calcium through an extensively branched root system with large numbers of root tips (Rao, *et al*., 1996; CIAT, [1984]; Miranda and Boddey, 1987). *Brachiaria decumbens* cv. Basilisk responds to low fertility by increasing the root to shoot ratio up to 30% in experimental conditions (Rao, *et al*., 1996).

Pitfalls

Contrasting with the otherwise resilient nature of Signal grass, this species is highly susceptible to spittlebug (several genus of Homoptera: Cercopidae) attack. *B. decumbens* reproduction is apomictic (asexual seeds), which, until recently, complicated its genetic manipulation so as to combine its broad edaphic adaptation with tolerance to such infestation (Miles and do Valle, 1997). *B. decumbens* pastures can develop hepatogenous photosensitization in cattle when consumed as a sole diet for long periods. Photosensitization is a widespread, but sporadic, toxicity syndrome causing losses in live weight gain. This disease has been associated with infestation

of the saprophytic fungus *P. chartarum*, although its definite role has not been stated (Keller-Grein *et al*., 1996; Lascano and Euclides, 1996). Lascano and Euclídes (1996) reported toxicity of *B. decumbens* causing vaca caída (fallen cow) syndrome during late gestation and early lactation.

Forage production

Different accessions of *B. decumbens* have been reported to produce 9.5 Mg DM ha^{-1} yr^{-1} in Costa Rica (Bustamante *et al*., 1998) and 11.4 Mg DM ha^{-1} yr^{-1}, in Brazil, with 26% of the total biomass production during the dry season and leaf to stem ratio of 1.07 to 1.51 (Valle *et al*., 1993). When fertilised with nitrogen and well managed, *Brachiaria* pastures give good quality, palatable forage enabling good animal performance (Valle *et al*., 1993).

Nutrient requirements

The most commonly limiting nutrient for the productive life of mono-specific swards of *Brachiaria* is nitrogen (Rao, *et al*., 1996). However, *Brachiaria decumbens* performs better than other *Brachiaria* species in unfertilised experimental conditions (Alvim *et al*., 1990). These authors obtained 10.3 Mg ha^{-1} with applications of 75 kg N and no increments in biomass production when doubling the doses, the nitrogen use efficiency being as high as 195 g biomass (shoots + roots) g N^{-1} taken up. The content of crude protein, however, increased linearly with incremental additions of nitrogen, from 7.2 to 10.6 to 13.4% for 0, 75 and 150 kg N ha^{-1} respectively. Nitrogen fertiliser requirements of *Brachiaria decumbens* are low and not accurately determined. However, its capability to obtain significant proportions of plant N from associative N_2 fixation under natural conditions, (estimated as up to 40 kg N ha^{-1} yr^{-1}, Boddey and Dobereiner, 1988), suggest that production is only partially contingent upon nitrogen amendments. Such estimates are consistent with field observations that stands of *Brachiaria decumbens* can remain productive for many years in the absence of N fixing legumes or N fertiliser (Rao, *et al*., 1996). *Brachiaria* species have much lower requirements, especially of P and Ca, than other grasses such as *Panicum maximum*, although there are inter-specific differences (Rao, *et al*., 1996).

3.2.2 *Leucaena leucocephala*.

Botanical description

Family: Leguminosae – Mimosoideae

Tribe: Fabaceae or Mimoseae

Subspecies: *Leucaena leucocephala* (Lam.) de Wit subsp. *glabrata* (Rose) S. Zárate

Synonym: *Leucaena glabrata* Rose

Vernacular names: Guaje blanco, guash de castilla (Chiapas), calloaxin (Mexican), yail ba'ade (Mixe), chalip (Guatemala), barba de león (El Salvador), frijol guaje (Honduras), wild tamarind (Belize), acacia ruidosa (Nicaragua).

Leucaena leucocephala subsp. *glabrata* (Figure 3.1) is a small tree 5-20 m tall, with a short clear bole to 3-5 m and an open irregular crown. Leafy shoots glabrous, bipinnate leaves 17-25 cm long with petiolar nectary gland oblong and a second nectary in the rachis tip, between the last pair of pinna and mucro 3-5 mm long. Leaflets 15-21 pairs per pinna, 11-21 mm long (Hughes, 1998). *L. leucocephala* is known to be tetraploid, 2n=104 and highly self-compatible.

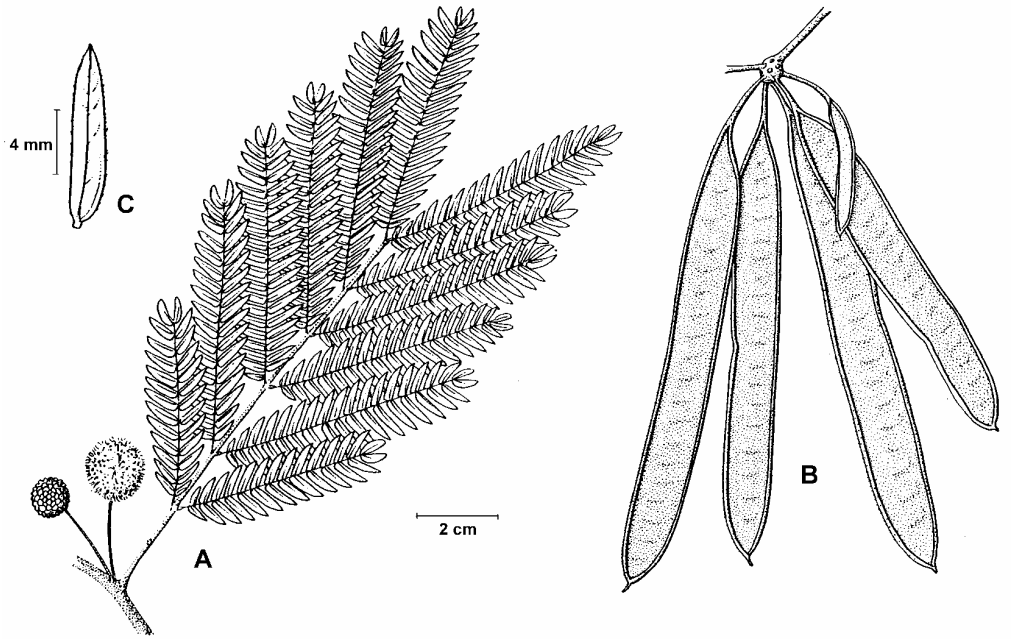


Figure 3.1 *Leucaena leucocephala* subsp. glabrata. A) Leaf and inflorescences, B) pods, and C) leaflet (Hughes, 1998)

Owing to the long story of distribution and cultivation of *Leucaena leucocephala*, cultivated varieties became the common currency, rather than any formal taxonomy, which has only recently recognised two separate subspecies: *leucocephala* and

glabrata. Unlike the "typical" shrubby subspecies *leucocephala* (Hawaii type), subspecies *glabrata* presents higher size as in the "giant" Salvador and the Peru types. More useful features to differentiate the two subspecies are that *glabrata* leaflets, buds and pods are slightly larger and are glabrous, whereas subsp. *leucocephala* leaflets are canescent, and buds and pods are pubescent (Stewart *et al*., 1992).

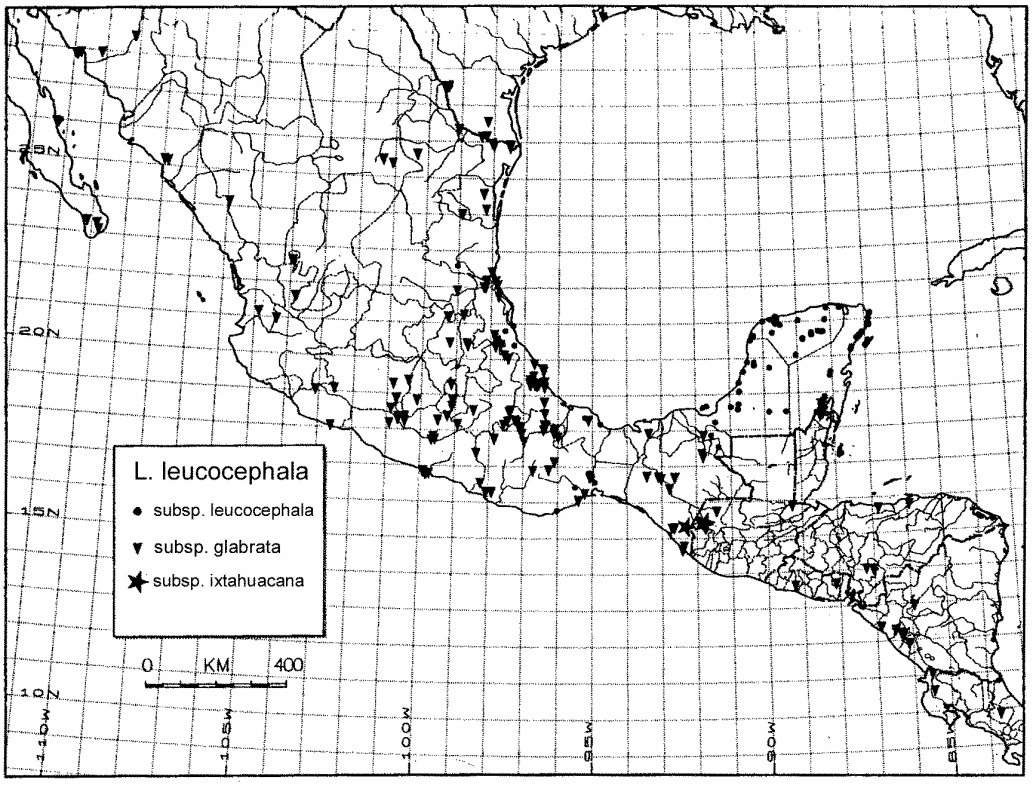


Figure 3.2 The natural distribution of the three subspecies of *Leucaena leucocephala* (Hughes, 1998)

Phenology: Flowering and fruiting throughout the year as moisture permits.

L. leucocephala associates with *Rhizobium loti* for biological nitrogen fixation (Singleton *et al*., 1992) and vesicular-arbuscular mycorrhizae also infect Leucaena roots (Binkley and Giardina, 1997). A monocrop stand of *L. leucocephala* can fix between 100 and 200 kg N ha^{-1} yr^{-1}, although hedgerow inter-cropping halves such amounts (Huxley 1997).

Distribution

Although the genus has its diversity centre in Mexico (Figure 3.2), it is native to tropical America (Zárate, 1994). The natural distribution of *Leucaena leucocephala*

subsp. *glabrata* remains unknown. It is a wildly distributed cultivated tree in Mexico and Central America, for the production of edible pods and seeds, fodder, green manure, shade in plantation crops and for land reclamation, the wood being used as timber, fencing and charcoal (Giller and Wilson, 1991; Stewart *et al*., 1992; Zárate, 1994). *L. leucocephala* subsp. *glabrata* is found in all tropical and subtropical Mexico except at elevations above 2000 m and has been actively introduced outside Mexico and Central America that now is cultivated pantropically.

Habitat

Subspecies *glabrata* has wider environmental amplitude than *leucocephala*, growing up to 1,500 m elevation and as far north as 27° N, with rainfall between 650 and 3,000 mm with 3 to 6 months dry season. However, yields are low in dry environments and are believed to increase linearly from 800 to 1,500; *Leucaena leucocephala* does best on neutral to calcareous soils, pH 5.2 or more and requires good levels of P and Ca for best growth but persist in sulphur deficient soils (Shelton and Brewbaker, 1994; Huges, 1998; Zárate, 1994; Stewart *et al*., 1992).

Pitfalls

This species is considered a fast growing, easy to maintain, widely adaptable multiple use tree. However, serious drawbacks have undermined the success of this species in many countries: *L. leucocephala* is notoriously limited by soil chemical characteristics and climatic regimes; Fusarium dieback and attack by Psyllids (*Heteropsylla cubana*) can be devastating (Hocking, 1991). Residue mulches of *L. leucocephala* have been reported to have allelopathic properties (Huxley, 1999). *L. leucocephala* show little content of tannins, so that animals find it palatable. However, it does contain mimosine which need to be detoxified by the right bacteria in order to eliminate deleterious effects in the metabolism of the animals (Huxley, 1999).

Production

There are only a few cultivated tree species in the tropics as diversified and widespread as *L. leucocephala*. This tree is grown in Asia as a high yielding hardwood. Its genetic improvement has been chiefly driven by agroforestry requirements such as in the selection of the arboreal Salvador-type varieties. Others

such as K8 yield 40 to 900% more wood than common varieties, and more forage by 100 to 300% (Chuntanaparb and MacDicken, 1991). Edible forage yields range from 3 to 30 ton. DM ha^{-1} yr^{-1} and higher with 1,500 mm rain or more. Pollarding every 6 to 8 weeks and up to 12 weeks in less productive locations. *Leucaena* paddocks are normally rotationally grazed with cattle moved to new areas when most leaf and edible stem have been removed. Appropriate stocking rates vary greatly from less than 1 beast to 1.5 ha in low rainfall environments (750 mm) up to 6 beasts ha^{-1} in fertile well watered or irrigated stands (Shelton and Brewbaker, 1994).

3.2.3 *Gliricidia sepium*.

Botanical description

Family: Leguminosae – Papilionoideae

Tribe: Robinieae

Species: *Gliricidia sepium* (Jacq.) Kunth ex Steud.

Synonyms: *Robinia sepium* Jacq.; *Lonchocarpus sepium* (Jacq.) D.C. and *Gliricidia lambii* Fernald.

Vernacular names: Cocoíte, kan-te (Mexico), madrecacao, cacahuananche (Guatemala), madreado (Honduras), madero negro (Nicaragua, Costa Rica), mata-ratón, etc.

Gliricidia sepium (Jacq.) Kunth ex Steud (Figure 3.3) is a tree 5-10 m tall and trunk 15-30 cm in diameter. Leaves are pinnate, deciduous, alternate or occasionally subopposite, 15-25 cm long, with 7-17 leaflets; these generally opposite, lance-oblong or elliptic, 3-7 cm long, (at maturity) upper surface glabrous to strigose, the lower surface glabrate to strigose (Lavin, 1996). Pink or lilac erect inflorescences, usually preceding the leaves. Pods are flat, about 15 cm long and explosively dehiscent, throwing the seeds up to 35 m (Stewart *et al*., 1992). Base chromosome number $\underline{x}$ = 10, 11 (Lavin, 1996). The name refers to the uses of the plant as rodenticide (bark and seeds) and hedge tree (easy propagation from stakes and because it tolerates frequent pollarding): *gliris*- mouse, *cidium*- killing and *saepes*- hedges (Giller and Wilson, 1991; McVaugh, 1987).

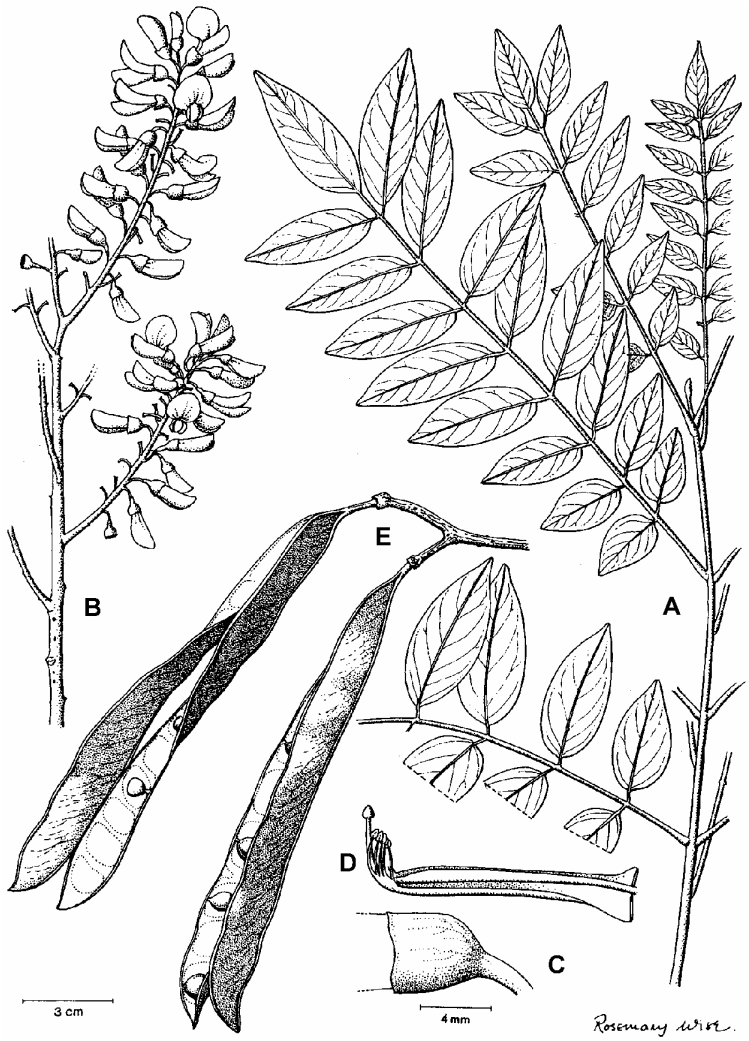


Figure 3.3 *Gliricidia sepium* (Jacq.) Kunth ex Steud. A) composed leaf, B) inflorescence, C) calyx, D) sexual organs, and E) pods (Lavin, 1996)

Phenology: Naturally flowering when the trees are leafless in the dry season, lower coastal sites flowering well before sites at higher altitudes (Simons and Stewart, 1994). Periodicity of pod typically takes 45-60 days. However, sprout, abscission and flowering can be greatly affected by management. (Stewart *et al*., 1992). It is nitrogen-fixing by association with *Rhizobium* and *Bradyrhizobium* (Sanginga *et al*., 1995). Although most of cultivated *Gliricidia* belongs to the species *sepium*, *Gliricidia maculata*, which is in fact a different species, is often used inaccurately as synonym.

Distribution

Gliricidia sepium natural distribution is probably limited to the Pacific coast of Central America and some inland valleys between 25ºN (Mexico) and 7ºN (Panama,

Figure 3.4). However, over the last 200 years it has been widely introduced and is now almost pantropical (Stewart *et al.*, 1992).

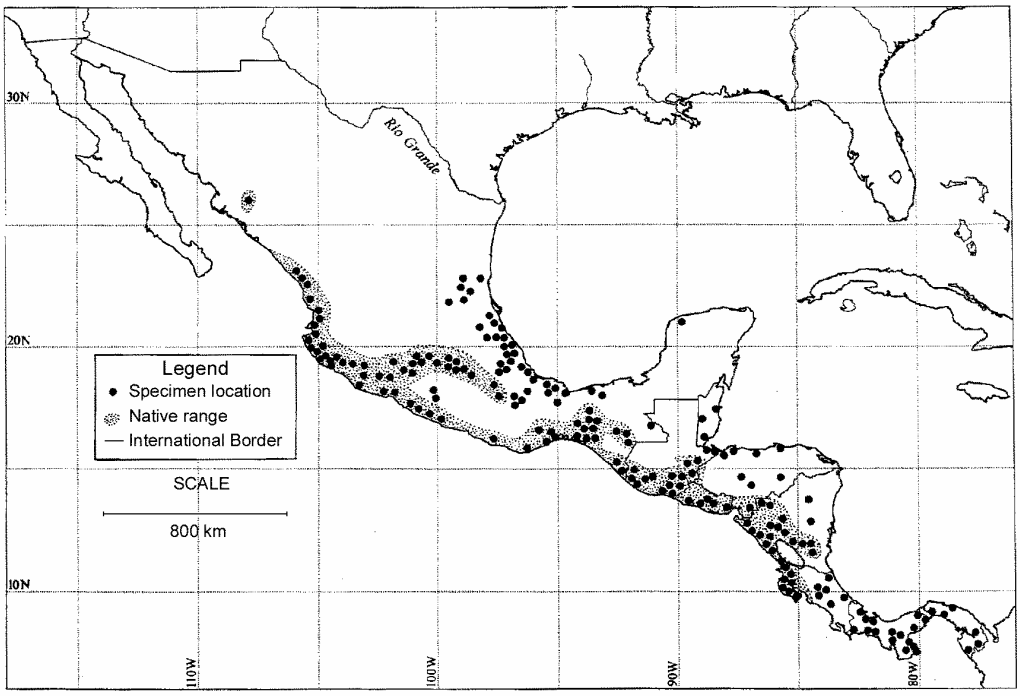


Figure 3.4 Natural distribution and collecting sites (Lavin, 1996) of *Gliricidia sepium* (Jacq.) Kunth ex Steud.

Habitat

Gliricidia sepium can be found up to 1,200m altitude. It tolerates inadequate soils from pure sand to eroded, skeletal volcanic soil to deep black vertisols and withstands salinity and acidity down to about 4.5 in pH, but does not tolerate waterlogging nor soil compaction and it prefers calcareous soils (Stewart *et al.*, 1992). Temperature range from 21 to 29°C (mean monthly temperature). Tolerates low calcium soils but have poor survival on soils with high aluminium saturation (Simons and Stewart, 1994).

Pitfalls

Gliricidia sepium produces high quality fodder for ruminants or nitrogen rich mulch, but reports of its palatability vary perhaps due to the concentration of coumarines or other substances that give *Gliricidia* supposed medical and poisonous properties (Stewart *et al.*, 1992). This toxicity is thought to be due to the conversion by bacteria of coumarin to dicoumerol, a haemorrhagic compound, during fermentation (Simons

and Stewart, 1994). Leachates from *G. sepium* mulch were found to produce chlorosis and to slow down growth in seedlings of associated crops, but this did not affect crop yield when applied one week before germination (Tian and Kang, 1994). The release of chemicals from *G. sepium* can be used to reduce weeds growth and thereby increase crop yields (Huxley, 1997).

Production

Gliricidia sepium is a fast growing, nitrogen fixing multipurpose tree that unlike *L. leucocephala* can be multiplied by rooting stumps (Huxley, 1999). *G. sepium* is commonly used in live fences and almost every part of the tree has some use: leaves are high in nitrogen that improves organic amendments and ruminant feeding, flowers are edible for humans, branches are good source of firewood and large stems make excellent posts for house building; also, roots and seeds contain poisonous chemicals traditionally used in the control of rodent pests. *G. sepium* is very low in tannins, and this leaves the crude protein ingested to be mostly degraded to ammonia and volatile fatty acids in the rumen (Huxley, 1999); when laid as mulch, in volume corresponding to the production of adjacent hedgerows, *G. sepium* reduced runoff by 50% and soil loss by up to 21% (Chiti, 1997). *G. sepium* can produce 20 ton. leaf DM ha^{-1} yr^{-1} at a planting dens of 4 trees m^{-2}. Cutting intervals of 6 to 12 weeks are usually recommended in stands of *G. sepium* grown for forage only in the humid tropics (Simons and Stewart, 1994).

3.2.4 *Delonix regia*.

Botanical description

Family: Leguminosae – Caesalpinioideae

Tribe: Caesalpinieae

Species: *Delonix regia* (Bojer ex Hook) Raf.

Synonym: *Poinciana regia* Bojer ex Hook.

Vernacular names: Flamboyant, alamboronala, sarongadra, tsiombivositra, hintsakinsa, tanahou, flor de fuego, guacamayo.

A deciduous tree 5-20 m tall. Cylindrical unbranched trunk of 50 cm or more in diameter. Pinnate or bipinnate stipules. Leaves mostly with 8-25 pairs of pinnae, with 30-60 or more opposite leaflets each, rachis grooved, leaflets oblong, 4-12 mm long,

not coriaceous. Flowers very large and showy, in corymbs above the foliage, bright scarlet-red, the upper petal with large white to creamy yellow blotch streaked and flecked with red and with a red margin. Pods very large, strap shaped, flattened, slightly curved, most 400-700 mm long, woody, brown to blackish, rather glossy, containing 20-50 seeds. All these characteristics make this species very distinctive within the genus (Du Puy *et al*., 1995). Branches brittle, leafless during the dry season. Wood almost white, feeble, soft and light in weight (Standley and Steyermark, 1946).

Phenology: "*It is extremely showy during its blooming period, however, is only a brief one… in the late months of the dry season*" (*ibid*.).

Distribution and Habitat

Delonix regia is native to West and North Madagascar, now widely cultivated in many tropical countries as an ornamental tree at up to 300 m altitude. In its natural habitat grows in limestone karst and escarpments, often in the taller forest of gullies and river gorges, or in sandy soil over limestone (Du Puy *et al*., 1995).

Uses

Ornamental, shade, its large pods are used as rattles.

3.2.5 *Lysiloma auritum*.

Botanical description

Family: Leguminosae – Mimosoideae

Tribe: Fabaceae or Mimoseae

Species: *Lysiloma auritum* (Schlecht.) Benth.

Synonym: *Acacia aurita* Schlecht. (Sare blanco)

Vernacular names: Chicharrón, gumara, tepequehuite, sicahuite (Martínez, 1979).

A 6 to 12 m high tree. The trunk sometimes with small buttresses, branchlets densely short-pilose; petioles short, bearing a conspicuous elevated gland [like in *Leucaena leucocephala*]; stipules large and deciduous; pinnae 10-25 pairs; leaflets 25-50 pairs, oblong-linear, glabrous, 4-5 mm long; racemes very short, oval, flowers distinctly pedicellate, densely puverulent, white corolla, scattered along an evident rachis; legume short-stipitate, 12-16 cm long, blackish or dark ferruginous, glabrous, rostate.

Spikes very short, oval or subglobose; sapwood thick and whitish, heartwood almost black with greyish bands (Standley and Steyermark, 1946).

Distribution

Lysiloma is an exclusively American genus, consisting of ten shrub and arboreous species. *Lysiloma auritum* has been reported in Southern Mexico, Guatemala, Honduras, El Salvador and Nicaragua (Hemsley, 1888).

Habitat

Moist thickets or often on dry, rocky, or thinly forested hillsides, sometimes in open pine forests, 1800 m. or less (, Standley and Steyermark, 1946).

Uses

"*Wood used locally for house construction, although it is said to be susceptible to the attack of termites, bark used for tannic hides…*" (*ibid.*).

3.3 Field trials

3.3.1 Description of the experimental site.

The field work was carried out on a small farm in the vicinity of Santa Fe y la Mar, Valle Nacional, Oaxaca State, Mexico (17.46°N, 96.18°W, 60m elevation). The experiment was conducted on gently undulated terrain at the foot of a valley and was about one hour walk from the road. The site is surrounded by primary and secondary rain forest, although there are hundreds of hectares of rubber and coffee plantations nearby. I decided to choose this farm because it is representative of the environmental and socio-economic conditions of an important portion of the Chinantla region, in Oaxaca State, a priority area for the conservation of natural resources. My previous research work in this region was in collaboration with the Fondo Regional de la Chinantla, which is the local authority for the administration of federal resources for Development. The Fondo Regional have a pilot programme for Sustainable Livestock Husbandry implemented in Santa Fe y la Mar, such a program consists on support to local organisation of farmers, credit and technical assistance. It is expected that the results from this research project can be used to derive recommendations for farmers.

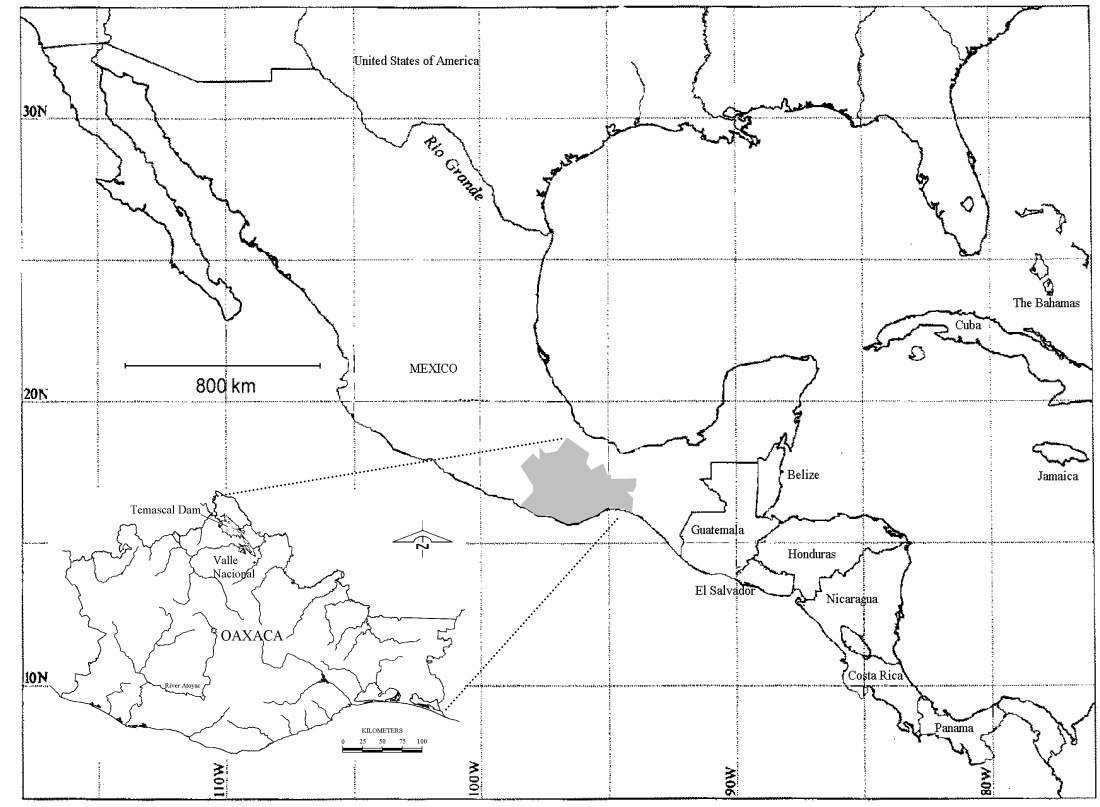


Figure 3.5. Map of Mexico, indicating the location of Valle Nacional, the nearest town council to the Silvopastoral Experiment.

3.3.2 Climate.

The mean annual temperature in Valle Nacional is 24°C, with mean maximum of 34.6°C, a mean minimum of 21.7°C. Annual precipitation average 3750 mm, with the driest part between March and May. However, even then there is rarely a large soil water deficit (López-Paniagua and Urbán, 1992). Total rain between Jul. 20 and Oct. 20, 1997 was 1879 mm, with 15 rain days over 50 mm, whereas total rain between Nov. 25 1997 and Feb. 2, 1998 was 214 mm, with one rain day over 50 mm (Figure 3.6).

3.3.3 Soil.

Soil in the experimental field was different between sections (Figure 3.4). Plots one to four were in the shallower and flat part, with big rocks at 20 to 50 cm but the topsoil was dark, organic, well mixed or slightly sandy. The rest of the field was on a terraced hillside, it was deeper, with some rocks at 40 to 60 cm but less dark, with

red tones and finer in texture. Plots 5, 6, 8, 9, 10 and 12 had little slope, whereas plots 7, 11 and 13 had moderate slopes.

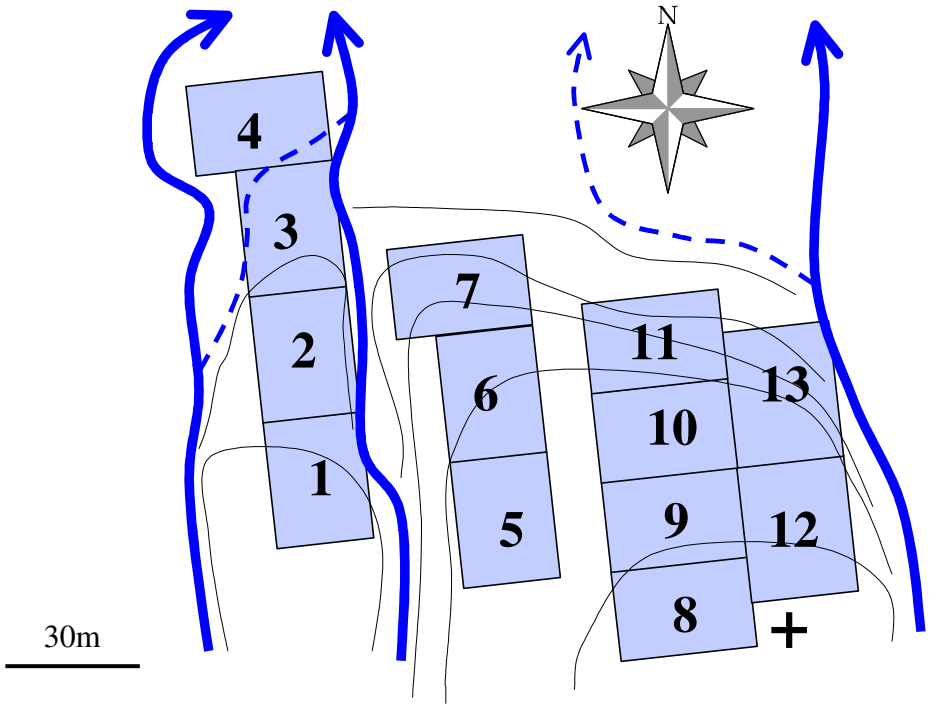


Figure 3.6. Free hand diagram of the plots of the Silvopastoral experiment. The thick lines denote streams and the dotted lines denote seasonal streams. Thin contours denote level curves of about 2 m intervals. The + sign indicates the highest point in the experimental field.

The soil in the experimental site was recently cultivated and infertile. There is no detailed map of the area. However, according to the FAO/UNESCO categories (Ahn, 1993), the soils in Valle Nacional are Luvisols (similar of Alfisols) and Acrisols (similar of Ultisols) and are present in two soil units (López-Paniagua and Urbán, 1992). The lists of plots in each soil class are my interpretation of my observations in the field:

- Calcimagnesitic on plateaux and terraces, associated with humus, characterised by incomplete decarbonation (plots 5, 6, 7, 8, 9, 10, 11, 12 and 13).

- Fersialitic associated with humus in plateaux and terraces, with complete decarbonation (plots 1 – 4).

3.3.4 Field experiment layout.

Experimental units and treatments

Thirteen 0.06 ha plots (20x30m) of *Brachiaria decumbens* were established in 1995 and treatments consisting of the combination of a tree species and planting density were randomly allocated to them(Plate 3.1). Four nitrogen fixing tree species (*Gliricidia sepium*, *Lysiloma auritum*, *Leucaena leucocephala* and *Delonix regia*) were planted and four planting densities used (500, 600, 700 and 800 trees ha^{-1}).

Plate 3.1. View of the Silvopastoral experimental field. Trees had been recently pruned. The digging of a run-off catchment is seen in the foreground. The background is secondary forest and native pastures.

Given the small number of some of the tree species, not all the treatment combinations (species x density) could be included. Plant density limits were established on the grounds that, on the one hand, 500 trees are considered capable of returning 100 kg N ha^{-1} in mulch and a similar amount from biological fixation. Inputs lower than 200 kg N ha^{-1} are unlikely to sustain stocking rates higher than 1.5 heads ha^{-1}. On the other hand, 800 trees per hectare result on an average distance of 3.5m between trees, which is the minimum advisable distance in order to allow free transit and avoid excessive damage from animals. The trees were deliberately not distributed uniformly over the plots. Instead, a 2m grid was drawn for every plot,

thus giving 150 squares of 4m^2 per plot. The squares were coded by row and column and a draw was carried out according to the desired plant density. Consequently each plot has a different distribution of planted and free squares. Trees were planted in the centre of the selected squares. Trees were planted in this way since this distribution matches better to the natural distribution of trees in pastures. In order to separate the effect of the tree component on grass, a control plot was retained without any tree. Each 0.06 ha plot was an experimental unit.

Table 3.1 Plots and corresponding tree treatments in the silvopastoral experiment.

Plot	Treatment		
	Species	Trees	trees ha^{-1}
9	*Delonix regia*	18	300[a]
10	*Delonix regia*	33	550[a]
1	*Gliricidia sepium* (seedlings)	11	183
8	*Gliricidia sepium* (seedlings)	13	216
3	*Gliricidia sepium* (seedlings)	49	817[b]
7	*Gliricidia sepium* (poles)	39	663
4	*Gliricidia sepium* (poles)	59	891
6	*Leucaena leucocephala*	18	300
5	*Leucaena leucocephala*	23	383
12	*Leucaena leucocephala*	37	616
13	*Leucaena leucocephala*	48	817
2	*Lysiloma auritum*	39	650
11	Control without trees		

a) The two *Delonix regia* plots presented very poor re-sprout and suffered rodents attack that weaken and killed many trees at the point that only 16 trees were able to be pruned in July and no pruning at all was possible in November. b) Plot 3 (*Gliricidia sepium*) re-sprout unevenly, only 19 (317 trees ha^{-1}) trees were useful for experimental purposes.

It was costly and difficult keeping small trees safe from grass overgrowing them during the establishment period, and the grass grew as high as 1.5m, literally covering the smaller trees and limiting the development of the plantation; many trees died before the trial was ready to start. There were two plots where the resulting tree population was severely diminished. The few remaining trees were then deliberately killed and *Gliricidia sepium* poles planted instead in January 1997. *Gliricidia* poles were ready for lopping after six months. The poles were planted in a square pattern 3.5x3.5m (900 trees ha^{-1}). Such an experience gives insights on the timing for tree

and grass establishment. Since no replacing of dead trees was done in the other ten plots, it resulted in a lower final tree density than was originally planned (T able 3.1).

Sampling units

The $4m^2$ squares in the experimental units were considered for most of the experiments as sampling units. The experimental units were divided into three sub-plots for sampling purposes according to the distance of the sampling unit from the nearest tree. The sample units containing a tree were designated *close* units; the sampling units without a tree but with at least one neighbouring *close* unit were designated *mid*; the sample units without a tree and without neighbouring *close* units were called *far*. The edge of the *far* sampling units was thus at least 3 from the nearest tree. *far* units cannot be considered completely free of influences of the trees (control units). However, a gradient was assumed where *close* units had direct shade and high tree root density, *mid* units had indirect shade and medium tree root density, and *far* units had very low shade and very low tree root density. The other difference of *far* units and the control plot was the application of mulch on the *far* units. Due to the random allocation of the trees and the criteria used for sub-dividing the experimental units, these sub-plots were inter-mingled within each of the 12 plots with trees.

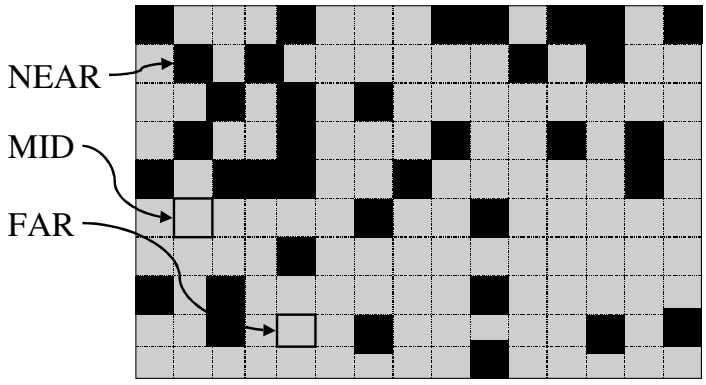


Figure 3.7. Model of a (20 x 30m) plot in the Silvopastoral experiment, the greed is $2m^2$. The grey area is grass and the black squares represent sampling units containing a tree in the centre. Examples of near, mid and far sampling units are pointed with arrows.

Variability and bias

It was possible for there to be eight *close* units neighbouring a *mid* unit. In practice there was typically one with a range of one to five neighbouring *close* units. That

means that the influence of the trees on the grass and soil could be different. Differences in the number of neighbouring *close* units are not considered a source of bias since such effect should be offset by increasing the number of sample units used. By doing so, the probability of each possible number of neighbouring *close* units relies on the tree density designated in the big plot.

Some variability between plots derived mainly from their position with respect to the two streams which flowed through the sample area; those plots near the water (1-4) were slightly more stony and sandy than those in the terrace and slope (5-13). 30 cm deep x 30 cm wide ditches were dug in order to prevent interference between plots such as runoff, which drags soil and litter particles across treatments, and roots from neighbouring plots. Most grass roots and shallow tree roots should have been intercepted, but clearly a 30 cm deep ditch would not prevent all roots invading the neighbouring plot. Sample units were located with an allowance consisting of one row of quadrates on every side of the plots for the edge effect. The isolating channels were maintained several times during the experiment. Individual experiments and monitoring studies had its own sampling schedule depending on the climatic season, the treatment (tree species, plant density), the distance to the nearest tree and the days of re-growth of grass and/or trees.

3.3.5 Time course of the experiment.

The nursery was established in February 1995 and the experimental plot in summer 1995. Trees were planted between July 15th and August 15th. The actual period of experimentation and data collection was from February 1997 to February 1998 (Table 3.2); thus the trees were two years old and the pasture was about eighteen months old. Because of the unexpectedly poor development of the trees by February 1997, the trees were left untouched for five months more to allow the stems to grow thicker and the recently established *Gliricidia* trees to root appropriately. Based on reported figures (Fernandes *et al*., 1994), it was assumed that 30 months was enough time for the trees to reach maturity in terms of potential biomass production (see Figure 2.1). In February 1997 the grass was cut with machetes to 5 cm height in order to even the sward, this action was the starting point of the experimental phase. The different experiments and sampling took place according to individual schedules

aimed to capture the dry and the wet seasons. The field work was finished in February 1998.

Table 3.2 Schedule of the field work, with indications of the months in which each activity was realised. For more details see the corresponding chapters.

					1997					1998	
ACTIVITY	A	M	J	J	A	S	O	N	D	J	F
Soil sampling (after Sep. 1995)			X	X	X	X					X
Grass biomass production	X	X	X	X	X	X				X	X
Grass leaf area index	X	X	X	X	X	X					
Root profile (vertical distribution)		X	X		X	X				X	X
Tree biomass production			X	X	X			X	X		
Root biomass production			X	X	X	X					
Mulch decomposition			X	X	X	X	X	X	X	X	X
Tree leaf area index								X			
Light interception								X			
Soil available nitrogen								X			
Chlorophyll content									X	X	
Root distribution (excavations)										X	X

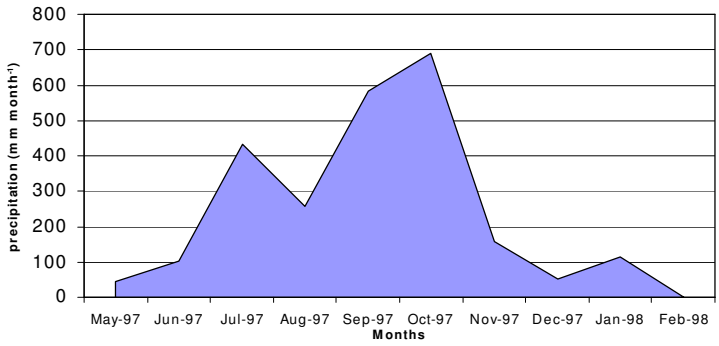


Figure 3.8. Monthly precipitation (mm) in the experimental field in Valle Nacional, Oaxaca, Mexico (1997-1998).

3.4 Laboratory analyses

The laboratory analyses consisted of a set of tests for the chemical characterisation of grass and tree leaves, mulch residues, litter and soil. Samples of rooting systems were analysed for their total dry matter. All the material was collected, dried and analysed according to the corresponding sampling schedule. More detail is given in Materials and Methods, Chemical quality of biomass section (4.2.2), Root biomass (5.2.1.1), Analysis of chemical factors affecting decomposition rate (6.2.1.2), Soil organic matter mineralisation rate (6.2.2) and Soil chemical characterisation (6.2.3).

Table 3.3 Types of samples collected from the silvopastoral experiment in Valle Nacional and from the root longevity experiment and analyses carried out in the Soil laboratory and Biochemistry laboratory.

Samples	**Analyses**
Grass leaves	Crude Protein Neutral Detergent Fibre Acid Detergent Fibre
Tree leaves	Crude Protein Neutral Detergent Fibre Acid Detergent Fibre Polyphenolics Lignin Ashes
Mulch decomposition samples	Total nitrogen Neutral Detergent Fibre Acid Detergent Fibre Polyphenolics Lignin Ashes
Grass + Tree Litter	Composition (grass, tree)
Grass + Tree Root samples (from the field)	Ash free biomass
Grass roots (from the growth room)	Ash free biomass
Soil samples	Organic Matter Total Nitrogen Nitrates Nitrogen mineralisation rate

3.5 Growth room experiment (Root longevity)

This experiment consisted on the determination of root longevity of *Brachiaria decumbens* as affected by the level of nitrogen fertilisation and depth in the soil. PVC duct pots 100cm deep, 10 cm diameter were filled with a mixture of 50% vermiculite – 50% perlite and sown with five seeds of *Brachiaria decumbens* grass and kept in a glass house until the plants were mature. The plants were fed with a liquid feed (treatments of 50, 150 and 250 kg N and 100 and 180 kg P and K ha^{-1} yr^{-1} respectively with full micro-nutrients). The pots had 5 cm windows cut out along one side of the tubes in order to allow root observation. The windows were covered with a rubber belt around the tube. The growth room was set up at 23ºC and 70% relative humidity. Maximum irradiance did not match the level under clear sky in the tropics. The experiment started as soon as the plants had reached full development (about 2 months after sowing). Data collection consisted of high resolution (S-VHS) video-recording of roots using a macro lens in a high resolution cam-corder (Panasonic

AG455 MB). The recording started on 26 November 1998, just before the first cutting of the grass, and then weekly for ten weeks. On every recording occasion, the roots were sketched on an acetate sheet from the video screen, noting the date (in a weekly basis) of appearance and disappearance of every root. The same acetate sheet was used for all the recordings in the same window. Details on the analysis of images and on the statistical analysis of results are presented in section 5.2.2.1.

3.6 Simulation Modelling

I developed a model for the introduction and management of a tree population in tropical pastures called The Silvopastoral Model. The model consists of five sub-models that represent the relevant processes for the simulation of the cycles of carbon and nitrogen in a tree-grass inter-cropping system and the interactions concerning light and nitrogen competition and transfers between them, namely: Grass, Tree, Animal, Mulch and litter and Soil. Grass, Animal and Soil are components taken from an existing model for nitrogen cycling in grasslands, the Hurley pasture model, (Johnson and Thornley, 1985; Thornley and Verberne, 1989). The tree component is based on a model for growth and partitioning of carbon and nitrogen in forest, the Edinburgh forest model (Thornley, 1991). The Silvopastoral model calculates the flows and pools of carbon and nitrogen on a $1m^2$ area.

The Silvopastoral model was developed and runs on ModelMaker 3.0.3 (Cherwell Scientific Publishing Limited, 1997, Oxford, UK, Walker and Crout, 1997). Description of the sub-models and the procedures to link the two models, as well as the adaptation of the original components in order to simulate the silvopastoral system are contained in Chapter 7 in this document.

4. Grass and Mulch Production and Composition in a Silvopastoral System

4.1 Introduction

4.1.1 Mulch production in tree-grass inter-croping

In the more extensive grazing areas of Australia, southern Africa and South America, tree legumes are increasingly being planted in association with improved grasses to increase carrying capacity and productivity of grazing cattle. In addition to shelter for animals and pasture, trees can provide considerable amounts of biomass for fodder or mulch. Muschler *et al*. (1993) obtained 1.0 Mg DM ha^{-1} of *Gliricidia sepium* leaves in six months re-growth in a dystric Fluvisol in Costa Rica (1600 trees ha^{-1}). Ezenwa *et al*. (1995) obtained 9.3 Mg DM ha^{-1} of forage in 180 days from a *G. sepium* – *Leucaena leucocephala* mixture (2857 trees ha^{-1}) in a *Panicum maximum* sward on an Alfisol in Nigeria. *G. sepium* (4760 trees ha^{-1}) associated with *Paspalum notatum* and *Digitaria decumbens* (C_4 pasture grasses) produced 10.5 Mg DM ha^{-1} of leafy dry matter in 120 days on an Ultisol in Guadeloupe (Nygren and Cruz, 1998). *G. sepium* in monocrop (5000 trees ha^{-1}), also on an Alfisol in Nigeria, produced 10.9 Mg DM ha^{-1} in 180 days (Sanginga *et al*., 1994). *L. leucocephala* growing in a granite-derived sandy soil in Zimbabwe on a contour bund system produced 4.3, 3.3 and 1.8 Mg leaf DM ha^{-1} (for Cunningham, Hawaii and Peru cultivars respectively) with 37000 trees ha^{-1} in 120 days (Nyathi *et al*., 1995).

In Central Queensland, over 20,000 ha have been sown to *L. leucocephala* in the past 15 years. *L. leucocephala* is sown in wide spaced rows 4-10 m apart and an improved grass such as Panic (*P. maximum* var. trichoglume), Rhodes (*Chloris gayana*), Buffel (*Cenchrus ciliaris*) or Signal (*Brachiaria decumbens*) sown between the *L. leucocephala* rows. Live weight gains of up to 1.0 kg $head^{-1}$ d^{-1} at stocking rate of up to 3-4 $heads^{-1}$ ha^{-1} can be achieved. A record live weight gain of 1,442 kg ha^{-1} for cattle grazing an irrigated *L. leucocephala*/pangola grass mixture was achieved in North Western Australia (Jones, 1994). MacDicken (1981) found that the *L. leucocephala* fallow period was less than half the length of the traditional bush fallow with no apparent decline in soil fertility and soil organic matter accumulation. Alongside *G. sepium* or alone, *L. leucocephala* is the more common species in alley cropping in the humid tropics because of its quick re-sprouting after pruning and its role in recycling nutrients to benefit the associated crop (Huxley, 1999). Its rapidly decomposing prunings would provide, however, little soil protection. Van der

Meersch *et al*. (1993) found that materials richer in nitrogen such as *L. leucocephala* (3.7% nitrogen content, half life 27 days) decomposed faster than poorer such as *Senna siammea* (1.8% N; half life 75 days). These authors obtained as much as 307 kg N ha^{-1} yr^{-1} from mulch of *L. leucocephala* on average of three years in Ibadan, Nigeria, but because release was faster than crop (maize) uptake, only 13% of the N released was taken up by the crop, 7% by weeds and 3% more by soil microbial biomass. N released at the end of the season accounted for 90% of total N applied as mulch. The poorer material (*S. siammea*) was found to slightly improve the percentage of plant N uptake, albeit less total N entered the crop, and to remarkably improve mulch contribution to soil microbial biomass. Both *L. leucocephala* and *S. siammea* mulch resulted in improved maize yields compared with the continuos mono-cropping system. Soil organic matter and tree roots are likely to be major sinks of the released N of leguminous tree prunings in alley cropping systems (Mulongoy and Van der Meersch, 1988).

These reports give insights on the high potential of some leguminous trees as a source of green manure since the biomass production is combined with high nutrients content. On the other hand, great variability can be observed on mulch yield and pasture productivity, which highlights the importance of choosing the adequate species for each particular inter-cropping system and for the soil and climate of a given region.

4.1.2 Effect of shade on grass production

Brachiaria decumbens uses the PEP-CK (phosphoenolpyruvate carboxykinase) type of C_4 photosynthetic pathway (Gutiérrez *et al*., 1976; Oliveira *et al*., 1973), producing a non-asymptotic light response curve. That means the continuous increment of net photosynthesis (μmol m^{-2} ground) in response to increments in photon irradiance. In general, tropical grasses reduce their root to shoot ratio and dark respiration rate in low light conditions (Wong *et al*., 1985). Stür and Shelton (1991) consider that *Brachiaria decumbens* maintains high dry matter as long as light was more than 70% of the light in the open, and yet this species ranked tenth among 46 accessions of tropical grasses grown at only 20% light (Stür, 1991). These results are in agreement with the findings of Smith and Whiteman (1983) and Chen and Bong (1983) that *B. decumbens* withstands the average level of shade under adult

plantations (50 to 75% light) and yet persists in densely shaded environments (less than 25% light). *B. decumbens* cv. Basilisk (66.7 kg DM ha^{-1} d^{-1}) performed the best among 21 *Brachiaria* accessions growing under coconut when shade and dry season were not restrictive (Sulawesi, Indonesia; Kaligis and Sumolang, 1991), yet its performance in high shade (42%) long dry season (7 months) was still average (33.0 kg DM ha^{-1} d^{-1}; Bali, Indonesia; Rika *et al*., 1991) among the other accessions. Shelton and co-workers (1987) and Wong (1991) classified *B. decumbens* as intermediate among various *Brachiaria* cultivars with respect to their tolerance to shade. Yields of *B. decumbens* cv. Basilisk growing under shadecloth (50% light transmission), were only 61% of that in full sun, although the total nitrogen content of the grass increased twofold and the amount retained in the animal increased fivefold. Concurrently the fibrous component of the grass (acid detergent fibre) was significantly lower and its retention was higher in the shaded treatment (Norton, *et al*., 1991). This is in agreement with the findings of Ludlow (1978) that shaded plants allocate a larger proportion of their dry weight increments to leaf blades. The ratio of the quantum fluxes in the 660 nm band of PAR and the 730 nm of near infrared has been suggested to determine such a shift in resource allocation; near infrared radiation penetrates the upper-storey canopy better than PAR (Ludlow, 1978). Even so, this is insufficient to counteract the decrease in net assimilation rate. However, increments in yield during the later harvests under shade suggested an interaction with soil in which, after the initial available nitrogen is depleted, the plant gained access to the N released by the augmented soil organic nitrogen mineralisation in the shaded plots (Wilson, *et al*., 1990; Norton, *et al*., 1991). Complementarily, enhanced water use efficiency has been demonstrated to occur under shaded conditions, this reducing the evaporative demand, thus improving net photosynthesis and reducing the periods of water deficit (Wilson and Ludlow, 1991). Cruz (1997) found that the mineral nutrition of shaded pastures was improved when compared with full sun, particularly under limiting water and mineral conditions. The nutritional quality of the forage was also increased under shade.

Tree density has direct implications on the effect of the tree stand on the sward, Eastham and Rose (1990) found clear evidence of the deleterious effect of high tree density on grass root depth in a *Eucalyptus* - *Setaria* inter-crop. Moreover, these

authors determined lower tree root to shoot ratio at higher tree densities, this shift in resource allocation affecting the harvest index of the tree plantation. Higher tree population densities reduce the fractional area of non-shaded grass of an area of pasture and clearly that part of the sward at short distance from a tree will experience more shade than that far from the nearest tree.

In order to characterise the silvopastoral system in terms of its productivity and how this is affected by the presence of trees (Objective 1, Chapter 1), two specific objectives were proposed:

1) To determine the production and quality of tree leaves for green manure (mulch) in inter-cropping.

2) To determine the production and quality of grass forage as a function of the associated tree species and the distance from trees.

4.2 Methods

This part of the work consists of three sections, biomass production, leaf area index and chemical quality, leaf area index being an indirect indicator of biomass production, but also an input for the analysis of light competition between the two strata in the inter-crop. Each section contains two pieces of information, grass and mulch, thus each section contributes to the accomplishment of the two proposed objectives.

4.2.1 Biomass production

Brachiaria decumbens

Grass forage biomass was estimated by harvesting samples of 50 cm x 50 cm quadrats. Samples were composed of five quadrats in each sub-plot (*near*, *mid* and *far*) for plots 2, 3, 6, 8, 10, 11 and 12. Sampling was repeated eight times during the experimental period, three of them at the end of three re-growth periods and five more at intermediate points in order to capture the rate of re-growth. In most cases each quadrat in a sample was weighed separately and then pooled for sub-sampling (approximately 100g) for dry matter; when help was scarce the five quadrats were, exceptionally, pooled before weighing. Dry matter samples were dried during at least three days in an *ad hoc* chamber with incandescent bulbs and ventilation. This

treatment brought the plant samples to 92% +/- 2 dry matter on average. Fresh and dry weights were measured with 0.1g accuracy.

I used two types of equations in the analysis of grass growth. Exponential regression was used as a first approach in grouping treatments by yield, avoiding late samples as they would not obey exponential growth rate. Secondly, sigmoidal regression was used to fit grass growth curves of longer span and for comparison with the control.

In order to make possible the comparison of treatments, yields were equalised at 45 days and the equation fitted to each treatment for June-July and August-September growing periods (Eq. 4.1). Fitting regression equations for the first sampling period (April) and the control plot was not possible due to an inadequate number of intermediate measurements. Predicted yield figures were tested for differences with two-way analysis of variance considering main plot and distance from the nearest tree. ANOVA was carried out both for wet season and the rest of the periods together using the data Analysis tool in Excel for Windows.

$$\textit{Forage biomass}\ (\text{Mg DM ha}^{-1}) = a * b^{t} \qquad (4.1)$$

Even though individual results from treatments could not generate growth curves themselves, they can be used to fit an equation of grass growth for general purposes. Results from different plots and periods were pooled together into high, medium and low yield according to the LSD test for multiple comparisons. The pooled datasets were used to fit sigmoidal regression equations (equation 4.2) using SigmaPlot 4.0 (SPSS Inc., 1997). Our discussion is based on this set of sigmoidal equations. A comparison table based on the sigmoidal fits was used to evaluate the inter-crops against the control.

$$\textit{Forage biomass}\ (\text{Mg DM ha}^{-1}) = \alpha/(1+ e^{-((t-to)/\beta)}) \qquad (4.2)$$

The data presented comprise four re-growth periods. The first was during the dry season (Feb-Apr 1997), the second was during the dry season and early in the rainy season (Apr-Jul 1997), the third was in the rainy season (Jul-Aug 1997) and the last corresponded to the late rainy season (Jan-Feb 1998). Due to the drought caused by El Niño, the last period was rather dry. These four periods are referred to as Dry season 97, Spring, Wet season and Dry season 98. When possible, the data of Dry

season 98 were pooled with the Spring data since the precipitation of both periods was similar. Some periods are not represented in all the treatments.

Trees

All trees were wholly lopped in June 1997 in order to give comparable re-growth periods to all treatments, the pruning consisting of lopping the stem at 1.8 m when first bifurcation was higher than that point. Alternatively, lopping each branch at the base when the tree branched between 1.5 and 1.8m. Any tree whose first bifurcation was under 1.5m was lopped between 1.5 and 1.8m. Although there was no control of the previous development of the canopy, leaf and woody biomass from this pruning was measured for further use. Two subsequent prunings were carried out on all treatments. Very young branches were not cut. The prunings were then separated into leaves + green twigs and wood immediately before weighing. The prunings of the whole plot were then pooled and five 100 g sub-samples of each fraction were used for determining dry matter content. No sub-plots were considered for the evaluation of tree biomass since any effect of the grass on the trees was assumed to be the same all along the plot and no inter-specific effects were considered. Dry matter sub-samples were treated as described for *B. decumbens*.

Allometric assessment of mulch production: Basal diameters (10 cm from base) of stems and branches (three centimetres from the insertion point) were measured prior to lopping in order to work out the cross sectional area. Branches were assumed to be elliptical and so the major and minor axes were measured. Weight of woody prunings, green twigs and leaves for every branch was recorded. Samples of every component and for every tree species were evaluated for dry matter content. Correlation analyses were performed to evaluate predictive functions for total biomass or green twigs + leaves against stem and/or branch biomass. It was intended to parameterise a prediction equation of (leafy and woody) harvestable biomass that can be used for non-destructive assessments in the future.

A calliper of 0.1mm precision was used. Linear regression equations were fitted for stem base cross sectional area (mm^2) to leaf or woody biomass (g DM) and branch cross sectional area to leaf or woody biomass supported by the branch (Eq. 4.3).

$$\textit{Tree prunings biomass}\ (\text{gr DM tree}^{-1}) = a + b\text{CSA} \qquad (4.3)$$

Where:

CSA is the cross sectional area at the branch (or stem) base.

Plate 4.1. Measuring stem base diameter in *Gliricidia sepium*.

4.2.2 Leaf area index

Brachiaria decumbens

Green leaf area was calculated using width (cm), length (cm) and green fraction (%) of each individual leaf in the tiller (Hoad *et al*., 1995). Width (*w*), length (*l*) and green portion (*f*) of each individual leaf were measured in samples of 3 to 7 tillers per quadrat (50 cm x 50 cm). Total number of tillers per quadrat was also determined. One to four quadrats were randomly allocated per sub-plot (distance) and per plot (treatment of species x tree density) for each sampling period in plots 2, 3, 6, 8, 10, 11 and 12. Green leaf area index (*L*) was calculated by adding up the individual green areas of each leaf in the tiller and averaging for all the measured tillers. The average green area per tiller was then multiplied by the total number of tillers in the sample (*P*) of n quadrats and then divided by the ground area sampled (Eq. 4.4).

$$L = P\frac{\sum wlf}{2500n} \tag{4.4}$$

Where:

n is the number of quadrats used in each sampling, and,

2500 is the area of one quadrat in square centimetres.

Gliricidia sepium

Leaf area index (LAI) in *Gliricidia sepium* was measured in two ways, destructive and non-destructive, this involving hemispherical photography. Destructive LAI was derived from the specific leaf area and the total leaf biomass at the time of pruning, after a six months re-growth period between June and November 1997. The specific leaf area was determined by measuring the area of 100.0 g fresh weight of leaves with an automatic planimeter (AMS, Delta-T Devices, Cambridge, CB5 0EJ, UK). Specific leaf area was calculated as the ratio of leaf area (m^2) per unit of mass (kg DM).

The prunings of every single tree in the two plots studied were weighed and separated into two fractions: woody branches and leaves and edible twigs (*G. sepium* prunings are normally used to feed cattle). The two fractions were weighed again separately. The fraction of leaves and twigs is the one utilised for this study. For the determination of the dry matter, three 100g replicates of leaves plus green twigs were sampled, which were weighed before and after drying to constant weight (65°C 48 hr). The fraction of petioles was subtracted from the bulk leaf biomass prior to the calculation of LAI. The specific leaf area, as well as the petiole fraction of the cover area was taken from the literature (Budelman, 1988; Muschler *et al*., 1993 and Muschler personal communication).

Use of hemispherical photography to estimate tree leaf area index of a sparse canopy: Hemispherical photography was used to investigate the tree leaf area index of *Gliricidia sepium* by the segmented method of the gap fraction analysis (van Gardingen, *et al*. 1999). Hemispherical photographs were recorded in ISO-100 and ISO-400 monochrome T-grain film to account for the different light conditions of the two days (T-Max 100, Kodak TMY 5053 and T-Max 400, Kodak TMX 5052, Kodak Ltd, Hemel Hempstead, Herts, HP1 1J, UK). An 8mm "fisheye" lens (Nikkor, 8mm, f/2.8, Nikon Corporation, Tokio 100, Japan) attached to a mechanical camera was used. The camera with the lens was mounted on a sturdy tripod and levelled and

orientated to North before use. Images were taken before and after pruning in order to calculate the difference of the gap fraction due to the leafy canopy.

Three random transects parallel to the long side of the plots were used, from which the first row of each side was discarded to prevent border effect. Four images were recorded on each transect by essentially random allocation of the camera. The first column of trees on each side was discarded to avoid border effect; the allocation of sampling points closer than 50cm was also avoided.

Images were analysed at a range of zenith angles with a commercial analysis package (Optimas 5.2, Optimas Co., Washington 98011, USA). The concentric annuli derived form the selected angles were segmented in order to determine the gap fraction of each segment. Individual gap fractions are log-averaged for each annulus (Eq. 4.5) and used to derive the log-average estimate of leaf area index (Eq. 4.6 and 4.7).

$$\overline{\ln P_i} = [-\Sigma \ln P_{in}]/s_i \tag{4.5}$$

Where:

$\ln P_i$ is the log-averaged gap fraction for annulus i,

P_{in} is the measured gap fraction for each segment and

s_i is the number of segments in annulus i.

$$-\ln P_i = \Sigma f_j k_{ij} \tag{4.6}$$

Where:

f_j is the leaf area index for each simulated angle class j and

k_{ij} is the extinction coefficient for a given azimuth angle i and a leaf angle class j

$$L=\Sigma f_j \tag{4.7}$$

Where:

L is the leaf area index of the plot.

The theory underlying the relationship between gap fraction and leaf area index uses an interpretation of the Beer's law (Eq. 4.8) described by Monsi and Saeki (1953): the fraction of solar radiation that is intercepted by a plant canopy is a function of the leaf area per ground area ratio. This is in turn, at the nether part of the canopy, inversely proportional to the gap fraction.

$$I/I_o = e^{-kL} \quad (4.8)$$

I is the radiative flux at the bottom of the canopy and I_o is the radiative flux on the top of the canopy. This approach can be used in subsequent studies as a means of estimating leaf biomass of scattered trees by a non destructive method.

4.2.3 Chemical quality of biomass

Brachiaria decumbens

Destructive method: Grass forage was analysed for its nutritional quality; sampling was performed in parallel with with biomass determination thus embracing the gradient of distances from the nearest tree. Different ages of the forage during the re-growth process as well as the different associations with nitrogen fixing trees and a control without trees were considered. Samples from the same treatment were pooled and mixed thoroughly and sub-samples of 20 g were dried in the chamber with incandescent bulbs. Samples were ground to pass 1.0mm mesh and a sub-sample was dehydrated in the oven at 65ºC for 72 hr for determining dry matter. Samples were analysed for total nitrogen (micro-kjeldahl), neutral detergent fibre (Van Soest, 1963a) and acid detergent fibre (Van Soest, 1963a, b) at the University of Chapingo, Mexico. Due to the different times of harvest between seasons, no statistical comparison between seasons was possible. However, plotting the results together gave insights on the tendency of the three attributes measured (crude protein, NDF and ADF); which resulted in considering the accompanying species and days after cutting as the more important sources of variation for samples from tree-grass mixtures. Analysis of results was performed through the Two-factor ANOVA in Excel97 for Windows and significant differences evaluated with Least Significant Difference test (Montgomery, 1991).

Leaf chlorophyll-meter readings: Chlorophyll meter (Minolta SPAD-502, Minolta Co., Osaka 541, Japan) readings in lamina were used to predict harvestable nitrogen. Chlorophyll concentration has been linked to specific leaf nitrogen (Chapman and Barreto, 1997). These authors found a relation specific leaf nitrogen (SLN) to SPAD readings of SLN = 0.039 SPAD - 0.47, for tropical maize in Mexico. Comparable relations have been proposed elsewhere (corn, Schepers, *et al*., 1992; rice, Peng *et al*., 1993; early dent stage of corn, Piekielek *et al*., 1995) showing that readings

depend on leaf thickness, species, sampling size and vegetative development of the crop.

In a preliminary survey, the effect of the position of the leaf in the stem (first, second and third fully expanded leaves), the inclination angle (flat, upright and intermediate) and the width of the leaf (wide or thin) on the chlorophyll content was determined. Analysis of variance in Minitab12 (Minitab Inc.) was used to determine significant differences considering the three sources of variation separately according to the model:

$$y_{ijkl} = \mu + position_i + inclination_j + width_k + e_{ijkl} \quad (4.9)$$

Based on the results of that study, chlorophyll measurements of the top fully expanded leaf were recorded. An array of 0.0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0 and 3.5 m from the nearest tree was surveyed, with 20 replications per distance and five replications per plot (associated tree species) for plots 2, 7, 9, 11 and 12. Each measurement consisted on the reading of transmittance of the leaf in two wavelengths simultaneously at the middle region of the leaf, avoiding the central nerve. The meter memorises 20 consecutive readings, thus allowing for the quick survey of each sample (20 readings). In order to ensure that the same distance was used for the whole set of readings, a cord was tied around the tree in order to take the readings in a circle, progressing through the different distances inwards to prevent damage to the grass to be sampled. General Linear Models procedure (SAS Institute, 1990) was used for the analysis of variance.

Trees

Destructive method: Prunings (tree leaves and branches) were collected for chemical analysis in order to evaluate its potential as green manure. The quality of tree leaves was considered not affected by any experimental factor other than species and leaf age. Thus, samples were collected once and results assumed valid for the whole study. Only full grown leaflets were pooled before sampling since the higher nitrogen concentration in young leaflets could affect the results of the chemical analysis even though the fraction of young leaflets in a developed canopy was no higher than 10%. Samples were weighed with 0.1 g precision before and after being dried in the chamber with incandescent bulbs and subsequently milled to pass a 1.0

mm sieve; finally a sub-sample was freeze dried for the correct assessment of dry matter content. In addition to nitrogen content, some limiting factors for decomposition of the cell wall were determined in the laboratory, namely hemicellulose, cellulose, lignin (Van Soest, 1963b) and total polyphenolics (Waterman and Mole, 1994). Samples for cell wall analysis were sealed into F57 filter bags (Ankom Technology, USA) to allow for the analysis of large amounts of samples simultaneously. Total phenolics were determined colourimetrically in 80% ethanol extracts by the Folin-Ciocalteu method and the absorbance determined in a Beckman DU-65 spectrophotometer at 760nm wavelength. Results are referred to as gallic acid equivalents. Residues of ignition (total ashes) were determined to the sealed sample residues after the lignin analysis. Carbon to nitrogen ratio was calculated assuming a 0.58 fraction of organic carbon (Tinsley, 1950) in plant material. Protocols of analysis are in the Appendix.

Leaf chlorophyll-meter readings: Chlorophyll readings were performed on new and fully grown leaflets of a tree, one sample integrated by 20 readings, with a Minolta chlorophyll meter (same as above). Five replications per plot (treatment: species x tree density) were practised in plots 3, 7, 9 and 12. Data were analysed for differences between and within species as well as for the stage of development (young vs. full-grown) of the leaflets. Statistical analysis was carried out with the general linear models procedure (GLM, SAS Institute., 1990).

4.3 Results

4.3.1 Biomass production

Brachiaria decumbens

Monocrop: The grass growth in the 43 days dry season period in the control plot was 1.81 Mg ha^{-1}, which was intermediate between that of the wet season period (2.24 Mg ha^{-1}, 39 days) and spring (1.34 Mg ha^{-1}, 55 days). The slower growth rate of spring followed an unusual prolongation of the dry season.

Silvopasture: Pasture productivity in the silvopastoral system was high and significantly different between plots, both in the June-July ($P=0.012$) and August-September ($P<0.001$) growing periods. No statistical differences were found between distances from the nearest tree. Interpolated figures of forage yield at 45 days

indicate that grass growing under *L. leucocephala* and *L. auritum* (300 and 650 trees ha^{-1} respectively) yielded significantly more forage during the dry season than other mixtures.

Table 4.1 Forage grass production (Mg ha^{-1}). Average of the three distances from the nearest tree, and interpolated to day 45 using exponential regression (Eq. 4.1).

Accompanying Species (plot)	Observed production (σ)	Re-growth (days)	Estimated yield (day 45)	
June-July (P=0.012)				
L. leucocephala (12)	5.53 (0.44)	70		
L. leucocephala (6)	2.87 (0.33)	55	1.49	a
L. auritum (2)	2.96 (1.34)	60	1.24	a
D. regia (10)	3.18 (1.12)	76	1.14	ab
G. sepium (3)	1.00 (0.16)	60	0.68	bc
G. sepium (8)	0.84 (0.16)	50	0.60	c
LSD $t_{(0.025)}$			0.47	
August-Sept (P<0.001)				
L. leucocephala (12)	2.01 (0.26)	39	3.45	a
L. auritum (2)	4.44 (1.10)	59	2.89	ab
G. sepium (3)	4.91 (1.93)	59	2.36	b
D. regia (10)	3.47 (0.44)	61	1.99	bc
L. leucocephala (6)	2.53 (0.23)	63	1.24	cd
G. sepium (8)	4.38 (0.08)	63	0.54	d
LSD $t_{(0.025)}$			0.99	

Grass under *G. sepium* (216 and 817 trees ha^{-1}) produced less forage during the dry season (Tables 4.1 and 4.2). Although exponential regression could not be fit for plot 12 (*L. leucocephala*) in the dry season because only final yield was recorded (5.5 Mg ha^{-1} in 70 days in average of distances), it can be classified high. Similarly, this treatment yielded the highest in the August-September period, along with the *L. auritum* association, (3.45 and 2.89 Mg DM ha^{-1} respectively). Most treatments increased yield from the June-July to August-September periods except for plot 6 (*L. leucocephala* 300 trees ha^{-1}), which showed a slight reduction.

Table 4.2. Forage grass production in nitrogen fixing trees-*Brachiaria decumbens* inter-crop and forage yield interpolations to the days of re-growth of the Control (Mg DM $ha^{-1} = \alpha/(1+ e^{-((t-to)/\beta)})$.

	Sigmoidal Regression Parameters			April	Jun-Jul	Aug-Sep
				Days after Cut		
Group	α	β	t_0	43	55	39
High yield	5.8	9.4	43.3	2.86	4.51	2.24
Mid yield	3.7	8.7	47.2	1.42	2.65	1.04
Low yield	32.1	19.6	122.9	0.53	0.97	
Control				1.81	1.34	2.24

Trees

G. sepium produced the highest among the three species evaluated in the wet season. Plots 4 and 7 (stakes) yielded 268 and 193 kg leaf + twigs DM ha^{-1}. Plot 3 (seedlings) yielded less biomass (160 kg DM ha^{-1}) even so the tree density was similar to plot 4, but only 40% of the trees were large enough to be lopped. *L. leucocephala* and *L. auritum* (91 and 46 kg DM ha^{-1}) presented very low biomass production (Table 4.3). Pruning biomass could not be statistically compared because of the different tree density and periods of re-growth.

Table 4.3. Mulch production in one re-growth period during the wet season. Yields per tree are interpolations assuming linear growth rates.

Species (plot)	trees ha^{-1}	Re-growth period (days)	Yield (Mg DM ha^{-1}) Leaves + Twigs	Wood	Yield per tree (g DM $100d^{-1}$)
G. sepium (4)	891	103	0.268	0.331	292
G. sepium (7)	663	100	0.193	0.184	292
G. sepium (3)	816	155	0.160	0.297*	317
L. auritum (2)	650	158	0.091	0.150	89
L. leucocephala (12)	616	131	0.046	0.096	56

*) Because of poor re-growth in this plot, only 19 out of 49 trees were lopped.

However, subjective comparison of treatments assuming linear growth rate between 100 and 158 days after pruning suggested *G. sepium* to have the highest productivity per tree (300 g leaf + twigs DM on average of 100 days) whereas *L. leucocephala* and *L. auritum* presented very low production per tree (Table 4.3).

Allometric estimation of mulch production: Primary branch cross sectional area presented good linear relation to mulch fresh weight (g $branch^{-1}$), especially in the second pruning period (November 1997), with determination coefficients of linear regression between 0.73 to 0.97.

Table 4.4. Regression equations of the fresh weight of total prunings (M_{Tot}), leaves and twigs (M_l) and woody branches (M_w) in grams per (primary) branch and per tree as a function of the primary branch cross sectional area and basal cross sectional area respectively (CSA) in cm^2, for the first and second pruning in the Silvopastoral experiment.

FIRST PRUNING Part	Equation	r^2
Primary Branch Cross Sectional Area		
Delonix regia		
Total biomass	M_{Tot}= 61.8 + 70.2 CSA	0.83 **
Leaves and twigs	M_l= 73.6 + 25.4 CSA	0.62 **
Woody branches	M_w= 44.2 CSA	0.86 **
Gliricidia sepium		
Total biomass	M_{Tot} = 319.8 CSA	0.84 **
Leaves and twigs	M_l = 162.3 CSA	0.74 **
Woody branches	M_w = 154.7 CSA	0.67 **
Lysiloma auritum		
Total biomass	M_{Tot} = 240.9 CSA	0.83 **
Leaves and twigs	M_l = 3.4 + 74.3 CSA	0.85 **
Woody branches	M_w = 154.2 CSA	0.79 **
Leucaena leucocephala		
Total biomass	M_{Tot} = 237.8 CSA	0.87 **
Leaves and twigs	M_l = 1.1 + 68.1 CSA	0.78 **
Woody branches	M_w = 157.0 CSA	0.86 **
Basal Cross Sectional Area		
Gliricidia sepium		
Total biomass	M_{Tot} = 2722.5 + 149.0 CSA	0.53
Leaves and twigs	M_l = 1561.0 + 63.6 CSA	0.83
Lysiloma auritum		
Total biomass	M_{Tot} = 194.7 CSA	0.73 *
Leaves and twigs	M_l= 58.3 CSA	0.78 **
Leucaena leucocephala		
Total biomass	M_{Tot} = 89.4 + 217.2 CSA	0.72 **
Leaves and twigs	M_l = 72.1 CSA	0.67 *
SECOND PRUNING		
Primary Branch Cross Sectional Area		
Gliricidia sepium		
Total biomass	M_{Tot} = 159.5 + 67.0 CSA	0.90 **
Leaves and twigs	M_l = 73.1 + 41.6 CSA	0.90 **
Woody branches	M_w = 87.6 + 25.3 CSA	0.83 **
Leucaena leucocephala		
Total biomass	M_{Tot} = 114.2 CSA	0.97 **
Leaves and twigs	M_l = 99.2 + 26.2 CSA	0.73 *
Woody branches	M_w = 99.2 + 21.5 CSA	0.89 **
Basal Cross Sectional Area		
Gliricidia sepium		
Total biomass	M_{Tot} = 89.4 + 217.2 CSA	0.72 **
Leaves and twigs	M_l = 270.4 + 30.0 CSA	0.61 **
Woody branches	M_w= 103.7 + 22.6 CSA	0.64 **

Note: One or two asterisks denote 95% or 99% of significance of the equation respectively.

In the first pruning the determination coefficients were slightly lower (0.62 to 0.87).

Gliricidia sepium regression equations fit better in the case of total mulch or leaf and

twig fresh weight than in the case of woody branches, whereas in *Leucaena leucocephala* the equations of total mulch and woody branches fresh weight presented better determination coefficient than the leaves and twigs equation. (Table 4.4). Basal cross sectional area did not correlate satisfactorily with mulch biomass.

4.3.2 Leaf area index and light interception in the tree canopy

Brachiaria decumbens

In June (Spring), *L. leucocephala* (plot 12) presented the highest green leaf area index (LAI); the control, along with plots 2, 6, 8 and 10 gave intermediate results. *G. sepium* in plot 3 was significantly lower than the rest of the treatments with other species ($\alpha = 0.05$). No statistical differences were found between treatments in the wet season. LAI in treed treatments was 1.9 for Spring whereas in August (wet season) it was 2.25, but no statistical differences were found between seasons (Table 4.5). This absence of difference was due to masking cross effects of treatments ($P<0.01$): t-tests for individual plots between seasons revealed that monocrop and pastures associated to *L. auritum*, *D. regia* and *G. sepium* increased in LAI, whereas grass under *L. leucocephala* diminished. However, only *L. leucocephala* and *G. sepium* varied significantly between seasons ($\alpha = 0.01$).

Table 4.5. Green leaf area index of *Brachiaria decumbens* under different nitrogen fixing tree-species and during the dry or wet seasons.

Accompanying species (plot)	June		August	
Leucaena leucocephala (12)	3.3	(0.37)	1.8	(0.35)
Lysiloma auritum (2)	2.4	(0.98)	2.8	(1.00)
Leucaena leucocephala (6)	2.2	(0.42)	1.8	(1.37)
Delonix regia (10)	1.7	(0.76)	2.1	(0.33)
Gliricidia sepium (8)	1.2	(0.06)	1.7	(0.56)
Gliricidia sepium (3)	0.6	(0.05)	3.3	(1.45)
Control (11)	2.0	(0.46)	2.2	(0.60)
LSD Columns $_{(0.025)}$	0.5		n.s.	
LSD Rows $_{(0.005)}$	1.2			

Note: LSD test for columns applies to June since no significant differences were found in August.

Gliricidia sepium

Specific leaf area of *G. sepium* in the present work was 15.1 m^2 kg DM^{-1}. Leaf area index in *G. sepium* trees, calculated by the destructive method and assuming a specific leaf area of 20.2 m^2 kg^{-1} DM (all figures cited in the literature were above 20 m^2 kg^{-1}; see section 4.4.3) , was 0.51 and 0.30 for plots 4 and 7 respectively; whereas when calculated by the log-average of segmented annulus of hemispherical photographs it was 0.37 and 0.31 in the same order. Photosynthetic irradiance under the tree canopy, calculated by combining estimations of direct and diffuse solar radiation (Efimova, 1967; cited in Pearcy, 1989) derived from the same images, was 79 and 78% of total photosynthetic photon flux density for plots 4 and 7 before pruning, whereas it reached 94% in both plots after pruning.

4.3.3 Chemical quality of biomass

Brachiaria decumbens

Crude protein

Monocrop: Crude protein decreased more rapidly during the first seven weeks of re-growth and the total contents varied according to the availability of soil water. In dry and wet seasons it averaged 11.26% at the optimum time for utilisation. Samples from the driest time of the year (Spring) were remarkably low (8.78% crude protein at 38 days of re-growth and 5.84 at harvest time). Neutral Detergent Fibre-NDF (cell wall) was less affected by the climatic season than for the span of the re-growth period. In general, NDF was low at week four (63.8%) and steadily increased to about 80.0%. It became stable after week 7. Acid Detergent Fibre-ADF (cellulose, lignin and other recalcitrant compounds in the cell wall) was also low at week 4 (33.21%), with further increment until week 7 (Table 4.6).

Table 4.6. Nutritional quality of *Brachiaria decumbens* in monocrop in an unfertilised Calcimagnesitic Acrisol at different times of the year and days after cutting (DAC).

Season (DAC)	CP%	NDF%	ADF%
Dry season (49)	11.43	82.43	44.40
Spring (38)	8.78	77.68	40.59
Spring (57)	5.84	83.34	44.89
Wet Season (27)	11.10	63.80	33.21

Silvopasture: Grass in inter-crop showed a similar tendency to the monocrop in the steady reduction of crude protein and increment of NDF and ADF during the first seven weeks of re-growth (Fig. 4.1a). Two-way ANOVA for plots 2, 3 and 12 revealed that grass crude protein content in plot 2 (*L. auritum*) at week 4 was superior ($P<0.0005$) to that in plots 3 (*G. sepium*) and 12 (*L. leucocephala*). No differences were found between distances from the nearest tree. However, when comparing interpolations at day 38 of re-growth with the control (Table 4.7), only plot 2 resulted significantly different ($\alpha = 0.05$). Later in the re-growth period (week 7) all treatments reached a steady state at about 6% crude protein. No statistical differences were found between distances to the nearest tree in the same plot. The parameter values of predictive equations for grass in inter-crop varied between plots; in general, the nutritional quality of inter-crop grass was initially better than that in monocrop (Fig. 4.1b).

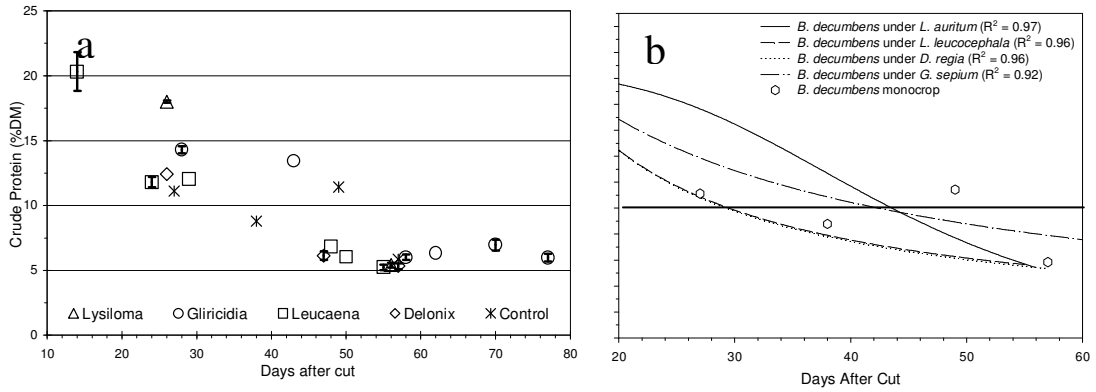


Figure 4.1. Crude Protein content of *Brachiaria decumbens* in inter-crop as affected by the length of the re-growth period. A) Averages by days after cutting and accompanying species (error bars are +/- one standard error). B) Exponential regression curves to facilitate comparison with control and evaluate the span of the optimum nutritional status (horizontal line at 10 % crude protein).

Table 4.7. Grass crude protein content at day 38 of re-growth in associations with nitrogen fixing trees.

Accompanying species	Regression Equation	Crude Protein (%Dry Matter)
Lysiloma auritum	$y=20.57/(1+(t/42.9)^{3.9})$	12.68*
Gliricidia sepium	y=1/(0.023+0.002t)	10.93
Leucaena leucocephala	y=0.6+(277.02/t)	7.90
Delonix regia	y=0.4+(280.3/t)	7.80
Control		8.78
Dunnett $_{0.05}$		2.67

The asterisk denotes significant difference with the control (Dunnett Multiple Comparison Test; Montgomery, 1991).

Chlorophyll measurement for estimation of nitrogen content in *Brachiaria decumbens*: With regard to the preliminary study on the effect of leaf position, inclination and width, the results indicate that chlorophyll level was significantly affected by leaf position and width. The youngest leaves (top position) were found more frequently to be wider than older leaves (third position). However, the two characteristics are independent (R=-0.27). Wider leaves were consistently higher in chlorophyll, regardless of the position in the tiller (P=0.002). On the other hand, first and second fully expanded leaves from the top showed no differences on chlorophyll content but the third leaf was significantly higher (P=0.004). The conclusion is that sampling wider leaves will produce higher readings regardless of the inclination angle or the position, although the third leaf will produce also higher readings than the top leaf. However, because of the possibility of a mistake in the identification of the third leaf in rapid samplings, we decided to sample always the first fully expanded leaf, provided it was subjectively wide.

Brachiaria decumbens leaves had, on average, 31.01 (σ^2=10.06) units of chlorophyll (SPAD reading). There were significant effects from some of the associated tree species and the distance from the nearest tree. Grass associated with *D. regia* and *L. leucocephala* presented the highest SPAD reading levels among the silvopastures (33.7 and 32.7 respectively); no differences were detected with the control (34.0) at any distance. In both cases the lowest reading was that at the tree base but the highest readings were between 0.5 and 1.5m from the trunk. *L. auritum* and *G. sepium* produced the lowest averages (29.8 and 28.4 respectively), with significant differences with the control (Table 4.8). Pasture associated with *L. auritum* presented

a similar trend to the previous two mixtures, with lower readings at the tree base and beyond 1.5 m, although the highest value was at the longest distance (3.5 m). Contrary to the trend of the rest of the mixtures, *G. sepium* was lower than the control at any distance, except for the tree base, where the highest value was reached.

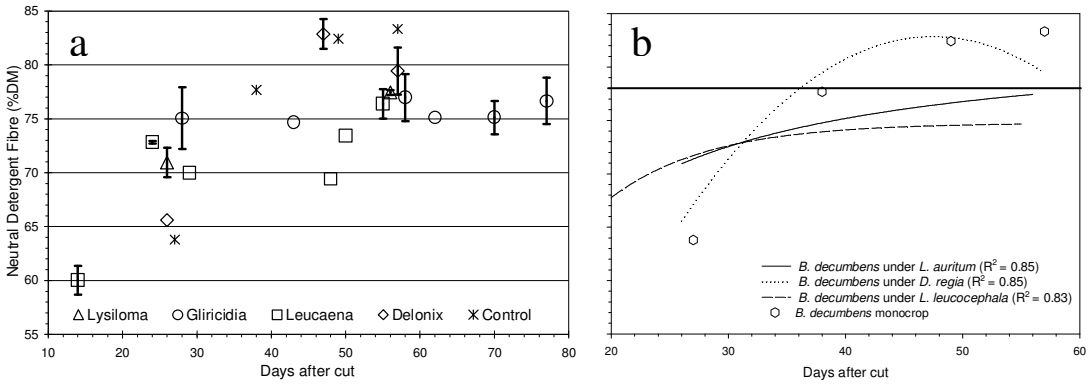
Table 4.8. Chlorophyll meter readings (SPAD units) in the top fully expanded leaf of *Brachiaria decumbens* at incrementing distances from the trunk of nitrogen fixing trees.

		Chlorophyll estimates at 0.5 m intervals							
Accompanying tree	trees ha^{-1}	0	0.5	1	1.5	2	2.5	3	3.5
Delonix regia	300	31.3	35.4	34.5	34.1	33.8	33.5	33.2	33.9
Leucaena leucocephala	616	30.3	32.8	33.4	34.0	32.4	33.2	32.5	32.7
Lysiloma auritum	650	28.3*	32.4	30.1	28.7*	29.7*	29.5*	29.9*	30.2
Gliricidia sepium	663	31.3	27.7*	27.9*	28.6*	28.1*	28.4*	27.9*	27.2*
Control	34.0								
Dunnett $_{0.05}$	4.0								

Note: asterisk denotes significant difference with the control according to Dunnett Multiple Comparison test (Montgomery, 1991).

Cell Wall

Neutral detergent fibre in the early stage of the re-growth period was higher in the silvopastures than the control, but as time passed the control reached higher levels, whereas the inter-crop plots increased, but at a lower rate (Fig 4.2). Values of 70 to 75% in DM for the 4th week increased to 75 to 80% at week seven. No statistical differences were found either between treatments (tree species and distance to the nearest tree) and with the control at day 38 (Table 4.9), probably because of the large



variability among samples of the same species.

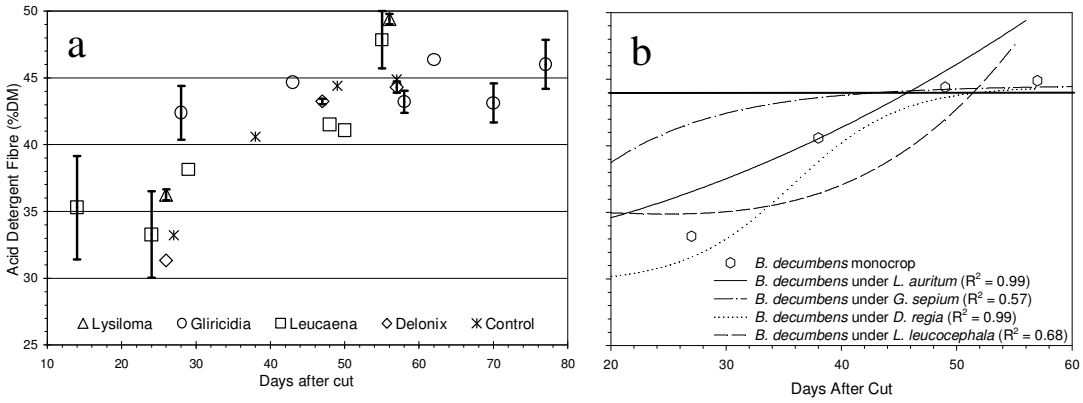
Figure 4.2. NDF content of *Brachiaria decumbens* as affected by re-growth period. a) By sampling date and accompanying species (error bars: +/- one standard error). b) Exponential regression curves for comparison with the Control (horizontal line at 68 %).

Table 4.9. Grass neutral detergent fibre content at day 38 of re-growth in associations with nitrogen fixing trees.

Accompanying species	Regression Equation	NDF (%DM)
Delonix regia	$y=-1.7+3.7t+-0.04t^2$	79.58
Lysiloma auritum	$y=83.1+(-315.6/t)$	74.77
Gliricidia sepium		74.69
Leucaena leucocephala	$y=74.8*(1-0.89^t)$	73.94
Control		77.68
Dunnett $_{0.05}$		4.82

Differences determined by Dunnett Multiple Comparison Test (Montgomery, 1991) against the control.

Acid Detergent Fibre, likewise Neutral Detergent Fibre, was higher than the control plot value at week four. The ADF of the mixtures underwent an increment of around 10% between weeks four and seven, when it reached steady state (Fig 4.3). Statistical differences were found ($p<0.05$) between plots but not between distances within the plot for treatments in plots 2, 3 and 12. Grass forage associated with *L. auritum* and *L. leucocephala* showed less ADF content (36.2 and 34.9% DM respectively) than that associated with *G. sepium* (42.37 % in DM). Interpolations at day 38 showed no



significant differences with the control (Table 4.10).

Figure 4.3. Acid Detergent Fibre content of *Brachiaria decumbens* in inter-crop as affected by the length of the re-growth period. A) Averages by sampling date and accompanying species (error bars are +/- one standard error). B) Exponential regression curves to facilitate comparison with control and evaluate the span of the optimum nutritional status (horizontal line at 44 % ADF).

Table 4.10. Grass acid detergent fibre content at day 38 of re-growth in associations with nitrogen fixing trees.

Accompanying species	Regression Equation	ADF (%DM)
Gliricidia sepium	$y=44.5*(1-e^{(-0.1t)})$	43.61
Lysiloma auritum	$y=31.4+0.07t+0.005t^2$	40.47
Delonix regia	$y=29.7+14.75/(1+e^{(-(t-35.7)/b)})$	38.83
Leucaena leucocephala	$y=33.4+0.3t-0.017t^2+0.00029t^3$	36.42
Control		40.59
Dunnett $_{0.05}$		4.48

Differences determined by Dunnett Multiple Comparison Test (Montgomery, 1991) for comparisons against the control.

Mulch Quality

Total nitrogen: *L. leucocephala* and *G. sepium* mulches contain the highest levels of nitrogen among the four species, *L. auritum* and *D. regia* the lowest (Table 4.11). Least significant difference test (LSD. Montgomery, 1991) showed significant differences ($\alpha = 0.05$) between species and sampling time between species, but not between sampling time within species.

Table 4.11. Nitrogen content (micro-kjeldahl) and estimated chlorophyll content (SPAD 502 chlorophyll meter) of young and mature leaves of nitrogen fixing trees in the Silvopastoral experiment.

Species (plot)	Total Nitrogen	SPAD reading (σ^2) New leaves	Mature leaves
June			
Leucaena leucocephala (12)	4.09a		
Gliricidia sepium (4)	3.79ab		
Lysiloma auritum (2)	2.85b		
November			
Gliricidia sepium (3)		29.5 (11.6)	25.2 (10.0)
Gliricidia sepium (7)		31.2 (1.4)	26.2
Leucaena leucocephala (12)	3.92ab	43.9 (35.4)	8.9 (0.2)
Lysiloma auritum (2)	3.11ab	25.6 (54.2)	16.8
Delonix regia (9)	1.87b	35.0 (104.3)	24.0 (62.5)
LSD ($_{0.025}$)	1.19	← 6.7	→

Note: LSD of total nitrogen comprises the two sampling times. LSD of chlorophyll estimates was calculated for the two ages and five plots together.

Chlorophyll measurement for estimation of nitrogen content in mulch: Chlorophyll estimations in new and mature leaflets of the trees were significantly different ($P<0.001$) for both leaflet age and species as well as for their interaction. *G.*

sepium mulch remained constant as the leaflets aged, whereas the rest of the species suffered significant reductions in chlorophyll (SPAD reading) with age. *L. leucocephala* presented the highest SPAD reading in young leaflets but the lowest in old ones (Table 4.11).

Cell contents: *D. regia* and *G. sepium* allocates a very high proportion of its leaf biomass to cell contents (73.1 % and 69.04 % respectively) whereas *L. leucocephala* averages 63.5 % and *L. auritum* has 60.9 %. $LSD_{0.025}$ test identified significant differences between *D. regia* and the treatments of lower cell contents (Table 4.12).

Cell wall: *L. leucocephala* mulch presents, in general, higher cell wall components contents than *D. regia*, *G. sepium* and *L. auritum* mulch being intermediate between them. The hemicellulose complex (hemicellulose, cell wall nitrogen and some tannin) is higher in *L. auritum* mulch but significant differences ($LSD_{0.025}$) were found only with the lowest result (*D. regia* and *G. sepium*). *L. leucocephala* in November was significantly higher in cellulose ($LSD_{0.025}$), than the other three species. There were no significant differences between *D. regia*, *G. sepium* and *L. auritum* mulch cellulose. Lignin in *L. leucocephala* was apparently higher than the other species, but only in November produced significant differences with the lowest value (*G. sepium*); *L. auritum* was among the lowest values of cellulose and lignin, but its levels of hemicellulose make this species the one with the highest cell wall content in mulch. *D. regia* and *L. auritum* contains significantly higher levels of total phenolics ($LSD_{0.025}$), *L. leucocephala* being intermediate and *G. sepium* at the lowest value (Table 4.12)

Table 4.12. Chemical composition (g $100g^{-1}$) of leaves of nitrogen fixing trees in the Silvopastoral experiment (Total phenolics expressed as g $100g^{-1}$ Gallic acid equivalents).

Species (Sampling time)	Cell Contents	Hemi-cellulose	Cellulose	Lignin	Total Phenolics
Delonix regia (Nov)	73.13a	8.66b	11.81ab	6.84ab	13.12
Gliricidia sepium (June)	69.04ab	11.32b	10.75b	6.19b	2.07
Leucaena leucocephala (June)	66.75ab	13.32ab	12.66ab	7.29ab	9.78
Lysiloma auritum (Nov)	60.95ab	22.10a	10.50b	6.92ab	14.07
Leucaena leucocephala (Nov)	60.32b	17.24ab	14.58a	8.03a	8.12
$LSD_{0.025}$	12.38	10.34	3.24	1.32	

4.4 Discussion

4.4.1 Grass biomass

Monocrop: Assuming 147 days of dry season and 218 days of wet season in an average year, the annual yield of the pasture can be calculated as:

1.58 Mg DM ha^{-1} x 3 periods of 49 days dry season: 4.72 Mg DM ha^{-1}

+ 2.24 Mg DM ha^{-1} x 5.6 periods of 39 days wet season: 12.52 Mg DM ha^{-1}

= 17.24 Mg DM $ha^{-1}yr^{-1}$

The figures for the dry season are the average of the April and June-July periods. These results suggest that the monocrop produced abundant forage during the experimental period if compared with *B. decumbens* results reported elsewhere. Macedo *et al*., (1993) obtained 0.93 Mg DM ha^{-1} per period during the dry season with *B. decumbens* cv. Basilisk in a fertilised Oxisol in Mato Grosso, Brazil. Carvalho (1997) reported 9.97 Mg DM $ha^{-1}yr^{-1}$ yields with *B. decumbens* in an Oxisol of low fertility in Minas Gerais, Brazil. Higher yields have also been reported: Eriksen and Whitney (1981) obtained 28 Mg DM $ha^{-1}yr^{-1}$ with optimum fertilisation; Wong *et al*. (1985) reported yields of 22 Mg DM $ha^{-1}yr^{-1}$ at six-week intervals. Most of the reported figures fluctuate between 11.4 and 13.9 t ha^{-1} yr^{-1} under experimental conditions (Valle *et al*., 1993; Alvim *et al*., 1990; Botrel *et al*., 1990). Figures commonly found in technical leaflets range between 9 and 15 Mg DM ha^{-1} yr^{-1}.

Such a difference can be explained for two major reasons; firstly the excellent environmental conditions at Valle Nacional, with high precipitation and temperature during most of the year and deep soils of mixed texture, which allows for deep rooting of the grass. These advantages were particularly noticeable in the experimental plot as the preceding fallow was only recently cleared. Moreover, the soil must have been especially enriched after the grass overgrown in the previous year. Secondly, the rains during the wet season were abundant and so the year may have been better than average.

Silvopasture: Forage biomass production in inter-crop in the present work was similar to that obtained by Bustamante *et al*., (1998) with a silvopastoral trial under similar conditions of weather and tree density. Inter-crop treatments with higher tree density yielded more than those of lower tree density both in the dry and wet seasons. In extreme dry conditions (June-July), the two *Gliricidia sepium* plots

produced the lowest, whereas the rest of the treatments performed in similar way to April (Table 4.13 and Fig. 4.4).

Table 4.13. Performance of forage yield in NFT-*Brachiaria decumbens* inter-cropping in average of the three distances from the nearest tree at different times in the year in the Silvopastoral experiment.

Accompanying species (plot)	trees ha^{-1}	Cutting period		
		April	Jun-Jul	Aug-Sep
Lysiloma auritum (2)	650	*Mid*	Mid	High
Leucaena leucocephala (12)	616		*High*	High
Leucaena leucocephala (6)	300	*Mid*	Mid	Mid
Delonix regia (10)	550	*Mid*	Mid	Mid
Gliricidia sepium (3)	817	*High*	Low	High
Gliricidia sepium (8)	216	*Low*	Low	Mid

Note: Italics denote ranking only based on average of samples of final harvest and interpolation, with no intermediate measurements.

Results from similar experiments showed the same tendency, where higher density treatments presented reduced yields in the dry season and enhanced yields in the wet season when compared with lower tree densities (Giraldo *et al*., 1995; Molina *et al*., 1996). By using Tables 4.1 and 4.2 it is possible to make comparisons of the mixed plots and the monocrop. *B. decumbens* monocrop yielded between high and medium during the dry season, as the rest of the treatments, except for *G. sepium* 216 trees ha^{-1}, which produced significantly less forage.

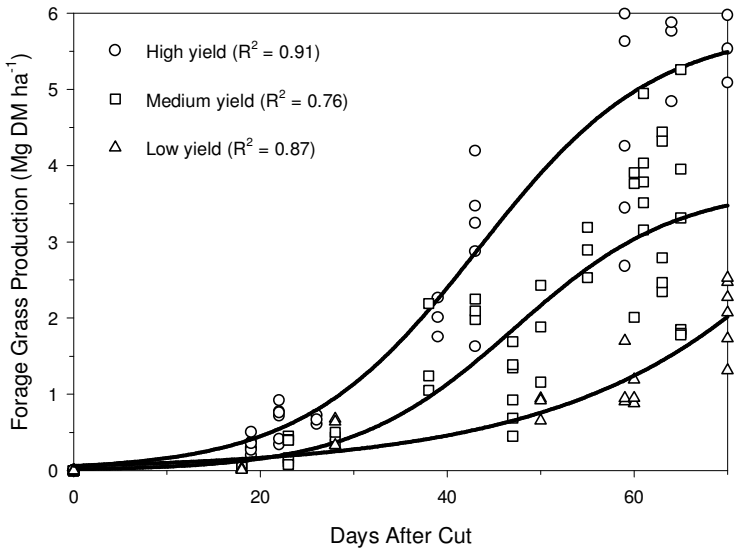


Figure 4.4 Forage grass growth in Nitrogen Fixing trees-*Brachiaria decumbens* inter-crop and sigmoidal curves fitted to three production levels.

By contrast, during June-July the monocrop performed between medium and low compared with the rest of the treatments. Nonetheless, only *L. leucocephala* at 616 trees ha^{-1} were high yielding at this time of the year. In the August-September period the monocrop ranked high yielding along with *G. sepium* 817 trees ha^{-1}, *L. leucocephala* 616 trees ha^{-1} and *L. auritum* 650 trees ha^{-1} wile the rest of the treatments grew at a medium rate.

It can be concluded that, at the tree density used, grass in inter-crop yielded the same as in monocrop except for *G. sepium* associations during the driest part of the year, in which the trees could have presented strong competition for water; this is in agreement with the healthier status of *G. sepium* roots, compared with the other tree species. A description of rooting system can be found in Chapter 5. Reports on forage grass yields in shade and sun show a tendency of reduction of grass production under shade (Acciaresi *et al*., 1994; Carvalho, 1997). However, neutral and slightly positive effects have also been reported (Daccarett and Blydestein, 1968; Cruz, 1997; Bustamante *et al*., 1998).

The sigmoidal growth rate proposed in this study is consistent with field data over time and is more realistic, during the vegetative growth phase, than the linear approach. Linear growth rates have been reported elsewhere (Rika *et al*., 1991); however, such an approach does not allow for predictions of standing biomass at intermediate times of the re-growth period since they have been based on final yield data.

4.4.2 Mulch production

Leaf yield in the experiment was low in overall terms. Production by individual trees was affected by poor root development (see Chapter 5) resulting on insufficient mulch production per hectare in terms of the requirements for grass production (see section 4.4.6). Even *G. sepium*, which showed better root systems, produced less foliage than similar experiences elsewhere (Figure 4.5).

Average production of individual trees in all *G. sepium* plots (3, 4 and 7) was similar, suggesting no effect of tree density on biomass production per tree between 660 and 890 trees ha^{-1}. However, other silvopastoral experiments with *G. sepium* show that while productivity per tree decreases at higher plant density, yield per hectare increases (Kass *et al*., 1989; Catchpoole and Blair, 1990a; Rosecrance *et al*., 1992;

Muschler *et al*., 1993; Sanginga *et al*., 1994; Fernandes, 1994; Ezenwa *et al*. 1995; Nyathi *et al*., 1995 and Nygren and Cruz, 1998).

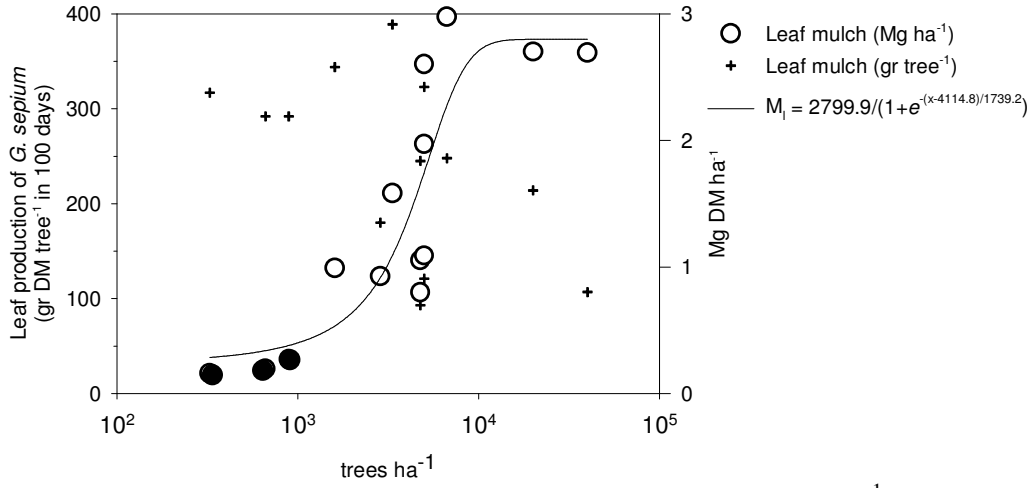


Figure 4.5. *Gliricidia sepium* leaves and twigs biomass production (gr DM tree^{-1} and Mg DM ha^{-1}) reported in the literature (○) and in the present work (●) at 100 days re-growth period, according to tree density (Kass *et al*., 1989; Catchpoole and Blair, 1990a; Rosecrance *et al*., 1992; Muschler *et al*., 1993; Sanginga *et al*., 1994; Fernandes, 1994; Ezenwa *et al*. 1995; Nyathi *et al*., 1995 and Nygren and Cruz, 1998). M_l is kg of leaves and twigs DM ha^{-1} 100 days after last lopping. Data from literature were selected only when managerial features were similar to those of the present work. Figures were transformed to kg DM ha^{-1} in 100 days assuming linear leaf production rate between three and six months after last lopping and adjusting for tree density.

Most of the variability of productivity per tree in the papers referred to can be attributed to the age of the trees and local precipitation regime. This suggests that under continuous pruning, tree densities higher than those used in this research would have increased mulch production. The question as to whether this alteration would affect grass production remains unsolved at this point, but insights are given in section 4.3.2 and discussed further in section 4.4.6.

Allometric assessment of mulch production: The trees in the experiment grew for 30 months before the first pruning. During that period, the grass also developed under the tree population. In fact, there was a clear evidence of the deleterious effect of the grass on the trees, especially during the establishment period (see Chapter 3). In spite of the generally poor growth of the trees, it can be assumed that the leaf mass of the trees at the time of the first pruning was a mixture of new and old parts, turning over according to the natural phenology of the species, especially during of the dry season (June 1997). On the other hand, the leaf mass of the second pruning corresponded to branches and leaves produced during the wet season of 1997. Such

different conditions between the two periods entail two consequences to be considered on the modelling of allometric relationships of tree parts. First, trees growing without pruning will have thicker branches than clipped trees because of the age of the respective branches. Measuring the base of the those branches directly attached to the trunk produced different CSA to biomass ratio in pruned and non-pruned trees. In non-pruned trees, one primary branch can carry more biomass because of the secondary branches, thus sustaining more leaves, whereas young branches usually have no bifurcations, carrying only their own leaves. This amount is limited by the number of leaf buds per surface unit in the branch.

Analysis of residuals indicated that *L. leucocephala* linear models underestimate the biomass of extremely large and small branches and overestimate intermediate ones, suggesting that better fits can be achieved from non-linear models. *G. sepium* presented larger residuals than *L. leucocephala* but according to the t-test, the mean residual did not differ significantly from zero. Nevertheless, no further attempts were made to improve the goodness of fit of the models because there were sources of variation that created an uneven effect across the experimental field, such as pests (rodents and ants) and diseases (an unidentified infection causing dark spots in leaflets and bark and further shedding of leaves). Moreover, the goal of demonstrating the feasibility of assessing the potential harvestable biomass by non-destructive methods was satisfactorily achieved.

4.4.3 Leaf area index

Brachiaria decumbens

Our results are similar, or slightly lower than, other *Brachiaria* sp. reported in the literature. Bustamante and co-workers, (1998) obtained 2.78 and 2.28 in leaf area index of four *Brachiaria* species growing under nitrogen fixing trees and in monocrop respectively. Although no significant differences were found between seasons in the present work, grass LAI during the dry season was slightly lower than in the wet season for most of the treatments. Considering that Plots 3 and 10 had most of their trees in a poor shape, this causing low potential for light interception, those treatments with a higher tree population in healthier condition (see Table 3.1)

presented higher grass leaf area index during the Spring. This effect disappeared during the wet season.

The results presented in this research suggest a morphological response of *B. decumbens* to water deficit that is different in different mixtures. The two *L. leucocephala* plots averaged the highest in grass LAI in the dry season but lowest in the wet season. On the other hand, *G. sepium* plot, which was the lowest in the Spring, averaged the highest in the wet season, except for *L. auritum* plot, which presented a slightly higher value.

It is noticeable that the treatments of poorer tree development, along with that of less tree density, produced lower grass LAI during the period of hydric deficit, and that no statistical differences were found in LAI when rain was abundant. The reduction in grass LAI under *G. sepium* when compared with the control could be attributable to the extent of soil water competition. This is supported by the larger size of the bulk of fine roots (Table 5.2) and the reverse of the problem during the wet season (Table 4.5), despite the fact that the tree fine roots grew even bigger.

The span of the dry period should be a reference for the adequate selection of tree species in silvopastoral systems. *L. leucocephala* allowed for higher grass biomass production during the period of maximum hydric stress (Table 4.1), perhaps because of the combination of higher tree population (616 trees ha^{-1}) and less fine roots (see Table 5.2). Apparently, such a blessing in disguise entailed a shift in the partitioning of resources within the grass plant in favour of leaf lamina due to lower temperature under the canopy and less water competition. A boost in forage production embracing the two following harvests ensued. The treatments with 300 trees ha^{-1} of *L. leucocephala* and 600 trees ha^{-1} of *L. auritum* produced the same effect but with more modest results. *L. auritum* leaf morphology is rather similar to *L. leucocephala*.

Gliricidia sepium

Specific leaf area was 34% lower on average than other figures reported (Budelman, 1988; Hairiah, 1992; Muschler *et al*., 1993 and Muschler personal communication). Such a difference could be partially attributed to the provenance of the plant material and the nutritional status of the crop. But more important, the method used in this work for the determination of the specific leaf area was found to be inaccurate as only fully expanded leaflets were used in the planimeter, whereas the total leaf

biomass included young leaves and green twigs. While including the twigs might lead to an overestimation of the LAI, separating each part would result in the need to split up new and old leaflets, both of different specific area, rendering an equally non perfectly representative portion to be analysed. This problem is commonly tackled by using proportionality constants such as the petiole fraction, when required. In the present study figures of specific leaf area reported in the literature were averaged and used further in the calculations of LAI.

Leaf area index (0.4) was rather small with respect to similar experiments. Tournebize and Sinoquet (1995) reported *G. sepium* LAI to vary between 1.7 and 2.6 in a silvopasture with 16 600 trees ha^{-1} one month after the last clipping. Nygren and Cruz (1998) obtained a LAI of 0.9 for *G. sepium* in a pasture with 4760 trees ha^{-1} after a re-growth period of six months. However, comparisons could not be made since very different plant densities and pruning frequencies were used.

Shade before pruning (22%) was within the recommended level (30%) for adequate growth in *B. decumbens* (Eriksen and Whitney, 1981). These authors found slightly higher, but not significantly different, grass production in fertilised swards of *B. decumbens* growing at 30% shade than under 100% full sunlight. Wong *et al*. (1985) reported yields of up to 91% of those under full sunlight in *B. decumbens* pastures with 40% shade. Carvalho (1997) obtained 63% of yields when growing *B. decumbens* under 60-70% shade compared with the open. The physiological effects of shaded environments on the photosynthetic efficiency of C_4 grasses have been described through three processes: a) Grass LAI increases under shade (Bustamante *et al*., 1998) and such increment can be explained as shelter improves the physical and chemical conditions of the soil, thus enhancing grass mineral nutrition (Cruz, 1997). Tavares *et al*. (1998) obtained incremental ($P<0.05$) levels of P, K and Mg in dry matter of *B. decumbens* when incrementing shade from 0 to 30 to 60%. b) Diffuse radiation, which is proportionally higher than direct radiation under the tree canopy, is richer in PAR (Ludlow, 1978), and c) Moderate shade induces a morphogenetic response of increased specific leaf area (lamina m^2 kg^{-1}) and thus the photosynthetic area (Tounebize and Sinoquet, 1995; Wilson and Ludlow, 1991; Farrell, 1999). Other morphogenetic responses of C_4 grasses to enable maximum radiation interception under shaded conditions are higher leaf to stem ratio,

associated to reduced tillering (Ludlow, 1978; Farrell, 1999) and higher shoot to root ratio (Wilson and Ludlow, 1991). It can be assumed that these transformations are beneficial for the efficiency of resource utilisation for forage production. However, shade leaves are thinner and there is an overall, but integrated, reduction in the capacities of biochemical and physiological processes at leaf level. Dark respiration rates and light compensation points of leaves developed under shade are reduced, but their photochemical efficiencies are unchanged. This results in only marginally higher net photosynthetic rates at low irradiances (Ludlow, 1978). Even though there is no measurable increment the production of forage biomass under moderate shade, the upper storey canopy retains its value as a source of green manure for the long term sustainability of the silvopasture.

4.4.4 Nutritional quality of *Brachiaria decumbens*

Crude Protein

Our results are in good agreement with other reports in non-fertilised pastures; Macedo *et al*. (1993) obtained 11.6% and 6.6% crude protein in unfertilised *Brachiaria* sp. during the wet and dry seasons respectively (the latter corresponds to Spring in the present work). However, forage production in fertilised *B. decumbens* pastures can average up to 13.6% (Alvim *et al*., 1990; Rao *et al*., 1996; Lascano and Euclides, 1996). The aim of the tree-grass inter-crop is to provide the conditions of soil fertility and shelter to allow for the grass to increase its crude protein levels in a sustained manner. At the plant densities used, *L. auritum* ($P<0.05$) and *G. sepium* (n.s.) silvopastures reached higher levels of crude protein than the control. However, their effect in different seasons could not be clearly established since differences between days after cutting and species were larger than the seasonal effects observed in this study. In further silvopastoral experiments, discontinuing time series and species comparisons in favour of a comparison between wet and dry seasons would be advisable. Larger tree densities should be established in order to achieve the requirements of soil nutrients, provided the level of shade is maintained under the threshold of net competition.

Similar improvements in crude protein in *B. decumbens* under shade have also been reported elsewhere: Carvalho (1997) found levels of 12.5 and 9.9% in *B. decumbens*

growing under trees and full sunlight respectively. Norton *et al*. (1991) obtained 8.8 and 10.9% crude protein in full sun and 50% shaded *B. decumbens* pastures. These authors found that N retained in the animal significantly increased from 0.9 to 5.5 g day^{-1} in sheep fed on grass grown in full sun and under shade respectively. Similarly, Acid Detergent Nitrogen (true protein insoluble in neutral detergent) retained in the animal increased from 29.1% to 61.1% when animals were fed on shaded grass.

Chlorophyll: Chapman and Barreto (1997), suggested a direct relation between leaf N and the SPAD but the experimental results indicate a negative correlation between leaf nitrogen and SPAD readings. However, no formal comparison was possible since crude protein samples were collected early in the wet season and the SPAD was available only until November 1997. The rank in chlorophyll measurements corresponded to tree density (r^2 = -0.80), with lower SPAD readings corresponding to the higher tree population. According to Ludlow *et al*. (1988) shade increases chlorophyll concentration in leaves of C_4 grasses. This suggest an explanation for low SPAD readings other than shade, but still related to the tree species, such as the soil status and below ground competition. *D. regia*, *L. leucocephala* and *L. auritum* mixtures shared characteristics in common such as low mulch production per tree and root development and a bipinnate leaf, with minute leaflets less than 1.0 cm^2, which allows higher transmission through the canopy. These tree species produced patterns of low-high-low chlorophyll concentration with a peak some where between 0.5 and 1.5 m from the base of the stem. *G. sepium* was high in chlorophyll under the tree (0.0 m) and low in the rest of the distances. The low chlorophyll level under the trees could be explained by direct nutrient competition, this condition disappearing beyond the tree cover. *G. sepium*, instead, produced more mulch per tree and had not such a weak root system. Its leaves are pinnate of larger leaflets (5-10 cm^2) which could prevent more solar radiation of reaching the grass under the tree canopy. These conditions of more shade and a root system reaching several meters along the soil surface would explain the enhanced chlorophyll level under the tree canopy and low levels beyond. However, causes for the lower readings in the silvopastures compared with the control remains unclear and might be due to the different length of the re-growth period.

Cell Wall

NDF in *B. decumbens* monocrop (77.68% DM) was slightly lower than other reports under similar conditions. Morais *et al*. (1998) determined an average of 79.8% under continuous grazing, and Norton *et al*. (1991) reported 78.4% after six weeks re-growth, in *B. decumbens* monocrop during the rains. However their values of ADF are remarkably higher than that in the present work (40.6% DM) with wet season averages of 47.5 and 47.3% ADF respectively. Non significant changes in NDF, but sensitivity of ADF when comparing shaded and full sunlight conditions, were also detected by Norton and co-workers (*ibid.*). They observed that NDF decreased in that work as well, although no significant differences could be demonstrated. On the other hand, they obtained significant reductions (3.6% DM) in ADF ($P<0.05$), in shaded *B. decumbens* pastures. In the present work, ADF varied significantly between plots, but no differences with the control were detected. Similar to chlorophyll levels, *G. sepium* appears to be the more pernicious association for the pasture.

Whereas the three indicators of the nutritive value of forage grass evaluated in this study showed a decrease during the first seven weeks of re-growth, no relevant changes in DM digestibility were found to be induced by shade. Instead, nitrogen in foliage increases in bulk and digestibility under the tree canopy, and as a consequence nutritive value is improved.

4.4.5 Mulch quality

Total Nitrogen

Total nitrogen values of *L. leucocephala* leaves in this work (4.09% and 3.92% DM for June and November respectively) are within the range of 3.63 to 4.4% of most published data (Flores *et al*., 1998; Molina *et al*., 1996; Islam *et al*., 1995; Kaitho *et al*., 1998b). Yet, lower average values have been quoted (Kaitho *et al*., 1998[a]: 2.45%). Perhaps the climatic season and the time after the last clipping were determinant in such variability. De Sousa *et al*. (1998) also stressed the variability between genotypes. As to *G. sepium*, the values obtained (3.79%) would be in the upper class among averages determined between provenances of 3.00% ($\sigma=0.2$) and 3.44% ($\sigma=0.2$) for dry and wet seasons respectively (Alayon *et al*., 1998; Sukanten *et*

al., 1995, n=16). These data suggest that no certainty can be claimed in quoting the nutritive value of plant material produced elsewhere or at different times of the year with the purposes of elaborating recommendations of soil or animal nutrition. Nonetheless such information is useful for approximate calculations and comparative exercises. With respect to *D. regia* and *L. auritum*, no reports of nutritive value were found in the literature.

Cell Wall

Regarding the cell wall components, the values obtained in this work appear to be from slightly to fairly lower than in the literature. *L. leucocephala* NDF content was 33.3% and 39.67% DM in the dry season and the rains respectively. Most reports average between 41.4% and 48.8% (Flores *et al*., 1998; De Sousa *et al*., 1998; Kaitho *et al*., 1998[a]). However, very low values have been reported in India and Ethiopia (34.19%, Kewalramani *et al*., 1986; 20.8%, Kaitho *et al*., 1998b). Likewise, *G. sepium* NDF (42.8% DM) presented values substantially lower than those of other authors, which range between 49.4% (σ=2.32) and 50.07% (σ=2.96) for wet and dry seasons respectively (Sukanten *et al*., 1995). On the other hand, Alayon *et al*. (1998) reported values as low as 35.7% for the same plant.

As a direct consequence of the lower NDF values, ADF values in this research were also low compared with other figures reported. *L. leucocephala* had 19.9% and 22.4% DM for dry and wet seasons respectively. The range of several documented analyses is between 20.6% and 27.9 % (Kewalramani *et al*. 1986; Flores *et al*., 1998; De Sousa *et al*., 1998; Kaitho *et al*., 1998[a]). Very low values have also been found (17.8%; Kaitho *et al*. 1998b). Due to the variability caused in the cell wall composition by the genotype and season, as well as the re-growth period, only general comparisons can be drawn. What is more important in terms of the use of plant material as mulch is the chemical composition of the cell wall. Different components of the cell wall are known to maintain a characteristic resistance to decomposition. Cellulose, Lignin and Total Phenols and their ratios to nitrogen are among the more documented biochemical groups in this regard (Tian *et al*., 1993; Palm, 1995; Singh *et al*., 1999). Organic carbon to nitrogen ratio is an important, yet empirical, determinant of the decomposition process (Tian *et al*., 1992; Vanlauwe *et al*., 1995; Bending and Turner, 1999).

Hemicellulose: Most of the literature on the degradability of hemicellulose (cell wall polysaccharides solubilized by acid detergents) refers to the rumen environment, but its unavailability to some major cellulolytic rumen bacteria (Dehority, 1993) suggest that low decay rate of hemicellulose is a possibility and put forward the need to explore the fate of hemicellulose in mulch decomposition.

L. leucocephala presented levels of hemicellulose in the dry season (13.3% DM) within the range reported by other workers (12.5% to 13.5%; Tian *et al*., 1992; Kachaka *et al*., 1993; Vanlauwe *et al*., 1995), whereas in the wet season it was raised to 17.2%. However very high (19.7%) and very low (6.25%) data can be found in the literature with no warning of distinctive sampling methods whatsoever (Flores *et al*., 1998; Kewalramani *et al*. 1986).

G. sepium was comparatively low in hemicellulose (11.3% in the dry season) since most reported figures average 13.45 (σ=1.66) for the dry season and 19.9% (σ=1.61) for the wet season (Sukanten *et al*., 1995; Alayon *et al*., 1998; Tian *et al*., 1992).

Cellulose: Cellulose content in *L. leucocephala* (12.7% DM in the dry season and 14.6% DM in rains) could not be properly compared since only two reports, widely different, were found (5.6%; Kachaka *et al*., 1993 and 21.1%; Tian *et al*., 1992). On the other hand, *G. sepium* (10.8% DM in dry season) was lower than other figures reported (16.04%, σ=0.7 in the wet season and 18.85%, σ=1.36 in the dry season: Tian *et al*., 1992; Sukanten *et al*., 1995).

Lignin: *L. leucocephala* (7.29% DM in the dry season and 8.03% DM in the rains) was in the lower limit of the range of figures found, which varied from 8.1% to 14.4% (Kaitho *et al*., 1998a; Kaitho *et al*., 1998b; Tian *et al*., 1992; Mulongoy and Gasser 1993; Kachaka *et al*., 1993). As with nitrogen content, De Sousa *et al*. (1998) found wide variation between genotypes. One very low value (5.0%) was reported (Vanlauwe *et al*., 1995). Lignin in *G. sepium* leaves (6.2% DM) was well below other materials. The average in the literature for the dry season is 17.8% (σ=4.3) and for the wet season is 13.3% (σ=3.0), these figures are derived from 17 genotypes (Sukanten *et al*., 1995; Tian *et al*., 1992).

Total Phenolics: Both in *L. leucocephala* (9.8% and 8.12% gallic acid equivalents -GAE- for dry and wet season respectively) and *G. sepium* (2.07% GAE) total phenolics resulted approximately 50% higher than the average of reports found,

which were 5.91% for *L. leucocephala* (Tian *et al*., 1992; Vanlauwe *et al*., 1995) and 1.31% for *G. sepium* (Alayon *et al*., 1998; Tian *et al*., 1992). It is worth reiterating the point that the results in the present work are referred to as gallic acid equivalents, whilst all the citations refer to tannic acid equivalents (TAE). Gallic and tannic acids are standards commonly used to express the relative contents of phenolic substances, but they have different molecular weight, and more important, different number of hydroxyl groups, thus the same plant extract will produce different figures for GAE and TAE (Waterman and Mole, 1994). Moreover, it may well be that there is no gallic or tannic acid present in the samples at all. These pitfalls make comparisons between species to be uncertain, and comparisons between figures of different standards to be futile.

Organic Carbon to Nitrogen ratio: Organic Carbon to Total Nitrogen ratio in *L. leucocephala* was 12.9 and 13.5 in the dry and wet seasons respectively. Such values were in the upper limit of the range of values reported in the literature, which goes from 12.8 for the roughest material to 8.8 for the more nutritious (Tian *et al*., 1992; Mulongoy and Gasser 1993; Kachaka *et al*., 1993; Vanlauwe *et al*., 1995) . *G. sepium* C:N ratio (13.7) resulted similar to the 13.1 reported by Tian *et al*., (1992) but smaller than 17.3 (based on 16 provenances reported in Sukanten *et al*., 1995).

4.4.6 Nutrient Cycling

Based on the present estimations of grass production, nitrogen demands would be of 240 kg ha^{-1} yr^{-1}. This amount can be partially self supplied by nitrogen fixation (50%, Boddey and Dobereiner, 1988); the rest is to be accomplished by combining organic and inorganic fertilisation. Not doing so turns to be the main cause for degradation of high yielding pastures (Sanchez and Salinas, 1981). Macedo *et al.* (1993) reported the consistent decline in N, P, K and S in three years of continuous grazing of *Brachiaria sp*. only fertilised when planted.

Because of the limited access to commercial inputs and the negative effect of inorganic nitrogen on biological nitrogen fixation in leguminous trees, the more desirable fertilisation strategy is such that inorganic nitrogen is minimised. This action must be accompanied by reduced nutrients demand and increased offer simultaneously. In addition, the strategy suggested considers incrementing the soil organic matter so as to reduce inorganic amendments in the future. However, at the

level of mulch productivity attained, tree population was lower than necessary to cope with grass nutrient requirements for all tree species. An increment in tree density of the appropriate species would cause lower grass growth rate (due to resource competition), and thus more chances for individual trees to develop satisfactorily in addition to the augmented mulch production per hectare.

In order to provide a minimum of nitrogen to maintain a good growth rate in the pasture (60 kg ha^{-1} yr^{-1} in amendments, Arosemena *et al*., 1996) different volumes of mulch should be applied depending on its nitrogen content. Nitrogen rich plant material must be produced through a fast growing tree, to allow frequent pruning of the stand, maximising light incidence at the sward level. According to the results reported in this work, a stand of 890 trees ha^{-1} of *G. sepium* could produce 950 kg leaf DM ha^{-1} yr^{-1}, resulting in 36 kg N. However, using the regression equation in Figure 4.11 to calculate the appropriate tree density in terms of the requirements of mulch, it would be 4500 trees ha^{-1}, with prunings every 100 days, the population required to produce 60 kg N ha^{-1}. There are reports of silvopastoral systems in which tree populations higher than 4500 trees ha^{-1} have been proven to allow grass growth satisfactorily, provided a programme of pruning and fertilisation is maintained (Nygren and Cruz, 1998; Catchpoole and Blair, 1990c).

The ideal mulch for *B decumbens* silvopastures should be one of C:N ratio lower than 20.0 (Frankenberger and Abdelmagid, 1985) but with a great deal of its nitrogen attached to the cell wall. This would retard pro rata the release of this element, thus maintaining its supply according to crop demands. Such a paradigm should be valid for most plant nutrients. Carvalho (1997) found levels of 2.16 and 1.80% K in grass dry matter in shade and sun respectively. Similarly 1.37 and 0.87% N and 0.16 and 0.20% K in litter in an induced silvopasture with *B. decumbens* under the tree canopy and full sunlight respectively. From the point of view of production of high quality green manure, *G. sepium* mulch can be considered to meet the requirements of the associated crop in a feasible way. *L. leucocephala* and *L. auritum* showed serious limitations in adapting to *B. decumbens* associations, but its high N contents suggest their exploitation when naturally available. However, *L. leucocephala* and *L. auritum* are rich in low degradability compound and phenolics, which are deleterious

for the percent of "initial nitrogen released" (Palm, 1995). The fractions of nitrogen initially released and retained in decomposing mulch will be analysed in Chapter 6.

4.5 Conclusions

The objective of assessing the potential for mulch production of trees in inter-cropping and their chemical quality was only partially achieved since every species presented different adaptation to the experimental conditions. The results of this study depicted the poor performance of the trees, this situation presumably due to the strong competitiveness of the pasture. Of the four species established, only *G. sepium* maintained most of the original population. Many *L. leucocephala* and *L. auritum* trees survived but the bad shape of many individual trees resulted in very low mulch production. Experiences of silvopastoral systems elsewhere reported better performance of the tree population at higher tree densities. This put forward that limiting grass growth by planting more trees per unit area would reach a balance point between the two populations.

The results of this study, nevertheless, confirm the potential of *G. sepium* and *L. leucocephala* as sources of high quality mulch reported in other studies (Tian *et al*., 1992; Van der Meersch *et al*., 1993; Mwiinga *et al*., 1994). Cell wall composition, phenolics contents and carbon to nitrogen ratio of mulch does vary between tree species and re-growth periods, thus modifying the performance of the association as to the synchrony of nutrient release and uptake by the crop. *L. leucocephala* and *L. auritum* are higher in cell wall than *G. sepium*. *L. leucocephala* combines low carbon to nitrogen ratio with relatively high lignin and phenolics, resulting in an ideal mulch for cropping systems in which there is a permanent, rather than seasonal, demand of nitrogen, such as tropical pastures.

Looking at the data in figure 4.5, the potential mulch production of *G. sepium* in agroforestry and silvopastoral systems can be achieved at a tree density of about 5000 trees ha^{-1}, yielding 7.5 Mg DM (or 340 kg N ha^{-1} yr^{-1}) in 100 days pruning intervals. However, its effect on grass production is uncertain because of increased above and below ground competition. Upon the hypothesis of limited grass competitiveness under higher tree density, species of high content of nitrogen, such as *L. leucocephala* that did not withstand inter-cropping under the current conditions, could become an alternative sustained source of mulch. Choosing species that

combine adaptation to pasture competition, high growth rate and nutrient contents a mulch decay rate that is in agreement with crop demand enables the adequate design of silvopastoral systems.

With respect to the objective of assessing the role of trees on grass production and its nutritive value, the results of this study suggest different effect of the tree-grass inter-crops according to tree species, tree density and climatic season. A helpful overview of the results of this study is one of three scenarios, the grass monocrop, the mixture of low tree density and the mixture of higher density (even so the latter is not as high as in other studies).

Grass production in the control plot was of intermediate yield during the dry season, as most mixed plots, except for the low performance of *G. sepium* mixtures. During the wet season, the control rendered high yield, like the higher density plots (those with more than 600 trees ha^{-1}), whereas plots of low tree density ranked remarkably low. *L. leucocephala* and *L. auritum*, at densities above 600 trees ha^{-1} consistently produced the highest grass yields in inter-cropping both in dry and wet seasons. As a general rule for the mixtures, high tree density yielded more grass than the low density treatments, both in dry and rainy season. As a whole, rainy seasons yields were conspicuously higher than during the dry season.

In summary, the monocrop yield was near to the low density mixtures during the dry season and near to the higher density mixtures during the rains. Even though both low and higher density plots experienced competition between trees and pasture, there was, apparently, a year round beneficial effect of the trees in the higher density treatments that offset competition and, moreover, enhanced resource availability during the dry season as described in Cruz (1997). These results were confirmed by the changes in grass leaf area index.

As to the nutritive value of forage grass, both crude protein and cell wall of the control plot were not significantly different to the silvopastoral treatments, except for crude protein in *L. auritum* associated grass, which was higher than the control. However monocrop nutritive value was always worst than the better treatments as in 38 day interpolations. Also, the role of the trees on preserving the good nutritional status of the grass for longer was demonstrated, and clearly, different tree species produced different results on grass crude protein and cell wall content. The

chlorophyll readings results suggest that the effect of the distance from the nearest tree was of smaller scale than the layout of the experiment. It seems that factors deriving from the above ground parts of the trees, such as shade or litter fall have been restricted to the crown cover area. Also, tree species of well developed root system (*G. sepium*) would have affected the nutritional status of the soil, hence the nutritive value of the grass near the trees.

5. Characterisation of Rooting Pattern in an Experimental Silvopastoral System

5.1 Introduction

5.1.1 The role of roots in nutrient cycling in agroforestry systems

Crop and tree roots in agroforestry can contribute an important amount of nutrients to the system through the decomposition-mineralisation of roots and nodules, and by nutrient exudation. Sometimes changes in physical environment affect root development through the response of micro-organisms to these factors. Also, exudation provides nutrients to soil micro-flora, which can either benefit or damage grass growth in different forms (Davidson, 1978). Whereas nutrient uptake and exudation are functional processes, decomposition and mineralisation only occur after abscission and senescence of fine roots, being an irreversible process. In order to manipulate the acquisition, retention and release of nutrients from the roots, it is necessary to identify and clearly understand the different factors affecting both decomposition-mineralisation and nutrients exudation, as well as the potential rate and the order of magnitude of the cycling of nutrients between components.

Growth in plant parts depends on an equilibrated assimilation of mineral nutrients, carbon dioxide and water. Roots absorb nutrients from the soil solution at a rate depending on the balance of water potential between soil and plant, the availability of soluble forms of nutrients in the soil solution, the size of the rhizosphere and on the development of microbial associations for fixation of nitrogen (*Rhizobium*) and phosphorus (mycorrhizae).

Nutrients entering the root system are distributed among plant parts depending on the phenological stage of the crop, which in turn is affected by environment and management. Anthesis and grain filling, as well as re-growth of vegetative parts after grazing entails a higher fraction of nutrients sent to the parts above ground, whereas senescing and storage in fully developed plants retain more assimilates in the roots.

5.1.2 Root systems of *Brachiaria decumbens* and nitrogen fixing trees

Improvement in tropical grasses has been targeted towards low fertility resistance and high yields as well as suitability for cattle nutrition. However, it has seldom been noted that these improvements depend on deeper root systems, which allow for both improved resource capture and more carbohydrate reserves for a quick re-

growth, even during the dry season. *Brachiaria decumbens* has an outstanding tolerance of infertile soils of low pH and high levels of aluminium, especially with deficiencies of nitrogen and phosphorus (Rao *et al*., 1996). The characteristics that contribute to this adaptability are: the relative reduction of shoot production (specially the stem fraction) and specific leaf area, as well as a shift in the carbon partitioning, favouring root development (Rao *et al*., 1993).

From the point of view of the sustainability of such a crop and the consequences of such an improved adaptability, questions arise as to whether the benefit of the exploration of lower layers of soil comes from the safety net effect (Hairiah *et al*., 1992) for leaching nutrients; the downward spread of processes in the surface horizons, such as decomposition of high quality root residues (Wardle and Lavelle, 1997) and nitrogen fixation (Boddey and Victoria, 1986), or the expansion of the root system resulting in a new balance between resource capture and turnover.

Root systems in agroforestry can be described as a spatial and temporal array of biomass where tree roots hypothetically occupy the full soil profile, whilst crop roots only reach a fraction of it. This distribution is consistent with the assumption that trees improve capture or utilisation of growth resources. This spatial distribution has been observed for agroforestry systems with annual crops (Jonsson *et al*., 1988; Hairiah *et al*., 1992; Rao *et al*., 1993; Vidhana Arachichi and Liyanage, 1998). However, it is not clear whether the same pattern occurs in silvopastoral systems with improved perennial pastures. The risk of implementing land use technologies based on uncertain assumptions is that yields and rent can drop as resource competition overcomes the benefits of the inter-crop depleting soil and biotic resources faster than in the traditional system. A better understanding of rooting patterns in tree-grass inter-cropping systems is required for designing sustainable agroforestry systems.

To understand to what extent roots can contribute to soil management and its mineral status, it is necessary to quantitatively determine the size and growth rate of root systems of both populations in inter-cropping (Objective 2, Chapter 1). In order to attain this goal three specific objectives were established:

1) To provide insights into the relationship between the rooting pattern and the carbon and nitrogen cycling of inter-cropping systems.

2) To evaluate the effect of agricultural practices on root density, root longevity and root distribution.
3) To characterise the rooting patterns of *Brachiaria decumbens* and the leguminous trees *Leucaena leucocephala*, *Gliricidia sepium*, *Delonix regia* and *Lysiloma auritum* in terms of their agronomic and agroforestry attributes.

5.2 Methods

5.2.1 Field Studies

It is an unfortunate side effect of root studies that the observation of the object under analysis modifies its otherwise normal behaviour since, almost unavoidably, roots must be excavated for measurement. The monitoring system developed for the present research is composed of several different techniques of survey, which are individually limited in some aspects but complementary when combined in a relatively large scale plot. The assumption is that because most of the methods in this study involve destructive but immediate observations of the variables, no significant disturbances should be expected that alter the reliability of the results. However, since our method entails the successive excavation (destruction) of sampling units, the investigation requires a larger experimental plot and involves a considerable amount of labour.
The combination of root trenches and core sampling allowed the estimation of total root biomass as affected by the particular tree-grass mixture and the climatic season. Root excavations were complementary to calculations of the below-ground woody biomass, which was not effectively sampled by coring. Repeated root observations allowed the dynamics of the root system to be investigated (Fig. 5.1).

Figure 5.1. Graphic representation of core sampling, vertical profiles, root excavations and root observation.

Root biomass

Root biomass was assessed in two simultaneous experiments, a distance trial, focused on the effect of the distance to the nearest tree, and a mulching trial, focused on the effect of the addition of the prunings to the soil surface as a source of green manure. This experiment was not in the original fieldwork plan but was conceived as the pruning of trees in July 1997 overlapped the study of root biomass. The pruning material was allocated in a section 0.25 the size of the plot, in order to obtain contrasting results on root biomass.

In order to determine root biomass in the topsoil in relation to agroforestry treatments, distance to the nearest tree and age of the canopy, root biomass was measured by core sampling as described in van Noordwijk (1993). Plots 8, 10 and 12 were included in this study. Samples were randomly allocated for every sampling period to one of three distances (close, mid and far). Three cores (2.54 cm in diameter and 30 cm deep) were taken from each one of five sampling units, these consisting of 2 * 2m quadrats, making up a combined sample of fifteen cores for each distance class. An allowance for the edge effect was made as described in Chapter 3, which combined with the division channels gave us the certainty of very little cross-over effect from neighbouring plots.

In the mulching trial, core sampling was laid out so as to allow the identification of the evolution of rooting systems after pruning. Part of plots 2, 3, 10 and 12 were treated with mulch. Sample management procedures were the same as in the distance trial. The sampling schedule in table 5.1 refers to the studies of the effect on root biomass of the distance to the nearest tree and mulching.

Table 5.1. Sampling schedule of core sampling for the effect of distance from the nearest tree and mulching on root biomass.

Date	Plot					
	2	3	4	8	10	12-13
	Lysiloma	*Gliricidia* (seed)	*Gliricidia* (poles)	*Gliricidia* (seed)	*Delonix*	*Leucaena*
20/Apr				Distance		
6/Jun				Distance	Distance	Distance
3/Jul				Distance	Distance	
7/Aug				Distance	Distance	Distance
21/Aug	Mulch	Mulch	Distance		Mulch	Mulch
13/Sep				Distance	Distance	Distance
24/Sep	Mulch	Mulch			Mulch	Mulch

When a shallow rocky horizon (plots 2-4) prevented 30 cm deep coring, calculations of root density were performed in accordance with the actual sampling depth. Three classes of roots were identified and treated separately: woody roots, suberised roots and fine roots. Woody roots were removed from each sample and washed. Suberised and fine roots were measured on sub-samples to 100g from which the soil particles were removed by washing on a 1.0 mm mesh; a variable but small amount of soil particles remained attached to the roots, the amount being higher in fine root than in suberised and woody roots. The roots were then dried to constant weight (105°C for 24h) and the weight recorded. Roots were incinerated in a muffle furnace to 550°C and the weight of the residue subtracted from the root sample weight to obtain the ash-free oven-dry root biomass in the corresponding volume of soil within the 0-30 cm soil top layer. Woody roots' content was calculated over the whole sample of fifteen cores, whilst that of suberised and fine roots was calculated over 100g sub-samples. No correction was made for the reduction in the incinerated sample weight due to soil organic matter since there was only little soil attached to the roots after washing. Since during the core sampling fine roots were recovered regardless of the class (primary, secondary, etc.), the total fine root biomass was divided according to the figures of the root maps (see below). These results were used to estimate root biomass.

The fine root results in the distance trial were lognormal transformed before analysis of variance so as to satisfy Bartlett's test for normal distribution of variances. Similarly, suberised root results were Weibull transformed in the distance trial. Plot

and distance from the nearest tree, or alternatively, plot and mulch application were considered as sources of variation in the analysis of variance. The statistical models for comparing treatments were:

$$Y_{ijk} = \mu + species_i + distance_j + interaction_{ij} + C_{recover} + e_{ijk} \quad (5.1)$$

Alternatively,

$$Y_{ijk} = \mu + species_i + mulch_j + interaction_{ij} + C_{recover} + e_{ijk} \quad (5.2)$$

Where $\mathbf{Y_{ijk}}$ is the root ash-free biomass – or lognormal/Weibull root biomass (g DM m^{-2}); $\mathbf{species_i}$ is one of the five tree-*B. decumbens* mixtures (*Lysiloma* at 650 trees per ha, *Gliricidia* at 216 trees per ha (distance trial), *Gliricidia* at 817 trees per ha (mulching trial), *Delonix* at 550 trees per ha and *Leucaena* at 616 trees per ha); $\mathbf{distance_j}$ represents one of three sub-plots (*close*, *mid* and *far*) in each mixture; $\mathbf{mulch_j}$ represents the addition or no addition of mulch from prunings of the same plot; $\mathbf{interaction_{ij}}$ refers to the species distance or the species mulch interaction; $\mathbf{C_{recover}}$ is a covariate to account for the period of time since the last tree pruning (one month before pruning, the same week of pruning, 35 and 70 days after pruning). General Linear Model procedure in Minitab v.12 was used for the analysis of variance. Homogeneity of variance and residuals distribution analysis were performed to check for errors on the assumptions of analysis of variance. Fisher's test was used to compare treatments.

Root profiles

Four trenches (150 cm wide and 1.0 to 1.3m deep) were excavated in plots 2 (*Lysiloma*), 8 (*Gliricidia*), 10 (*Delonix*) and 12 (*Leucaena*) in order to identify rooting patterns of the *B. decumbens*-tree mixtures. Root measurement consisted of counts of root tips in the plane of the profile. The resulting rooting patterns were used to characterise the potential interactions between the two species and also to work out the total root biomass at different times in the year. Profiles were excavated in March 1997 and the first root maps recorded in May the same year. That was the driest time of the year. The rest of the profiles were obtained during the wet season, except for the last one (early 1998), which was unexpectedly dry. The schedule of root mapping was:

Accompanying species	Dates
Lysiloma auritum	11/Aug/97 and 2/Feb/98
Gliricidia sepium	2/Jun/97, 8/Aug/97, 11/Aug/97, 16/Aug/97 and 15/Jan/98
Delonix regia	13/May/97, 10/Aug/97, 27/Sep/97 and 2/Feb/98
Leucaena leucocephala	14/May/97, 8/Aug/97, 11/Aug/97 and 16/Jan/98

Root profiles were drawn on polythene sheets in trenches as described in TSBF (1993). The trenches were dug 150 cm from selected trees. After excavating the profiles with shovel and pick we carefully removed a vertical soil layer with a small blunt spatula to reveal root tips. The trenches were used more than once, after removal of a 10 cm thick soil layer. Different colour markers were used to identify roots by diameter class on a large sheet of polythene. A 10 or 15cm^2 grid was drawn on the opposite side of the polythene sheets to ease the counting and calculation of root sections and root tips population. Woody roots, primary fine roots and secondary fine roots were recorded; primary roots refer to those fine roots that branched and secondary roots to terminal root tips.

Plate 5.1. Trench dug to 1.5 m for root tip counting in the study of vertical distribution of roots.

It was not until the final part of the survey that we gained the ability to reliably differentiate between *Gliricidia* and grass roots, thus only one map contains information with that level of detail. The outcome of the work was an array of data representing the count of root tips. The columns and rows of the array were the sections in which the trench was divided to ease the survey (usually every 10cm). Negative exponential functions were fitted to the vertical distribution of roots (Eq. 5.3). Models were tested and parameters produced through non-linear regression with Minitab v.12.

$$D = ae^{-cd} \tag{5.3}$$

Where D is the number of roots for $10cm^2$, a and c are constants and d is the depth interval in the soil. The combination of core sampling, as an indication of root biomass at the soil surface, and the root maps, was used to elucidate the status of roots deeper in the soil at set times after cutting in both the dry and wet seasons. Trees and grass roots are presented together. In order to estimate total root biomass, several assumptions had to be made:

- All counted roots within the same class (woody, primary and secondary fine roots) were considered to be alive. In fact, dead roots were seldom found, probably because temperature and humidity resulted in high decomposition rates, and those roots with obvious signs of decay were avoided.
- Roots were assumed to be homogeneously distributed within map rows as well as having the same specific density (root tips per kg root) at different depths.
- Root distribution patterns were assumed not to vary with distance from the tree; the only difference consisting of the total root biomass of each distance.
- There are some maps where no data on suberised roots are recorded. Real suberised roots were assumed to be mixed with primary fine roots. This assumption is more conservative than attempting to split the count of primary fine roots into two classes.

Root maps and core sampling were always performed at approximately the same time so that the data sets were compatible. The profiles from the rainy season (August - September) were averaged before being used to calculate total root biomass. Thus three stages of the silvopasture are analysed, namely dry season 1997, wet season 1997 and dry season 1998.

Calculation of total fine and suberised root biomass in the silvopastoral experimental field: Values of fine root biomass from soil cores in the top 30 cm of soil, were divided into two categories, primary and secondary fine roots, according to fractions from the corresponding root map. Suberised roots were added to primary fine roots for root biomass calculations. Each fraction was further extrapolated to the whole profile by matching with the fraction of root tips in the top 30 cm and calculating the corresponding figure for the rest of the profile. The same procedure was performed for the two categories of roots and the three distances, namely *close*, *mid* and *far* from the nearest tree. The aggregate of root dry matter per hectare was worked out from the three distance classes according to the plant density of each plot.

Tree root form (full excavation)

In plots 7 (*G. sepium* poles), 8 (*G. sepium* seed), 9 (*D. regia*) and 12 (*L. leucocephala*) tree lateral roots were excavated in order to uncover their natural distribution in the soil and to estimate the abundance of nodules for biological nitrogen fixation: one root in plot 8, one root in plot 12, three roots in plot 9 and the whole tree in plot 7. Excavations were performed carefully in order to avoid damage to thin roots. First, the soil around the trunk of the selected tree was thoroughly watered and left to soak overnight. This procedure softened the soil aggregates. Next, excavation was performed mostly by hand and with wooden rods when possible. More water was added once the softened soil was removed and after one day's work, since softening takes a long time (overnight). At some point water was also useful to wash loose soil from the excavation. Because the removal of soil depends on the softening action of water, the excavation of a single whole lateral root takes several days. Very few *Rhizobium* nodules were found after excavating several root systems. Even so, excavation continued as interesting results on tree root distribution emerged, providing insights into the nutrient status of the soil profile, which determines root distribution and competition. The variables considered in this study were lateral root diameter class, depth and length as well as branching pattern.

5.2.2 *Brachiaria decumbens* root turnover rate

This experiment was established in order to assess the longevity of *Brachiaria decumbens* roots in response to increasing N fertilisation. Plants were sown in PVC tubes 100cm high * 15cm in diameter (service duct). An artificial soil of vermiculite and perlite was used to fill the tubes. 8.5 cm diameter windows were cut out on one side of the tubes in order to allow root observation, of which, those at 5, 15 and 65 cm deep were used for root observation. The windows were sealed with a rubber belt to prevent the soil behind the windows becoming loose. Two *Brachiaria decumbens* seeds were sown at a depth of 3.0 mm. Temperature in the glasshouse was kept at 23°C and day length to a minimum of 11 hours, using artificial light when necessary. Only one plant was preserved after germination and this plant was maintained to five tillers, removing the new tillers by hand every week. Owing to serious damage to the glass house during a storm in December 1998, two weeks after the experiment started, the pots were transferred to a growth room, where control over the environmental conditions was better than that in the glasshouse. However, the photon flux density was lower in the growth room.

Treatments:

Three nitrogen fertilisation levels (100, 200 and 300 kg N ha^{-1} yr^{-1}) were compared. Nitrogen was applied in feeding solution composed of Vitafeed-Q4® (19-19-19), 0-7-0, K_2SO_4, ammonium nitrate and Vitax® *foliar* feed high nitrogen (35-5-10), in adequate proportion to make 100-100-180, 200-100-180 and 300-100-180 kg ha^{-1} yr^{-1} treatments. Fertiliser was supplied twice a week in combination with watering. Although length of cutting interval was a treatment considered at the beginning of the experiment, it was impossible to carry out since the plants grew very slowly. The experiment started once the plants reached full development (about 2 months after sowing). The plants were cut the day when the recording of roots (video-recording) started in order to promote the production of new roots that could be measured. The recording continued every seven days until preliminary analysis of results in week 11 showed that most of the roots under study were dead or had disappeared. The weekly schedule of recording was based on the reports of other authors suggesting that fine roots become moribund very quickly because the most active absorption occurs in

the root-hair zone behind the root cap or near the apex (Davidson, 1978). Longevity can be in the order of one to three weeks (Black, 1997).
Drawings of the roots were sketched on acetate sheets directly from a monitor, denoting the cohort and disappearance of every root on a weekly basis. Since the same acetate was used for the whole series of records of the same observation window, it was necessary to:

a) Record the window number in the top left corner of the acetate.

b) Use different coloured permanent markers every week in order to allow for the identification of roots from every cohort during the analysis.

c) Mark the position of the acetate on the first week's image, so as to enable the accurate replacement of the acetate for subsequent acetate recordings.

d) Record the death/disappearance of each root using the colour corresponding to the current week.

Total alive and dead roots within the same cohort (produced in the same week) and for each depth were counted and root longevity estimated from the difference between the time (in days) the roots appeared and died/disappeared. Treatments and cohorts were tested (χ^2) through the `LIFEREG` procedure for survival analysis using SAS (SAS Institute Inc. Cary, NC 1990) in order to determine significant effects of sources of variation, namely doses of N fertilizer, observation depth and cohort.
Nitrogen treatments were compared in their effect on root longevity over time on two groups of cohorts through the `LIFETEST` procedure for survival analysis (SAS Institute Inc. Cary, NC 1990). Six cohorts were monitored during a period of seven weeks. Monitoring of the earlier cohorts finished earlier. The data for each cohort were put together according to the week number and the starting week of all cohorts. Since we decided to stop monitoring before the last root under observation disappeared, a survival analysis (Black *et al*., 1996) procedure was used to give insights into the probability distribution of root longevity of those surviving longer

than the duration of the experiment. The LIFEREG procedure fits a linear regression model (Eq. 5.4) for the transformed vector of observations (ε). Weibull distribution was found the most appropriate to transform the dataset.

$$y = x'\beta + \varepsilon \quad (5.4)$$

Where **y** is the vector of the log of the event-time variable, **x** is the matrix of covariate values and **β** is a vector of unknown parameters to be fit. χ^2 test was used to compare the estimate values of the covariates: nitrogen fertilisation, depth of the observation and cohort group. The LIFETEST procedure computes the Survival and Hazard life table estimates. Survivor functions *S(t)* and Hazard rate functions *h(t)* were used to calculate the probability of survival at least up to time *t* and the instantaneous probability of death at time *t* respectively. Survival distribution was modelled with a two parameters distribution (Weibull). Survivor function and hazard rate function were described as:

$$S(t) = \exp(t/\theta)^{\gamma} \quad (5.5)$$

and

$$h(t) = (\gamma/\theta)[t/\theta]^{\gamma-1} \quad (5.6)$$

Where θ is the **Scale** parameter of the Weibull probability distribution and is the main determinant of the level of hazard and thus the level of life span. High θ values correspond to a large proportion of individual roots surviving a long time (low hazard) and vice versa. The **Shape** parameter (γ) determines the change in the level of hazard; when $\gamma = 1$ the probability distribution reduces to an Exponential of mean θ, and hazard θ^{-1} (Black *et al*., 1997). Because of the properties of the Weibull probability distribution $\gamma < 1$ are associated with high Coefficient of Variation and decreasing risk (hazard) and vice versa.

5.3 Results

5.3.1 Root biomass in the top soil

Fine and suberised root biomass in tree-grass mixtures showed significant differences when distances from the nearest tree were compared ($P<0.05$). Result are presented as average of four sampling periods, although some mixtures showed

differences between sampling periods (Table 5.2). Fine roots accounted for the largest bulk of root biomass, averaging 629 g DM m^{-2} for *G. sepium-B. decumbens*, 405 g DM m^{-2} for *L. leucocephala-B. decumbens* and 586 g DM m^{-2} for *D. regia-B. decumbens* mixtures. Suberised roots represented 25.0, 33.1 and 24.6 g DM m^{-2} for the same mixtures respectively, which is a small part of the total standing biomass (4.0, 8.2 and 4.2% of the fine root biomass respectively).

Woody root biomass values differed inconsistently between sampling dates. This suggests that this category of roots was undersampled as it is unlikely that woody roots grow and disappear repeatedly in one season. Most woody root biomass recovered in the core sampling, however, concentrated in the surroundings of the base of the stem. This is in agreement with root excavation results, which showed a profuse ramification of the lateral roots at a short distance from the trunk root and a maximum length of approximately 4 m. The data on woody roots ranged between 50 and 600 g DM m^{-2}.

The *close* distance caused a slight positive effect on the fine roots (especially in the *G. sepium-B. decumbens* mixture) in the early rainy season. This effect was reversed in the second sampling of the wet season (August), which took place four weeks after the first pruning of the tree stands. The effect on *mid* and *far* distances remained more even along the experimental time. By the last sampling period (September), the overall fine root biomass was lower than that of the previous samplings in all species and distances, except for *Leucaena* and *Delonix* (*far*).

Table 5.2. Average fine root biomass, in the top 30 cm of soil, of *Brachiaria decumbens* - leguminous tree inter-crops at $2m^2$ sampling unit scale, and plot scale weighted by fraction of plot area in each distance to the nearest tree.

Tree species	Fine root biomass g m^{-2}			Fraction of plot area (%)			Plot fine root biomass Mg ha^{-1}		
	Close	Mid	Far	Close	Mid	Far	Close	Mid	Far
G. sepium (216)*	623^b	506^b	744^a	8	45	47	0.48	2.29	3.57
D. regia (550)	483^b	668^a	625^a	22	67	11	1.07	3.74	0.66
L. leucocephala (616)	477^b	580^a	454^b	30	69	1	1.68	4.29	0.03

*) Equivalent trees ha^{-1}. Letters in the same row denote statistical differences between distances ($LSD_{0.05,24}$). Average of four sampling periods.

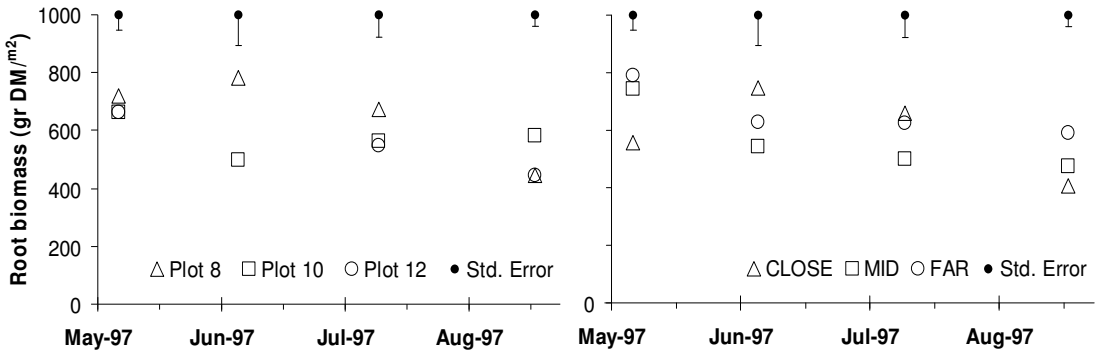


Figure 5.2. Fine plus suberised roots biomass in the top soil (30 cm) in three tree-grass mixtures (left) and at three distances (right); plot 8 (*G. sepium*), plot 10 (*D. regia*), plot 12 (*L. leucocephala*). Error bars are one standard error.

The undifferentiated behaviour of the root biomass in the *D. regia-B. decumbens* mixture must be interpreted in the light of the poor re-growth of the stand after pruning. Likewise the other treatments, there was more variation in the *close* quadrats (fig. 5.2 right). The mulching trial produced no statistically different responses in fine or suberised roots biomass. The averaged values of day 51 and 84 after pruning for mulched and non mulched treatments suggest that the four mixtures might have different responses to pruning and mulching, but the sampling was just not enough to detect such changes (table 5.3).

Table 5.3 Root biomass in Mulched vs. Non-mulched plots of leguminous trees-*B. decumbens* mixtures in the Silvopastoral experiment (g DM m^{-2} in the top 30 cm of soil). Values after pruning are average of 21 Aug. and 24 Sep. 1997.

	Fine Roots			Suberised Roots		
Acompanying	Before	After Pruning		Before	After Pruning	
species	Pruning	No-Mulch	Mulch	Pruning	No-Mulch	Mulch
D. regia	507	558	687	29.6	16.1	33.0
L. auritum	705	1500	1359	21.1	26.4	147.2
L. leucocephala	710	321	498	43.9	17.0	20.4
G. sepium	788	1336	386	23.3	35.2	23.6
Average	668	929	733	29.5	23.7	56.1

Note: Each figure is the result of a composite sample (n=15 cores per sample) covering the whole plot at random, there is no replication within categories.

Responses were as low as 518 and 338 g fine + suberised root DM m^{-2} in *L. leucocephala – B. decumbens* with and without mulch respectively, and up to 1506 and 1527 g fine + suberised root DM m^{-2} in *L. auritum – B. decumbens* in the same order. These figures range from reductions of more than 50% in root biomass to twofold increments when compared with the biomass one month before pruning.

5.3.2 Vertical distribution

The vertical distribution pattern was shown to perform consistently between the treatments with half of the root population in the top 20 cm of the profile and a steady diminishing downwards. Considerable amounts of very fine roots were found to a depth of 1.20 m. Primary fine roots were about 20% of the secondary fine roots but reached the same depth. Root profiles consistently contained 25% of the fine root tips within the first 10 cm, 25% more within the next 10 cm and another 25% more or less evenly distributed between 20 and 45 cm, and up to 50 cm during the dry season. The rest of the roots populated the remainder of the profile with decreasing density (table 5.4).

Table 5.4. Density profiles of fine root tips (depth at which 25,50,and 75% of total root tips appeared) by treatment at two different times in the year.

Fraction of total root tips	*G. sepium*	*L. leucocephala*	*D. regia*	*L. auritum*
	Soil depth (cm)			
	Dry season 97 (May – June)			
25%	7	10	10	
50%	20	20	20	
75%	50	50	50	
	Wet season 97 (August-September)			
25%	10	10	10	10
50%	26	20	20	17
75%	45	40	42	30
	Dry Season 98 (January- February)			
25%	12	8	10	9
50%	27	20	20	20
75%	45	40	40	36

Note: All figures from one profile each, except for *G. sepium* wet season (n = 3) and *L. leucocephala* wet season (n = 2). *D. regia* third profile (20-45-70, 27 Sep.) was not included in the average as its values resulted in a highly irregular pattern when compared within and between treatments.

Although a negative exponential function ($D = ae^{-cd}$) fits the general shape of fine root tip density with depth (table 5.5), for both primary and secondary fine roots, there was in most cases a steeper reduction at 35-50 cm (fig. 5.3 a-d). Apparently *Brachiaria decumbens* roots were found deeper than any of the tree species roots. Woody roots were scarce and normally occurred only in the top 30 cm of the soil.

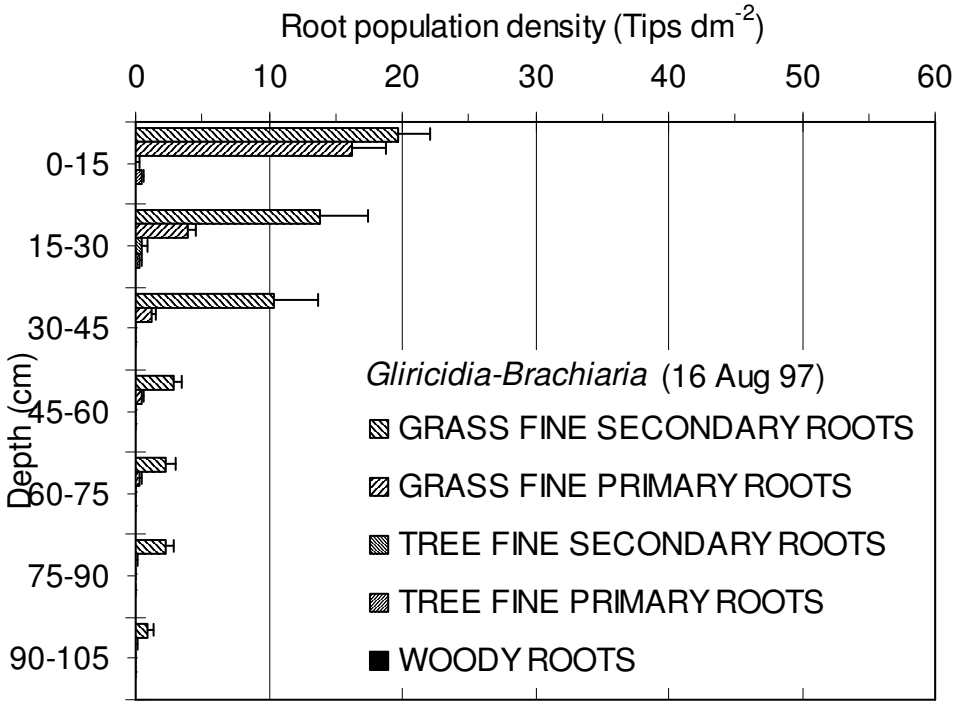


Figure 5.3.a. *Gliricidia sepium* - *Brachiaria decumbens* root counts of vertical profiles at different times in the year. Error bars are one standard error of 10 columns 10 cm wide and the indicated depth.

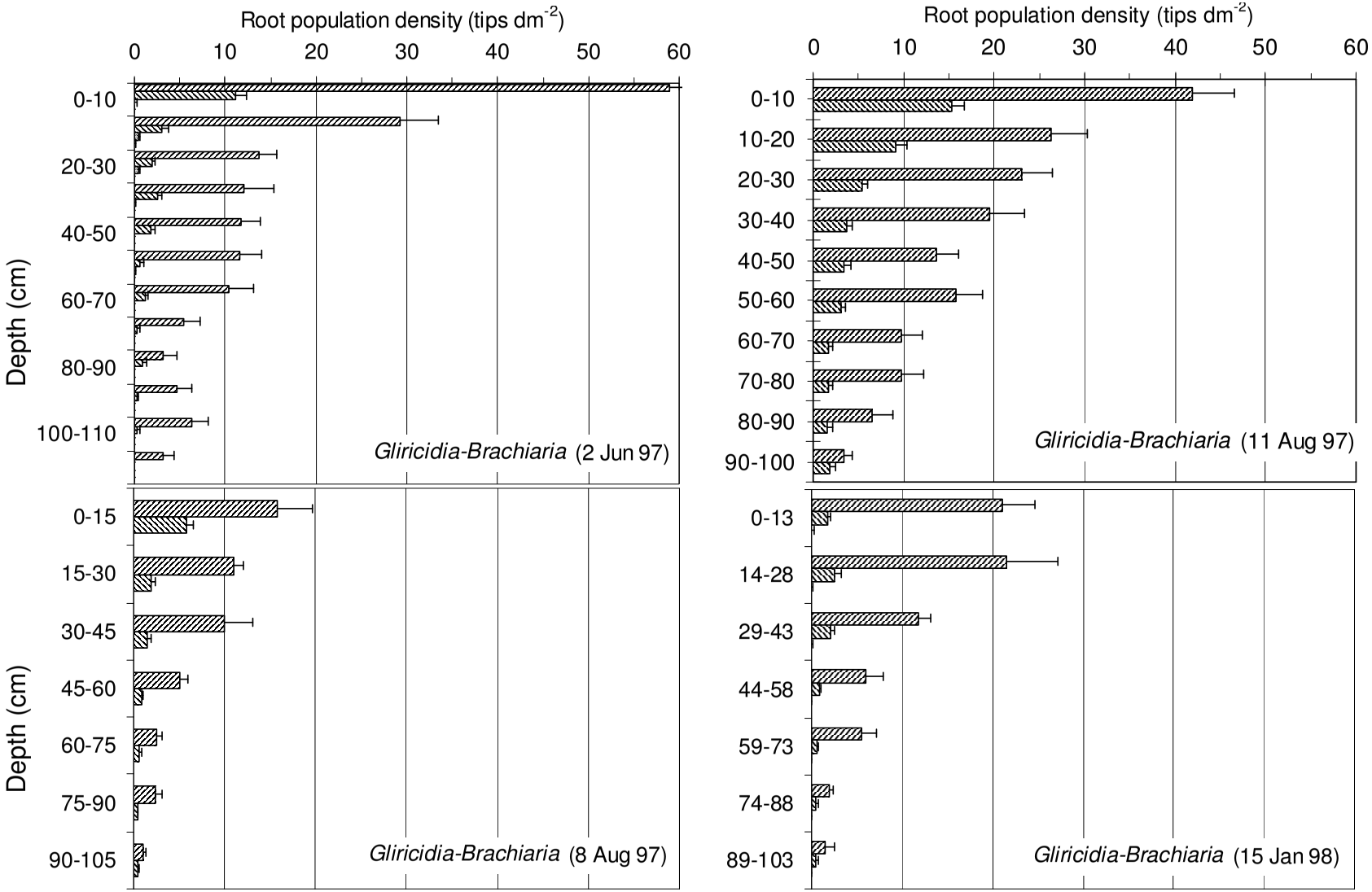


Figure 5.3.a. (Continuation) Grass and tree roots are in the same columns.

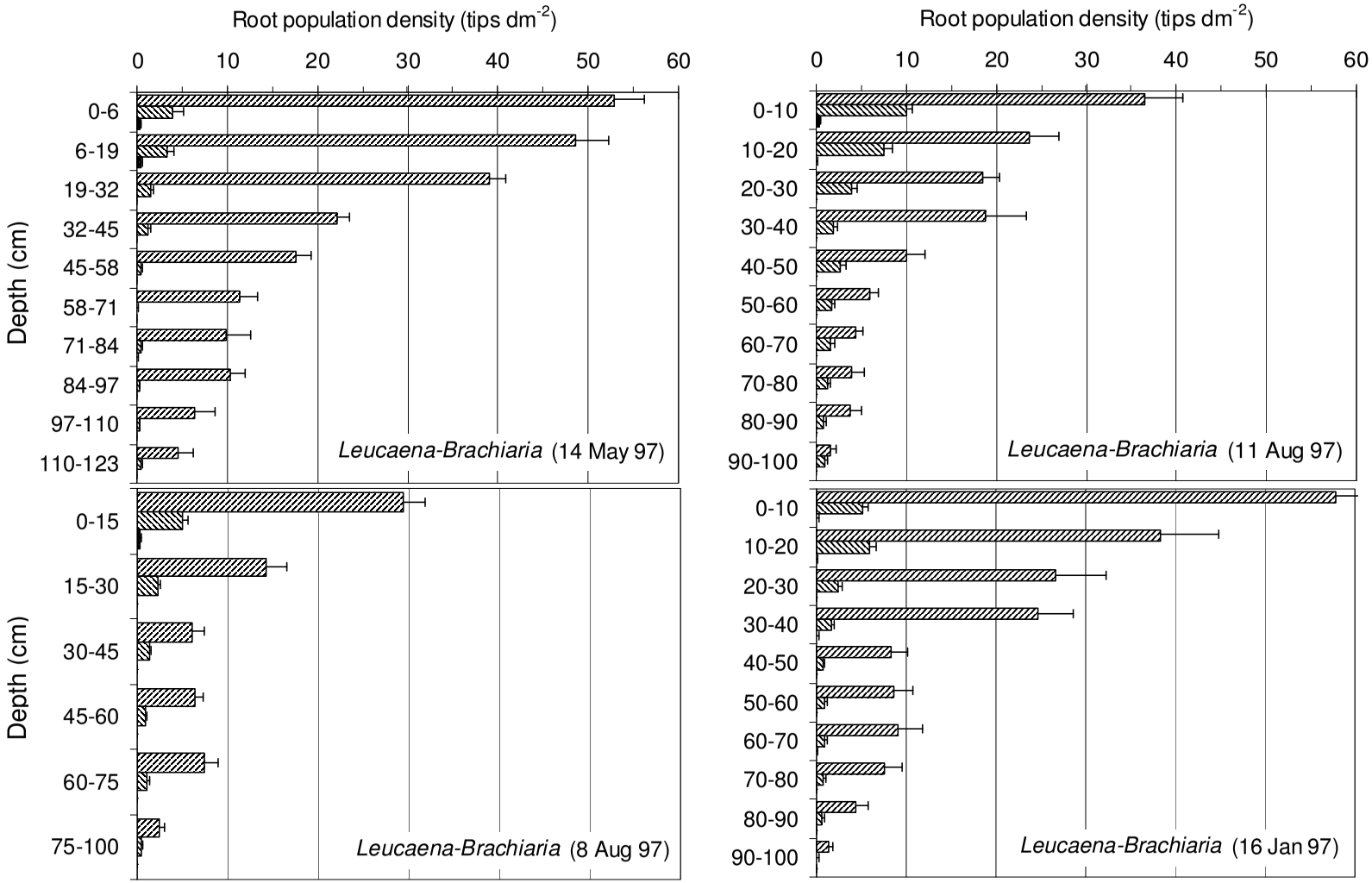


Figure 5.3.b.*Leucaena leucocephala Brachiaria decumbens* root counts of vertical profiles at different times in the year. Error bars are one standard error of 10 columns 10 cm wide and the indicated depth. Grass and tree roots are in the same columns.

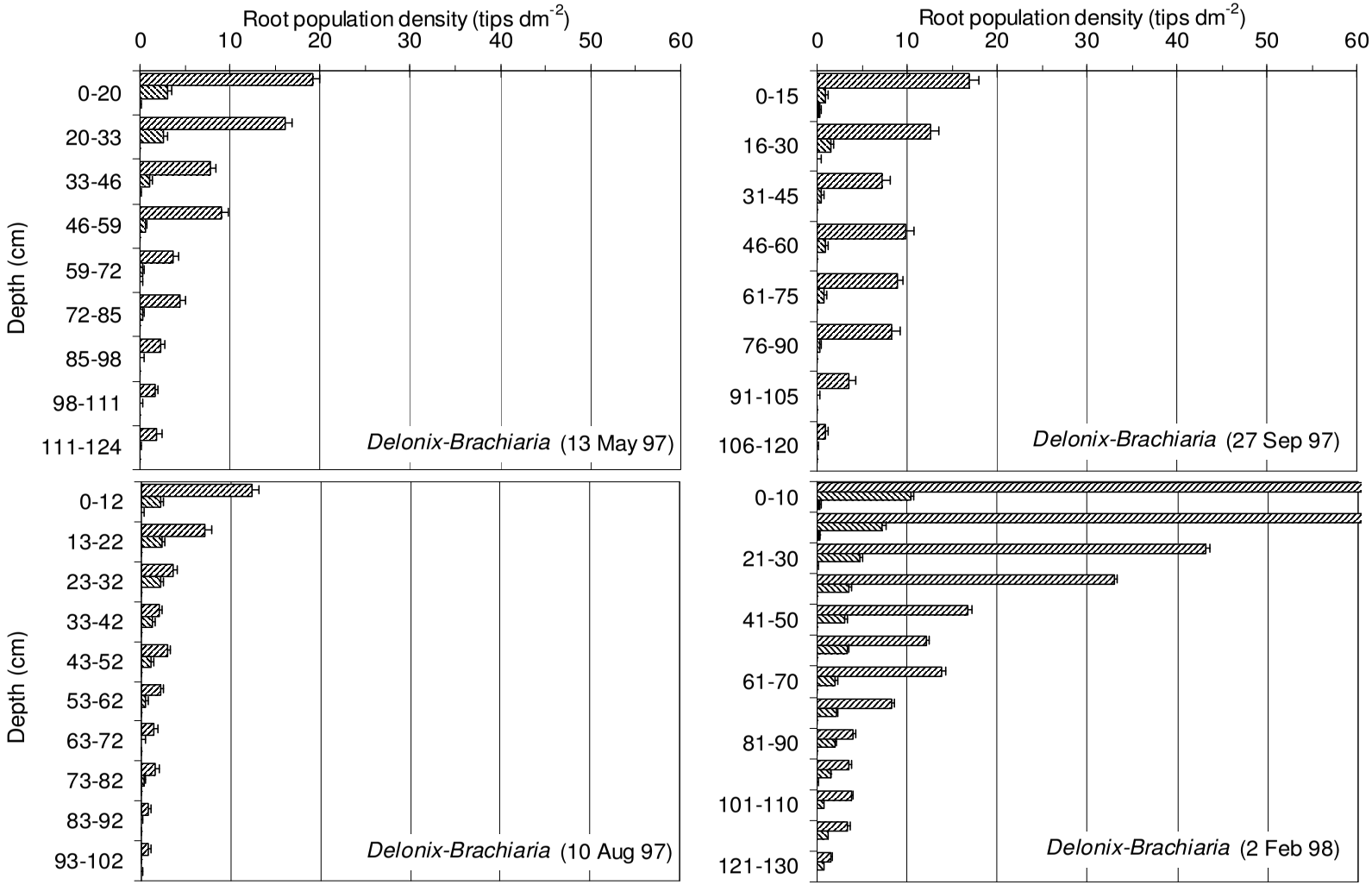


Figure 5.3.c. *Delonix regia - Brachiaria decumbens* root counts of vertical profiles at different times in the year. Error bars are one standard error of 10 columns 10 cm wide and the indicated depth. Grass and tree roots are in the same columns.

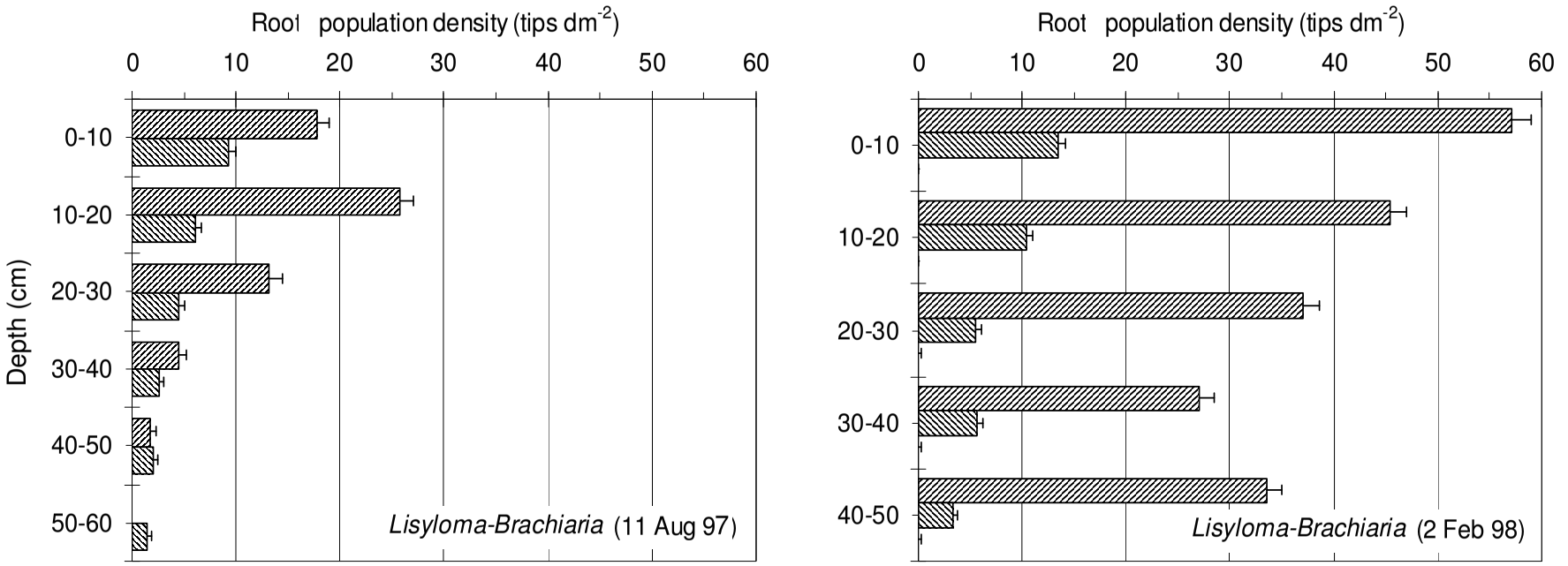


Figure 5.3.d. *Lysiloma auritum* - *Brachiaria decumbens* root counts of vertical profiles at different times in the year. Error bars are one standard error of 10 columns 10 cm wide and the indicated depth. Grass and tree roots are in the same columns.

Table 5.5. Intercept **a** and shape coefficient **d** and significance of predictive equations of root density **D** (tips dm^{-2}) of secondary fine roots per dm (depth) for four different Nitrogen Fixing Trees-*B. decumbens* mixtures.

Accompanying tree	a	d	P	R^2	S.E.	Comments
D. regia	21.31^{**}	0.03^{**}	<0.0001	0.61	4.4	4 profiles
G. sepium	36.99^{**}	0.03^{**}	<0.0001	0.67	6.7	5 profiles
L. auritum	27.87^{*}	0.04n.s.	0.059	0.63	6.3	Aug. '97
L. auritum	60.34^{**}	0.02^{*}	0.022	0.87	5.0	Feb. '98
L. leucocephala	52.81^{**}	0.03^{**}	<0.0001	0.81	6.9	4 profiles

* = 95% significance. ** > 99% significance. S.E. stands for one standard error.
Note: Profiles of the same species are from the same wall.

Roots grown in 1 m deep pots in the root longevity experiment (see section 5.2.2) measured on average 122 cm (σ = 19.4) from the base of the culms to the tip of the tap root. Because they grew in pots 15cm in diameter, there was uncertainty as to the length of the lateral roots and whether some roots that developed downwards would spread horizontally in real soil, thus only three pieces of roots were considered, 0 to 10 cm, 10 to 50 cm and the rest of the tap roots. 76.4 % of the root biomass (ash free DM per plant, n = 8) was found in the top 50 cm of the root system (Table 5.6), one plant being up to 5 tillers growing from the same meristem. Some pieces of root were rendered loose during the extraction, they could not be assigned to any part of the root system as they were recovered from the sieve; after putting the dead pieces apart, they were processed as a separate fraction for general calculations, this part constituted 7.4% of the total root biomass.

Table 5.6. Fractions of root biomass in *Brachiaria decumbens* grown in 1 m long cylinders for root observation.

Root part	Root biomass (g DM per plant)	σ
0 to 10 cm	0.600	0.4
10 to 50 cm	0.795	0.4
50 cm to tip	0.263	0.2
Loose roots	0.130	0.1

5.3.3 Total Root biomass:

The total living root biomass (kg ash free DM ha^{-1}) is presented as the sum of the weights of tree and grass fine and suberised roots. These values were obtained by

applying the fractions derived from root profiles to the top soil biomass results from the core sampling. Each chart represents two categories of roots (secondary fine roots and primary fine plus suberised roots) in three *zones* of the plot with respect to the nearest tree (*close*, *mid* and *far*).

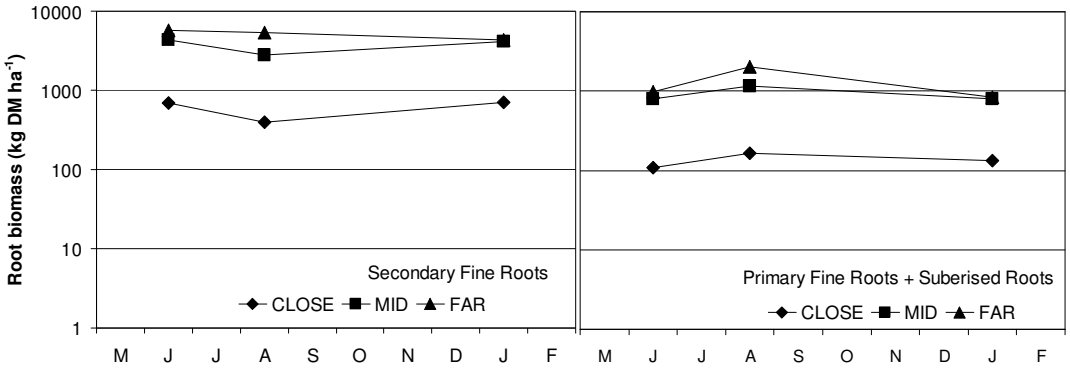


Figure 5.4. Secondary (left) and primary fine plus suberised root biomass (right) of a *G. sepium-B. decumbens* mixture during dry and wet season 1997 and dry season 1998 according to distance from the nearest tree. These figures derive from the combination of field data of root profiles and core sampling, thus the variability of this results is that of the data on which they are based (see sections 5.3.1 and 5.3.2).

Secondary roots are about ten times more in biomass than primary plus suberised root. Root biomass grew from the dry season 1997 (May-June) to the wet season (August-September), and then slightly decreased or remained more or less stable until the next dry season (January-February) for most distances and the two categories, except for the secondary fine roots in plot 8 (*G. sepium-B. decumbens*). Roots in the *G. sepium-B. decumbens* mixture abound at *mid* and *far* distances, being one order of magnitude higher in biomass than in *close* distance (Fig. 5.4). *L. leucocephala-B. decumbens* showed a steep increase of secondary fine roots between the dry and the wet season 1997. *Far* root biomass grew slightly higher by the last sampling period, whereas primary and suberised roots at close and mid distances diminished at that time of the year (Fig. 5.5).

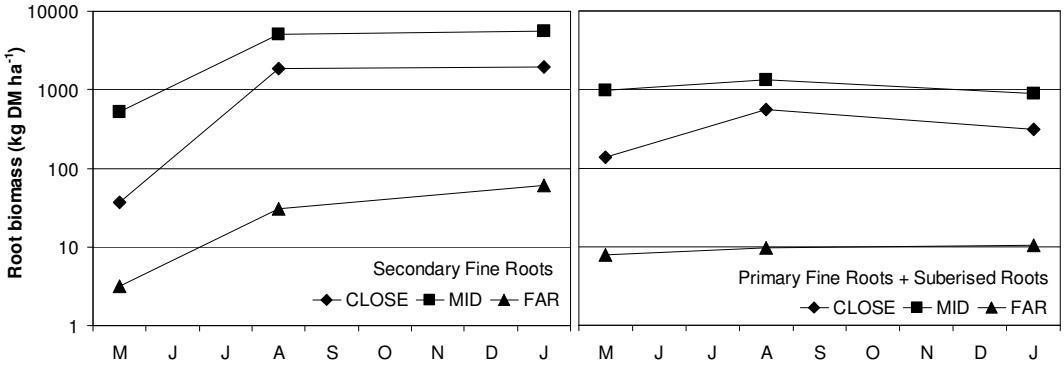


Figure 5.5. Secondary (left) and primary fine plus suberised root biomass (right) of a *L. leucocephala-B. decumbens* mixture during dry and wet season 1997 and dry season 1998 according to distance from the nearest tree.

The *D. regia-B. decumbens* mixture presented a high level of secondary fine root biomass in the dry season of 1997, which was slightly increased during the wet season and maintained in the dry season of 1998 (Fig. 5.6). In *L. leucocephala-B. decumbens* and *D. regia-B. decumbens* inter-crops root biomass is the highest at the *mid* distance and the lowest at the *far* distance, the *close* being high in *L. leucocephala-B. decumbens* and low in *D. regia-B. decumbens*.

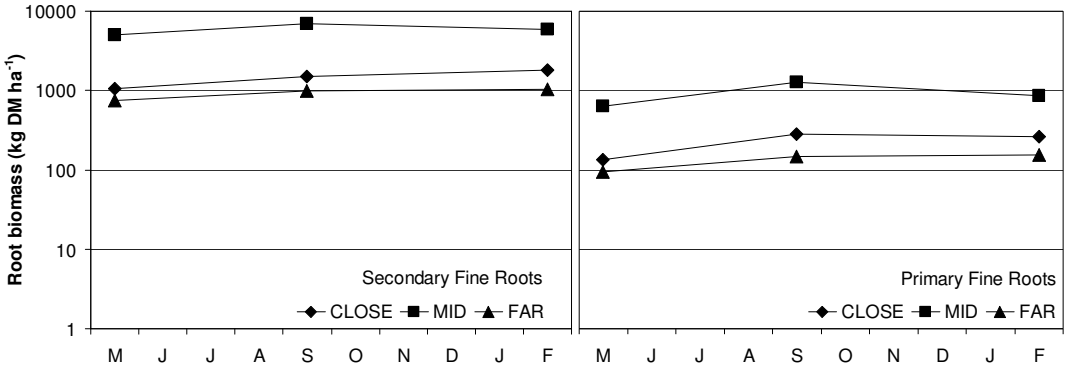


Figure 5.6. Secondary (left) and primary fine root biomass (right) of a *D. regia-B. decumbens* mixture during dry and wet season 1997 and dry season 1998 according to distance from the nearest tree. Note the logarithmic scale.

Significant differences in fine root biomass were found between distances to the nearest tree (P=0.02). No other differences in root biomass were detected, either for time after cutting and for mulching treatment, at any root class, perhaps because of a larger variability within than between treatments. The average ash free root biomass in the top 1.20 m during the experimental period for plot 8 (*G. sepium*) was 11.82 Mg DM ha^{-1} (σ = 1.3), Likewise, the average for plot 12 (*L. leucocephala*) was 7.05 Mg DM ha^{-1} (σ = 3.6) and for plot 10 (*D. regia*) was 9.93 Mg DM ha^{-1} (σ = 1.8).

These figures can be taken as good approximations to total root biomass considering the rooting patterns described (Table 5.4).

5.3.4 Tree root form

The general pattern of the tree roots was one of long shallow lateral roots reaching more than four metres from the trunk base. Since trees were planted either as small trees grown in a nursery or as poles, the original bulk of roots branched at a depth of 30-40 cm. No tap roots were found. In fact, lateral roots often grew upwards at first. New lateral roots grew from the upper main root spreading near the surface with branches exploring downwards. Some of the excavated long, shallow tree roots showed localised growth of root tips down to 0.80 m, although no physical obstruction or favourable condition was observed. Possible explanations are that there were patches of low density of grass roots, thus less competition, enabling tree roots to proliferate. The growth of the tree roots was affected by rodents and the massive presence of grass roots.

Case studies

1. The excavation of a *L. leucocephala* tree in plot 12 was completed on 13 October 1997. The tree was located in an area where large stones reached the soil surface, which made digging difficult. Because of this, only the main lateral root was fully excavated. The stem base was 5.0 cm in diameter. The lateral root, which was 94 cm long and 1.3 cm in diameter, ran at a depth of 8.0 cm below the soil surface with no bifurcation in the first 40 cm. Only two small woody roots (0.3 cm in diameter) grew from this root at 40 and 64 cm respectively, the first one of 25 cm with three fine roots 30 cm long on average, the second one of 38 cm with two fine roots 15 cm long on average. The far end of the root split into three branches of a 0.5 cm in diameter average, one 78 cm long without ramifications, the other 63 cm long with two ramifications (11.5 cm on average) and several short fine roots. The third branch was 121 cm before the first bifurcation; in the next 15 cm the root split into four roots of 41, 60, 33 and 154 cm. The first one was accidentally cut during the excavation. The second one had no ramifications but only a few fine roots. The third one proliferated in fine roots 30 cm long on

average. The fourth one branched profusely, and its far end was the only part of the whole lateral root found to penetrate to 40 cm depth.

Plate 5.2. *Leucaena leucocephala* excavated lateral root.

2. The *Gliricidia sepium* excavation in plot 8 was completed on 13 October 1997. The selected lateral root derived from the tap root at 10 cm depth. No search was made of the form and depth of the tap root. The lateral root was 3.5 cm in diameter and the longest branch reached 4.44 m, being 4.04 at 10 cm from the soil surface and 0.40 m downwards. The lateral root was shallow and short (28 cm) and so were its two branches (50 cm on average). There were ten third order branches which were rather long (50 to 295 cm) and nine fourth order roots (4 to 225 cm). There were nine fifth order roots (11 to 317 cm). Finally, there were eleven sixth order roots (8.5 to 157 cm). The total number of root tips of the whole lateral root was 87. Of this network, nine roots penetrated soil layers deeper than 10 cm, with an average of 0.63 m and maximum of 1.40 m. Very few nodules were found and they were apparently not active at the time of the excavation according to the pale yellow colour inside.

3. The *G. sepium* root in plot 7 belonged to a tree developed from a pole of 7.0 cm basal diameter. The excavation was completed on February 1998. In this case a full excavation was carried out, except for the root tips of 0.2 cm in diameter, in order to keep the tree alive. The soil in this area was deep and soft and with few stones. Even so, the roots preferred the top soil, and in contrast with plot 12 and plot 8 roots, no sign of deep penetration was found at the root ends. There were four roots (2.0 cm in diameter on average) growing from the bottom end of the pole; one of them was cut by rodents and three roots re-grew from the cut end. The four roots grew upwards and so did their bifurcations, which accounted for twenty branches (0.7 cm in diameter on average). Like the *G. sepium* root in plot 8, the third and fourth order roots (0.3 cm in diameter on average) were many and appeared near to the trunk.

Plate 5.3. *Gliricidia sepium* full root excavation.

4. The *D. regia* root excavated in plot 9 originated from a seedling that reached the bottom of the bag in the nursery, causing premature bending of the tap root. The tree was 5.0 cm in diameter at the base and the bend was 50 cm deep. Every

original root in the tree was cut by rodents, and only three very small lateral roots that also showed signs of damage from such animals remained. The first root, 0.5 cm in diameter, was 25 cm in length before splitting into three surviving branches of 29, 49 and 24 cm, each of them with further ramifications. The second root was only 0.3 cm in diameter, with 4 cm before the bifurcation, and each branch bifurcated again into two more at 8 cm on average. The fine roots were between 12 and 54 cm in length. The third lateral root was 0.5 cm in diameter, the first bifurcation was at 15 cm and each branch split several times at short distances, producing nine root tips of up to 43 cm long. There was no clear tendency in the direction of the root tips in this case. Nevertheless, there was no tap root and some root tips were found to penetrate deeper soil horizons down to 0.80 m. However, there were also root tips that were found growing upwards to the top 6 cm of soil. Among the excavated roots, *D. regia* was the most severely damaged by rodents. This is in agreement with the high mortality of *D. regia* trees at the end of the experimental period. There were cases when trees, full of foliage, were suddenly killed by rodents eating the whole root system.

Plate 5.4 *Delonix regia* Root excavation.

5.3.5 Root turnover rate

Survival analysis demonstrated significant effects of the nitrogen fertiliser doses, the depth of the observation point and the cohort on *B. decumbens* root longevity. As to nitrogen fertilisation, the intermediate fertiliser doses (200 kg N ha^{-1} yr^{-1}) resulted in the highest root longevity, with half survival time (50% remaining of the initial roots) of 18 days (average of the six cohorts), 19.9% of roots in this treatment survived after 42 days. 100 N treatment produced a half survival time of 13 days, but only 9.8% of roots survived after 42 days, whereas in the 300 N treatment 15.4% of roots survived at day 42, with a half survival time of 11 days. The switch in half survival time and survival at day 42 between the 100 and 300 treatments, resulted from the different hazard values of new and old roots in each treatment; hazard was higher in young roots of the 300 treatment, whereas it was higher in old roots of the 100 treatment (Figure 5.7).

Table 5.7. Calculated values of the scale parameter θ and the shape parameter γ and the surviving roots of *B. decumbens* grown in vermiculite - perlite, as affected by different levels of nitrogen fertilisation (kg N $ha^{-1}yr^{-1}$) under controlled conditions; figures in parenthesis are the survival estimates.

N	θ	γ	Total roots	days 7	14	21	28	42
				Cohorts 1-3				
100	19.8	1.45	45	31 (0.69)	17 (0.38)	4 (0.09)	4 (0.09)	3 (0.07)
200	34.3	1.49	72	61 (0.85)	49 (0.68)	32 (0.44)	22 (0.31)	19 (0.26)
300	15.3	1.57	16	9 (0.56)	2 (0.13)	1 (0.06)	1 (0.06)	1 (0.06)
				Cohorts 4-6				
100	22.6	1.59	169	105 (0.62)	86 (0.51)	57 (0.34)	45 (0.27)	19 (0.11)
200	25.5	1.58	194	129 (0.66)	101 (0.52)	88 (0.45)	62 (0.32)	32 (0.16)
300	22.4	1.57	88	54 (0.61)	42 (0.48)	31 (0.35)	22 (0.25)	15 (0.17)

Shorter life span of roots corresponded to small scale parameter θ values, thus hazard value is high and only few roots survive for long time (Table 5.7). Also, shape parameter is higher than unity, thus there is an increasing hazard rate; note that the 100 N treatments, of lower scale parameter θ, but contrasting shape parameter γ present higher mortality of young roots when γ is higher, although both groups end with little survival at day 42. Similarly, treatments 200 N, of high θ and contrasting γ, presented different mortality of young roots (7-14 days), but similar, and high, survival at day 42 (Figure 5.7).

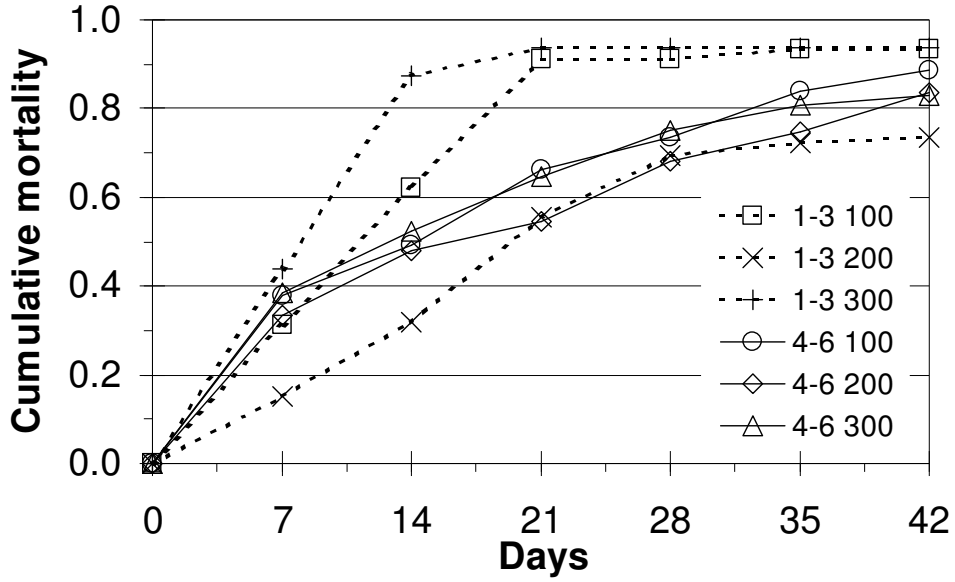


Figure 5.7. Cumulative mortality (dead roots / initial roots) of *B. decumbens* fine roots of two groups of cohorts as affected by different nitrogen fertilisation treatment.

Comparisons showed significant differences ($P<0.05$) between groups of cohorts, scale parameter increased between early and late cohorts with 100 and 300 N treatments, representing a population that moved from a small number of roots living a long time to a moderate number of roots living a long time. The scale parameter in the 200 N treatment of N decreased in the later cohorts, reducing the survival of this group.

As to the depth of the observation point, comparison between depths shows statistical differences in survival, top soil roots lasting longer. Two thirds of the roots in the top 5 cm of the pots disappeared during the first four weeks (66%), but at 15 cm and 65 cm mortality was 71 and 76% respectively. This increase can be attributed to reductions in oxygen availability, especially in the conditions of high water holding capacity of a perlite - vermiculite environment.

5.4 Discussion

5.4.1 Root biomass

Total root biomass (0 to 1.2 m depth) on average in the present study was 1182 g ash free DM m^{-2} in *G. sepium - B. decumbens*, 705 g ash free DM m^{-2} in *L. leucocephala- B. decumbens* and 993 g ash free DM m^{-2} in *D. regia - B. decumbens*. Comparable results were found in Campo Grande, Brazil, where *B. decumbens* monocrop presented 959 g DM m^{-2} of roots in the top 40 cm in an experimental field (Corrêa, *et al*., 1999), although the absence of trees and the different depths in each study make the results difficult to compare. The present results can be considered high if compared with pure or *Arachis pintoi* associated stands of *B. decumbens* in Carimagua, Colombia, which averaged 265 ± 62 and 267 ± 42 g DM m^{-2} in the first 1.0 m of soil for the pure stand and the mixture respectively (Fisher and Kerridge, 1996). This difference may be partially attributed, on the one hand, to the high aluminium saturation of soils in Carimagua (90%; Sanchez and Salinas, 1981), which reduces phosphorus availability. The value of *B. decumbens* is its ability to withstand in such adverse conditions. On the other hand, as stated in chapter 4, the good environmental conditions of the rainy season in Valle Nacional in 1997 may have boosted grass growth (the results of this study refer to a single year of measurements that may not be representative of the long-term average). Temperate pastures, on the other hand, have been reported to have up to 18.75 and 27.30 Mg DM ha^{-1} of roots in the 0-0.15 m soil layer in contrasting locations in Italy and the UK respectively (Black, 1997).

As to the effect of the distance from the nearest tree on root biomass, *G. sepium - B. decumbens* and *D. regia-B. decumbens* presented less root biomass *close* from the nearest tree and more biomass *far*, whereas *L. leucocephala- B. decumbens* had more root biomass in the intermediate distance. In the interpretation of these results, however, the different areas of each *zone* (distance) must be taken into account, since at low tree densities, *close* fraction of the land is rather small, whereas *mid* and *far* fractions are similar; at higher tree density, *close* fraction of the land increases linearly, whereas *mid* fraction increases only fractionally because of overlapping and *far* fraction quickly disappears. It is likely that such overlapping affected the

fractional area more than the actual root biomass per hectare (Table 5.2). The results of Jonsson *et al*. (1988) confirm that no clear pattern can be observed in fine root biomass in *L. leucocephala* inter-crop. Eastham and Rose (1990) found similar results to this study but with opposite trend, i.e. lower root biomass *far* from the trees, with total root mass of approximately 1050, 1040 and 750 g DM m^{-2} in 0 to 4.4 m soil depth, measured at 0.6, 1.2 and 3.25 m from the nearest tree in an *Eucalyptus grandis – Setaria sphacelata* tree-grass inter-crop in Brisbane Australia. Apparently the difference due to the horizontally shorter root system of *E. grandis*.

Variation in root standing biomass was found to be related to three important events during the experiment, namely the beginning of the rains, grass cutting and tree pruning; all of them occurring between late June and early July 1997. Although the wet season was expected to be associated with increments on standing root biomass in the top soil layer, whereas above ground harvest would cause the opposite process, that was not the case. No consistent behaviour was found between plots with respect to changes on climatic season. Whilst an increment in standing root biomass was recorded in plot 10 (*D. regia-B. decumbens*) as the wet season progressed, there was a reduction in plot 8 (*G. sepium - B. decumbens*). Likewise, contrasting results were found in relation to grass cutting, although grass roots showed a general low sensitivity to above ground cutting:

Tree pruning was, in these two plots, associated with periods of increment in fine root biomass *near* the trees. It can be that higher soil moisture retention by tree shade facilitated both higher decomposition rate and nutrient uptake by roots. It is suggested that such an increment corresponded mostly to grass roots near the tree rather than tree fine roots, since root excavations showed that the vast majority of tree fine roots appeared near the root far end; more over, total tree roots biomass did not reach a volume to self-explain such increment. However, fine grass root biomass quickly returned to its normal volume as the boost of assimilates is offset by the transference to new green tissue. The response to pruning + mulching was only marginally higher than the untouched samples and lower than the non-mulched treatment. The association of *D. regia* and *B. decumbens* did not show big changes, suggesting no important effect of the management of the tree component; this can be explained by the sparse tree rooting system, associated with very little leaf biomass.

5.4.2 Root profiles

The volume of root tips was highly variable between plots and within profiles of the same wall. There was, however, a typical pattern as to the proportion of roots by depth. The profile can be divided into three parts, the top two with grass and tree roots and the bottom one mostly with grass roots. The shape of the whole curve, however, is mainly explained by the grass roots population. The shift in the slope between the first two parts is explained by both the nutritional and physical status of the soil, which favours root growth in the top layer. The shift between the second and third parts might be due to the water table depth, deeper in the dry season. It is also partially explained by the end of the bulk of tree roots. When the rains begun in July 1997, the mid part of the root system became shallower, whereas the top part remained more or less unaltered in terms of the proportion of roots and the depth in the soil. This suggest that the changes in soil moisture are particularly important at 35 - 50 cm depth and that plant species adapt better to the dry season if their root system posses the plasticity to produce longer roots when water level is deeper in the soil. This explains the improved adaptability of *B. decumbens* to drought, compared with non-improved tropical grasses. These observations are in agreement with the experiment on root longevity in the glasshouse, where *B. decumbens* roots grown in 100 cm pots occupied the whole profile. Despite many roots concentrated in the top 10 cm (0.60 g DM per plant), an important proportion of the total root biomass was beyond 50 cm deep. The total length of the grass roots in the root longevity experiment averaged 122 cm (σ = 19.4). Similar figures have been obtained in real soil, Corrêa, *et al*. (1999) determined that the volume of *B. decumbens* roots in the top 20 cm of soil was seven to ninefold than in the 20 - 40 cm soil layer. Nevertheless, their figures (0.66 g DM 100 g^{-1} of dry soil) are, apparently, vastly higher than those of the present study, although no comparison is possible since the number of tillers in each experiment could have been very different.

With respect to the tree roots, the results of the present study are in agreement with the findings of Jonsson *et al*. (1988) where *L. leucocephala* - *Zea mays* inter-crop consistently presented between 60 and 70% of the root biomass in the top 40 cm of soil both in two and six year old stands and in stand densities of 890 and 1800 trees ha^{-1}. The shallowness of the roots of *Gliricidia* and *Leucaena* have been broadly

documented. Hairiah *et al*. (1992) in Lampung, Sumatra, measured the great majority of fine roots of these two species, grown in hedgerows with *Imperata cylindrica* (speargrass), in the top 20 cm of soil. Vidhana Arachichi and Liyanage (1998), studying coconut plantations inter-planted with leguminous trees in Sri Lanka found *Gliricidia* roots showing a pattern of 77, 10 and 13% of total root biomass for 0-15, 15-50 and 50-100 cm respectively, whereas *Leucaena* produced 83, 16 and 1% of roots in the same strata. The apparently deeper roots of *B. decumbens* compared with the tree species in this study is in agreement with the findings of tree root excavations, where woody roots were found chiefly in the top soil.

However, tree roots were not the more important part of the bulk of fine roots. Apparently only less than 5% of fine roots in this study (particularly in *Gliricidia sepium* pit) belonged to the tree species. This is less than the findings of other authors in annual alley cropping systems, Shroth and Zech (1995) reported 50% of fine roots in the top 10 cm of soil (661 kg ha^{-1}) in a *Gliricidia sepium* + maize alley cropping at 1.0 m from the hedgerow. This resulted in an increment of 17% from the sole crop at the 0-10 cm top soil, whereas the increment at 0-50 cm was 30%.

The apparently poor growth of the tree roots can be explained on the one hand by the young age of the stands and the negative effect of lopping on the below-ground development, and on the other hand on the effect of *B. decumbens* whose roots are strong competitors that prevented tree roots from capturing resources. Also, allelopathic effects of *Brachiaria* roots could have affected tree growth, although the four tree species showed different levels of tolerance in terms of the observed production of above ground biomass. Finally, rodents attack was determinant for the survival of *D. regia* and also affected *L. leucocephala* and to a lesser extent *G. sepium*.

Sources of error: The different total root counts among profiles, gave insights on the limited potential of wall profiles on the study of root density in large grass clumps as the size of the profile (150x120cm) was not enough to embrace several grass plants. Subsequent profiles of the same wall would not be independent as the presence of plants at one point affects the distribution of plants for the following measurement. They cannot be taken as time series data as every excavation entailed the elimination of the plants or part of the plants recorded previously.

B. decumbens roots are massive, a single clump root covered some times up to one half of the profile area, the large standard deviation of root tips density, particularly in the top soil, were associated with such a patchy distribution. In addition, up to three profiles from the same wall were recorded within one week by removing a 10 cm layer of the wall, which could affect the plant response on retaining or killing transport roots due to contact of root tips with air and light. Moreover, although *Brachiaria* roots spread widely, they concentrate within a relatively narrow collar at the stem base, making feasible to cut entire plants off when excavating for a new map. Unlike the agroforestry hypothesis of the safety net from deep tree roots (Van Noordwijk *et al*., 1996b), grass roots established a solid network for resource capture and transport, reaching more than 120cm deep in the soil, whereas tree roots systems in this experiment may represent weak, although true, competitors to grass roots that operates mostly in the top soil.

Total Root biomass: The variability in the composition between mixtures is noticeable, both in the fine and suberised categories. In the *G. sepium-B. decumbens* plot an important part of the roots consisted of secondary fine roots from the *mid* and *far* locations. However, the primary plus suberised roots represent between 17 and 23% share of the total biomass. The relative low share of the *close* roots is due to the comparatively low plant density (216 trees ha^{-1}) thus a small proportion of the plot in that category. In *L. leucocephala-B. decumbens* mixture, instead, the fraction of land *far* from the trees was low, owing to a higher plant density (616 trees ha^{-1}), thus there was only very little root biomass in this *zone*. Likewise in the *G. sepium – B. decumbens* mixture, the primary fine plus suberised roots played a significant part in the total root biomass. In all cases the weight of the primary plus suberised roots during the wet season is approximately twice that of the dry season,

5.4.3 Longevity

Brachiaria decumbens roots longevity is shorter than that shown in other species (Hooker, *et al*., 1995; Black, *et al*., 1996), although a variable fraction of roots remained alive at the end of the experiment. It can be assumed that, as a result of the different environmental conditions and soil fertility, two categories of roots were produced, short and long lived roots. Two attributes are considered in the

characterisation of root longevity, survival and hazard. Survival is best viewed in the *final* surviving fraction of the cohort (Table 5.7, day 42), and hazard determines how rapidly the short lived roots disappear (Figure 5.7). The shortest life span of roots was obtained preferably in the glasshouse with 300 N, and the longest lived roots were produced better in the growth room and at 200 N level. On the one hand, earlier cohorts may represent mainly primary and secondary roots, whereas later cohorts would contain a higher proportion of tertiary and quaternary roots (Black, 1997; personal communication). Tertiary and quaternary root categories are more sensitive to harvest, presenting higher rates of mortality some days after cutting and then recovering steady state. Such differences between cohorts can be partially attributed to the change from glass house to growth room. On the other hand, more roots were observed in the 200 N treatments and less roots in the 300 N treatments (Table 5.7); this is an indirect indicator of biomass, as every root in the observation window was recorded. The 100 N treatment was intermediate in survival, hazard and number of roots recorded. No clear reason was found for the results in this group.

Apart from the 100 N treatment, these results are in agreement with Nadelhoffer and co-workers (1985). These researchers compared fine root turnover in temperate forests sites with a gradient of soil fertility. They found that the production of fine roots (< 0.5 mm diameter) is higher in richer sites, whereas total fine root biomass can be higher in poorer sites and stated that low turnover rates in poor soils might be analogous to the observed lower leaf turnover in such conditions compared with the same species in more fertile soils. The different categories of roots behaved differently in terms of distribution in the profile. Roots with higher longevity dominated the top of the containers whilst shorter lived roots populated the bottom. The shift in longevity between these two groups is given by the probability of the individual roots failing to survive until reaching the condition of transport root. Fine roots can be considered meristems that can derive into transport tissue according to environmental conditions. When no water, oxygen or nutrients are available, fine roots will die. When adequate conditions remain, fine roots survive for longer, eventually developing transport tissue and new meristems.

5.4.4 Nitrogen Cycling

Grass root mortality constitutes an important share in the cycling of nitrogen in pastures. Considering the findings of this research work as to root turnover rate and the mass of roots present in the system, an equivalent of 27 times the nitrogen present in the root standing biomass is returned to the soil in the form of dead roots in one year (Table 5.8). The assumptions for these calculations are:

- There is no nitrogen retranslocation prior to root death (Nambiar, 1987). Nitrogen concentration used in the calculations derived from a forage to root N yield of 6.8 referred for *Digitaria decumbens* (Whitney *et al*., 1967). Forage crude protein was taken to be 10.4% (see section 4.3.3 in this study). Nitrogen content of crude protein is 16%.
- Root weight is constant throughout the year. The figure used is the average root biomass of the fraction of grass root in the *G. sepium – B. decumbens* mixture reported in this study (see Figure 5.3.a and section 5.3.3). This is not completely realistic since root biomass was demonstrated to vary during the experimental period. However, aiming to simplify the calculation, as no consistent trend could be determined in such a short term (May, 1997 – February, 1998), no temporal changes were assumed.
- The upper end of the age group is taken as the age at root death (e.g. for 0-7 age group: 7 days). This allows for a more robust calculation, despite the entailed underestimation of nitrogen release from each age group. Using the average age of the group (e.g. 0-7: 3.5 days) instead, would mismatch the root mortality value, which refers to the end of each interval. Thus the group of 28 days longevity can turnover 365 ÷ 28 = 13.04 times its N content in a year (Black, 1997).
- No consideration of the nitrogen mineralised out from the decaying roots is made. It is expected that a high proportion of the nitrogen released from dying roots decomposition is being taken up by the new grass roots, thus the results of this calculations are necessarily higher than the total volume of nitrogen in the system. Castilla (1992) reported a lignin to nitrogen ratio of 13 for *B. decumbens* dead roots; according to the CENTURY model (Parton *et al*., 1987; modified by Castilla, 1992), this would lead to 60% of the root litter towards the fast

decomposing soil organic matter pool, i.e. this fraction of nitrogen in dead roots will become available within the same year of root death.

- The growing period is taken to be of 365 days a year. Constant longevity fractions were used for the age groups. This is likely to be inaccurate as dry and wet seasons were found to affect root behaviour in the field (see section 5.3.3). An average of crude protein content in dry and wet seasons was used in order to reduce such disagreement.

Table 5.8. Calculated year flows of nitrogen from live to dead roots pools using growth room derived root mortality figures (Table 5.7).

Longevity Interval	Root mortality (fraction of cohort)	N lost by root death Mg ha^{-1}	Average longevity(days)	N lost Mg $ha^{-1}yr^{-1}$
0-7	0.37	0.0105	7	0.547
7-14	0.13	0.0036	14	0.094
14-21	0.12	0.0035	21	0.061
21-28	0.10	0.0028	28	0.037
28-35	0.08	0.0022	35	0.023
35-42	0.05	0.0015	42	0.013
42-365	0.09	0.0025	203	0.005
Totals	0.94			0.779

B. decumbens turns over up to 80% of its roots in 35 days, thus suggesting that rooting system demands a bigger share of assimilates for NPP than above ground biomass. Nitrogen uptake seems to reach 779 plus 240 kg ha^{-1} yr^{-1} to satisfy below and above ground demand respectively. However, as stated in the previous paragraph, much of this demand is covered by recycling of nitrogen released from the dying organs. Two aspects that can affect the recycling of nutrients and particularly nitrogen are the shorter longevity of deeper roots and the production of new roots mainly from the culms base (Davidson, 1978), leading to an unbalance on the vertical stratification of release and uptake, and worst, the release in zones where nutrients are prone to leaching. Unfortunately, this study could not embrace the assessment of such items. The importance of nutrient export in animal feeding and leaching and other forms of losses to the environment have been described in detail (Jordan and Kline, 1972; Haynes and Williams, 1993; Cadisch *et al*., 1994; Romney *et al*., 1994). Summarising the works referred above, it seems that losses in pasture systems (including animal removal and other animal transfers) range from 105 % of the inputs in unimproved hill pastures to 96 % of the inputs in intensively managed

farms. However, improved pastures have been proved to drastically reduce leaching and gaseous losses, totalling about 25 % of the inputs (both fertiliser and organic additions), the reason being the extended rooting system that readily absorb the nutrients released from urine and dung patches, preventing from leaching and volatilisation that would occur as urine urea is hydrolysed at rates higher than unimproved pasture demand (Haynes and Williams, 1993; Romney *et al*., 1994). Cadisch and co-workers (1994) calculated the nitrogen outputs (animal, excreta and soil) of *B. decumbens* swards to be of about 80 kg ha^{-1} yr^{-1}. When no additions are made, the system relies only in the diazotropic bacterial fixation and the atmospheric deposition of nitrogen. According to these authors, such sources are not sufficient in monocrop pastures, leading to soil degradation. For the soil organic matter N mineralisation to sustain pasture productivity, an input of high quality litter is required (polyphenol + lignin to N ratio lower than 12, Handayanto *et al*., 1995), such level can only be attained by associating legumes whose foliage is mainly entered to the litter pool (e.g. low palatability herbaceous legumes, prunings from legume trees) rather than browsed. Low quality litter such as that from *B. decumbens*, with C to N ratio as high as 117 (above ground litter), is likely to revert mineralisation of nitrogen (immobilisation), thus reducing pasture productivity in the long term (*ibid*). Chapter 6 in this study deals with these issues.

5.5 Conclusions

With respect to the objective of assessing the potential of the roots in the Silvopastoral system for nutrient cycling (Objective 1), indications of root net primary production (NPP) and nitrogen cycling were established. Based on the turnover rate of grass roots it seems that more biomass and more nitrogen turnover occur below than above ground. These situations put forward the hypothesis that the benefit of an extended rooting system is, at least, partially offset by the increased hazard of nitrogen leaching by deep roots of high turnover rate. This process is opposite to the hypothesis of nitrogen sequestration sought by planting leguminous trees in inter-crop as the former actively carries nutrients to the deep soil, where the probability of leaching is high, whereas the latter converts mineral nitrogen into organic forms, of slow release rate, that are deposited, hopefully, under the soil surface.

Less certainty was derived from the analysis of causes of variation in root biomass and root distribution (Objective 2). No significant differences were obtained from the comparison of tree-grass mixtures, this is related to the fact that the variability of measures of the same treatment was larger than the differences between treatments. Likewise, no significant differences were found between the three distances, although root biomass *close* to the trees was more variable, suggesting that the effect of the trees is restricted to a narrow band around each individual tree, rather than over the whole field. This is in agreement with the results of the chlorophyll readings (see section 4.4.4) as to the size of the zone of influence of an individual tree. Unlike annual crops, *B. decumbens* opposes a permanent pressure against trees growth, this put forward the idea of growing trees at closer spacing so as to restrict grass growth and reach full establishment of the association.

G. sepium trees could have had an effect of reducing grass roots growth by improving the fertility of the soil. This effect of mulching, although no significant, is in agreement with the findings of Nadelhoffer and co-workers (1985) that suggest less roots in enriched environments. The cases of *L. leucocephala* and *D. regia* are less clear, but these species were certainly in a poorer shape than *G. sepium*.

Differences due to changes in climatic season were clearer, with less roots during the driest part of the year (May – June) but with relatively more roots down at 50 cm than during the wet season (except for *B. decumbens* - *G. sepium* secondary fine roots). The same tendency was observed in January, as the soil started to dry out. Root longevity was also affected by changes in the environment. Even so the experiment did not aimed the evaluation of such source of variation, the move from the glass house into the growth room was reflected in the longevity of earlier cohorts.

The objective of characterising the rooting system of the Silvopastoral experiment (Objective 3) was achieved as to the determination of root biomass, and root architecture. Root longevity of *B. decumbens* was also determined. The results presented provide insights on the standing root biomass of grass and trees, as well as on the vertical and horizontal distribution in the soil. With 7.1 to 9.9 to11.8 Mg ash free DM ha^{-1} for *L. leucocephala*, *D. regia* and *G. sepium* mixtures respectively, roots in the Silvopastoral system account for up to five fold the aboveground grass standing biomass, being grass roots the more abundant part. Tree fine and suberised

roots were affected by both grass roots competition and rodents attack, rendering high tree mortality and poor general performance of the tree populations. The *B. decumbens* – leguminous trees inter-crop presented an abundant root system that reached invariably depths beyond 1.2 m, although most of the roots at any part of the profile belong to the grass species. *B. decumbens* root longevity does vary according to environmental conditions and soil depth. It is also affected by soil nutritional status. However, it can be concluded that most of the roots disappear within 35 days and that the half live (50% of the initial number of roots) is about 15 days.

6. Soil Fertility in an Experimental Silvopastoral System

6.1 Introduction

6.1.1 A quantitative description of soil nitrogen dynamics

The vast majority of carbon and nitrogen in tropical forest is in the biomass. However, when forest is replaced with pastures, up to 90% of carbon is allocated in the form of soil organic matter. Most of the 10% remaining integrates in the biomass, of which roots can constitute up to 60%. Nitrogen figures are likely to be proportional to carbon as the carbon to nitrogen ratio in both soil organic matter and in plants are relatively constant. However, there is a third component in the balance of nitrogen of particular interest to this study: the mineral nitrogen, which can be 100 to 1000 times smaller than the whole soil organic nitrogen pool. These figures refer to the instantaneous balance of the system; cumulative year values are less contrasting.

Compounds deriving from decomposition of plant litter have most of the nitrogen attached to carbon molecules. During organic matter mineralisation, carbon is released to the atmosphere as carbon dioxide. There is no real mineral carbon pool in soil. In summary, carbon and nitrogen balance in grazing systems is characterised by a predominant component, soil organic matter, with quantities of 50 to 300 Mg ha^{-1} dry matter (C = Organic Matter/1.72, N=C/50) containing 30-170 Mg carbon and 0.6-3.5 Mg nitrogen ha^{-1}. The next important component of tropical grazing systems is biomass with up to 2 Mg ha^{-1} above ground and 1.0-2.5 Mg dry matter below ground.

Nitrogen mineralisation implies the combustion of 10 to 20 times its volume in carbon, which is released to the atmosphere. Nevertheless tropical pastures have levels of net photosynthesis of up to 20 Mg CO_2 ha^{-1} yr^{-1}, they still can be net producers of carbon when high SOM mineralisation rates occur. Although mineral nitrogen is 2 to 3 orders of magnitude lower than that in soil organic matter, its quick "turnover" rate requires strict control in order to efficiently maximise crop yields.

6.1.2 Nitrogen translocation from dying organs

The amount and quality of plant litter is determinant for the content of organic matter in soil and for the rate at which nutrients become available for crops and associated plant populations. Agricultural practices, particularly the pruning of leaves for

mulching, causes an acceleration of nutrient cycling by preventing translocation of nutrients from old to new tissues, meaning that the fraction of the canopy being removed from the stem will drag all its nutrients to some sort of "improved" litter pool called mulch.

Translocation, ultimately, produces changes in biomass to a lesser degree than it does in litter quality, as it mainly refers to the withdrawal of soluble compounds (cell content) from dying tissues, which account for no more than 10% of the dry matter. Translocation has no significant effect on the structural components (cell wall), which account for c. 90% of dry matter. Lignifying of old structural components escalate -or worsen- the effect of translocation on litter quality.

Although pollarding is primarily an above ground agricultural practice, it has an effect on processes at root system level. As to litter production, pruning causes fine roots to die, whether this response occurs at a rate proportional to the fraction lopped, is an issue that requires clarification. In the longer term, mulch will generate a higher soil nutrient status, thus modifying the requirements of new roots. It is also unclear whether or not roots translocate nutrient before natural death, although it is likely that translocation is very limited when death occurs as a consequence of above ground pollarding.

The rationale behind this hypothesis is that this particular modality of root turnover occurs as a means of self-balance of plant parts. On the one hand, in the absence of leaves, the supply of photosynthates to maintain the root system suddenly collapses, causing the massive and more or less immediate death of fine root. We assume that no storage of soluble carbohydrates in roots occurs as this is normally associated with soil environment conditions that become adverse to root development during one climatic season, or, aged, less efficient foliage; both situations being unexpected in frequently coppiced trees in the humid tropics. On the other hand, the demand of mineral nutrients in the canopy for the build up of new tissue is temporarily interrupted, creating a virtual surplus of nutrients at root level, minimising the need for retaining-translocating the stock.

This perspective grants, in the first instance, an enriched process of soil amendment by pruning and mulching. Nutrients in leaves are released from the plant to the soil surface in the form of high quality green manure, and nutrients in roots are also

rapidly released to the soil. In the second instance, this cause-effect relationship provides the grounds for agricultural technologies where available nutrients are temporarily sequestrated in the form of root biomass and subsequently conveniently released to the soil when the roots of the accompanying crop are sufficiently spread to take them up.

6.1.3 Nitrogen from dying nodules

Many plant species, especially within the leguminous family, are able to develop symbiotic associations with nitrogen fixing micro organisms like *Rhizobium* spp. and *Frankia* spp. (nitrogen fixation being the transformation of atmospheric nitrogen N_2 into ammonium nitrogen NH_4^+). In general, the symbiosis occurs only under conditions of low soil fertility conditions and consists on the interchange of soluble carbohydrates from the tree for ammonium nitrogen. The infection causes the root hair to wrap itself around the bacteria so as to increase the interface (contact) area. This arrangement constitutes the origin of the nodules, in which nitrogen is reduced to ammonium. In tropical legumes (Phaseoleae), nitrogen is further transformed to Ureids and stored in the host plant.

When the infected roots die, nodules are rendered loose and then die as a consequence of the interruption in the supply of energy. The death of nodules -rich in nitrogen- produces an increase in available nitrogen in soil. Because of their low carbon to nitrogen ratio and low cell wall-lignin content, dead nodules promptly decay into a labile form of soil organic matter whose components, in turn, suffer mineralisation at rates in the order of 0.03 to 0.1 (g/g) d^{-1} in the humid tropics. However, since the natural turnover of root hairs is chiefly driven by the inability to cope with plant nutrients demand, *Rhizobium* infected (nodulated) root hairs are not expected to show high turnover rate (short longevity). Nodule mortality after pruning, nonetheless, can be quite high and often constitutes itself sufficient reason to introduce nitrogen fixing species in inter-cropping with the economic crop or during the fallow. The principle behind green-manuring with nitrogen fixing tree prunings is that the nutrients from one species (roots) can eventually be utilised by a second species, provided that the processes of decomposition and mineralisation remain under the control of the farmer.

6.1.4 Soil organic matter production

Agricultural systems based on natural supplies of fertilisers, as organic farming, agroforestry and most indigenous systems (extensive livestock husbandry, fallow agriculture, etc.), rely to a great extent on the same paradigm, decomposition of dead plant parts into soil organic matter and the subsequent mineralisation of nutrients from it. The rates at which decomposition and mineralisation occur depend on the activity of soil fauna and microbes, whose metabolism relies on the carbohydrates in litter and SOM.

Organic matter in soil embraces both live microbes and the decaying tissues of dead organisms. Microbial organic matter (decomposers) feed on the dead organic matter. All litter particles that are incorporated into the soil by the action of soil fauna and microbes, but not readily decomposed and further mineralised to their soluble chemical constituents, become the soil dead organic matter. Different components of litter present different decomposition rates partially depending on their carbon to nitrogen ratio. When high quality litter is decomposed, nitrogen is released to the soil solution; when rough material of high carbon to nitrogen ratio is attacked by decomposers, nitrogen from the soil solution is immobilised in order to satisfy microbial requirements (Killham, 1994). The quantity of nitrogen held in soil organic matter greatly exceeds annual inputs and outputs (Porter, 1975). The key issue in manipulating the recycling of nitrogen in tropical pastures is knowledge of the fractions of organic matter with different mineralisation rates and the interactions between the turnover of nutrients and the plant uptake (Powlson and Jenkinson, 1990; Heal and Harrison, 1990).

Turnover rates

Decomposition in plant debris is a consequence of carbohydrate assimilation, as a source of energy for soil microbes. This process is characterised by a respiratory cost, producing carbon dioxide release to the atmosphere. The compromise between gain and consumption of energy underlies the selectivity of microbes toward those compounds with lower molecular weight (Moody *et al*., 1995).

It is assumed that mineralisation of nitrogen is given at the same rate as those fractions to which it is attached. Jordan (1989) emphasised the effect of temperature, moisture and soil fertility on biogeochemical processes and suggested that it is the

concurrence of these three factors, rather than mere geographic position, which determines the rate of decomposition of plant litter. More recently the importance of soil texture and the level of inhibitors among the plant chemical constituents has also been emphasised (Feller, 1991). Clay soils reduce the contact surface between litter and decaying agents, effectively diminishing the decomposition rates of litter. Some compounds associated with the cell wall in senescent tissues, inhibit decomposition by soil microbes, e.g. phenolic metabolites.

6.1.5 Management options

Tree species

Different tree species in the leguminous family have intrinsic properties that make each one more or less suitable for a given agroforestry purpose. Fast growth rate, nitrogen fixation, deep rooting or multiple use are characteristics that seldom appear in one cultivar simultaneously. Screening for the appropriate species requires both the precise definition of the objectives of production and knowledge of the individual characteristics of the alternative species to choose from. As to the definition of objectives, a scenario of multiple objectives is common in small farming systems, and so the need for assisted decision making can arise since the proper combination of species may require experiments whose time and space the farmer cannot afford. With respect to the characteristics of every possible species, this is a vast area of research that still shows numerous gaps, especially at local level, as physical environment determines the expression of genotype. At present, there is no direct way to correctly select the appropriate tree species for a set silvopastoral system. Much help can be provided, however, by stating what characteristics have to be sought when studying trees for tree-grass inter-cropping and by systematising the knowledge so as to reveal the gaps. This is, to a great extent, the purpose of the present research. Tree species that are useful for mulch production should match the system's requirements for re-sprout rate after pollarding, low specific leaf area to allow for maximum light transmission through the canopy, nutritive value of prunings, adequate content of cell wall compounds and other inhibitors of decay, and so on.

Tree density

Individual trees can be claimed to have positive and negative effects on associated crops, the more pronounced the effect as the distance between tree and plant is shorter. On the other hand, tree populations may have positive or negative effects to the crop at plot scale, in proportion to the tree density, regardless of the effect on the neighbouring plants, i.e. shade can be deleterious to the grass growing near to very dense tree canopies, but beneficial for the water status of the grass and soil in a broader area of the plot. Clearly the more trees per hectare the more pronounced effect will occur both above and below ground. Tree density is then a matter of complex thinking as to the maximisation of beneficial effects but certainly not for preventing the deleterious ones, thus the optimum tree density combines minimisation and maximisation of different processes simultaneously. Yet, the result of a set tree density on the pasture is one of dynamic nature, according to the climatic season and the vegetative stage of crop and tree stands.

Tree pruning

In the silvopastoral system we propose, pruning trees for green manuring is considered as a means of controlling nutrient availability for the crop. Lopping entire branches produces an immediate input of green manure on soil surface and an input of dying fine roots (and nodules) to soil litter. The amount of nutrients that becomes available for uptake by grass roots depends on the volume of mulch produced and on the decomposition rate of such material. Once the system is established, pruning becomes the practice that controls the whole interaction between grass and trees (Figure 6.1). The options available range from pruning frequency and intensity to the spatial distribution and burial of mulch to root pruning. Tree species, tree density and tree pruning should be considered simultaneously when designing tree-crop systems in order to attain the maximisation of benefits and minimisation of competition.

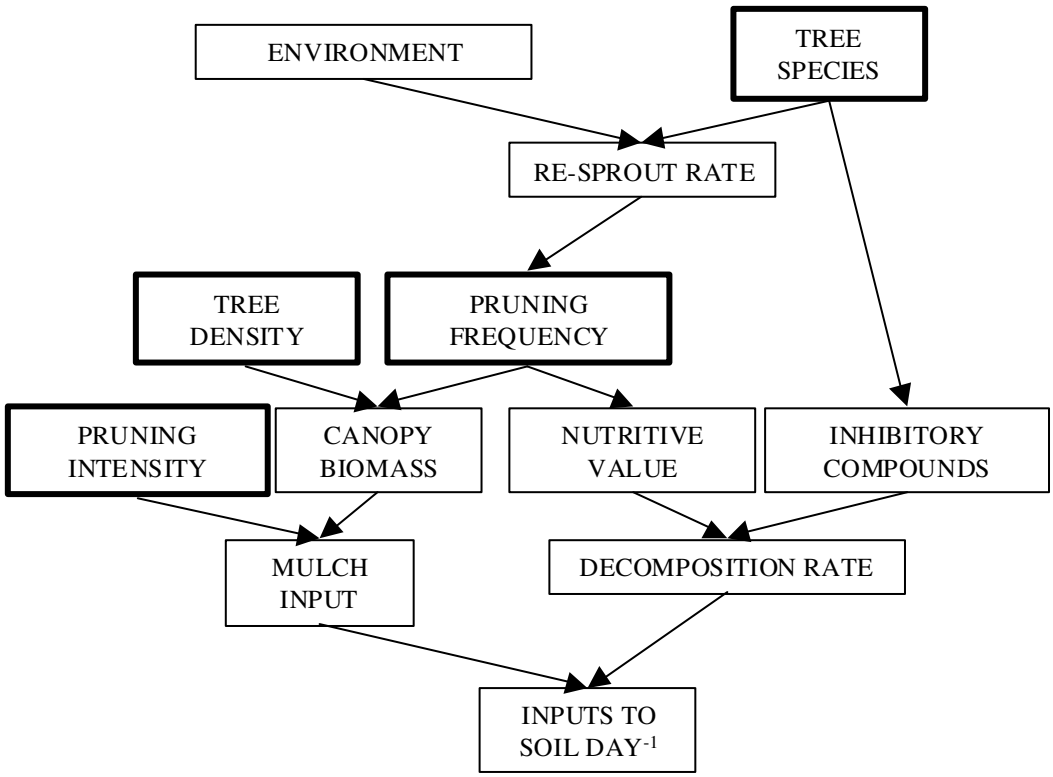


Figure 6.1 Simple flow diagram of factors affecting the input of nutrients into soil in a mulch based tree-crop system. Thick boxes indicate the management options.

In order to satisfy the objective of determining the decomposition rate of mulch from leguminous trees for pasture systems (Objective 3, page 15), three specific objectives were proposed:

1) To determine the decomposition rate of mulch from the tree legumes *L. leucocephala*, *Gliricidia sepium*, *Delonix regia* and *Lysiloma auritum* under field conditions.

2) To characterise the fate of substances and plant tissues that affect the potential for green manuring of mulch from *L. leucocephala*, *Gliricidia sepium*, *Delonix regia* and *Lysiloma auritum* subject to decomposition.

3) To evaluate the effect of accompanying trees on the soil organic matter and soil nitrogen of a silvopastoral system.

6.2 Methods

6.2.1 Decomposition rate of mulch from trees

Determination of the rate of decomposition of mulch

Decomposition was assessed on two occasions, wet and dry season, using litter bags. The trial in the wet season was established in Jun/Aug 1997 and the litter bags collected on five successive occasions at an interval of 25 days on average. The trial in the dry season was established in Nov/Dec 1997 and the litter bags were collected at five intervals of 15 days on average (for pluviometric characteristics of the two seasons refer to sections 3.3.2 and 3.3.5). Mulch decomposition presented two phases, one of rapid loss of dry matter and one of more stable residual dry matter, the shift occurring approximately one month after the beginning of the trials. These parts are hereafter referred to as first and second phase. The hypothesis model discussed here focuses on the variation of the different fractions of the unused substrate by soil microbes, namely: cell contents, cellulose, hemi-cellulose, lignin and silica (Figure 6.2).

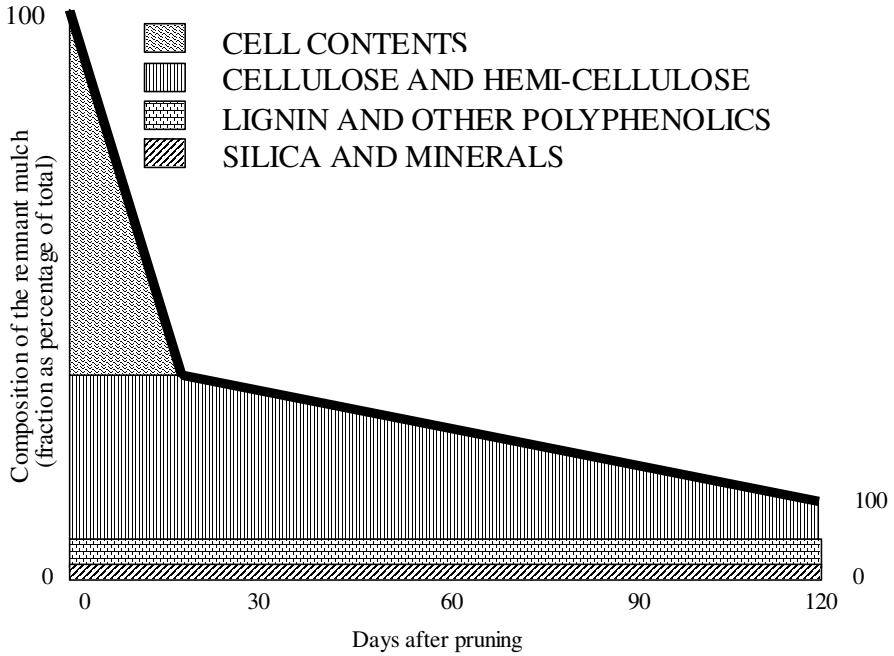


Figure 6.2 Schematic representation of the fractionation of tree mulch and the residues in mesh bags after progressive decomposition. The thick line denotes weight loss. The total remnant mulch is expressed as 100% at any time.

The use of cumulative decay functions as a mathematical approach to decomposition rate can inhibit the understanding of the process kinetics. They can, however, help in

the interpretation of the two phases of the process. In the analysis, the first phase of the decomposition process (the section of the curve with a steeper slope) is related to the disappearance of the cell contents. The second phase of the curve has a closer relation with the decomposition of the labile fraction of the cell wall. However, I also use the analytical approach of one continuous curve to stress the use of the equation for predicting the rate and extent of decomposition in the long term (3 to 12 months). Mulch disappearance was described by fitting a negative exponential equation (Eq. 6.1).

$$Y_t = Y_0 + e^{-ct} \quad (6.1)$$

Where Y_t is the remnant mulch dry matter after a period t and Y_0 is the original weight of the sample. It was common in the second phase of decomposition that the remnant mulch at a certain sampling period was higher than can be expected by the interpolation of the adjacent sampling periods, representing the retarding or lag of the decay process. This lag could be defined as the difference between the baseline remnant mulch (straight line between any sampling period and the next lower value) and the observed average remnant dry matter. This approach still underestimates decomposition, since the mere presence of decomposing mulch promotes the production of insect and microbial biomass, which combines with unused substrate in dry matter measurements, masking the extent of substrate utilisation.

Analysis of chemical factors affecting decomposition rate

In Chapter 4 the use of tree prunings as a source of fertiliser in the silvopastoral system is described. Here, the analysis of how nutrients present in mulch become available to grass and tree roots is presented. Assumptions are made that woody components of pruning material are low in nutritive value and in decomposition rate, and so their effect on soil fertility would not be measurable or important in the short term.

Leaf mulch was assessed for chemical composition, especially for those attributes regarded as limiting factors for decomposition to soil organic matter. We assessed total nitrogen (Kjeldahl) and lignin content (Klasson) to work out the nitrogen to lignin ratio, which is considered determinant for litter decomposition potential. Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF) analysis were

carried out as indicators of cell wall content, since it is considered that carbon in the cell wall (cellulose + hemi-cellulose) will present a slower decomposition rate than that in the cell content (metabolic carbon). We also analysed total phenolics (Folin-Ciocalteau) content since their influence on reducing the decomposition rate of aged material has been demonstrated. Samples were dehydrated into a chamber with incandescent bulbs, milled to pass a 0.5mm sieve and then freeze dried; sub-samples were assessed for dry matter content.

Dry samples of residues from litter bags were ground to pass a 0.5 mm sieve and analysed for total nitrogen, NDF, ADF, Klasson lignin and total phenolics with the same methods described for original mulch. Results were studied in relation to remaining biomass (g DM in the bags) to determine the importance of each factor, and the combination of factors, on the decomposition rate of mulch under field conditions.

Total nitrogen

0.5000g samples and duplicates were analysed for total nitrogen (Kjeldahl), consisting in acid digestion and distillation and titration of recovered compounds with 0.1 M Sulphuric acid. See appendix on methods for the full procedure.

Cell wall

Neutral Detergent Fibre

Neutral Detergent Fibre and Acid Detergent Fibre were developed as a more meaningful alternative method to evaluate plant cell wall. The detergent system provides a rapid procedure to estimate hemi-cellulose, cellulose and lignin content in plant materials. NDF recovers all major (hemi-cellulose, cellulose and lignin) and most minor parts (protein and bound nitrogen, minerals and cuticle) of cell wall. Since NDF is an non hydrolytic extraction, only non-bound components of the lignified cell wall matrix, such as pectin, are lost during the process (Van Soest, 1994). NDF consists of a non hydrolytic extraction with a neutral (pH 7) solution of sodium lauryl sulphate with the chelating agent ethylenediaminetetraacetic acid (EDTA), which prevents heavy metals and alkaline earth metal ions from interfering in the preparation of the fibre residue (Van Soest, 1963a).

Acid Detergent Fibre

ADF is essentially useful as an intermediate step towards the partitioning of cell wall components since it recovers only very low nitrogen complexes such as cellulose and lignin in conjunction with the highly insoluble non-carbohydrate fractions (Van Soest and Moore, 1965; Van Soest, 1994). ADF is based on the extraction of plant tissue with a strong acid solution (1.0 N sulphuric acid) of a quaternary detergent such as (2%) cetyltrimethylammonium bromide (Van Soest, 1963b).

Lignin

Acid Detergent Fibre bags with residues were assessed for lignin with 72 % Sulphuric Acid. Bags with lignin residue were washed with distilled water to eliminate sulphuric acid (until pH 5.0) and then with acetone to eliminate water. Dry weight was determined before and after incinerating.

Analysis of results

Five fractions of the plant cell are described, either because they are known to affect decomposition rate (cellulose and lignin) or because they are useful for the interpretation of the estimates of other fractions (cell contents, hemi-cellulose complex and biogenic silica plus some pectin, Figure 6.3). Lignin complex contains lignin, cutin and minerals, but it is often found to be contaminated with non lignin phenols, Maillard products and synthetic plastics. Hemi-cellulose complex contains mostly hemi-cellulose but also cell wall nitrogen and some tannin.

This fractionation approach is routinely used for the analysis of digestibility in foodstuffs. It was first proposed by Van Soest (1963a,b) and its suitability for the analysis of green manure is based on the parallel of rumen digestion and the decomposition of soil organic matter, particularly in the case of enhanced litter (e.g. mulch from legumes) during the earlier stages of decay (Chesson, 1997). Two reciprocal sequences of analysis are combined in order to derive the five fractions, which respond different to neutral and acid detergents. The core sequence consists of the NDF analysis followed by ADF since the residue of NDF is representative of the entire cell wall and the residue of ADF can be used as a intermediate step for the determination of cellulose and lignin, provided other fractions (biogenic silica, pectin, cell wall minerals) have been dissolved and their interference thus minimised.

The difference between ADF and NDF residue can be considered mainly hemi-cellulose, although some compounds can be expected to cause interference (Bailey and Ulyatt, 1970) since litter bag residues are particularly rich in insoluble cell wall components.

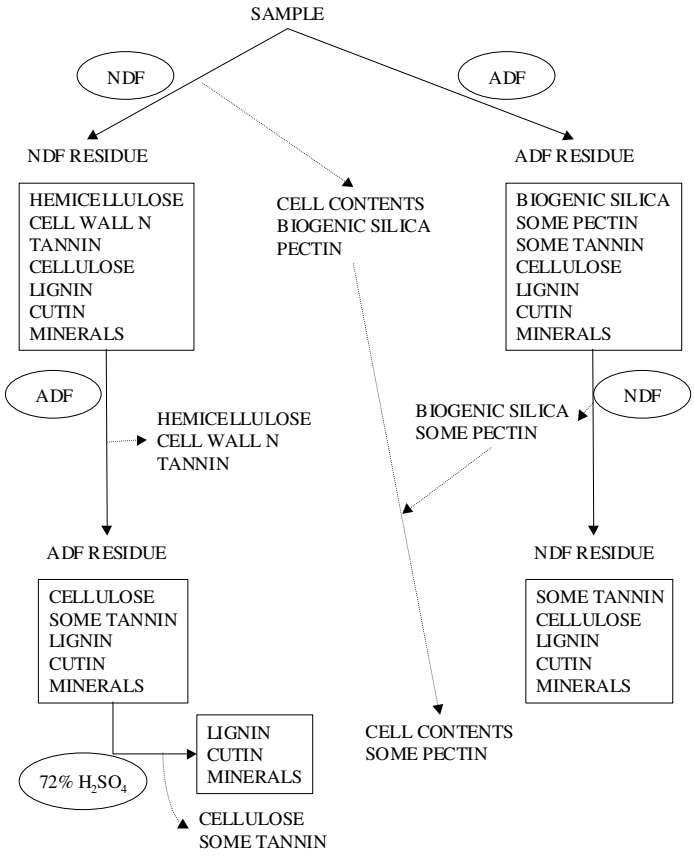


Figure 6.3 Flow diagram for sequential analysis of plant cell wall; continuous arrows and boxes denote residues of analysis (ovals), dotted arrows denote fractions measured as weight loss (based on Van Soest, 1994, p. 147).

This is normally achieved through the pre-digestion with neutral detergent of high sodium concentration (Van Soest, 1994). The reverse sequence is useful for the assessment of biogenic silica, pectin and cell wall minerals, which interfere with the determination of cell contents, calculated by weight loss in the sequence ADF - NDF. Results from the subsequent fractionation were submitted to Repeated Measures Analysis of Variance and differences between adjusted means were determined with multiple comparison T test for Least Square Means, both in the General Linear Models procedure of SAS (SAS Inc., 1990). A multiple linear regression model was fitted for residual dry matter, considering all the components of variance derived

from the layout of the experiment and the analyses, namely, climatic season, sampling period, total nitrogen, cellulose, hemi-cellulose, and lignin. Regression analysis was performed with the REG procedure in SAS (SAS Institute Inc., 1990). Species, cell content and silica were not included as they caused problems of collinearity to the other variables.

Total phenolics: Phenolics were assessed colourimetrically with the Folin-Ciocalteau method (Folin & Ciocalteau, 1927) slightly modified by Waterman and Mole (1994). This method consists of the extraction and oxidation of phenolate ions and the determination of absorbance of the reagent complex. Extraction of phenolics from plant residues is based on solvation and diffusion of phenolics into the selected solvent (ethanol 80%) at 60. Oxidation of phenolate entails the reagent complex (phosphotungstic-phosphomolybdic acid) to turn blue during reduction. The more phenolics, the more blue the reagent becomes, provided alkaline conditions are created by adding saturated sodium carbonate solution. Molybdenum – tungsten blue was assayed at 760 nm in an spectrophotometer (Beckman DU-65) and the absorvance readings transformed into total phenolics (g 100g DM gallic acid equivalents^{-1}). Waterman and Mole (1994) reviewed the more common techniques for total phenolics assessment and concluded that there is no ultimate method to suit all necessities but different choices that each researcher has to evaluate in terms of the type of material and facilities available.

6.2.2 Soil chemical characterisation

In order to assess the effect of tree-grass mixtures in soil fertility and in some factors affecting soil fertility, namely organic matter (OM), total nitrogen (N_{tot}), available nitrogen (NO_3) and aluminium (Al) content were determined in soil samples taken at the end of the experiment (February, 1998) for chemical characterisation. Soil cores (1.5 inch) were taken at two depths (0-15 and 15-30cm) from Plot 2 (*L. auritum-B. decumbens*), 3 (*G. sepium* seed *–B. decumbens*), 4 (*Gliricidia sepium* poles *–B. decumbens*), 9 (*D. regia-B. decumbens*), 12 (*L. leucocephala-B. decumbens*) and 11 (control without trees). Five samples from three distances from the nearest tree and from each depth were pooled and sub-sampled for dry matter and bulk density determination, and subsequently for laboratory analysis. Organic matter and total nitrogen were assessed as a general appraisal of the effect of the establishment of

silvopastures. Organic matter gives information about the improvement of the input of C and N from the atmosphere to the system; organic matter is proposed to act as check of the status of soil total nitrogen since it can be assumed that soil total nitrogen perform proportionally to soil organic matter. Nitrates were assessed as a measure of the nitrogen available to plant roots, which might not show significant increments since the root systems will deplete it soon after its mineralisation. Aluminium was measured to provide insights into the availability of phosphorus for the crop. Tests were assessed in duplicate for each sample. Analysis of soil samples from February 1998 (end of the experiment) was carried out in the soil analysis laboratory of the University of Chapingo, Mexico. Analyses of samples from other sampling periods were performed in Edinburgh University. Results were statistically analysed with the GLM procedure of SAS (SAS, Inc. 1990) through the model:

$$y_{ijk} = m + plot_i + distance_j + plot * distance_{(ij)} + depth_k + e_{l(ijk)} \qquad (6.2)$$

Where y is one of the variables of study (OM and N_{tot}). NO_3 and Al data sets did not comply the assumptions of ANOVA because NO_3 is discrete and Al insufficiently accomplished. Therefore results are T-test compared instead. Plot and distance are the class variables and depth is a covariate to adjust for the two depths of the sampling (0-15 and 15-30 cm).

Soil organic matter content

Total Organic Matter was calculated in two different forms. Samples from February 1998 were analysed with the rapid titration method (Walkley and Black, 1934). Samples from previous sampling periods were brought to Edinburgh and incinerated after determination of moisture content, i.e. loss on ignition method. The difference between the weight before and after incinerating is assumed to be the soil organic matter (Allen *et al.*, 1974). Organic matter content in soil (kg m^{-2} in the top soil) is calculated from the residue of incineration, soil layer thickness in metres (L) and bulk density (ρ_b Mg m^{-3}).

$$TOM = OM\ L\ \rho_b\ 10^3 \qquad (6.3)$$

Where OM is fraction of soil that disappears after ignition.

Total nitrogen

One set of samples was analysed in the Kjeltec-auto analyser 1030 in Chapingo. A second set was analysed by a similar method in Edinburgh. Total Soil Nitrogen (N_{tot}) calculations were based on soil layer thickness, L and bulk density, (ρ_b).

$$N_{tot} = N\ L\ \rho_b \tag{6.4}$$

Since mineral nitrogen is considered negligible in air dried bulk soil, results from Kjeldahl analysis can be considered mostly nitrogen from organic matter.

Available nitrogen (NO_3)

Nitrates were extracted with 1.0 M KCl at 20:1 v/w and assessed in a Kjeltec-auto analyser 1030 after extraction with 2N KCl in the Soils Department Laboratory, University of Chapingo, Mexico

Soil organic nitrogen mineralisation rate

Mineralised nitrates were determined colourimetrically with Nitrachek strips (Merckoquant Nitra test strips, MERCK Co.) before and after incubation. Colour was measured with a Nitrachek meter (Nitrachek 404, Challenge Agriculture, UK) according to the method described by Rees *et al*. (1996).

6.3 Results

6.3.1 Decomposition rate

The tree-grass treatments differed in the rate of decay during the first phase, and the percentage of residual dry matter (extent of decomposition) at the end of the second phase. Decomposition results are referred to as apparent decomposition to stress the difference between the variation of mulch residue weight and the actual decay process.

Table 6.1. Regression equations for cumulative apparent decomposition in mulch from tree NFT species in a Tree-Grass Inter-Cropping System in the Humid Tropics (g $100g^{-1}$).

Species	Regression Equation	R^2	P
Leucaena			
Wet season	$y = 8.7 + 88.4e^{-0.01x}$	0.76	0.0002
Dry season	$y = 18.2 + 72.9e^{-0.01x}$	0.72	0.0016
Gliricidia			
Wet season	$y= 51.4e^{-163.1x}+48.6e^{-0.003x}$	0.71	0.0028
Dry season	$y = 30.7 + 69.0e^{-0.12x}$	0.95	<0.0001
Lysiloma			
Wet season	$y = -129.9 + 225.9e^{-0.001x}$	0.60	0.0025
Dry season	$y = 52.5 + 47.2e^{-0.09x}$	0.90	<0.0001

G. sepium mulch presented the highest rate of apparent decomposition compared with *L. leucocephala* and *L. auritum*, with 0.039 and 0.035 d^{-1}, for the first phase of decomposition during the dry and wet season respectively (these figures were generated by linear regression between the original sample weight and the remnant one sampling period). *G. sepium* and *L. leucocephala* presented more extended decomposition than *L. auritum* at the end of the second phase of the trials. The extent of apparent decomposition in *G. sepium* during the dry season was more pronounced (Figure 6.4). A decay lag occurred between the 30 and 45 days in the dry season, whereas an absolute increment in the bags content occurred in the whole second phase of the rainy season trial, retarding the decomposition process. Negative exponential functions fitted the results (Table 6.1).

Plate 6.1. Litter bag. Note the wider mesh at the top to facilitate arthropods to gain access to mulch. This bag was on a thick bed of dead grass, this was unfortunate.

Plate 6.2. *Delonix regia* litter bag contents, 30 days after cutting; very little decomposition occurred as can be seen in the shape of the leaflets, which remain untouched. Note the two sources of contamination: roots (bottom centre) and grass shoots (right) proliferating into the bag.

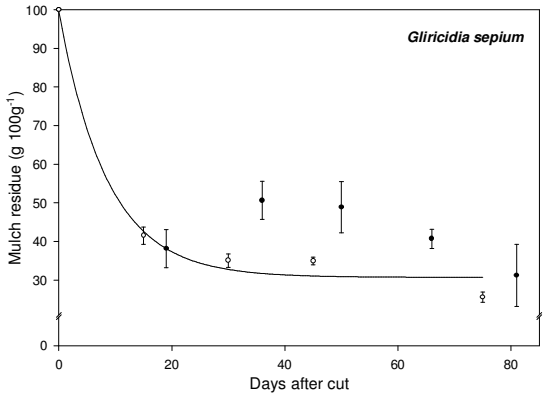


Figure 6.4 Cumulative apparent decomposition of mulch of *Gliricidia sepium* according with the climatic season in a Tree-Grass inter-cropping system in Oaxaca, Mexico (Wet season ● and Dry season ○). Fitted curves correspond to the dry season.

L. leucocephala results refer to the first 75 days of the trials, although the trial during the rainy season last longer (110 days). *L. leucocephala* lose weight to the same extent during rains as during the dry season (51and 53 g 100 g^{-1} in 75 days respectively). The initial apparent decomposition rate of the dry season (0.018 d^{-1}) was determined by the quick reduction of remnant biomass in the early dry season. However, a slight increment during the third sampling period suggests the build-up of the bag contents (Figure 6.5). Nevertheless the calculated initial rate of the wet season (0.011 d^{-1}) cannot be assumed as the absolute maximum since the first sampling period only happen until day 27. The results from rains suggest a slightly slower process than in the dry season. An exponential decay function adequately fitted the results (Table 6.1). Likewise for *G. sepium* residues, an apparent rise in the contents of the bags was observed in the last sampling period.

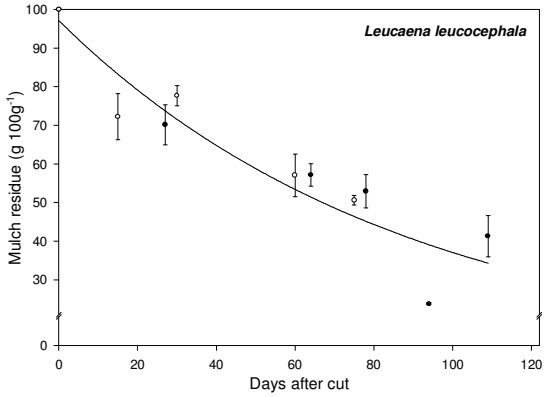


Fig. 6.5 Cumulative apparent decomposition of mulch of *Leucaena leucocephala* according with the climatic season in a Tree-Grass inter-cropping system in Oaxaca, Mexico (Wet season ● and Dry season ○). Fitted curves correspond to the dry season

In the case of *L. auritum* mulch, apparent decomposition occurred less rapidly during the early stage of the rains trial but steadily continued for the span of the experiment, remaining about 60 g $100g^{-1}$. Mulch disappearance during the dry season was similar to *G. sepium*: rapid in the early stage and becoming asymptotic afterwards (Figure 6.6). There was no lag detected during the dry season, but the lag in the rainy season was very high and long. The initial apparent decomposition rate was 0.023 d^{-1} for the dry season and 0.005 d^{-1} for the rains. An exponential negative function fitted the disappearance of *L. auritum* mulch (Table 6.1).

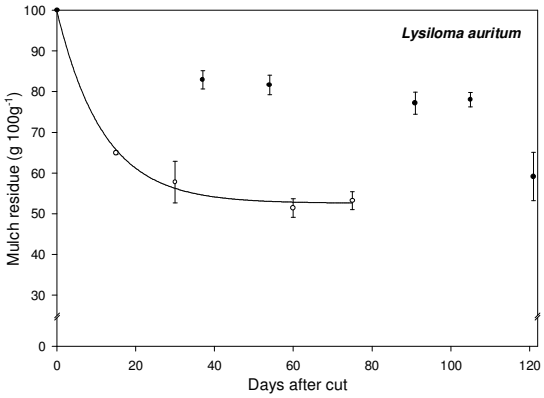


Fig. 6.6 Cumulative apparent decomposition of mulch of *Lysiloma auritum* according with the climatic season in a Tree-Grass inter-cropping system in Oaxaca, Mexico (Wet season ● and Dry season ○). Fitted curves correspond to the dry season.

6.3.2 Chemical factors affecting decomposition rate

Stepwise linear regression analysis denoted that Total nitrogen and Cellulose content in mulch, as well as the length of the decomposition period are the factors that affect the most on the rate and extent of decomposition of prunings residues of the leguminous trees included in this study (Table 6.2). The linear model that best fitted the results with a minimum of components was that of four variables (P=0.0001), namely the intercept, days after lopping, cellulose content and total nitrogen in mulch, with r^2 of 0.78. Further addition of variables resulted in only marginal enhancements of this indicator.

Table 6.2. Stepwise Linear Regression results of factors affecting decomposition of mulch from leguminous trees in litter bags in a Silvopastoral system with *B. decumbens*.

Variable	Parameter Estimate	Standard Error	r^2
Intercept	**77.1**	**13.1**	
Cellulose content	**-2.4**	**0.4**	**0.49**
Days after lopping	**-0.3**	**0.1**	**0.68**
Total nitrogen	**10.8**	**2.5**	**0.78**
Climatic season	9.4	2.6	0.83
Hemicellulose content	-0.6	0.4	0.84
Lignin content	0.1	0.3	0.84

Each row present the next variable added to the model, its best parameter estimate, standard error and r^2 of the model. Bold typing indicates the minimum set of variables of a satisfactory linear regression model.

Table 6.2 (Continuation). Pearson correlation coefficients / P>|R| matrix of factors affecting the weight of remnant biomass of litter bags with mulch of leguminous trees.

	Season	Days after cut	Total Nitrogen	Cellulose	Hemi-cellulose	Lignin
Remnant	-0.004	-0.48	0.67	-0.70	0.16	-0.49
	n.s.	0.0003	0.0001	0.0001	n.s.	0.0002
Season		0.03	-0.33	0.17	-0.12	0.48
		n.s.	0.0211	n.s.	n.s.	0.0003
Days after cut			-0.23	0.06	0.06	0.66
			n.s.	n.s.	n.s.	0.0001
Total Nitrogen				-0.44	0.37	-0.42
				0.0019	0.0114	0.0037
Cellulose					-0.25	0.40
					n.s.	0.0033
Hemi-cellulose						-0.11
						n.s.

Note: n.s. stands for not significant ([P> |R| under Ho: Rho=0] > 0.05). n = 47.

Total nitrogen

Total N in mulch residues from different species presented significantly different patterns of disappearance, according to season and time (P=0.0001). Mulch residues of *G. sepium* released nitrogen faster than either *L. leucocephala* and *L. auritum* (P=0.0002) Fresh mulch of *G. sepium* (leaves & twigs) contained an average of 3.8%

N at the beginning of the two decomposition trials (wet and dry seasons). Total N loss in the trial established in August was rapid during the first phase (1.48 % of the residue DM) and stabilised at 2.2% in the second phase. In the trial established in November total N loss was only 1.04% of residue dry matter during the first phase of decomposition and then there was a gradual recovery of 0.26% in the N content of mulch residue in the litter bags (Figure 6.7).

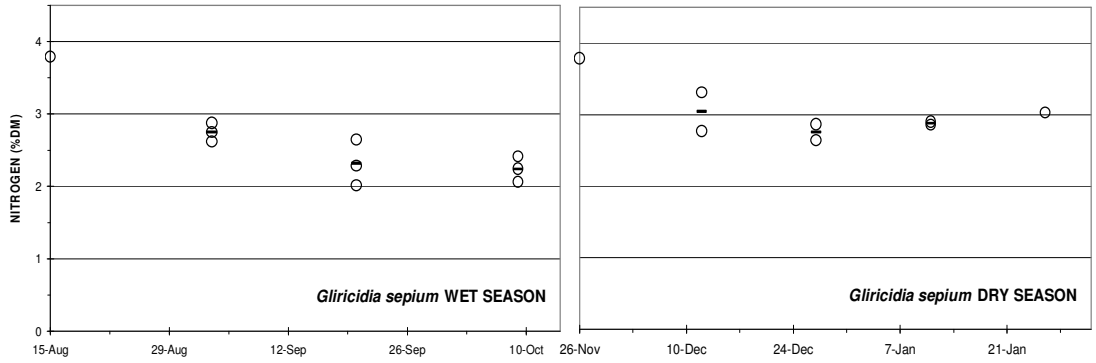


Fig. 6.7 *Gliricidia sepium* mulch and mulch residues total nitrogen content (samples O and average -) after different periods of decomposition. The trials started on August 15 and November 26, 1997.

L. leucocephala had the highest total N content in the original mulch (4.09 and 3.86 % DM in June 1997 and November 1997 respectively); Shelton *et al.* (1991) reported an average concentration of 5.4% N in young leaves of *L. leucocephala* cv. Peru in several sites in Australia. Total N in *L. leucocephala* residues did not show the two phases of disappearance observed in *G. sepium*. No statistically significant differences were found between seasons, but it is noticeable that the trial in the wet season had a slight linear reduction in total N content during the 75 days of monitoring, whereas the data from the dry season showed a slight increment during the first 45 days and a small reduction by day 60 (Figure 6.8).

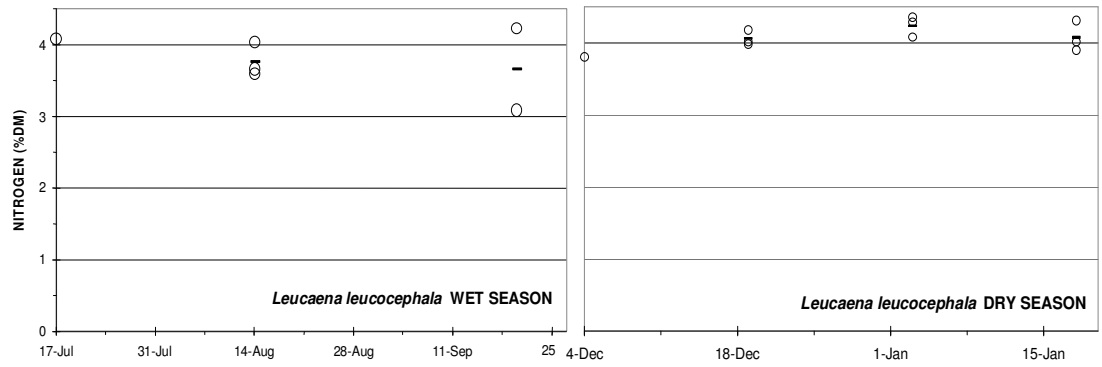


Fig. 6.8 *Leucaena leucocephala* and mulch residues total nitrogen content (samples O and average -) after different periods of decomposition. The trials started on June 17 and December 4, 1997.

L. auritum presented total N of 3.28 and 2.85% in original mulch in dry and wet seasons respectively, although only data of decomposition during the dry season are presented. Likewise *L. leucocephala*, *L. auritum* mulch residues presented an increment in total N content of the residual dry matter in the first month and stabilisation between day 30 and 45 of the trial (Figure 6.9). Because of the lack of further data it is not possible to describe the fate of the contents of total N in the residue, but the only data at 60 days shows no changes from previous values.

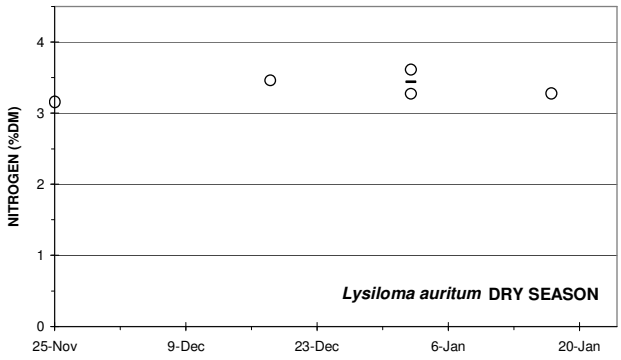


Fig. 6.9 *Lysiloma auritum* and mulch residues total nitrogen content (samples O and average -) after different periods of decomposition. The trial started on November 25, 1997.

Table 6.3. Residual mulch fractions as original and at the third sampling period (this level is representative of the composition of the residue after stabilisation. Values are % of total dry matter).

Species	Decay (days)	Cell Content (%)		Hemicellulose Complex (%)		Cellulose + Some Tannin (%)		Biogenic Silica + Some Pectin (%)		Lignin Complex (%)	
Lysiloma (dry s.)	0	57.7		22.1		10.5		2.8		6.9	
	45	36.3	(0.34)	20.2	(0.13)	13.8	(0.18)	13.4	(0.23)	16.2	(0.55)
Gliricidia	0	69.0		11.3		10.8		2.7		6.2	
Wet season	55	16.4	(1.45)	14.4	(0.60)	17.2	(0.67)	11.3	(0.09)	40.6	(1.15)
Dry season	45	34.7	(3.83)	14.2	(0.23)	23.7	(1.45)	6.8	(0.43)	20.6	(0.95)
Leucaena (wet s.)	0	64.0		13.3		12.7		2.7		7.3	
	65	22.6	(3.05)	19.7	(0.51)	16.8	(1.72)	11.3	(0.46)	29.6	(0.98)
Leucaena (dry s.)	0	56.5		17.2		14.6		3.7		8.0	
	45	30.0	(3.38)	16.4	(0.51)	18.0	(1.35)	10.1	(0.51)	25.5	(1.23)

Note: Values in parenthesis are Standard error.

Cell Contents

Cell contents also refer to some pectin that is dissolved during ADF analysis. *Gliricidia* original cell contents (69.05% DM) were higher than *Leucaena* (60.25% DM) and *Lysiloma* (57.7% DM) for the wet and dry seasons in average. Cell contents presented a significant reduction in weight during the first 45 days of the experiment (P=0.0001). All treatments reached stability in remnant cell contents weight within one month of decomposition (Figure 6.10), thus no further chemical analyses were performed in samples from longer periods of decomposition. Cell contents diminished faster than any other fraction of the cell, the climatic season being the only component of variation (not considering time of decomposition) with significant effect on the remnant cell contents (P=0.0001). However, there was an interaction between time of decomposition and season, i.e. mulch released different amounts of cell contents during each climatic season (P=0.0001). Mulch from all the species during the rains lost cell content at higher rate than in the dry season (40% and 30% average in 45 days, Table 6.3).

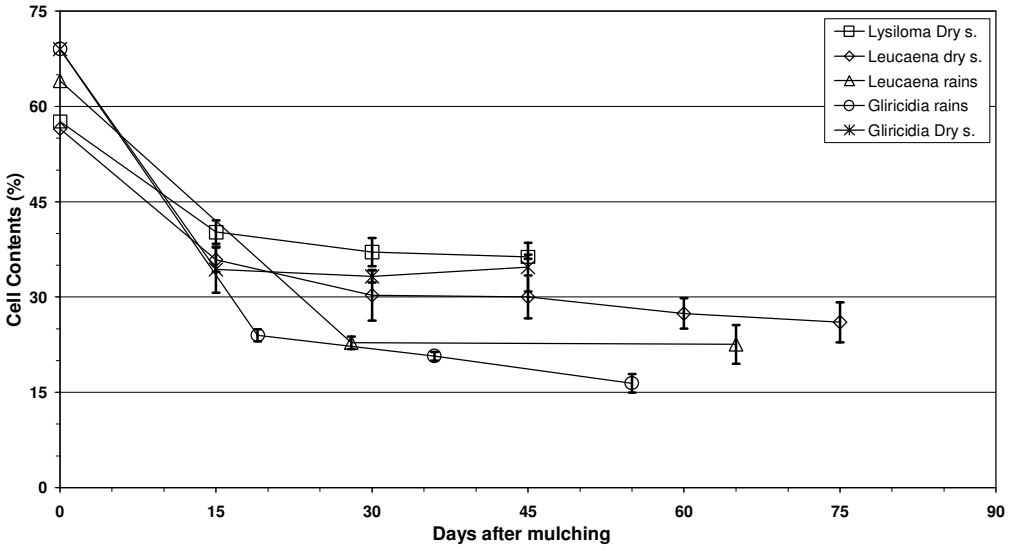


Fig. 6.10 Cell contents (plus some pectin) fraction of mulch residues of tree legumes in a tropical silvopasture. The error bars are one standard error to both sides.

Hemi-cellulose complex

Hemi-cellulose complex contains also the nitrogen attached to the cell wall and tannins dissolved during ADF analysis. *G. sepium* original hemi-cellulose content (11.31% DM) was lower than *L. leucocephala* (15.27% DM) and *L. auritum* (22.11%

DM) in average of wet and dry season values. There was a significant increase in the proportion of hemi-cellulose in remnant mulch (P=0.0001) after 45 days of decomposition (Figure 6.11). Similarly to Cellulose, hemi-cellulose behaved differently between tree species mulches (P=0.0001). Likewise, season affected differently the rate of disappearance of hemi-cellulose. The interaction time/species/season was also significant. *L. auritum* retained more hemi-cellulose than *L. leucocephala* and the two were higher than *G. sepium*. *G. sepium* presented similar levels of hemi-cellulose during both dry and wet season, whereas *L. leucocephala* had slightly higher levels in the wet season (Table 6.3).

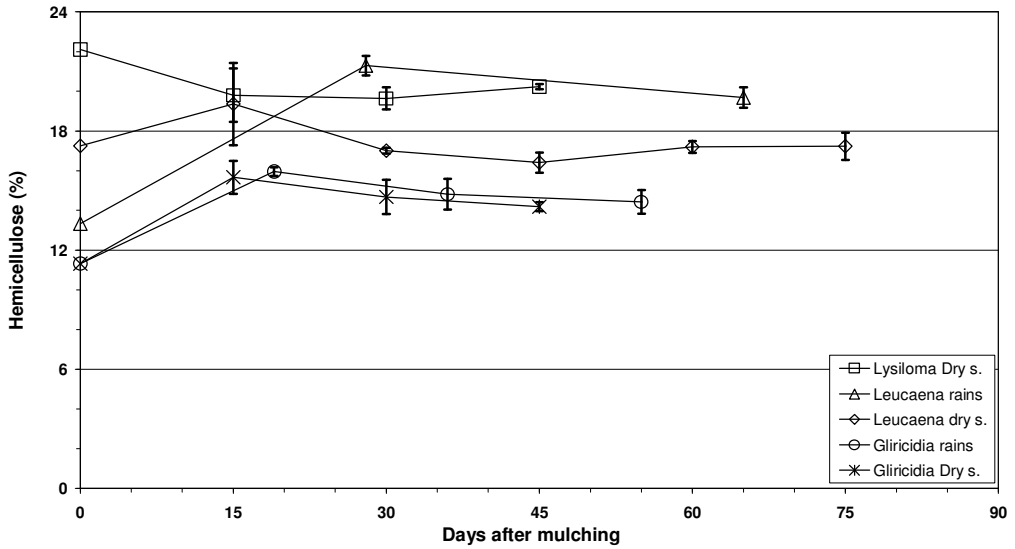


Fig. 6.11 Hemicellulose complex (hemicellulose, cell wall nitrogen and some tannin) fraction of mulch residues of tree legumes in a tropical silvopasture. The error bars are one standard error to both sides

Cellulose

This fraction also contains some tannin not dissolved during ADF analysis. Cellulose was originally lower in *Lysiloma* (10.50% DM) and *G. sepium* (10.75% DM) than in *L. leucocephala* (13.62% DM) in average of wet and dry season values. Cellulose significantly reduced its volume from the time the trials were established, but since the cell content disappeared more quickly, the proportion of Cellulose in the remnant decomposing material increased (Figure 6.12, P=0.0001). Cellulose fraction also increased differently between species during the monitoring period (P=0.0001). A significant time/season interaction revealed different rates of cellulose disappearance between seasons (P=0.0016). Remnant cellulose fraction in *G. sepium* was higher

than *L. leucocephala* and these two were higher than *L. auritum*. Yet, *G. sepium* mulch cellulose was higher during the dry season than in the rains, whereas in *L. leucocephala* it was lower in the dry than in the wet season (Table 6.3).

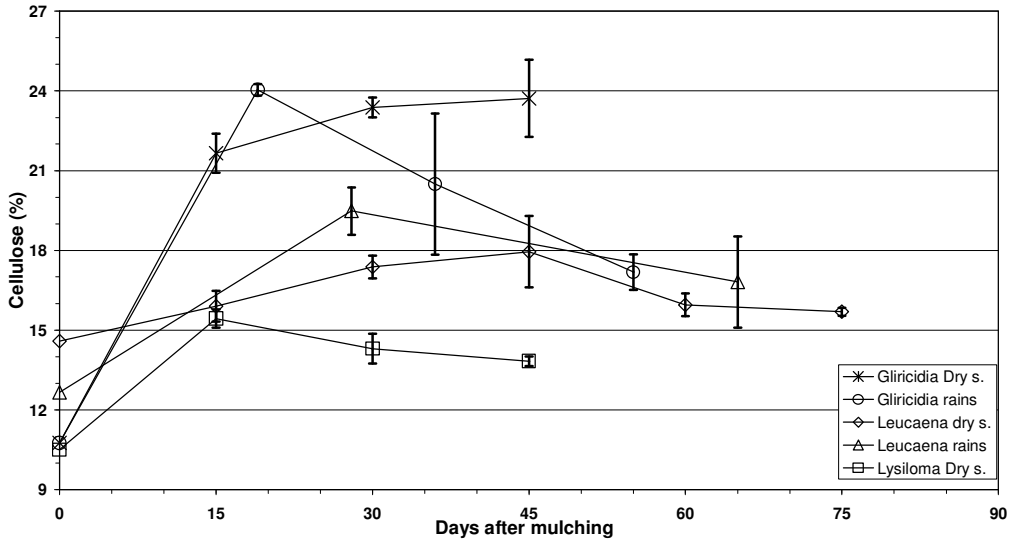


Fig. 6.12 Cellulose plus some tannin fraction of mulch residues of tree legumes in a tropical silvopasture. The error bars are one standard error to both sides

Biogenic Silica

The results reported include biogenic silica plus some pectin that was not dissolved in the ADF analysis (Table 6.3). *G. sepium* had originally less biogenic silica (2.69% DM) *L. auritum* (2.81% DM) and *L. leucocephala* (3.17% DM) biogenic silica fraction in residual mulch increased significantly during the monitoring period (P=0.0001). Species, season and species/season interaction were also significant (P=0.0001, 0.002 and 0.04 respectively). Likewise, the rate at which it varied between species (time/species) was significantly different (P=0.0001) and so was the effect of the interaction time/season (P=0.0001).

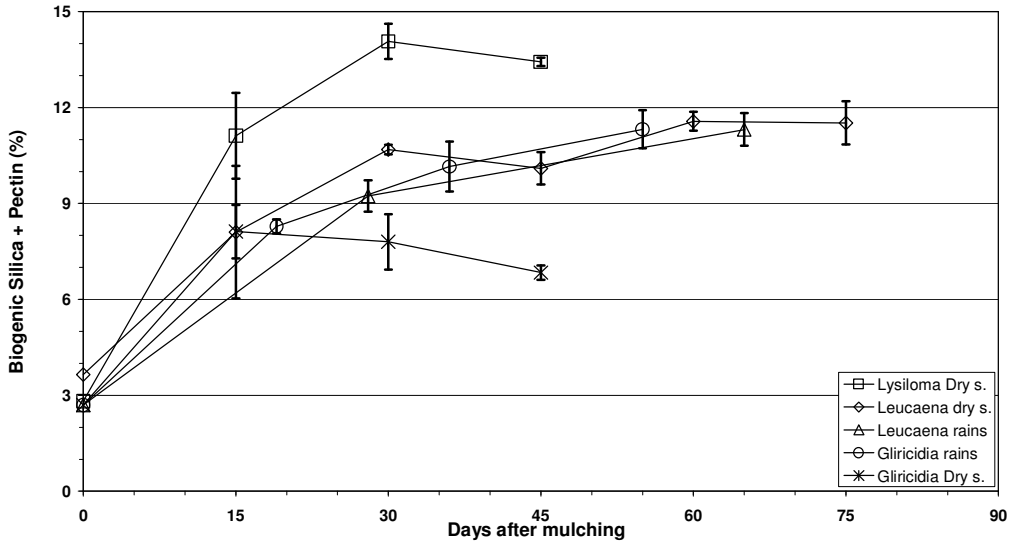


Fig. 6.13 Biogenic silica plus pectin of mulch residues fraction of tree legumes in a tropical silvopasture. The error bars are one standard error to both sides

L. auritum presented the higher level of remaining Biogenic Silica, *L. leucocephala* having an intermediate value and *G. sepium* the lower (Figure 6.13). *L. leucocephala* and *G. sepium* effects are different between climatic seasons, with constant levels in *Leucaena*, but a higher level in *G. sepium* during the rains than in the dry season (Table 6.3).

Lignin complex

The lignin complex includes cutin and minerals that are not dissolved in the NDF-ADF sequence. *G. sepium* presented the lower lignin complex content (6.19% DM), followed by *L. auritum* (6.92% DM) and *L. leucocephala* (7.67% DM) in average of wet and dry season values. The fraction of lignin complex in the remnant mulch significantly increased during the 45 days of monitoring (P=0.0001). All the components of variance and their interactions were significant, so that the results are difficult to describe. *G. sepium* mulch retained more lignin complex on a percentage basis than *L. leucocephala* during the wet season but less than *Leucaena* during the dry season. Both species retained more lignin complex than *L. auritum* (Figure 6.14, Table 6.3).

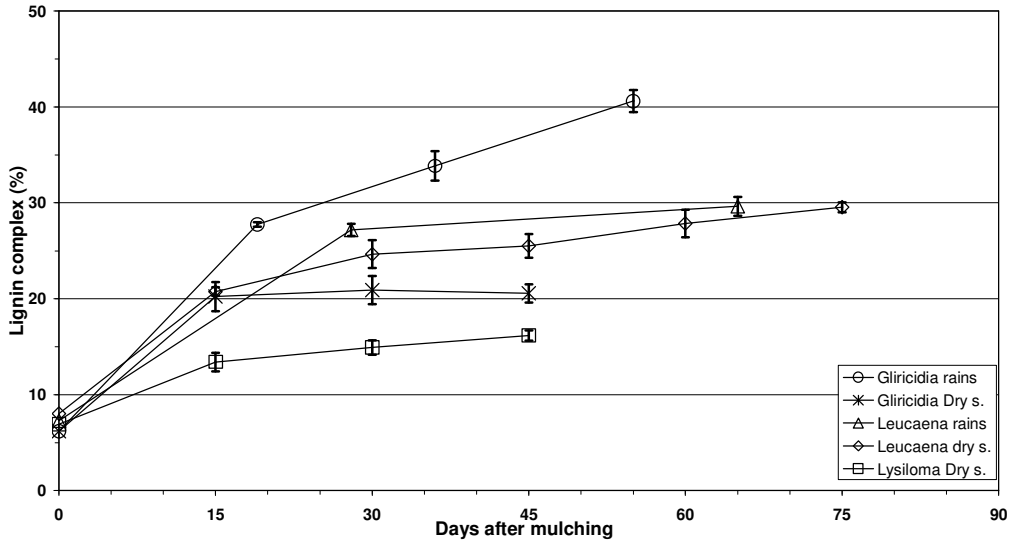


Fig. 6.14 Lignin complex (lignin, cutin and some minerals) fraction of mulch residues of tree legumes in a tropical silvopasture. The error bars are one standard error to both sides.

Phenolics

Total phenolics in tree prunings residue decreased during decomposition. *L. auritum* has the highest level of phenolics in plant material (16.5 and 13.0 g 100 g^{-1} Gallic acid equivalents GAE in June and November 1997 respectively); prunings of *L. auritum* of November 1997 released most of its phenolics after 30 days and reached stabilisation at 1.6 g 100 g^{-1} GAE for the rest of the trial.

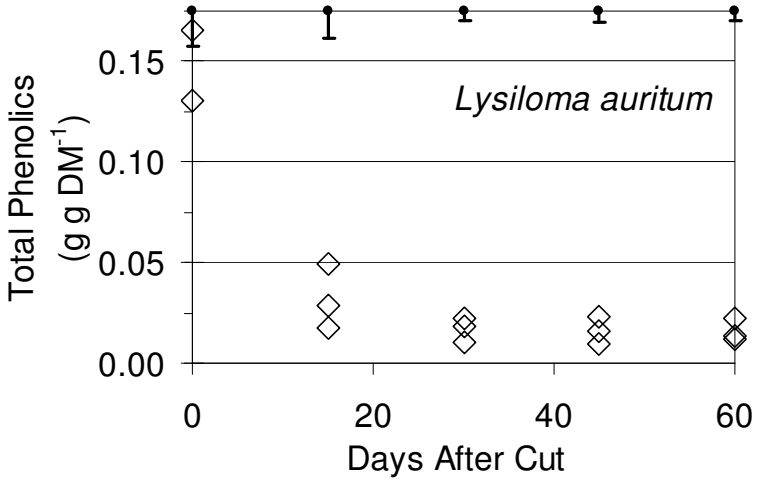


Figure 6.15. Total phenolics in *Lysiloma auritum* mulch after different periods of decomposition in litter bags in a Silvopastoral system with *B. decumbens*. Error bars represent one Standard Error of the sampling period.

L. leucocephala presented an intermediate level of total phenolics (9.02 and 7.52 g 100 g^{-1} GAE for June and November 1997 respectively), but it suffered a steep

reduction of this compounds during decomposition. This species lost phenolics more rapidly in the early 28 days of decomposition and keep losing along the whole trial but it reduced the rate of release of phenolics after reaching approximately 1.0 g 100 g^{-1} GAE. In the wet season, mulch of *L. leucocephala* lost phenolics in the same rate and extent than in the dry season.

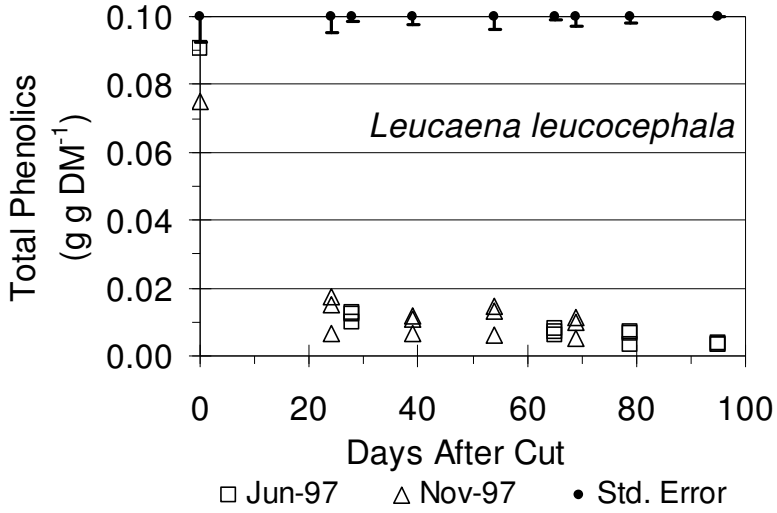


Figure 6.16. Total phenolics in *Leucaena leucocephala* mulch after different periods of decomposition in litter bags in a Silvopastoral system with *B. decumbens* during the wet and dry seasons (starting in June and November 1997 respectively). Error bars represent one Standard Error of the sampling period.

G. sepium presented the lowest level in original material (1.92 g 100 g^{-1} GAE, this value correspond to the sample of June 1997) and there were consistently less phenolics in older residues. In the rainy season *G. sepium* lost phenolics within the first sampling period (17-18 days) and remained stable during the rest of the trial. In the trial starting in August 1997, this species fist lost phenolics to a level of 0.2 g 100 g^{-1} GAE in the second sampling period (36 days) but then recovered to present 0.4 g 100 g^{-1} GAE in the fourth sampling period (64 days). Similarly, in the dry season, the mulch lost phenolics during the first two sampling periods (30 days) and then gained 0.1 g to reach about 0.4g 100 g^{-1} GAE in average (Figure 6.17).

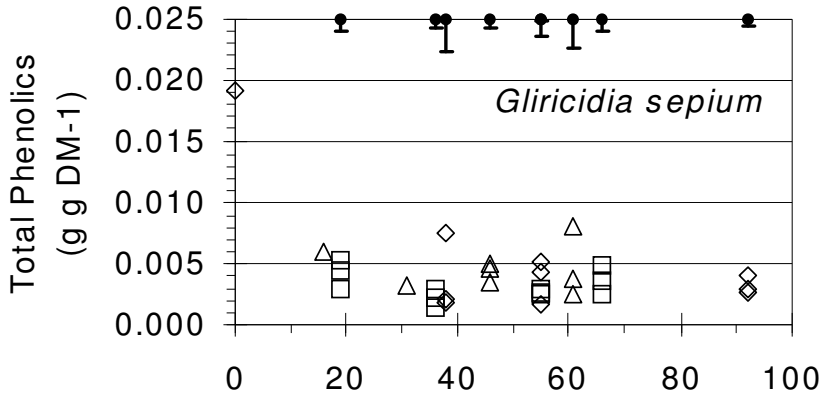


Figure 6.17. Total phenolics in *Gliricidia sepium* mulch after different periods of decomposition in litter bags in a Silvopastoral system with *B. decumbens* during the wet (starting in June and August 1997) and dry seasons (starting in November 1997). Error bars represent one Standard Error of the sampling period.

6.3.3 Soil chemical characterisation

Soil organic matter content

Tree-grass mixtures affected soil organic matter SOM in the experimental site. Two tailed t test showed that soil from a series of samples from 1997 presented significant differences with the original soil at 0 to 15 cm of soil surface (P = 0.001). In a separate analysis, no differences between distances in the mixed plots as a whole were found, but SOM in the top soil was significantly higher than in the 15 to 30 cm layer (P<0.01). Least significant difference test (Dunnett) for comparison against the Control (Montgomery, 1991), showed that most tree - grass inter-crops in the top 15 cm of soil and *close* from the nearest tree, have significant differences (α=0.05) in SOM with *B. decumbens* mono-crop after three years of establishment (Table 6.4). *L. auritum* presented the highest level of SOM in the top 15 cm of soil and in the 15 to 3 0 cm layer, with 6.2 and 3.9 % in average of the three distances, whereas *G. sepium*, both at lower and higher tree density, presented the lowest SOM content, having in some points values statistically lower the control (3.6 and 3.1 % in plots 3 and 4 respectively). With respect to the experiment of green manuring, no significant differences were found between *mulched* and *non mulched* treatments.

Table 6.4. Soil Organic Matter (kg m^{-2} in the top 0.3 m) in a *Brachiaria decumbens* - leguminous trees inter-cropping system as affected by grass mono-crop and accompanying trees and by distance from the nearest tree, after three years of establishment.

Plots	Depth	General	Zone		
			Close	Mid	Far
Initial values (September 1995)					
1 to 4	0-15	9.21			
5 to 13	0-15	11.62			
Average values 1997					
4 *G. sepium* (pole)	0-30		11.96	12.71	
8 *G. sepium* (seed)	0-30		12.95	11.70	13.16
10 *Delonix regia*	0-30		15.52	15.16	14.51
Final values (February 1998)					
11 Control	0-15	10.45			
	15-30	3.59			
2 *Lysiloma auritum*	0-15		13.55 *	21.09 *	13.73 *
	15-30		6.50 *	18.17 *	5.82
3 *G. sepium* (seed)	0-15		9.59	8.22	10.63
	15-30		3.43	3.93	6.34 *
4 *G. sepium* (pole)	0-15		7.54 *	8.58	
	15-30		3.07	4.29	
10 *Delonix regia*	0-15		10.63	10.30	10.30
	15-30		4.45	3.59	4.11
12 *L. leucocephala*	0-15		6.01 *	9.93	7.72 *
	15-30		10.45 *	3.59	4.73

Samples from 1995 and 1997 were analysed by loss on ignition (550°C) and samples of 1998 were analysed with the rapid titration method (Walkley and Black, 1934). Asterisks denote significant differences with the Control in 1998 according with the LSD Dunnett test (α=0.05).

Soil Nitrogen

No significant differences were found in total nitrogen N_{tot} between tree - grass combinations but the values in the top soil were statistically different ($P< 0.05$) from those in the 15-30 cm layer. Available nitrogen NO_3 was significantly affected by the presence of trees (Table 6.5). *L. auritum* - *B. decumbens* mixture presented the highest value of NO_3 (39.2 mg NO_3 kg^{-1}) and was significantly different from the lowest value (Control plot, 16.8 mg NO_3 kg^{-1}), *G. sepium* - *B. decumbens* (30.8 mg NO_3 kg^{-1}) was also superior to the control ($P=0.05$). Distance to the nearest tree was not determinant for any apparent difference in the two characteristics presented.

Soil acidity

Different tree-grass mixtures caused significant changes in soil acidity ($P<0.05$) at any depth in the soil. Treatments with *G. sepium* (plots 3 and 4) presented soil acidity higher than the rest of the treatments at any distance from the nearest tree. Fisher test for Least Significant Differences showed statistical differences between plots 4 and 3 and between them and the rest of the treatments (Table 6.5).

Table 6.5. Soil chemical properties in the Silvopastoral experiment, as affected by the distance from the nearest tree. Data refer to the final status of the experimental field, 30 months after the establishment of the silvopasture.

Accompanying sp.	Total nitrogen ($g\ m^{-2}$)		Available N (NO_3) ($mg\ kg^{-1}$)		pH 1:2	
	0-15a	**15-30b**	**0-15**	**15-30**	**0-15**	**15-30**
2 *Lysiloma*	709	518	39.2	36.4 a	5.63	5.86 c
10 *Delonix*	455	195	25.2	28.0 bc	5.86	5.53 c
3 *Gliricidia* (seed)	397	225	30.8	25.2 b	6.09	6.42 b
12 *Leucaena*	345	338	28.0	25.2 bc	5.67	5.56 c
4 *Gliricidia* (pole)	332	169	25.2	25.2 bc	6.24	6.63 a
11 Control	449	180	16.8	25.2 c	5.74	5.40 c

Note: Different letters in the same subject denote differences of entire colums (depth) or rows (plot) according to a t test ($\alpha=0.05$).

Soil organic nitrogen mineralisation rate

SOM mineralisation rate was slightly differently affected by different tree - grass mixtures ($P=0.05$) (Table 6.6) but no statistical differences were found between distances from the nearest tree. However, an increment in this rate could be noted at longer distances (5.07, 5.39 and 5.55 kg N ha^{-1} d^{-1} for *close*, *mid* and *far* averages of all plots respectively).

Table 6.6. Nitrogen mineralisation rates under laboratory conditions in soil organic matter from *Brachiaria decumbens* - leguminous trees associations.

Plot (accompanying trees)	N mineralisation rate (kg N ha^{-1} d^{-1})	σ
12 *Leucaena leucocephala*	7.37 a	5.8
3 *Gliricidia sepium* (seeds)	6.81 a	2.1
2 *Lysiloma auritum*	6.10 ab	1.4
4 *Gliricidia sepium* (poles)	6.05 ab	2.5
9 *Delonix regia*	5.95 ab	2.5
8 *Gliricidia sepium* (seeds)	5.28 b	1.9

Different letters indicate significant differences (α=0.05) according with the t test (LSD).

6.4 Discussion

6.4.1 Decomposition

This study characterised the mulch from different tree species in terms of the rate and extent of decomposition. These attributes are useful for the control of nutrient release and the input of resistant litter to the soil in agroforestry systems by the adequate selection of tree species. Mulch in litter bags underwent processes that led to an effective reduction in biomass. However, this reduction should not be described by a simple process rate. There were two phases in the decaying process that help on the characterisation of sources (tree species) of mulch. First there was a rapid reduction of biomass, that is related to the decomposition of cell content. The ensuing part, representing the decomposition of the more digestible parts of the cell wall ran at a slower rate. The first phase lasted only a few days, whereas the second phase did not show an end and could last from a few months to even years depending on the weather and the presence of soil microbes (Parton *et al*., 1987; Palm *et al*., 1996; Tian *et al*., 1997). Some build up of the litter bag contents overlapped with the second phase, making difficult the interpretation of results. It is noticeable that in all species both the rate and extent of apparent mulch decomposition were larger during the dry season.

Cell wall

L. auritum mulch underwent decomposition to a lesser extent than *G. sepium* and *L. leucocephala* during the time of the experiment. *L. auritum* leaves presented the

lower level of total nitrogen and the higher level of cell wall in the original material compared with *G. sepium* and *L. leucocephala* leaves. There seems to be a natural relationship between nutritional quality and decomposition rate. Tian and associates (1997) demonstrated that the "mulching effect" on soil moisture and temperature can make a big difference in decomposition. The mulching effect refers to the physical role of the prunings on preserving mild temperature and high moisture in the soil underneath. The principle is that plant materials that are rich in recalcitrant components will last longer, prolonging such beneficial environment for decomposers. The apparent disagreement with the present results could be explained considering that empty litter bag itself produced more "mulching effect" than the actual bag content, allowing for the process to rely exclusively on the very quality of the different materials. Whether the search is for rapid or slow decomposition is up to the decision maker, the discussion here is about the factors affecting the process.

Histology

The decay process can be partially explained by the structure of the leaf. *G. sepium* mulch presented more rapid and extensive decomposition than the other three species. *G. sepium* leaves are pinnate, with folioles of about 4 cm^2 whereas *L. leucocephala* and *L. auritum* leaves are bi-pinnate, with foliolules of one or less than one cm^2. This anatomic difference entails a higher proportion of mesophyll in *G. sepium* than in the bi-pinnates. Mesophyll is related to a more rapid penetration of bacteria into leaf vascular tissue (Hanna *et al*., 1973), but more important, is related to easy physical disruption (irrespective of microbial digestion), resulting in particles of less than 150 μm (Kennedy and Murphy, 1988). Unlike *Gliricidia*, bi-pinnates show no macroscopic innervate vascular tissues apart from the midrib, thus, the decay of the blade would be expected to be faster. The lower decomposition rate during the first phase both in *L. leucocephala* and in *L. auritum* could be attributed to a possibly earlier thickening of the cuticle and waxy layer of the epidermis that is apparent in the foliolules, and the higher levels of biogenic opaline silica found in these two species. The overall extent of decomposition in the bi-pinnates was reduced by the intrinsic decomposition rate of petiole and rachis, that constitute most of the structural tissues of the composed leaf. These structures contain more than 70% of parenchyma and phloem fibres (Wilson, 1993). Although parenchyma

probably does not lignify, it occupies the central pit of the petiole, remaining beyond the reach of decomposers. Phloem fibres present thick cell wall that although do not lignify, may take phenolic staining at the outer edge of the bundles, thus becoming resistant to decomposers (Wilson, 1993).

Decomposition Lag

An apparent lag on the decomposition process was observed at some stage of the second phase, especially in the wet season. It is unlikely that the climatic season determines such a lag, but it was always in the dry season when the maximum apparent decomposition was achieved, denoting the importance of this variable for the occurrence of lags. *G. sepium* and *L. leucocephala* presented weaker and shorter lags than *L. auritum*. From the present results, it is not possible to elucidate the causes of large and small lags. However, results from the dry season approximate better the true decomposition of litter, whereas those of the rainy season combine decomposition with processes that made the bags' contents to build-up, such as dying microbes and plant roots. No direct reference to such a problem was found in the literature, but fine roots were often found growing into the litter bags during the rainy season.

Total nitrogen and Lignin

Losses of N_{tot} in *G. sepium* both in the wet and the dry seasons were similar during the first phase of decomposition. The apparent rise in N_{tot} content of the residue in the second phase of the dry season may be partially explained by the composition of the residues. The contents of the litter bags after 30 days, was only 35-40% of the original sample. The petiole fraction in *G. sepium* leaves is 18% (Muschler, *et al*., 1993), thus N_{tot} from different collecting dates derives from qualitatively different materials. It is likely that the remnant mulch (half of which could be petiole and, clearly the other half rachis and other recalcitrant tissues) is rich in nitrogen but high in fibre that prevent the nitrogen from being released. An additional source of nitrogen in decomposing mulch was the contamination of the samples with fine roots growing from the soil under the bags. This problem only happen in the trial of the dry season. In a drier environment, the bags maintained soil moisture, allowing higher microbial activity and encouraging the plants to root trough the mesh into the

carpet of litter particles at the bottom of the bag. Although the roots did not reach too deep inside the bags, they might have effectively increased the nitrogen content of the sample; N_{tot} thus combined mulch and root derived N. Increments on the relative content of N_{tot} were also observed in *L. leucocephala* and *L. auritum* in the dry season, but at an earlier stage. This can be explained by the slower decomposition rate of these two materials.

The importance of N_{tot} on decomposition derives from its role on cellulose degradation. Cellulose led the rate of decay during the second phase of the trials. Steep reductions in residual cellulose after two weeks in the dry season's trial corresponded to N_{tot} levels higher than 3.5%. These results are in agreement with the high correlation coefficient between remnant mulch in the litter bags and both N_{tot} (0.67) and cellulose content (-0.7). Van Soest (1994) says that degradability of complex carbohydrates such as cellulose depends on microbes nutritional status (i.e. nitrogen availability).

Nitrogen is not expected to accumulate in decaying tissues since it is required for microbial activity. The present results suggest that lignified parts in *L. leucocephala* and *L. auritum* were not nitrogen deficient although N attached to such parts was less prone to decay. What can be seen in these results is the rapid disappearing of "metabolic" litter followed by the decomposition of the low N lamina cell wall (cellulose). The remaining of the litter bags content was anatomically different (petioles-rachis), but probably higher in N than lamina cell wall, creating the apparent increase in N content.

Lignin distribution in broad-leaved plants is, to some extent, different to that in monocots (Hatfield, 1993). That is essentially due to the differentiation of support and photosynthetic tissues at leaf level. Whereas lignin in monocots is more or less evenly distributed along the lamina, such compound in dicots is concentrated in nerves and petiole-rachis. Bi-pinnate leaves have so small folioles that no nerves are required for supporting the lamina, making more notorious the different allocation of labile compounds and lignified compounds. The micro-Kjeldahl N results, however, only reflect the overall average of the whole residue (Fig 6.7-9). The nitrogen content of ADF of forages has been positively correlated with lignin content -and negatively with digestibility (Van Soest, 1994). Because of the C to N requirements of microbial

decomposing agents, such hypothesis would not be feasible in an hostile environment where moisture, heat and/or soil organic matter are lacking. None of these were an issue in our field, in which soil microbes would immobilise N from elsewhere in order to gain access to the carbohydrate rich amendment. In addition, it is a household concept in foodstuff analysis the occurrence of higher amounts of insoluble, lignin bound nitrogen in legumes than in grasses (Van Soest, 1994). Wide mesh litter bags were meant to facilitate large insects to access tree prunings. The drawback of this alteration is that insects could have progressively contaminated the samples with non soluble forms of nitrogen such as keratin. Another problem associated with the use of litter bags is the potential lose of intact material through the mesh. This factor affects more to diminutive leaflets (*L. leucocephala* and *L. auritum*) than bigger ones (*G. sepium*) and more to petiole - rachis than lamina. *G. sepium* mulch presented a more discrete recovery of nitrogen during the second phase of decomposition because the fraction of mulch corresponding to petiole, rich lignin, is smaller and more succulent compared with petioles of *L. leucocephala* and *L. auritum*. From the point of view of the long term amelioration of soil fertility, it is perhaps more desirable to incorporate materials that retain nitrogen into the litter-organic matter phase, provided the bulk of this phase is large enough to sustain, trough the slow release of nutrients, an economic cropping system.

Total phenolics

G. sepium phenolics content (1.92 g 100 g^{-1}) was similar to other reports: 1.62 g 100 g^{-1} (Tian *et al*., 1997, Folin-Denis method), 2.83 g 100 g^{-1} (Vanlauwe *et al*., 1997, King and Health method, ball-milled dry samples), 3.0 1.5 g 100 g^{-1} in fresh regrowths and oven-dried prunings respectively (Mafongoya *et al*., 1997, soluble polyphenols), 1.34 g 100 g^{-1} (Jones *et al*., 1997, Folin-Denis method). However, comparisons are not fully reliable because of the variety of methods utilised. *L. leucocephala* phenolics content (9.02 and 7.52 g 100 g^{-1} for June and November respectively), resulted slightly higher than other figures reported. Tian and co-workers (1997) obtained 5.02 g 100 g^{-1}, Vanlauwe *et al*. (1997) reported 5.84 g 100 g^{-1}, Mafongoya *et al*. (1997) determined 4.3 and 2.7 g 100 g^{-1}, in fresh regrowths and oven-dried prunings respectively, Jones *et al*. (1997) found 3.3 g 100 g^{-1}.

Unlike other agents that are deterrent to decomposers (cellulose and lignin), total phenolics presented a strong reduction during the early stage of decomposition, suggesting that most phenolics are present in the cell contents and are rendered loose rapidly. It also suggest that phenolics can be classified according with the way they affect decomposition rate. Himmelsbach (1993) says that the composition of polyphenols, oligomeric phenols and monophenols in plant tissues may depend on the species, plant part and maturity. Harborne (1997) reports the presence of phenols on the leaf surface that have some solubility in aqueous environment; these antifungal agents must be permanently synthesised within the leaf. These compounds would constitute an important share of fresh mulch but would also readily disappear in dead material under open air conditions. This is in agreement with the findings of Handayanto *et al*. (1995) that obtained a loss of polyphenols after standing *Calliandra* prunings in water for five days. Unfortunately, the method used to assess phenolics in this study is unable to identify different phenolics separately; moreover, it takes all phenolics to be gallic acid (or other standard), that may well not be actually present at all (Waterman and Mole, 1994). The drawback of this technique is that it is based on the assumption of equal number of phenolate groups per mol of extract for any different phenolic group present. This hypothesis, clearly inaccurate, was taken as useful when comparing plant materials of unknown, but presumably similar composition, such as samples of the same species at different stages of decay. It is, however, less reliable for comparisons of different tree species. Nevertheless, these results gave some degree of certainty about the differences between species insofar as the numbers of each species are one order of magnitude different, at least-between *G. sepium* and the other species.

In the light of the present results, it seems that there are at least two groups of samples of the same species that can not be straightforwardly compared, fresh and decomposed material. Instead, these results give insights into the different chemical quality of phenolics and put forward questions as to how much each class is affecting decomposition. With respect to phenolics in fresh material, *G. sepium* presented the lowest phenolics content and the highest rate and extent of decomposition in the first two sampling periods (first phase); similarly, *L. auritum* presented the highest phenolics content and the lowest rate and extent of decomposition in the same

period. The same relation can be seen between decomposition during the first phase and phenols in the second phase, but at different scale. During the second phase, phenolics and decomposition become more stable but the relationship was not as clear: On the one hand *G. sepium* retained very low residual dry matter in the bags, as well as phenolics; moreover, the observed lag in biomass decay was, to a certain extent, mirrored by the phenolics. On the other hand, *L. leucocephala* mulch disappeared to a lower rate but to a similar extent than its phenolics, whereas *L. auritum* mulch decomposition extent was only a fraction of the decomposition of its phenolics, particularly in the wet season.

6.4.2 Soil Chemical Characterisation

This part of the study relied on a minimum set of samples. Distance between the experimental field and soil laboratories combined with the high cost of soil analyses to constrain the amount of samples that could be analysed. Extensive sample collections were bulked prior to chemical analysis. This explains the lack of indicators of variability of results.

Soil Organic Matter

With respect to soil organic matter, some samples were analysed in the Soil Analysis Laboratory at The University of Chapingo, Mexico, 600 km away from Valle Nacional, whereas the rest were brought to be analysed in Edinburgh (Biochemistry laboratory, Scottish Agricultural College). These two facilities hold different techniques for the determination of organic matter in soil, and no standard was produced for the two procedures, thus the results could not be compared. Apparently, Walkley - Black (1934) produces lower results than the loss on ignition method. Despite such a pitfall, some conclusions can be drawn within the experiment.

Average Soil organic matter in the top soil in *G. sepium*, *D. regia* and *L. leucocephala* mixtures (6.01 – 10.63 kg m^{-2} in the top 20 cm, depending on the accompanying tree and the distance from the nearest tree) was in agreement with other pasture systems in the tropics. Neill *et al*. (1995) reported between 3.55 and 4.74 kg m^{-2} in the top 10 cm of soil under *Brachiaria brizantha* pastures in the Amazon Basin. Nygren (1995) reported levels of 9.9 to 10.6 kg m^{-2} at 0 – 25 cm depth in field amended with leguminous tree prunings in Costa Rica. However, soil

under *L. auritum* mixture resulted rather high in organic matter (13.55, 21.09 and 13.73 kg m^{-2} for the top soil, *close*, *mid* and *far* zones). No clear explanation for such a high value can be drawn, but samplings from all distances and depths in plot 2 (*L. auritum*) were consistently higher in SOM than the rest of the experiment. Plot 2 was particularly stony (bed rock at 20 to 30 cm depth); this could make the root system to concentrate in the top soil and indirectly enrich SOM with root turnover.

Plot 4, with higher tree density (891 Mg ha^{-1}) and larger trees (planted as poles of about 7 cm in diameter) had SOM and total nitrogen in the top soil lower than the Control, whereas in plot 4 (816 trees ha^{-1}, trees grew up under grass competition after being transplanted from the nursery, poor re-growth after pruning, only 317 useful trees, see section 4.3.1) neither parameter was different to the Control. Lower SOM in Plot 4 can be explained in terms of the longer turnover period of grass under shade. It is worth recalling that trees in plot 4 were planted in a regular pattern in the paddock. Thus, less dead grass tissues enter the litter pool. In addition, tree derived litter has little effect on long term SOM build up since most of the tree mulch and litter decomposes to the labile SOM pool.

Accepted figures of organic matter in tropical rain forest soils are about 3.3 kg m^{-2} (Wood, 1995) It appears that the present results confirm the household paradigm that pasture and silvopastoral systems increases organic matter in soil (Neill *et al*., 1995; Römkens *et al*., 1999). This process can be explained in the context of the addition of green manure from tree prunings, but more important, from the rapid turnover of grass and tree roots.

Soil nitrogen

The results on total soil nitrogen presented in this work (332 to 709 g N m^{-2}) are in agreement with or slightly higher than similar research reports (Handayanto *et al*., 1995; Neill *et al*., 1995; Srivastava, 1998). The lack of significant differences, despite of the large virtual differences in total nitrogen between treatments might be explained by the reduced degrees of freedom in the analysis owed to the limited number of samples that were analysed. Results on available nitrogen (16.8 - 39.2 mg NO_3 kg^{-1}), however, were comparatively high among reports of pasture system soils elsewhere, although the figures are rather variable. Srivastava, (1998) determined values between 9.8 and 13.1 for savannah pastures in an ultisol in Uttar Pradesh,

India. Neill and co-workers (1995) reported an average of 0.8 mg NO_3 kg^{-1} in *Brachiaria humidicola* swards on an ultisol in the Amazon Basin, Brazil.

Organic Nitrogen Mineralisation

The results obtained in the silvopastoral experiment are comparatively high with respect to other reports on tropical soils. Matson *et al*. (1987) obtained net rates between 1.5 and 3.1 kg N (NO_3 + NH_4) ha^{-1} d^{-1} in re-grown tropical hardwoods. Pfadenhauer (1979, cited in Binkley and Hart, 1989) reported values from 0.06 to 1.6 kg N (NO_3) ha^{-1} d^{-1}. It is worth mentioning that the present results correspond to an experimental aerobic incubation that should be taken as per day estimates, and may not be representative of seasonal variations in the field. Binkley and Hart (1989) concluded from an extensive review, that seasonal maximum NO_3 mineralisation rate is usually 1.5 times that of the seasonal minimum, but it can be more than tenfold the minimum rate. Moreover, this short term assessment (five days incubation) might have been affected by an eventual high level of ammonium in the original sample, unfortunately this compound was not measured. Palm *et al.* (1993) reported that ammonification rates in the first seven days of incubation of tropical soils were about six times higher than between 14 and 28 days. This is in agreement with the fact that the plot where incubation last one day less (plot 12, *L. leucocephala - B. decumbens*), resulted the highest on nitrogen mineralisation rate. Nevertheless, high mineralisation rates are indirectly supported by the high available NO_3 nitrogen found in the silvopastoral treatments soil. Total soil nitrogen was also high enough to allow high microbial activity.

With respect to *G. sepium* plots, even though no significant differences were found between plot 3 (317 trees ha^{-1}) and 4 (891 trees ha^{-1}) in available nitrogen and mineralisation rate, plot 3 was superior. The approach used in calculating mineralisation rate in this research work is bound to the assumption of equal SOM between treatments. This is not the case, Plot 3 had higher SOM level; this may have determined the higher nitrate concentration in the incubation trial. Mineralisation rate in Plot 8 (216 Mg ha^{-1}) was significantly lower than the other *G. sepium* plots perhaps because the volume of high quality mulch entering the litter pool was lower, thus less N was available for microbial metabolism.

6.5 Conclusions

The specific objective of determining the decomposition rate of mulch from the four tree legumes in this study under field conditions was satisfactorily achieved. Two main phases were described, one of rapid reduction of biomass (about 30 days in *G. sepium* and *L. auritum* and not defined in *L. leucocephala*), and other of slow weight loss, whose span exceeded the time of the experiment. During the first phase, *G. sepium*, *L. auritum* and *L. leucocephala* lost weight at an average rate of 0.4, 0.02 and 0.018 day^{-1} respectively. The two-phase approach for litter decomposition find extensive documentation in Heal *et al*. (1997). Warnings arouse from the interference of processes such as proliferation of crop roots and arthropods litter into the litter bags and the reliability of figures derived from mulch samples containing both high and low lignin structures, namely rachis-petiole and leaf lamina, particularly in bi-pinnate leaves.

With respect to the characterisation of the fate of substances and plant tissues that affect the potential of tree prunings for green manuring, the objective was accomplished. The first phase of decomposition was characterised by the fraction of plant cell contents that was removed; the second phase was determined by residual nitrogen and cellulose, as well as the remaining total phenolics in the plant sample. Although lignin presented high correlation coefficient with most of the components of variance of the model of decomposition (Table 6.2 …*et seq.*), it was not as important on explaining mulch decay as cellulose and total nitrogen (R = -0.49). This is in agreement with previous studies on factors affecting decomposition (Vanlauwe *et al*., 1997; Wachendorf *et al*., 1997). Berg (1986), however, put forward the hypothesis that the second phase of decomposition is mainly governed by lignin decomposition rate, which in turn, is increased by high cellulose content and reduced by high nitrogen content. The results of the present work do not entirely support that conclusion. *G. sepium* mulch released the cell contents at a higher rate and at larger extent during the first phase of decomposition, only remaining about 25 and 50% of this fraction in the wet and dry season respectively, whereas cellulose fraction increased 60 and 120% in wet and dry season respectively during this phase. Lignin fraction in *G. sepium* increased more than 550% (wet season) and 230% (dry season) during the first phase. *L. leucocephala* was the species of slower decomposition rate

and the one whose residues suffered decomposition to a lesser extent. Whilst cell contents fall to 35 and 50 % of its original value in the wet and dry season respectively, cellulose risen more than 30 and 20 % in the wet and dry seasons respectively and lignin increased 300 and 220%. Such different features stress the importance of taking into account the proper selection of species for agroforestry systems where tree prunings are to be utilised as a source of green manure. Species of rapid degradability can be as valuable for fast growing, seasonal crops, as species of slow degradability can be for permanent crops, such as tropical pastures.

The objective of evaluating the effect of accompanying trees on the soil organic matter and soil fertility was achieved, but the results of this part of the study are less robust. Due to the difficulties for expanding or repeating sampling and assessments, these results must be interpreted cautiously. It could be better to use the plot averages to compare between treatments than any comparison against external datasets. However, Organic matter, Total nitrogen, Available NO_3 nitrogen and Net NO_3 mineralisation rate were measured and results were similar to or higher than other reports from comparable conditions.

G. sepium mulch produced the expected effect on soil carbon and nitrogen. Tree population may have influenced grass growth, and indirectly affected SOM. More and larger trees reduced grass turnover rate; thus reducing the production of soil organic matter. Total soil nitrogen in *G. sepium* plots can be partially explained by soil organic matter content (Table 6.5). Mineralisation rate was retarded by lower nitrogen content SOM.

The *L. auritum* - *B. decumbens* mixture produced the highest levels of organic matter and nitrogen in the top soil, as well as high nitrogen mineralisation rate. *L. leucocephala* - *B. decumbens*, was lower than the control both in SOM and total nitrogen. *L. auritum* and *L.* leucocephala mulches were scarce and of high cell wall fraction, resulting in little SOM labile fraction being released from decomposition. The difference between the two species is the production of recalcitrant SOM that is encouraged by high cell wall C to N ratio and (total phenolics + lignin) to nitrogen ratio, both parameters higher in *L. auritum* mulch. *L. leucocephala* mulch is rich in nitrogen, this could determine an enhanced microbial activity, hence higher mineralisation rate.

7. A simulation Model of Carbon and Nitrogen Cycling in a Tree-Grass Inter-Cropping System in the Humid Tropics.

7.1 Introduction: Why using models?

The diffusion of sustainable technologies for natural resource management has been limited by the difficulty of extrapolating research findings and knowledge from different sources between locations, even when they show points of similarity. Even so progress has been made in sciences and it is quickly being disseminated to more sectors of the society, the possibility of direct extrapolation of technologies is constrained by a long list of factors that affect, in a set environment, the processes under study. This restriction is especially handicapping for heterogeneous regions of patchy landscapes and is particularly valid for poorer economies, which can not afford extensive research programmes.

Between research in experimental fields and farm technical assistance, simulation models can play an important role as decision support tools. In the context of agricultural extension, a model may be developed to represent the environmental or land use variability occurring in a region, ecosystem, biome, etc., to allow for virtual experimentation, prior to the establishment of on-farm trials.

Simulation is complementary to field research and knowledge. Models can be used to solve problems by experimenting with a broad variety of options that would be impossible to test in the field. Nevertheless, the more we want the model to accurately predict reality, the more complex and the more unaffordable it becomes as it needs more parameters. Also, the complexity can reduce its potential for extrapolation (Haefner, 1996).

Sharing information and co-ordinating research in order to reduce duplication of projects is the way to tackle the bottleneck of parameterisation of complex models. The same way human populations share solutions to solve common problems, researchers world-wide are testing technologies from other regions with similar conditions through simulation models to solve similar questions (Parton *et al*., 1993; Lauenroth *et al*., 1993; Smith, *et al*., 1997) . In addition, parameterising models world-wide can make them more robust.

7.2 The silvopastoral system

One of the problems that many tropical regions share is the replacement of natural vegetation by pasture for cattle. Whether or not this process is in agreement with the demand for food and the well being of small farmers is not the focus of this paper. However, a fact is the reduction in soil productivity following the clearance of the rainforest.

The common practice after slash and burn of forest is the establishment of annual food crops which benefit from both “induced” fertility and relative lack of weed competition. Weed proliferation begins some time between the first and fourth cropping cycle as the farmers normally do not rotate crops. In areas where land is spare but climate is seasonal (i.e. long dry season), farmers will shift to a new/regenerated piece of land to slash and burn and grow their crops again. In areas with short dry season farmers may plant grass along with the last cycle of cultivation of their food crop in order to establish pastures to raise cattle. Under this system, they have to clear new areas of forest to grow their crops every time.

Due to the traditional utilisation of natural recovery of soil fertility after land has lain fallow, farmers do not normally use fertilisers or herbicides. The same premise can be applied to pasture cultivation as the poor natural potential of the grass species

commonly utilised, combined with low stocking rates, permits the lengthening of the life span of soil natural fertility, actually allowing for a limited regeneration of soil fertility.
Concern about natural resources and scarcity of land are pushing institutions and farmers towards more intensive technologies. The introduction of new species of grass, aiming to permit increased stocking rates and consequently the reduced pressure on the surrounding forest makes such a system rely more on nutrient availability from the soil.
New grass varieties root deeper in the soil and withstand more acid soils, which means that the extraction rate of soil nutrients is more rapid. The use of such species of grass by traditional small-scale farmers should be restricted to the establishment of a system in which a strategy for soil fertility maintenance is assured. Many agroforestry systems in which trees interact with herbaceous vegetation under natural or induced conditions have been described, from the nomadic silvopastoralism in the Sudan-Sahel region of north Africa (Sissoko, *et al*., 1994) to the sheep grazing under poplar plantations system in temperate regions (Acciaresi *et al*., 1994) to the cattle grazing under coconut system in Asia and South Pacific (Wong, 1991). Apart from savannah, most of these systems are conceived for the commercial utilisation of the tree products, either directly (timber, fruit) or indirectly (fodder), while the soil fertility is maintained through chemical fertilisation or via the recycling and resilience of some low productivity systems. Unlike most of the tree-grass agroforestry systems, the Silvopastoral system proposed in this work is one where the trees are introduced as a substitute of inorganic fertilisers for high yielding forage grass species. Trees are planted scattered or on a regular layout within the paddock, with allowance for free transit of the animals. The trees are pollarded regularly so that the mulch is of best quality – and high decomposition rate– thus providing a permanent source of nutrients to the crop. Additionally, by pollarding the trees frequently, light competition is minimised and incident solar radiation interception on the grass canopy is maximised.
The objective of this part of the research project was to develop a model prototype that can be used in combination with field trials to test the potential of fast growing nitrogen tropical trees as a source of green manure for improved pastures so as to integrate the understanding of physiological and biochemical processes and to enable effective decision making where extensive field trials are not feasible.

7.3 The silvopastoral model

The use of trees in inter-cropping with pastures increases the complexity of the system and reduces its predictability even when the understanding of every component is satisfactory. Apart from the representation of the components of the two crops, a model of an inter-cropping system has to take into account the interactions between them, which lead the two populations towards either resource competition or complementarity. Another important cause of complication is the management exerted to the inter-cropping system, which differs from the practices for sole crops. A model of such a system will provide insights into the ability of trees to incorporate nitrogen to the system and the amount of this nutrient that can be expected to be available for grass utilisation. The model addresses specific questions as:

- Are the model results consistent with independent field data sets? If not, why not?
- To what extent does the tree population supply green manure to the pasture?
- What are the management practices the system needs in order to prolong soil fertility?
    - Stocking rate (the model assumes continuous grazing)
    - Tree pollarding frequency

The Silvopastoral model was built by coupling two established process-based ecosystem models, the Hurley Pasture (HP) model (Thornley and Verberne, 1989) and the Edinburgh Forest (EF) model (Thornley, 1991; Thornley and Cannell, 1992). Here the HP and EF models are described insofar as necessary to understand the Silvopastoral model. Each model consists of a Plant submodel and a Soil submodel. First the soil processes were treated very simply (Johnson and Thornley, 1985), but as new features such as the ability to handle organic and inorganic inputs were added, the soil submodel became more complex (Thornley and Cannell, 1992; Arah, 1996; Arah *et al*., 1997). Additionally, there are environmental variables such as solar radiation (PAR), air and soil temperature and soil moisture. The HP model has an Animal submodel (sheep) that is fairly simple.

7.3.1 Plant submodels

HP and EF plant submodels are based on the growth of structural carbon pools and partitioning of assimilates (carbon from photosynthesis and nitrogen from soil) to the different components (Figure 7.1). By component we understand the readily identifiable anatomical entities of the plant. These have been separated into sub-submodels in the two Plant submodels. The grass has two general components: leaves and roots, both disagregated into an array in which the ageing of individual leaves is simulated.

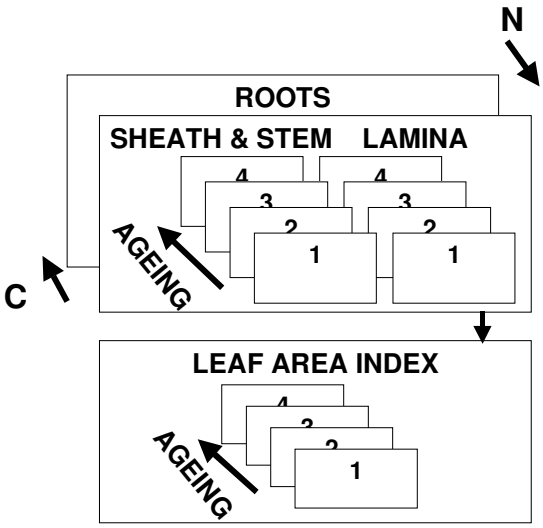


Figure 7.1. Structure of the Hurley Pasture model as in Johnson and Thornley (1985). Each numbered rectangle represent state variable and a pool of structural dry matter. Arrows represent flows of substrate C or N or the ageing of structural dry matter.

The tree consists of five components: leaves, branches, stem, coarse roots and fine roots constituted as an array of similar processes governed by different parameter

values (Figure 7.2). The five tree parts are connected in a row, i.e. substrate carbon passes the branches, stem and coarse roots one after another in order to get to fine roots. Similarly, substrate nitrogen goes through coarse roots and so on to arrive to the leaves.

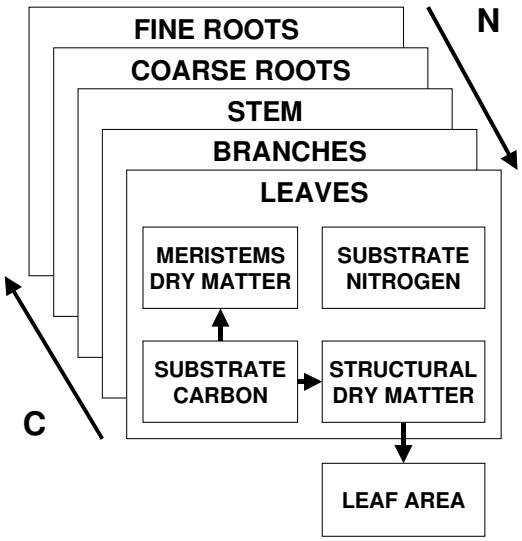


Figure 7.2. The Plant sub-model of the Edinburgh Forest model as in Thornley (1991). Each rectangle represent either substrate carbon or nitrogen or meristem or structural dry matter pool state variables. Arrows represent flows of substrate C or N.

The HP and EF models use the single leaf photosynthesis approach of Johnson and Thornley (1984), which describes the rate of simple leaf gross photosynthesis (P_g) as a non-rectangular hyperbola. Instantaneous Canopy Photosynthesis (P_c) is based on the integration of P_g along the Leaf Area Index ($0 \rightarrow L_0$) for a given leaf irradiance (I_λ) defined by the light attenuation model of Monsi-Saeki (1953).
Both grass and tree are assumed to consist of a structural and a non-structural (substrate) components. Substrate carbon depends on the daily carbon input ($P_{c\text{-}grass}$) and recycling from dying organs. Grass substrate carbon is partitioned teleonomically towards shoot and root growth (structure), i.e. more resources are dedicated to develop the smallest component in order to maximise growth rate based on the existing structure. There are two major losses of substrate carbon from shoots, maintenance and grazing; and two more from roots, nitrogen uptake and exudation. Tree substrate carbon originates from $P_{c\text{-}tree}$ and can be either retained at leaf level or derived to branches substrate. Each tree part substrate carbon is subsequently split into retained (and the correspondent maintenance respiration costs) and derived to the next part downwards (Figure 7.2). Within each part, substrate carbon is partitioned, first to meristem, the rest to structure. The specific growth rate of tree components is determined by a growth coefficient (activity parameter) and the substrate carbon and nitrogen concentrations of the component. The rate of synthesis of both grass and tree structural dry matter is determined by substrate carbon and nitrogen concentration and a growth coefficient. Substrate nitrogen is also dynamically calculated from the rate of N uptake (or flow from previous tree part) and the rate of synthesis of structure (assuming constant N content in structure). There is an input of recycled substrate N from dying plant structure.

7.3.2 Animal submodel

The animal submodel (HP) represents the pools of carbon and nitrogen in faeces dynamically, based on the nitrogen FN_{faeces} and carbon FC_{faeces} to faeces flow rates and the faeces to soil *ammonium* mineralisation rate. It calculates the fluxes of carbon and nitrogen to faeces based on animal intake and C and N fraction parameters. Fractions of nitrogen to urine (0.52; Haynes and Williams, 1993) and faeces ($1 - fN_{urine}$) are modified by C to N ratio of forage.

7.3.3 Soil Submodel

The Soil submodel consists of three submodels, representing the litter, the soil organic matter (SOM) and the mineral pools of nitrogen, connected by the Soil Microbial (live SOM) pool. As with the other submodels, the dynamics of nitrogen in litter and soil organic matter are essentially driven by the fate of carbon. The size of the pools of soluble nitrogen depends on the abundance of microbial biomass, whose activity obeys temperature and soil moisture potential dependent process rates. An adequate C:N ratio in soil solution is also essential for the microbial activity, for which mineral nitrogen may be removed from the ammonium and nitrate pools, in order to attain the proper C:N ratio of live SOM.

Litter

HP and EF consider two groups of decomposing materials, namely surface and root litter, each group subsequently producing Metabolic (comparable to cell contents) and Structural (comparable to Cell Wall) litter. Structural dry matter, depending on lignin content, is split into cellulose and lignin fractions. There are two submodels that contribute to the HP Litter submodel: Animal, and Grass. Clearly all litter in the EF model comes from the Plant submodel. The Animal produces C and N faeces flows, the Grass produces C and N litter from shoots and roots, the Tree produces C and N litter flows from leaves, branches, coarse roots and fine roots. The rates of partitioning of the live carbon pools to Litter are fixed (Figure 7.3). However, a dynamic approach as in CENTURY (Parton *et al*., 1993) should be considered.

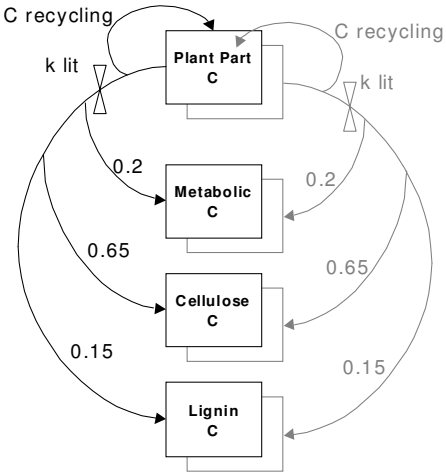


Figure 7.3. C partitioning in litter above (black) and below-(gray) ground. Figures are the fraction of each live compartment to each litter compartment.

The metabolic and structural components of decomposing material are represented by the addition of dead fractions from every live component of the model and

subtracting the flows to Soil Solution and to soil organic matter (SOM). Pools of surface litter (derived from shoot litter and faeces –HP, and leaves and branches litter –EF) and soil litter (derived from grass root litter –HP, and coarse and fine root litter –EF) are split into metabolic, cellulose and lignin compartments, with "standard" first-order decay constants (k_{20}), respiratory losses on transformation (ϕ_R), and C:N ratios (ρ) given in Table 7.1. The C:N ratios of the metabolic litter pools are not fixed; they depend on the C and N contents of the root, shoot and faeces pools feeding them, all of which are deemed to comprise 65% cellulose and 15% lignin (these fractions could be tailored to reflect different biomass compositions).

Table 7.1. First-order decay constants (k_{20}), respiratory losses on transformation (ϕ_R), and C:N ratios (ρ)of the three Litter pools.

	k_{20} (d^{-1})	ϕ_R	ρ
metabolic	0.2	0.6	-
cellulose	0.1	0.4	150
lignin	0.02	0.2	100

Breakdown of *metabolic* and *cellulose* litter pools produces *soluble* C as well as CO_2. Soil *ammonium* and *nitrate* are produced according to the C:N ratio of each pool (Figure 7.4) Breakdown of lignin produces protected and unprotected SOM in a ratio ($\phi_{protected}$:(1-$\phi_{protected}$)) dependent on the clay fraction of the soil. The standard first-order transformation rate constants k (Eq. 7.1) are modified by, litter C:N ratio ρ (7.2) and lignin fraction λ (7.3). For temperature T and moisture potential ψ modifiers see 7.3.4. (environmental variables).

$$k = k_{20} f_T f_\psi f_\rho f_\lambda \tag{7.1}$$

$$f_\rho = \frac{m_\rho}{\rho} \tag{7.2}$$

$$f_\lambda = \exp\left(-m_\lambda \frac{C_{lig}}{C_{lig} + C_{cel}} \right) \tag{7.3}$$

Temperature T in (7.3) is measured in Kelvin; elsewhere it is in degrees Celsius. The parameters m_ρ (default 50) and m_λ (default 3) determine the sensitivity of litter incorporation litter quality variables.

Soil Organic Matter

This submodel elaborate on the processes by which the nitrogen contained in products and by-products of the live components of the systems becomes available to the roots in its way throughout the soil. Attention is drawn to three factors affecting the action of micro-organisms on their substrates: carbon to nitrogen ratio, lignin content and soil texture. High C:N ratio is considered a **biological** constraint to mineralisation as nitrogen becomes a limiting factor for microbial growth. Lignin constitutes a **physical** constraint for microbes action onto organic matter since it prevents the fractionation of cellulose to a microbes-bite-size. Nevertheless phenolic polymers as a whole have been demonstrated to counteract organic matter decay (Palm and Sanchez, 1990; Lehmann *et al.*, 1995), it is mainly lignin that has been

individually described and considered when modelling SOM dynamics. Clayey or silt soils foster the aggregation of mineral and organic compounds, **physically** constraining the action of microbes (Wood, 1995; Koutika *et al*., 1999).
The development of the Soil Organic Matter model has been ongoing for more than two decades, originally based on the long term experimental datasets from Rothamsted Research Station (Jenkinson and Rayner, 1977). These authors first proposed the dissagregation of litter and organic matter into dynamic C and N pools. The PHOENIX model (McGill, 1981) elaborated on the dynamics of C and N for soil microbes and proposed a single resistant pool. The CENTURY model (Parton *et al*., 1987; Parton *et al*., 1988) divided the *humads* (labile) pool into *active* and *slow* SOM pools according to lignin content of *structural litter* and introduced lignin to nitrogen ratio as a more robust criteria for differentiation between *metabolic* and *structural* litter pools in dying material. They also introduced soil silt-plus-clay content determining the split of microbial SOM between mineralisation (ammonium pool) and immobilisation (passive SOM). Sandy soils (at field capacity) facilitate dying microbes carbon to leach, whereas silt-clayey soils favour the flow to the *passive* pool as small mineral particles adsorb organic substrates into silt micro-aggregates, thus *protecting* organic matter from microbial attack and reducing microbial respiration and turnover (Heal *et al*., 1997). Parton and co-workers (1988), based on data of Martel and Paul (1974), used CENTURY to model the decay rates of SOM. The active pool mineralises at a rate equivalent to 1.5 years for the complete disappearing of the existing organic matter; the slow pool fully mineralises in 2.5 years. Old organic matter fraction dates from around 1200 years and comprises more than 50% of total SOM.
The Hurley Pasture model split the *active* pool into soil soluble carbon *soluble*C and microbial biomass carbon *mSOM*C and the *slow* pool into two compartments of different decomposition rate: unprotected and protected *SOM* carbon (*unprotected* and *protectedSOM*C), both fed on *lignin* litter. The more clayey soil, the larger the fraction of *lignin* litter entering the *protectedSOM*C. *Unprotected* and *protected* SOM contribute to the *stabilised* pool. Decay of the *stabilised* pool represents an input to the *soluble* C pool (Figure 7.4). The derivative equations of Soil Organic Matter in HP are:

$$\delta\, unprotectedSOMC/\delta t = (mSOMC_{\text{dead, labile}} - m\phi_{R_u}) + (ligninLitter_{\text{labile}} - lignin\phi_{R_u}) - unprotectedSOM_{\text{min}} - unprotectedSOM_{\text{st}} \quad (7.4)$$

$$\delta\, protectedSOMC/\delta t = (mSOMC_{\text{dead, resistant}} - m\phi_{R_p}) + (ligninLitter_{\text{resistant}} - lignin\phi_{R_p}) - protectedSOM_{\text{min}} - protectedSOM_{\text{st}} \quad (7.5)$$

$$\delta\, stabilisedSOMC/\delta t = (unprotectedSOM_{\text{st}} - u\phi_{R_{st}}) + (protectedSOM_{\text{st}} - p\phi_{R_{st}}) - stabilisedSOM_{\text{min}} \quad (7.6)$$

Where:

$mSOMC_{\text{dead, labile}}$, $mSOMC_{\text{dead, resistant}}$ are the fractions of dying microbes entering the *unprotected* and *protected* SOM pools (labile fraction is higher in sandy soils)

$ligninLitter_{\text{labile}}$, $ligninLitter_{\text{resistant}}$ is the fraction of C in decaying litter *lignin* component entering the *unprotected* and *protected* SOM pools (labile fraction is higher in sandy soils)

$unprotectedSOMC_{min}$, $protectedSOMC_{min}$, $stabilisedSOMC_{min}$ are the fluxes of *unprotected*, *protected* and *stabilised*SOM C into the *soluble*C pool

$m\phi_{R_u}$, $m\phi_{R_p}$ are the respiratory cost incurred in microbial decay into *unprotected* and *protectedSOMC* pools

$unprotectedSOMC_{st}$, $protectedSOMC_{st}$ are the fluxes of *unprotectedSOMC* into *stabilisedSOMC*

$lignin\phi_{R_u}$, $lignin\phi_{R_p}$ is the respiratory cost incurred in decomposition of *lignin* into *unprotected* and *protectedSOMC*

$u\phi_{R_{st}}$, $p\phi_{R_{st}}$ are the fractions of C in fluxes of stabilisating *unprotected* and *protectedSOMC* which are respired.

Mineralisation and stabilisation rates are modelled with first order kinetics, with a standard rate (process speed at 20°C) that is modified by microbial abundance, soil temperature and moisture potential.

$$k_i = k_{i20} * mSOMC * f\Gamma_{soil} * f_\psi \quad (7.7)$$

Standard mineralisation and stabilisation rates k_{20} and losses to respiration (ϕ_R) attendant on these processes are reported in Table 7.2.

Table 7.2 Mineralisation and stabilisation rates (k_{20}) of SOM pools and ratio of losses to respiration (ϕ_R)

	mineralisation		stabilisation	
	k_{20} (x10^{-3} d^{-1})	ϕ_R	k_{20} (x10^{-3} d^{-1})	ϕ_R
unprotected	3	0.4	0.2	0.2
protected	0.15	0.4	0.02	0.2
stabilised	0.03	0.4	-	-

Soil organic nitrogen is not dynamically modelled but attending C:N ratio of each SOM C pool. C:N ratios of the SOM pools are dynamic properties of the system, changing over time. The C:N ratio ρ_i of new material entering each of the SOM pools varies within a set range (eq. 7.8) according to the current mineral N content (N_{min} = nitrate + ammonium):

$$\rho_i = \rho_{max_i} - \left(\rho_{max_i} - \rho_{min_i}\right)\frac{N_{min}}{\left(K_i + N_{min}\right)} \quad (7.8)$$

where the suffix *i* runs from *unprotected* to *protected* to *stabilised*SOM. Default values of ρ_{max}, ρ_{min} and *K* are shown in Table 7.3.

Table 7.3 Default values of C:N ratios (ρ_{max} and ρ_{min}) and *K* of SOM pools

	ρ_{max}	ρ_{min}	K (kg N m^{-2})
unprotected	12	6	0.002
protected	12	6	0.002
stabilised	ρ'_{max}	$\rho'_{max}/2$	0.002

Soluble C and microbial SOM C Pools

The *soluble*C pool facilitates the simulation of a more effective microbial compartment, from which immobilisation of *ammonium* and *nitrate* N are represented. The flow from *soluble* C to microbial SOM C (*mSOM*C) is represented by a self-limiting (asymptotic) equation (k_{mG}*$mSOMC^{2/3}$) with maximum growth rate

of microbial biomass k_{mG} modified by two thirds of the available microbial pool. The power of two thirds is meant to prevent exponential growth, based on the physically vacant attachment sites in the microbial substrate i.e. *u*, *p* and *s*SOM (Thornley and Verberne, 1989). Growth depends on the relative size of the *soluble*C and *mSOM*C pools and is driven by a bisubstrate Michaelis-Menten dependence to maintain the C:N ratio of soil microbes. The size of the *mSOM*C pool is governed by growth rate v_g and death rate v_d, modified by the size of the total SOM stock, moisture and temperature.

Nitrogen is either entrained (immobilised) from the mineral N pools or released to them depending on the C:N ratios of the various source pools and the magnitude of the C fluxes, so as to maintain a fixed soil microbial biomass C:N ratio. Mineralisation and immobilisation fluxes are divided equally between the nitrate and ammonium pools. Biomass growth and mineralisation on death both involve respiratory loss of C to CO_2. The growth yield coefficient *Y* is taken to be 0.5 – thus twice as much C is lost from the *soluble* C pool as appears in new biomass. Carbon made available by biomass death is apportioned between CO_2, *soluble* C, and the SOM pools (Figure 7.4, fluxes to CO_2 not shown) in the ratio 0.5:0.1:0.4 respectively. The flux to the *unprotected* and *protected* SOM pools (note that none enters the *stabilised* pool) is divided according to the clay content ϕ_c of the soil.

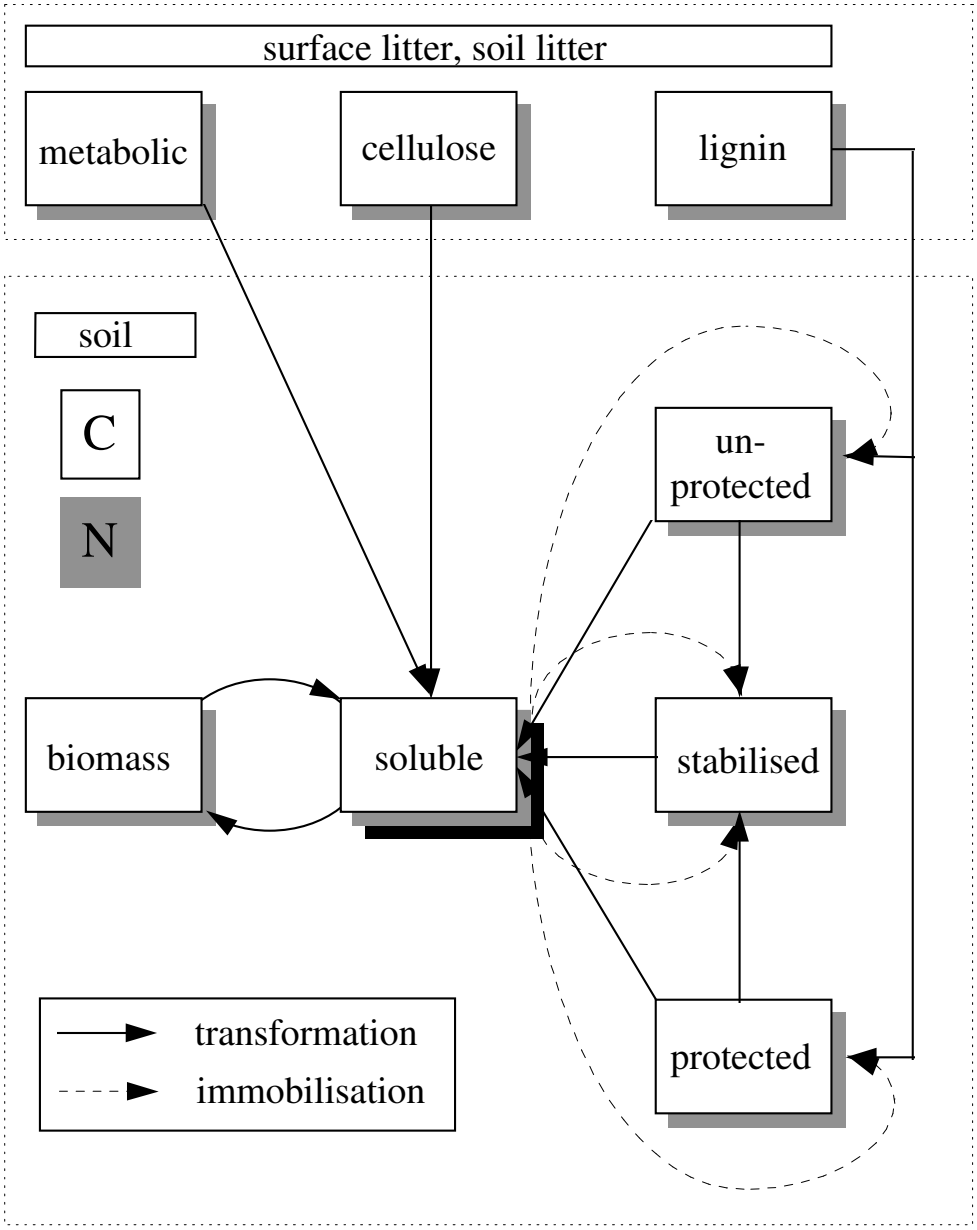


Figure 7.4. The modified soil submodel (1996) of the HP model. White boxes represent C pools, grey boxes the corresponding N pools (the two shaded compartments underlying the soluble C pool represent ammonium and nitrate); C and N fluxes are indicated by solid arrows, N fluxes alone by dashed ones. Nitrification, denitrification, volatilisation, leaching, atmospheric and fertiliser N inputs and plant N uptake are not shown.

Mineral nitrogen

Mineral nitrogen exists in two forms, ammonium and nitrate. Each pool is simulated dynamically with inputs of Organic and inorganic amendments and non-symbiotic fixation and outputs of plant uptake, volatilisation, nitrification, denitrification and leaching. Plant uptake is driven by root biomass and soil mineral N concentration

(ammonium + nitrate * t°C/20). Root biomass effect on N uptake is limited by low root C and high root N. The intrinsic N uptake constant (k_{up}) is taken to be 0.1 kg N kg^{-1} d^{-1} in EF and 0.25 kg N kg^{-1} d^{-1} in HP, and is modified by temperature and root moisture potential. Grass roots exude soluble C and ammonium. Non-symbiotic nitrogen fixation intrinsic rate constant k_{fix} ($5x10^{-5}$ kg N kg^{-1} biomass C d^{-1}) is modified by a bisubstrate Michaelis-Menten kinetics relation (K_{Csol} and K_{Nmin} are Michaelis-constant analogues 0.0005 kg C m^{-2} and 0.001 kg N m^{-2} respectively) and is inhibited by low soil soluble C and high mineral N. Transformations other than fixation are first order kinetics processes upon intrinsic rate constants (affected by temperature and soil moisture tension) times the respective N ion concentration: Ammonia volatilisation rate constant (k_{vol}) is taken to be 0.005 d^{-1} in EF and 0.02 d^{-1} in HP (pastures are likely to be less acidic); nitrification rate constant (k_{nit}) is 0.1 kg ha^{-1} d^{-1} and denitrification rate constant (k_{denit}) is 0.05 kg ha^{-1} d^{-1}. Nitrification and denitrification depend on microbial biomass. Denitrification occurs only in near-saturated soil. Nitrate N leaching depends on the drainage exchange rate and occurs when soil is above field capacity.

7.3.4 Environmental variables

Temperature affects nutrient cycling via the rate modifier f_T (Arah, 1996):

$$f_T = 0.075T\text{-}0.00125T^2 \quad (7.9)$$

which is asymptotic in 1.125 at temperature T of 30°C.

The moisture potential rate modifier $f\psi$ (Arah, 1996) takes the form:

$$f\psi = \left(e^{(\mu_w * \psi / (R * T°K))}\right)^{q\psi} \quad (7.10)$$

where μ_w is the molar mass of water (18×10^{-3} kg mol^{-1}), ψ is the moisture potential (J $kg^{-1} \equiv$ kPa). R is the universal gas constant (8.314 J K^{-1} mol^{-1}) and T°K is the absolute temperature. ψ is affected by soil texture and is always less than or equal to zero thus $f\psi$ is always less than or equal to unity, falling off sharply in dry soil. q_ψ default value is 20 for soil and 30 for surface.

7.4 Description of the Silvopastoral Model

The silvopastoral system is based on the potential of leguminous tree species to provide the main source of nitrogen fertiliser for grass production. Pollarding for green-manuring is the process by which competition (nutrients, light, water) is minimised and nutrients are released from tree to soil. An important additional advantage of these fertilising method is that it makes possible the synchronisation of nutrient release and nutrient demand, eventually maximising resource utilisation by the grass.

The silvopastoral model was designed to represent such a system by assessing the potential of dead tissues (prunings, leaves litter, dead roots, etc.) on supplying enough nutrients to maintain soil fertility according to the following premises: High yielding tropical pastures are strongly demanding of soil nutrient availability. Nitrogen fixing trees can contribute to the restoration of soil fertility, although external inputs can be eventually required to amend soil fertility. Inter-specific competition for soil nutrients is based on root biomass-root activity and root resilience. Light competition arises when the upper-storey canopy results in insufficient solar radiation reaching the grass. Nitrogen cycling is accelerated by pollarding the tree canopy, such action produces both mulch and dying roots and

nodules, all them high in readily decomposable organic matter. Additionally, it allows more solar radiation to reach the grass canopy. Soil organic matter decomposition depends on the quality of the mulch and litter produced and on the natural abundance of soil microbial biomass. Soil and air temperature and soil moisture drive all soil processes.
The Silvopastoral Model calculates the pools and flows of carbon and nitrogen in a $1m^2$ basis. Although the tree submodel was originally conceived to calculate its budgets on a stem basis, it has been set up to output in a $1m^2$ basis by adjusting: radiation interception, the inputs to the *Mulch and Litter* submodel and the outputs of the *Mineral Soil* submodel. The model consists of four submodels containing the relevant processes for the simulation of carbon and nitrogen cycles within an agroforestry system with trees, pasture, animals and soil.
The Silvopastoral Model can be used to predict the availability of mineral nitrogen for the system over a long period as well as for the evaluation of the permanence of the pasture and the tree population. Another application of this model is the design of inter-cropping systems (tree-pasture), where the species to be planted, the plant density and the management of the trees (pollarding) are of interest.

7.5 Modifications in parent models for the Silvopastoral model

7.5.1 Light competition

The distribution of radiation approach of Conijn (1995) was adopted and further scalated from 1 hectare to $1m^2$. PAR transmitted to the grass canopy is calculated by an attenuation coefficient (Lambert-Beer's law) based on the thickness of the tree canopy. Dealing with isolated trees entails the adjustment of tree leaf area index since the Lambert-Beer's law obeys closed canopy light attenuation. Knevel (1993) suggested that the ratio between absorbed PAR of a solitary tree A_s and an individual tree in a closed tree canopy was 1.7 for savannah tree species, thus A_s can be readily approximated upon the Monsi-Saeki equation. Even so these measurements correspond to the savannah ecosystem and to different tree species, the modelling approach resulted convenient and simulations resulted satisfactory. The proper parameterisation of absorbed PAR in our trees requires further attention. The assumptions are that the tree canopy is homogeneously distributed over the pasture, and varies according with the leaf area index of the tree. The tree canopy extinction coefficient k_{tree} is taken to be 0.57 and the leaf inclination angle is randomly distributed between 0 and 90^o. Provided competition between individual trees is not an issue, total absorbed canopy PAR by a solitary tree A_s, is:

$$A_s = q_{sc}\, I_{total}\, (1 - r_p)\, (1\text{-}e^{-(k_{tree} L_{tree})}) \,/\, N_c \qquad (7.11)$$

where:
q_{sc} is the ratio between absorbed PAR of a solitary tree A_s and an individual tree in a closed tree canopy A_c
I_{total} is the daily PAR ($J\ m^{-2}\ d^{-1}$)
r_p is the reflection coefficient (0.08; Lövenstein *et al.*, 1992)
k_{tree} the extinction coefficient of tree canopy, and
L_{tree} the leaf area index of the tree canopy.

N_c is the tree population density (trees m^{-2}) necessary for a closed tree canopy at maximum crown cover for pollarding ($4m^2$). N_c is taken to be 0.25 (i.e. 2500 trees ha^{-1})

The daily reflected PAR by the tree population I_r is:

$$I_r = q_{sc}\, I_{total}\, r_p \qquad (7.12)$$

The PAR transmitted through an homogeneous canopy to the understorey I_{grass} is calculated as follows:

$$I_{grass} = I_{total} - A_s - I_r \qquad (7.13)$$

Disaggregated model: Disaggregating the model into *near*, *mid* and *far* zones required an estimation of the fractional shade that individual trees cast over each zone. Knevel (1993) modelled the cumulative fractional shade as a function of the distance from the tree base relative to crown cover radius in savannah trees. Conijn (1995) suggested non-linear interpolation at the boundary of each *zone* to approach the corresponding shade fraction. The assumptions are that trees are homogeneously distributed in the field and that near zone is the aggregated of $3.14m^2$ circles with one tree at the centre, mid is the aggregate of 2m thick surrounding areas and far is the rest of the field (in which every point is +3m from the nearest tree). The shade of individual trees is the same to all directions and does not reach the *zones* of adjacent trees (Figure 7.5).

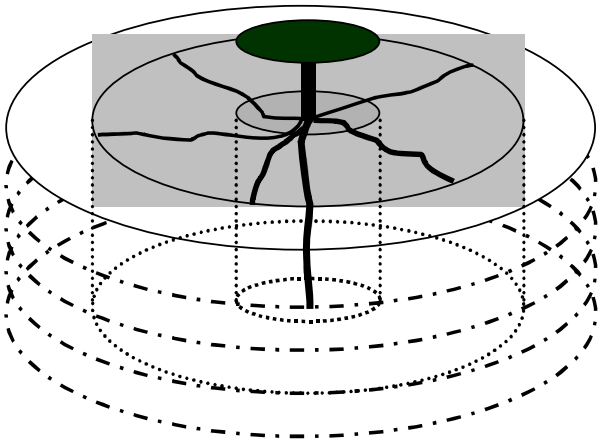


Figure 7.5. A tree-grass diagram with three zones at different distance from the trunk (Conijn, 1995); soil could also be compartmentalised in each zone. In the dissagregated Silvopastoral model, the zone *near* to the tree is 1 m in radius, zone *mid* is a doughnut of 3 m external radius; zone *far* is the outer space within the field (i.e. the area not included in zones *near* and *mid*).

The PAR transmitted to the understorey in *zone* (n) (I_{grass}(n)) is calculated as follows:

$$I_{grass}(n) = I_{total} - f_{sh}(n)\{(N\, A_s) + I_r\} \qquad (7.14)$$

where:

I_{total} (n) is the daily PAR in *zone* n (J m^{-2} d^{-1})

zone (n) refers to the distance from the nearest tree (near, mid and far)

f_{sh}(n) is the fraction of the intercepted PAR by the tree population with respect to each *zone* (n). f_{sh}(near) is 0.25, f_{sh}(mid) is 0.30 and f_{sh}(far) is 0.45 (Knevel, 1993)

N is the actual tree population density (trees m^{-2})

A_c is the absorption of PAR by an individual tree in a closed tree canopy

I_r is the daily reflected PAR by a tree population
The total transmitted radiation of the mixture could be expressed as:

$$\sum_{n=near}^{far} A(n) \bullet I_{grass}(n) \qquad (7.15)$$

where:
$A(n)$ is the *zone* (near, mid or far) surface (m^2)

7.5.2 Mulch and Litter

In the Silvopastoral model *mulch* was introduced as a diversion of tree *leaf* and *branch* biomass, alternative to *litter*. Both *mulch* and *litter* contain metabolic and structural dry matter but in different proportions (Figure 7.6). Unlike the *litter*, *mulch* is removed from the trees before the tissues undergo senescence, thus preventing the reduction of quality of plant material. Two major features regarding that issue were considered in the model: C:N ratio, which rises due to the recycling of substrate before any plant part dies, and the *lignin* fraction of plant structure, which grows with ageing of the tissues. For the purposes of the model, the *lignin* fraction is considered to be fixed for each outflow, being lower for *mulch* and higher for *litter*. *Mulch* + *litter* carbon pools on soil surface $(ML)C_i$ feed on all the above-ground live components of the system and contribute to *soluble* and *organic* (SOM) C pools of soil:

$$\delta(ML)C_i / \delta t = sh_i + l_{lit\,i} + l_{mulch\,i} + b_{mulch\,i} + fa_i - FC_i \qquad (7.16)$$

Where:
i is the *metabolic*, *cellulose* or *lignin* fraction of litter in soil surface
sh_i is *grass shoots*$_i$ litter
$l_{lit\,i}$ is *tree leaves*$_i$ litter
$l_{mulch\,i}$ is *tree leaves*$_i$ mulch
$b_{mulch\,i}$ is *tree branches*$_i$ mulch
fa_i is animal *faeces*$_i$
FC_i is mineralisation/humification of *i* mulch and litter

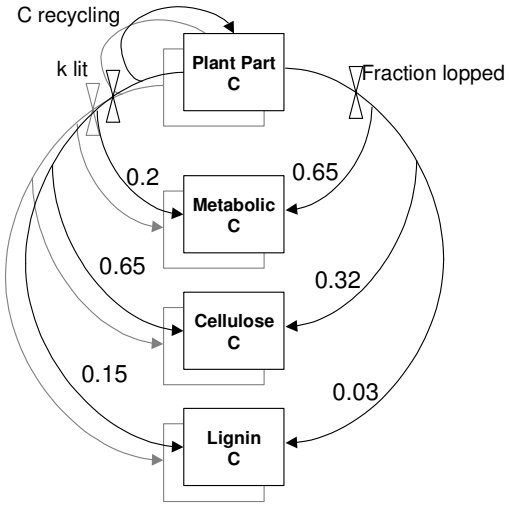


Figure 7.6. Structural C partitioning in Litter and Mulch above (black) and below (grey) ground. Figures beside arrows are the fractions of each plant part C pool to each Litter and Mulch compartment. ***k lit*** is the rate of naturally occurring

plant part death. Lopped fraction is a management option and can be tuned according to the interest of the user. Figures of mulch fractions correspond to *Gliricidia sepium*.

7.5.3 Soil Submodel

The parent models originally shared a common soil submodel, described in Arah (1996), but it was modified in the HP, following evaluation against several long-term soil organic matter datasets, to make it less responsive to changing inputs (Arah *et al*., 1997; John Thornley, 1996, personal communication). Linking the EF and HP models could have used either soil submodel. The earlier EF submodel, described by Arah (1996), is attractive because it is relatively simple and because published versions of both models employ it. However, as it is outlined in sections 7.3.3 and 7.3.4, the newer HP submodel offers more scope for site-specific tailoring. It follows the majority of current SOM models in introducing a recalcitrant ("stabilised") pool in order to buffer input response (McGill *et al*., 1981; Parton *et al*., 1987; Verberne *et al*., 1990; Nicolardot *et al*., 1994b,c; Chertov and Komarov, 1995), but it retains a degree of flexibility by allowing the C:N ratios of various pools to vary over time, depending on the overall mineral N content of the system. Moreover, all inputs (whatever their provenance) are characterised by their quality (metabolic:cellulose:lignin fractions) rather than by single decay constants, which must be more appropriate for a model in which, eventually, management options such as pollarding and litter incorporation are to be explored. The two models were thus brought into line by sharing the HP soil submodel.

7.5.4 Pollarding

Pollarding and subsequent litter incorporation differs from leaf and branch litter since substrate C and N recycling within the plant does not take place in pruned parts thus it has higher N content than shed biomass. Apart from modifications to the Litter submodel components, one new management routine was introduced. The programming code consist on

- determining the size of the tree that triggers pollarding for the first time and for subsequent prunings,
- removing a fraction of structure, meristem and substrate from branch and leaves this fraction (0 to 1) being the pollarding intensity defined by the user,
- reducing tree Leaf area index according to the reduction in leaves biomass
- allocating the prunings into the corresponding litter pools (metabolic, cellulose and lignin)
- adjusting the partitioning of substrate carbon in favour of tree parts other than stem to respond to lopping of the tree tip (i.e. apical meristem)

4.3 Parameterisation

The EF and HP models contain many parameters describing plant (and animal) growth, as well as the SOM turnover parameters identified above. All of these are potential candidates for site-specific parameterisation. The aim of the this was to identify the more important parameters in order to make the adaptation to a different environment tractable. In adapting EF/HP to produce a tropical silvopastoral model some of these parameters have been examined. Following is a list of EF/HP parameters, which were changed in the parent models (table 7.4):

Table 7.4. Parameters in the Silvopastoral model that were modified from the original in HP and EF

Parameter	Definition	Value	Units	Source and comments
$I_{0,avg}$	Average light receipt on the ith day (PAR)	11.6	(MJ m^{-2} d^{-1})	Wilson and Ludlow (1991)
$I_{0,range}$	Seasonal oscillation amplitude of $I_{0,avg}$	0.5	(MJ m^{-2} d^{-1})	
$\alpha_{MAXgrass}$	Leaf photosynthetic efficiency under moderate shade	2.5	(kg CO_2 J^{-1})	Johnson, Parsons & Ludlow (1989); Wilson and Ludlow (1991)
k_{grass}	Grass canopy extinction coefficient	0.7	(m^2 leaf)$^{-1}$	Cruz (1997) quoted a k_{grass} of 0.73 for Dichathium aristatum, C4, which is assumed more similar to B. decumbens than the 0.5 reported for latifoliates.
k_{tree}	Tree canopy extinction coefficient *G. sepium*	0.57	(m^2 leaf)$^{-1}$	Harrington & Fownes (1995)
k_{tree}	*L. leucocephala*	0.58	(m^2 leaf)$^{-1}$	Harrington & Fownes (1995)
$n_{stemsZ1}$	fraction of a fully developed tree that corresponds to 1 m^2 in zone near	0.19		this work; Knevel (1993)
$n_{stemsZ2}$	fraction of a fully developed tree that corresponds to 1 m^2 in zone mid	0.03		this work; Knevel (1993)
$n_{stemsZ3}$	fraction of a fully developed tree that corresponds to 1 m^2 in zone far	n.d.		Variable, depending on tree density and array, maximum of 277 trees in a squared layout
$k_{branch}M20$	Activity of branch meristem at 20°C	5		this work
$K_{coarsert}M20$	Activity of coarse root meristem at 20°C	5		this work
$K_{finert}M20$	Activity of fine root meristem at 20°C	5		this work
$K_{leaf}M20$	Activity of leaf meristem at 20°C	5		this work
$K_{stem}M20$	Activity of stem meristem at 20°C	5		this work
$f_{pruning}$	fraction of canopy that is cut to the mulch and litter sub-model	0.0-0.99		this work
$LAI_{pruning}$	Tree leaf area required to trigger pollarding	5.25	(m^2 leaf stem^{-1})	this work
Parameter	Definition	Value	Units	Source and comments

$Stem_{max}$	Maximum size of stem for lopping tip top	10	(kg DM $stem^{-1}$)	
$f_{mulchZ1}$	Fraction of prunings deposited on zone near	0.25		this work, optional
$f_{mulchZ2}$	Fraction of prunings deposited on zone mid	0.75		this work, optional
$f_{mulchZ3}$	Fraction of prunings deposited on zone far	0.0		this work, optional
f_{NlX}	N concentration of leaf structure *G. sepium*	0.034	[kg N (kg Structure DM)$^{-1}$]	this work
f_{NlX}	N concentration of leaf structure *L. leucocephala*	0.04	[kg N (kg Structure DM)$^{-1}$]	this work
f_{NlM}	N concentration of leaves meristem *G. sepium*	0.034	[kg N (kg Meristem DM)$^{-1}$]	this work (same as structure)
f_{NlM}	N concentration of leaves meristem *L. leucocephala*	0.04	[kg N (kg Meristem DM)$^{-1}$]	this work (same as structure)
f_{NbM}	N concentration of branch meristem	0.005	[kg N (kg Meristem DM)$^{-1}$]	Binkley, (1993)
f_{NplX}	Fractional N content in grass structural DM	0.016	[kg N (kg Structure DM)$^{-1}$]	this work
$f_{Ngrass,dead}$	Fraction of N in grass degradable structure	0.005	[kg N (kg Structure DM)$^{-1}$]	Assuming c. 3% crude protein in grass leaf litter
$grassroot_{depth}$	rooting depth grass	1.8	(m)	this work
$SLAmax_{grass}$	Maximum Specific Leaf Area of grass	21.1	m^2 leaf kg^{-1} DM	Wong (1991)
$kLAI_{an}$	Grass Leaf Area Index for half-maximal animal intake	1.4	m^2 leaf m^{-2} ground	this work
$intake_{max}$	Maximum animal intake rate, saturating LAI	13.5	(kg DM $head^{-1}$ day^{-1})	450 kg LW steers eating 3.0% LW
fN_{urine}	Fraction of nitrogen to urine	0.52		Haynes and Williams (1993)
$mulch_{met,l}$	Metabolic fraction of tree mulch *G. sepium*	0.65		this work; Parton et al. (1987)
$mulch_{met,l}$	*L. leucocephala*	0.30		this work; Parton et al. (1987)
Parameter	Definition	Value	Units	Source and comments

$mulch_{cel,l}$	Cellulose fraction of tree mulch *G. sepium*	0.315		this work; Parton et al. (1987)
$mulch_{cel,l}$	*L. leucocephala*	0.613		this work; Parton et al. (1987)
$mulch_{lig,l}$	Lignin fraction of tree leaf mulch *G. sepium*	0.035		this work; Parton et al. (1987)
$mulch_{lig,l}$	*L. leucocephala*	0.027		this work; Parton et al. (1987)
N_{fert}	N fertiliser application	65	(kg N ha^{-1} yr^{-1})	requirements of B. decumbens monocrop
k_{leach}	Nitrate leaching rate constant	0.004		
k_{vol}	Ammonia volatilisation rate constant	0.002	(d^{-1})	Century; pastures are likely to be less acidic
$T_{air,avg}$	atmospheric air year average temperature	23	(°C)	weather records (30 yr)
$T_{air,range}$	Atmospheric air temperature year oscillation amplitude	2.5	(°C)	
$T_{soil,avg}$	soil year average temperature	30	(°C)	Wood (1995)
$T_{soil,range}$	soil temperature year oscillation amplitude	2.0	(°C)	

7.5.5 Modelling platform

The Silvopastoral model was developed by encoding the relevant parts of HP and EF on ModelMaker 3.0.3 (Cherwell Scientific Publishing Limited, 1997, Oxford, UK, Walker and Crout, 1997). ModelMaker is a graphic modelling software that also allows prototype model simulations to be executed, thus facilitating the edition of the code (prior to compilation with a programming language) and the understanding of the processes by visualising the relationships and performance of the components during and after the simulations. An additional reason to choose ModelMaker for this work was the possibility of virtually programming-free mathematical modelling, that allows concentrating on the biological process of the study. A fourth-order step Runge-Kutta integration method was used in this simulations, the initial time step 0.007 days (10 minutes), and the accuracy of seven significant figures. Longer time steps during the stabilisation process caused the program to be interrupted due to arithmetic errors. However, since the Silvopastoral model has not been compiled and there is a rather large number of components and variables, a single year run can take up to 40 minutes. Moreover, each run involves an initial period of stabilisation (one year), which is not useful for analysis. The model consist of 55 state variables and about 200 other variables and fluxes depending on nearly 150 parameters (Figure 7.7).

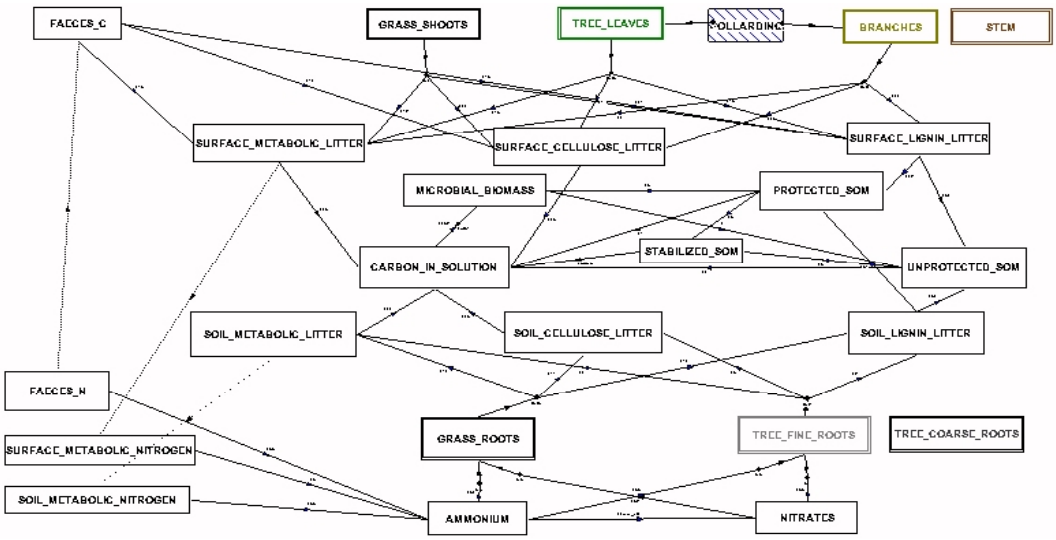


Figure 7.7. Middle level overview of the Silvopastoral model as represented in ModelMaker 3.0.3 (Cherwell Scientific Publishing Limited, 1997).

7.6 Simulations

References to comparable observations reported are presented where available. However, as discussed by Thornley and Verberne (1989), measurements in grasslands are highly variable and, one way or another, often incomplete with respect to the scope of a particular piece of work. Nevertheless, when steady state simulations were carried out, the results were compatible with those in the literature. The model produced the following solutions:

- Are the model results consistent with independent field data sets? If not, why not?

Above and below ground biomass production:

Brachiaria decumbens forage production predictions were within the bounds of independent field datasets (Table 7.5). However, seasonal variability was reproduced less accurately. Perhaps the weather functions in the silvopastoral model (air and soil temperature and especially atmospheric humidity) were too simple to cope with the seasonal variability measured in the silvopastoral experiment.

B. decumbens root biomass predictions in the model are low compared with the experimental results and independent datasets (Table 7.5). This is explained by the different management of the pasture in each situation. Corrêa and co-workers (1999) used fertilisation doses of 50 kg N ha^{-1} yr^{-1} and sufficient K and P, whereas in the silvopastoral experiment in Valle Nacional, no fertiliser was added, but there was no grazing. In the model, only an initial addition of inorganic fertiliser was used and green manure was applied subsequently. Grazing is used at 3.5 heads ha^{-1} stocking rate. Higher stocking rate and continuous grazing in addition to more frequent tree pollarding would lead to lower fine root biomass in the model simulation.

Gliricidia sepium foliage production predictions were 15% above the highest figures found in the literature. This can be taken as a satisfactory approximation since growth rate in the tree submodel is a function of many variables (canopy gross photosynthetic rate, N substrate conductance rate, partitioning ratio between structure and meristem, intrinsic specific growth rate of leaf meristems) and parameters (leaf photosynthesis parameter, light extinction coefficient, activity of leaf meristem, potential leaves meristem size). In the transformation of the tree model for the Silvopastoral model, only measured parameters were updated, whereas many others remained the same as in the original model. Model predictions in the same order of magnitude were considered acceptable as this is a prototype model.

Table 7.5. Comparison of model outputs, experimental results and independent results on above ground biomass production of grass and trees.

Species	Model (steady state)	This work	Independent datasets
B. decumbens forage prod. (Mg DM ha^{-1})	0.85 to 0.98 (40 days)	0.54 (63 days) to 3.45 (39 days)	0.93 (Macedo *et al*., 1993) 1.09 in 40 days (Carvalho, 1997) 3.06 (Eriksen and Withney, 1981)
B. decumbens - *G. sepium* root biomass (kg DM m^{-2})	0.07 – 0.12 *B. decumbens* 0.003 – 0.008 *G. sepium*	0.53 – 0.81 (ash-free biomass, grass + tree)	0.83 – 1.54 (Corrêa *et al*., 1999, Personal Communication.; grass monocrop, washed roots)
G. sepium mulch producn. (g DM $tree^{-1}$)	370 (100 days)	292 (100 days)	90-320 (100 days)
Fractions of Soil Organic Matter	*stabilised*: 0.17	-	Passive: 0.39 (0.1 S.D.) (Schimel *et al*., 1994)
	protected + *unprotected*: 0.56	-	Slow + Detrital: 0.57 (0.12 S.D.) (*ibid.*)
	microbial: 0.02	-	Microbial: 0.03 (0.005 S.D.) (*ibid.*)

Soil organic matter:
A steady state simulation of the Silvopastoral model under regular pollarding schedule predicted the Silvopastoral system to maintain the *stabilised* pool of SOM (c. 2.2 kg C m^{-2}) relatively constant, and the *unprotected* (0.06 kg C m^{-2}), *protected* (3.7 kg C m^{-2}), *microbial* (0.14 kg C m^{-2}) and *soluble* (2.0 kg C m^{-2}) pools to gradually increase during a 2500 days simulation (one year stabilisation + 5.8 years useful output) (Figure 7.8). These results are at the top bound of reported figures of total soil organic matter in pasture systems world wide (1.0 to 11.0 kg C m^{-2} in the top 20 cm of soil; Parton *et al*., 1993; Carter *et al*., 1993; Motavalli *et al*., 1994). Uncoupling the tree model in the silvopastoral model (grass animal and soil remain) produced solutions of c. 6.0 kg C m^{-2} as *unprotected*, *protected* and *stabilised* SOM did not vary during the six years simulation. The model estimations are in agreement with the fractions of soil carbon determined by Schimel *et al*. (1994) in a global scale simulation (n = 38 sites in five continents) (Table 7.5). Soils in Valle Nacional ranged between 2.58 and 6.17 kg C m^{-2} (Table 6.4; C = organic matter / 1.724) which is lower than the model estimates. The size of the pools of soil organic matter in short simulations (i.e. less than 30 years) in the Edinburgh Forest model depends, primarily, on their initial value (Thornley and Cannell, 1992). Perhaps the soil sub-model in the Hurley Pasture model responds in the same manner. It is likely that the decomposition – mineralisation rates and the initial values of the different pools of litter and organic matter from the parent model do not hold for the new conditions, thus new k_i parameters are required. Also, the temperature and humidity functions (see above) might be inappropriate for Mexico.

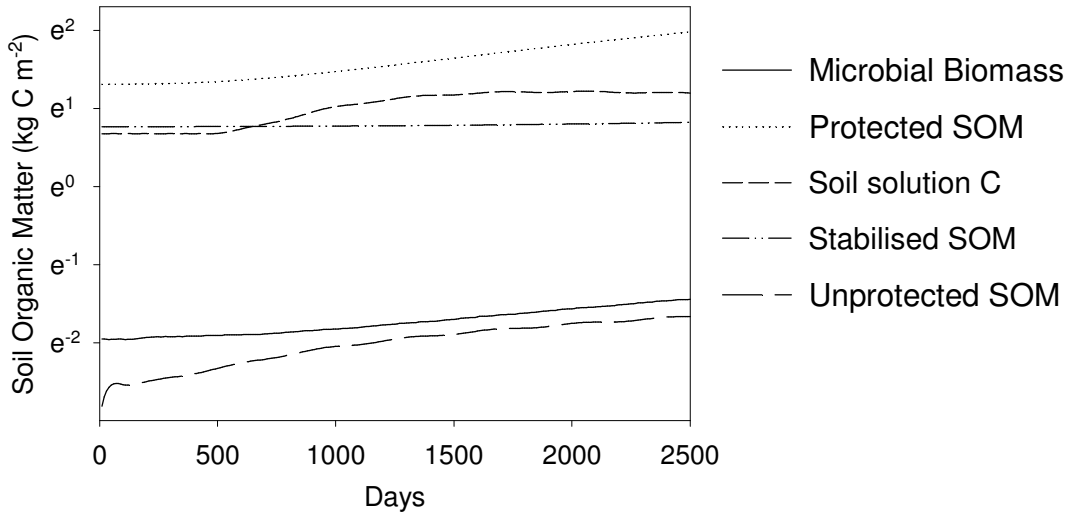


Figure 7.8. Soil Organic Matter Pools in a steady state simulation of the Silvopastoral model.

- To what extent does the tree population satisfy the nitrogen demand from the pasture?

The Silvopastoral model was compared with one in which the tree component was removed, the later required the application of 150 kg N ha^{-1} yr^{-1} in order to complete

the 2500 days simulation, whereas the former required one single application of 150 kg N during the stabilisation period (Figure 7.9). Production of grass biomass increased in the mixture due to improved photosynthesis and sustained supply of mineral nitrogen. The chart shows how photosynthesis essentially mirrors grass shoot biomass, since light is not limiting and no direct effect of nitrogen is considered in the model equation (Section 7.3.1). In a later version of the photosynthesis procedure, Thornley (1998) integrates substrate nitrogen and photosynthesis nitrogen into leaf photosynthesis calculations.

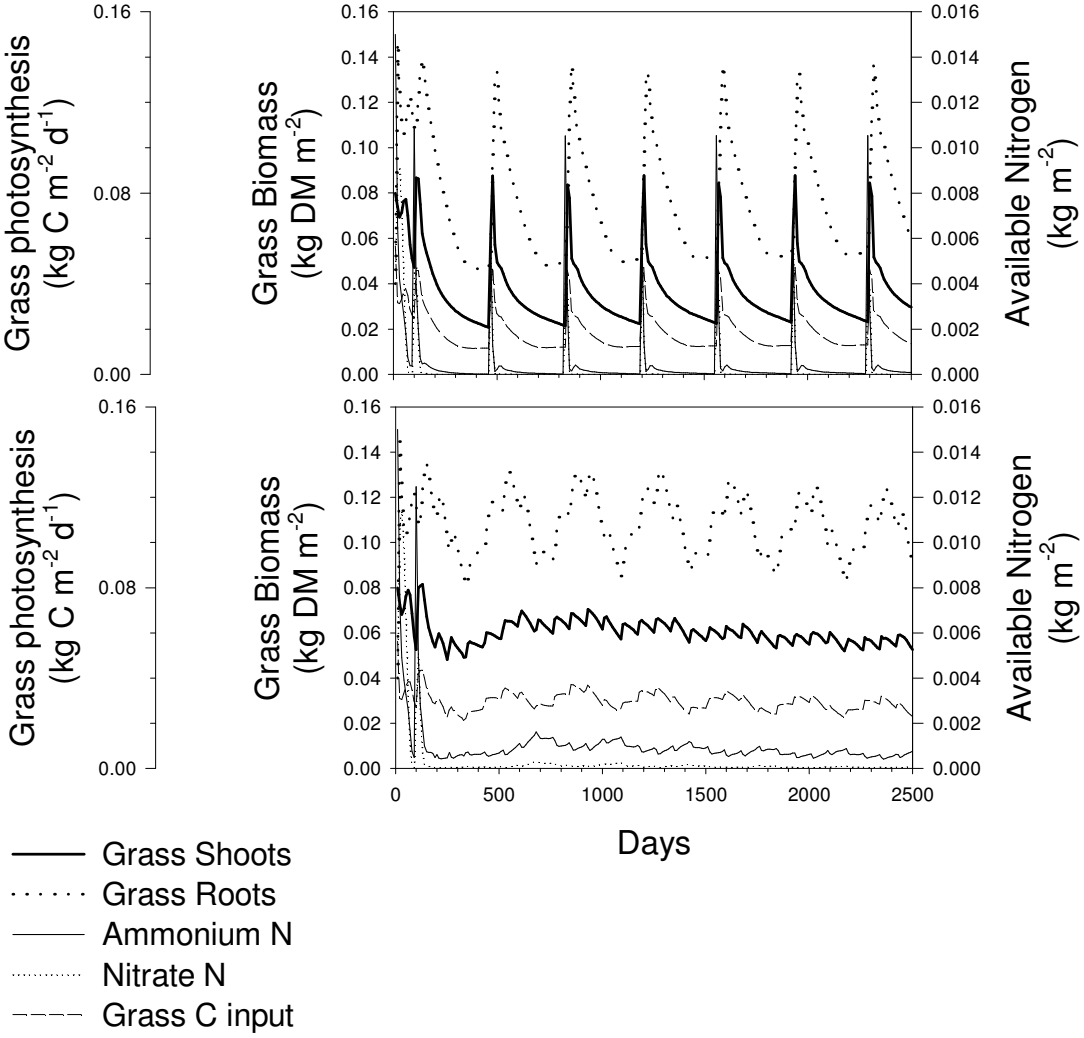


Figure 7.9. Grass standing biomass, Carbon input via Grass photosynthesis and Available Nitrogen in grass monocrop (top) and the Silvopastoral model (bottom). In grass mono-crop, inorganic N is applied in doses of 150 kg ha^{-1} yr^{-1}.

Litter above and below ground increased in the silvopasture model by about twofold, but cellulose and lignin litter below ground grew ten times the level of the mono-crop (Figure 7.10). This may be in association with a high turnover of tree coarse roots caused by pollarding. Coarse roots are assigned 65% towards cellulose litter and 20 % to lignin litter. This response is relevant for the capability of the trees to

populate and remain in the deep soil. Apparently frequent pollarding is deleterious for this purpose.

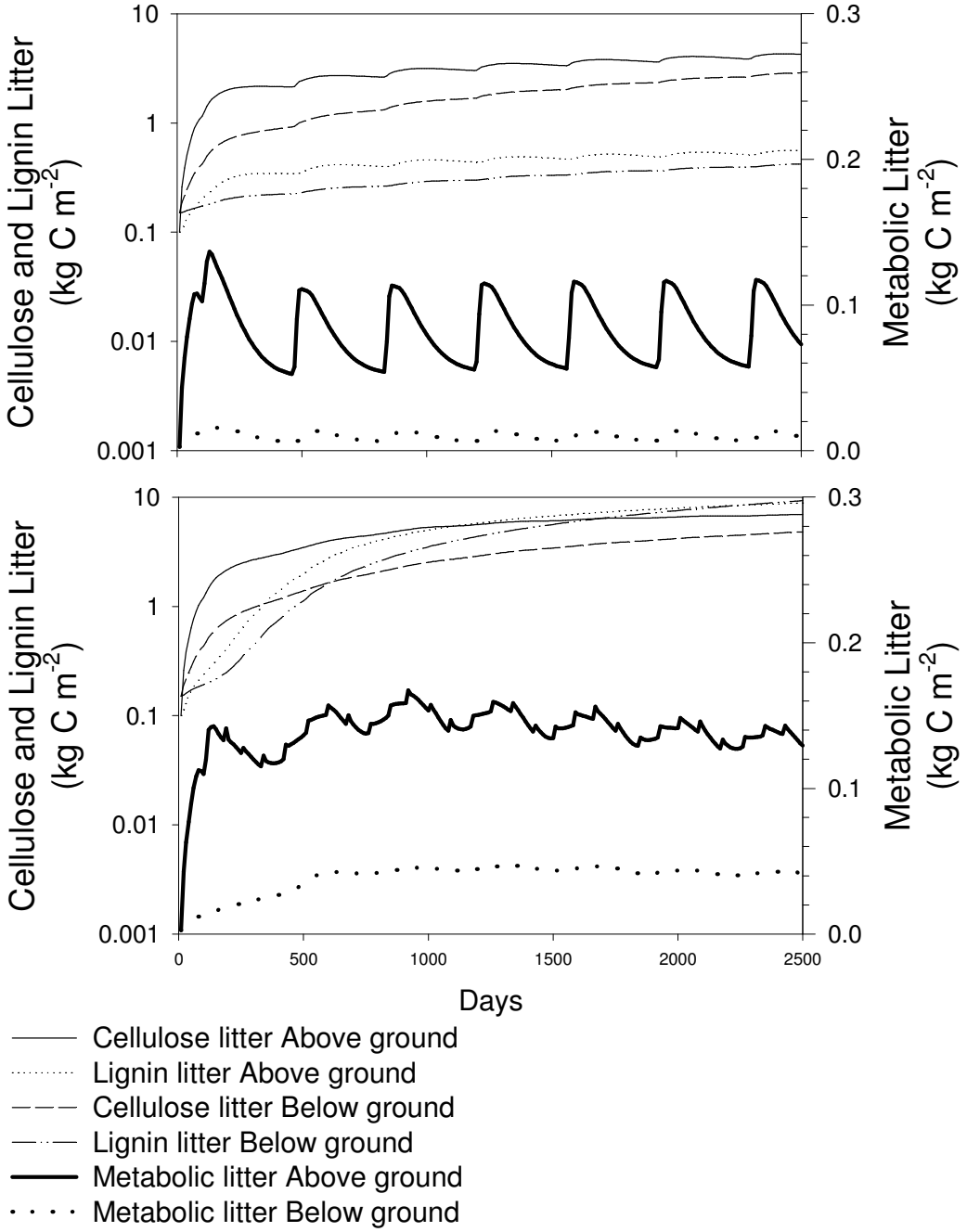


Figure 7.10. Carbon litter fractions in grass monocrop (top) and the Silvopastoral model (bottom). In grass mono-crop, inorganic N is applied in doses of 150 kg ha^{-1} yr^{-1}.

Trees provide four separate sources of nitrogen to the soil: natural dead leaves, root turnover, branch plus leaf mulch and fine root exudation. Some of this nitrogen becomes rapidly available to roots, but some is bound to low decay rate fractions of litter. Assuming that this less labile fraction acts to restore the baseline soil organic

matter lost through mineralisation, a single overall figure of nitrogen from each tree part has been calculated as follows:
The pasture demand of nitrogen is 285 kg ha^{-1} yr^{-1}. The tree population (*G. sepium*, 2500 trees ha^{-1}, 3.4 % N in leaves and 0.005% N in branches) supplies 111 kg N ha^{-1} yr^{-1} through the (above-ground) mulch, 3.75 kg N ha^{-1} yr^{-1} from leaves litter, and 100.1 kg N ha^{-1} yr^{-1} from coarse + fine root turnover and root exudation. Trees themselves take up 149.7 kg N ha^{-1} yr^{-1} leaving 65.1 kg N ha^{-1} yr^{-1} for grass consumption. The difference would be expected to be obtained from mineralisation of soil organic nitrogen and inorganic additions. Myers and Robbins (1991) suggest that improved tropical pastures without external additions of N are technically not sustainable; the damage piles up as gaseous loss rises and grazing degraded pastures accelerates N removal. In order to increase pasture productivity, external nitrogen must be added and organic N mineralisation enhanced.
Tree growth is faster in the model than observed values, according to the figures for mulch harvested (Table 7.5). The tree component of the Silvopastoral model is based on a forest model in which the stem is the main component. In the Silvopastoral model the growth of the stem is limited soon after the establishment by clipping the top, which prevents the trees from growing in height; the substrate is then allocated to branches and leaves. This could explain the elevated growth rate of leaves and branches observed in Figure 7.13.

- What are the management practices the system needs in order to prolong soil fertility?

In order to elucidate the effect of stocking rate and pollarding frequency on the fertility status of the soil under silvopastoral systems, sensitivity analysis procedure of ModelMaker 3.0.3 (Cherwell Scientific, 1998) was applied. The procedure is fully functional from an *ad hoc* dialog box. The parameter to be tested is selected and the spaces for bounds and steps of the analysis filled. Finally, the run is configured as to the length of both the simulation and time step. Indication of the integration method and the accuracy with which error is to be controlled can also be handled by the user. I used mid point integration method and time step of 12 minutes. The 11 variables tested were as follows: Grass N uptake, Soil NO_3-nitrogen, Soil NH_4-nitrogen, Mulch plus Litter carbon and nitrogen in three pools (Metabolic, Cellulosic and Lignin), Mulch and Litter Metabolic nitrogen, Soil organic matter carbon in three pools (unprotected, protected and stabilised). Results in this section describe those variables that were significantly affected by changes in the experimental variable.

- Stocking rate (assuming continuous grazing)

The number of animals in the paddock in continuous grazing was shown to be important for the sustainability of the system. Sensitivity analysis showed the effects of an increase from 4 to 10 heads ha^{-1} on litter and soil organic matter composition. The higher stocking rate treatment suffered a significant reduction in litter stock, this reduction being more conspicuous in the highly decomposable fraction of litter (Figure 7.11), Litter nitrogen behaved similarly (not shown).

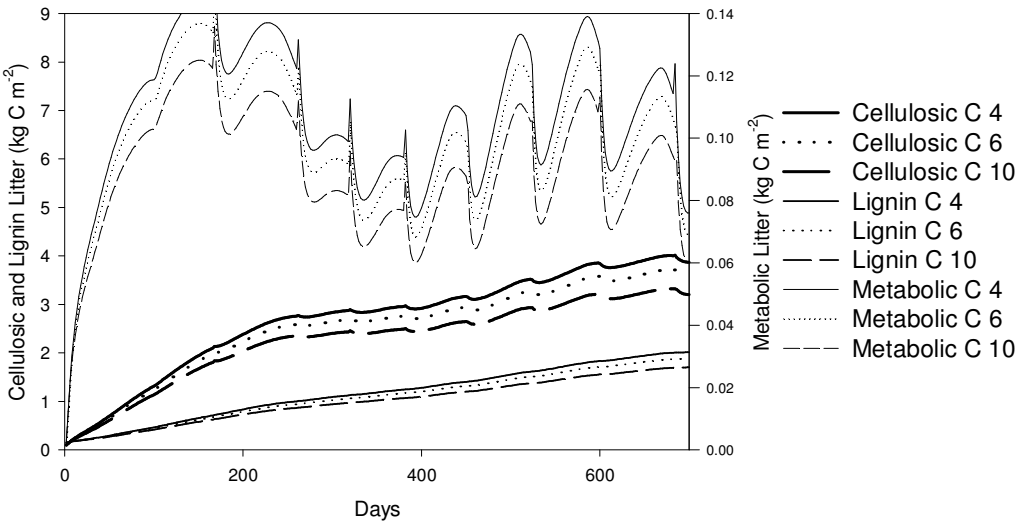


Figure 7.11. Carbon litter fractions in the soil surface, as affected by increasing stocking rate (4, 6 and 10 bovine head ha^{-1}) under continuous grazing.

Likewise, higher stocking rates produced reductions in the labile fraction of soil organic matter and as a result, less available carbon in the soil for microbial metabolism (Figure 7.12). This is important in terms of the short term sustainability of the system since recycling of nutrients is the core process for the maintenance of soil fertility.

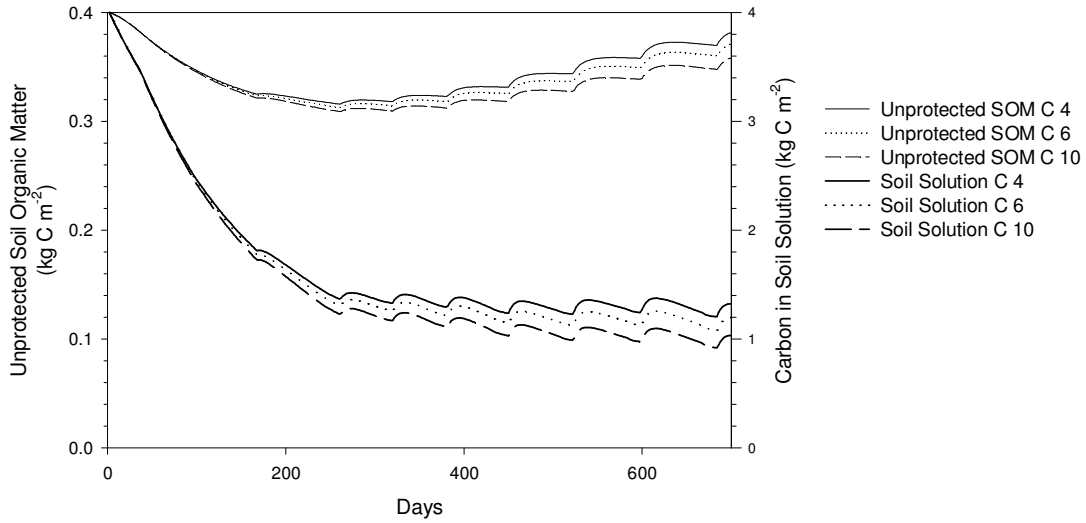


Figure 7.12. Microbial biomass carbon and unprotected soil organic matter carbon as affected by increasing stocking rate (4, 6 and 10 bovine head ha^{-1}) under continuous grazing.

- Tree pollarding frequency

Pollarding was conceived as an option to enable the user to control the cycling of nutrients (Figure 7.13). In fact, pollarding trees is the technique normally used in the field. Various aspects of the system are described in response to this practice. One of

the substantial modifications introduced to the Edinburgh Forest model when developing the silvopastoral model was the possibility of pollarding, which consists of the translocation of branch and leaf structural dry matter to the *mulch and litter* pool.

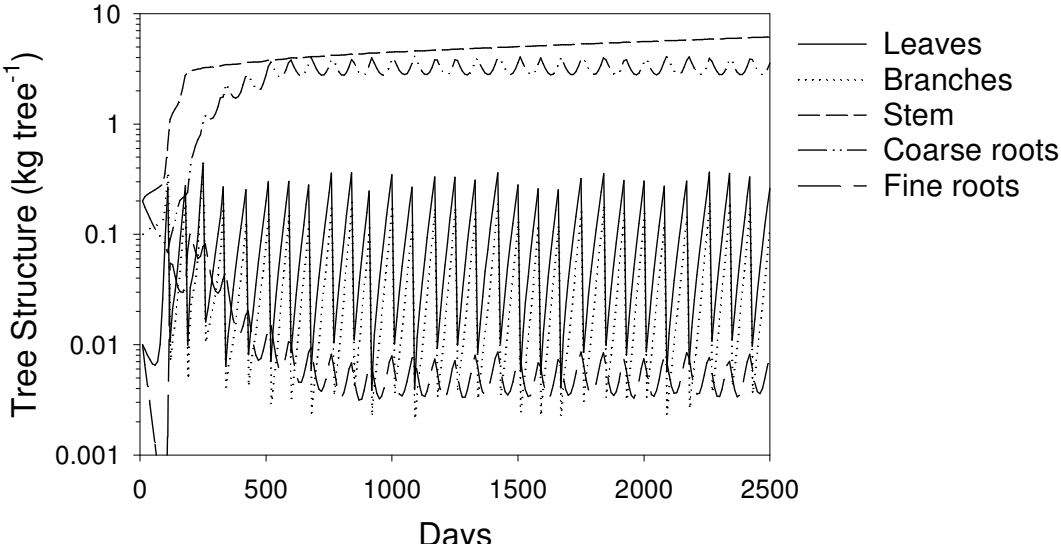


Figure 7.13. Tree biomass in the Silvopastoral model following sequential pollarding of branches and leaves.

During the current simulations, pollarding events were controlled by a short routine that read the size of the tree leaf area - provided the trees were six months or older. Once this pool reached 5.25 m^2 $tree^{-1}$, the program triggers a number of processes in the system that the user can monitor throughout the model run-time.
The fraction of leaves removed from the tree canopy is proportional to the transmitted radiation reaching the grass canopy. The model predicted a consistent increase in substrate carbon in the grass in the days following pollarding, suggesting that grass photosynthesis sensitivity to light interception by the tree canopy is correctly simulated by the model (Figure 7.10).
The pollarding interval is also an important factor influencing several other processes in the tree, and indirectly in the other components of the system. Longer pollarding intervals produced a higher biomass harvest per cycle from the trees. This is explained because pollarding occurs within the vegetative growing phase of the tree canopy (i.e. the growth curve is ascending). However, grass forage production was not shown to be strongly sensitive to this variable, at least within the range of the sensitivity analysis performed here. Even so, a slight diminishing in shoot biomass was observed as the pollarding interval became longer (Figure 7.14).

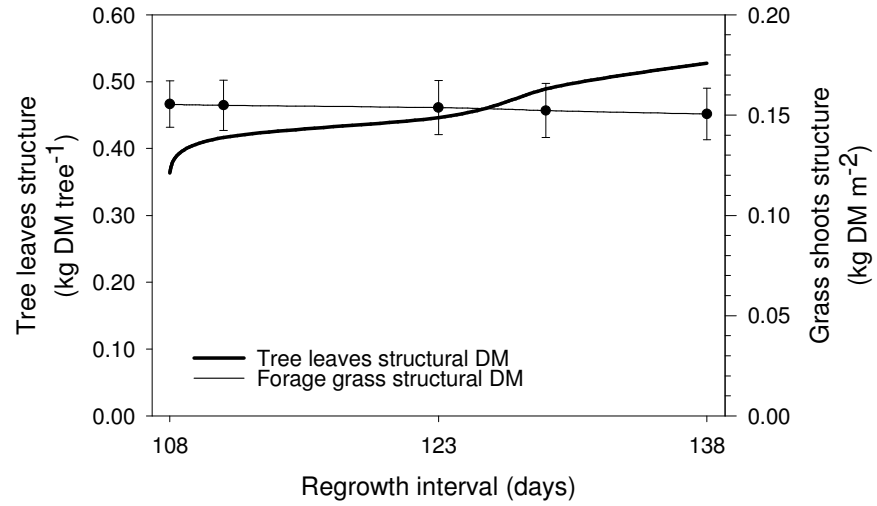


Figure 7.14. Tree leaf and grass shoot structural dry matter according to the length of the pollarding interval.

With respect to the competition for soil nitrogen, longer intervals between prunings produced a bigger pool of tree fine roots, enabling the tree component to capture more nitrogen from the soil (Figure 7.15). This might be connected with the reduced grass shoot biomass observed in Figure 7.14.

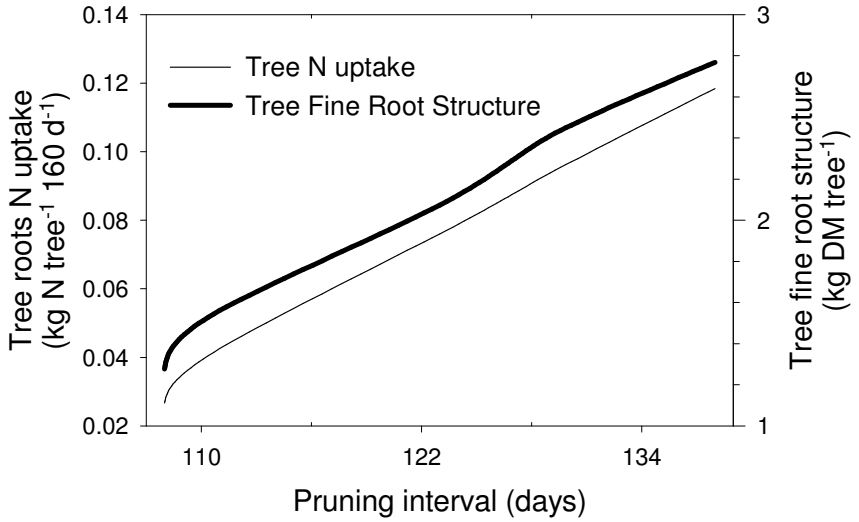


Figure 7.15. Nitrogen uptake and root structural C as affected by pollarding frequency.

One of the species attributes that drives many aspects of the tree management is specific leaf area. Specific leaf area (SLA, m^2 lamina kg^{-1} DM) must be addressed when selecting tree species for agroforestry purposes. It involves, on the one hand, light competition to the grass and, on the other, the mulch biomass that constitutes the benefit to the system. Lower SLA implies more biomass for less leaf area. The silvopastoral model simulates the expansion of leaf area based on an **incremental SLA** parameter which relates the allocation of photosynthesis carbon to leaf structure and the actual size of the *leaf structural dry matter* pool to work out the increment on

leaf area on a stem basis. This parameter was shown to strongly affect the tree gross (Figure 7.16.a) and maximum (Figure 7.16.b) photosynthesis.

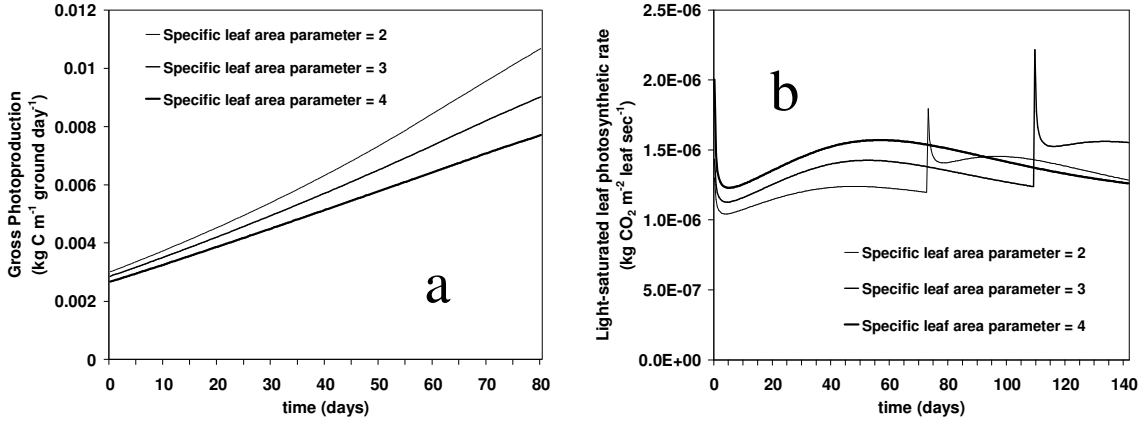


Figure 7.16. Tree canopy gross photosynthesis (a) and Maximum leaf photosynthesis (b) as affected by the Cumulative SLA Parameter ($[C]^{-1}$) of the tree canopy .

The maximum photosynthetic rate increases and the gross photosynthesis decreases as the SLA parameter increases. Apparently this parameter controls the feedback of leaf production to canopy photosynthesis. Single leaves assimilate more CO_2 as the concentration of nitrogen in leaf structure also increases but canopy gross photosynthesis decreases as it accounts for the total leaf area per stem. The second parameter determining SLA defines the maximum ratio between leaf area and structural dry matter (**SLAmax**). We were interested in the effect of the tree SLA on inter-cropping. The model suggests that higher SLA will reduce radiation transmittance faster (Figure 7.17.a), increasing competition among species and requiring a more intensive pollarding schedule compromising the survival of the trees. Higher tree SLA also affected grass shoot structural dry matter (Figure 7.17.b) which might be a result of a reduction in transmitted PAR.

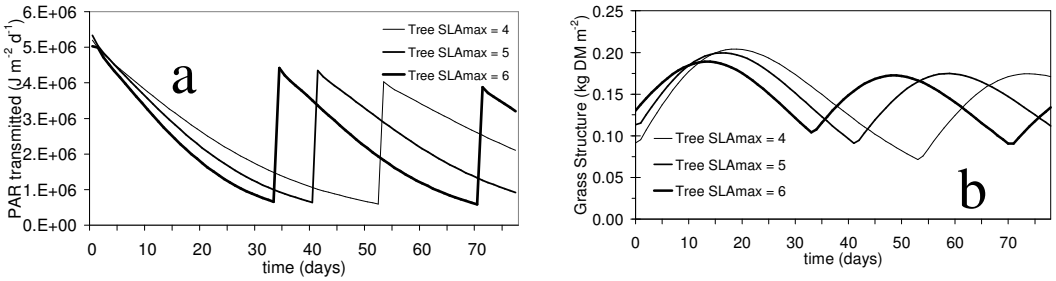


Figure 7.17. Radiation (PAR) transmitted through the canopy (a) and Grass shoots structural dry matter (b) under tree canopies of different Specific Leaf Area. Higher **SLAmax** parameter causes higher Specific Leaf Area in the tree leaves and more rapid recovery of ground cover of the canopy, thus shorter pollarding intervals.

7.7 Discussion

The model produced steady state simulations that are in agreement with independent pasture datasets. However, there is more disagreement with results from the Silvopastoral experiment, which served for the parameterisation of the model. Even

though such disagreement is not one of large differences, further field work is required in order to make the model to produce more reliable predictions. Attention should be drawn to factors affecting the interaction between the species, such as light transmission in the tree canopy and the light intercepted by the grass canopy (tree light attenuation coefficient, fraction of direct and diffuse transmitted light, fraction of tree shade that reaches each zone –*near*, *mid* and *far*-, grass specific leaf area). Another set of parameters that must be attended to are those of the partition of dead plant material to litter and mulch and these into soil organic matter. Perhaps the Century approach (Parton *et al*., 1987) should be introduced. Environmental driven flows of mineral nitrogen (leaching, volatilisation, denitrification) are only roughly described. A more mechanistic approach should be considered. Much of these recommendations have ignored insofar the complexity of the mathematics involved slow down the model simulations. This problem can be tackled with faster computer processors now available and more adequate programming languages, that allows for debugging – compilation of programs.
Despite these deficiencies, the results obtained in the simulations suggest that the model can be used to predict the status of the pasture according to pollarding frequency, it is also useful to analyse plant attributes that lead to the adequate selection of species, such as tree specific leaf area. Tree species with a lower specific leaf area allow more light to penetrate the tree canopy for the same leaf biomass. One of the management implications of reducing specific leaf area is to prolong the interval between prunings. A more efficient leaf shape in terms of light capture will reduce the need for pollarding when light competition is of concern. Thus, the model allows us to assess the amount of radiation that can be intercepted by the tree canopy before grass survival is impaired and provide some insights into the characteristics the tree species has to have to allow complementarity in inter-cropping. By the appropriate parameterisation of the model, it is possible to calculate the fraction of radiation which is intercepted in the tree canopy by correlating it with non-destructive estimates of leaf biomass.

7.8 Conclusions

The Silvopastoral model is based on existing models that are comprehensive in their description of the biogeochemical cycles of carbon and nitrogen and have been widely tested for different environments and crops/ecosystems. This gives confidence about the correct performance of the models chosen to build the Silvopastoral model. Based on this premise more attention was paid to the interactions when the two crop models work together, sharing soil resources and solar radiation. The suitability of the HP soil submodel (Arah, 1996), as a coupling component of pasture and forest models was confirmed. The present chapter has explored the relationship among components in terms of the trends of the biological effect of the inter-cropping on the two species based on the adaptation of the parent models to the new species and environment. Future research will involve the parameterisation, spatial disaggregation of the tree canopy and the soil, and full validation of the Silvopastoral model. Thus, it is not yet certain whether the Silvopastoral model agrees with real data in aspects other those evaluated in this study.

From the preliminary results of the simulations described here, I consider that the model works satisfactorily as a description of the behaviour of grass and tree populations in inter-cropping. The satisfaction of this first goal permits the modelling of the Tree-Grass Inter-Cropping System in the Humid Tropics of Mexico to be continued with confidence. However, the full incorporation of crucial limiting factors, such as availability and diffusion of phosphate, into the nitrogen cycling, as suggested in Whitmore (1993), is necessary if the Silvopastoral model is to be of real benefit to decision makers.

The original objective of this part of the research project was at least partially achieved as the Silvopastoral model was produced and it provides reasonable outputs. However, if the model is to be used in decision making, the correct parameterisation of every process and its validation with independent datasets must be carried out.

Much of the beneficial effect of the trees is as shelter for better resource capture and net photosynthesis of the pasture. However, the Silvopastoral model lacks responsiveness to shade in terms of air and soil temperature. Research results were not available on this matter.

8. General Discussion

8.1 Introduction

Maintaining fertility of tropical forest soils (mostly Oxisols and Ultisols, Szott *et al*., 1991) involves the transformation of three main factors affecting the balance of nutrients: (i) introduction of germplasm adapted to low fertility, acid soils, (ii) increasing high quality soil organic matter and (iii) reducing aluminium and iron toxicity. Managing organic fertilisers is associated with high labour costs, especially when green manure is cultivated not *in situ* (Sanchez and Salinas, 1981).

Although green-manuring is almost equivalent, in the short run, to using inorganic fertilisers in terms of the nitrogen use efficiency in annual crops (with respect to the harvest in the following year), in the long run, green-manuring has advantages for the soil physical and chemical properties of soil (*ibid*.). Soil organic matter becomes the main pool of nutrients of forest soils after slash and burn; it is also important for conferring soil structure to reduce soil erodibility and nutrient leaching. Organic matter buffers soil pH, thus can contribute to ameliorating Al and Fe toxicity that retains phosphorus in forms unavailable for plant uptake.

Silvopastoral systems in the tropics have been proposed as an alternative to high input agriculture for land reclamation, but more important, for preventing land degradation and even increasing the productivity of livestock systems. By combining appropriate tree and grass species it is expected that the inter-crop provides forage for more animals and sustains this production for longer periods of use of the same field. This is particularly topical in the light of the limited access to pristine forest land for cattle owners and the growing demand of food.

This research project was proposed as part of search for a suitable combination of leguminous trees with *Brachiaria decumbens* in the humid tropics of South East Mexico, both in terms of the tree species and of some management options such as plant density and pruning frequency. The experiment was used in combination with a simulation model to establish the grounds of viability of high yielding tropical grasses and fast growing nitrogen fixing trees in inter-cropping.

8.2 Establishment of the silvopastoral system

Establishing a silvopasture has proved to be twice as difficult as establishing the mono-crop of grass and tree separately. In addition to the cost and time involved in

growing and transplanting the trees from the nursery, the success of the plantation is compromised by its adaptability in the inter-crop. Grass must be kept down in order to allow for light reaching the tree foliage until the trees have passed the grass canopy. Alternatively, poles can be used when the desired species is able to be reproduced in this fashion.

The cost of establishment is the first but not the only limiting factor on introducing trees in *B. decumbens* swards. In general terms, it appears that *B. decumbens* kept the surviving trees in poor shape if compared with trees of the same nursery growing outside the grass area. Also, it is likely that *B. decumbens* was partially responsible for the low re-growth of the trees after pruning. However, diverse responses of tree species to inter-cropping suggest not to lay all the blame on *B. decumbens* for the poor development of the trees. The balance between the population density of the two species would be possible within a band in which the population of species A is low to allow the presence of species B, but at the same time restricts the expansion of species B, assuring the survival of species A. However, according to Westoby and colleagues (1989) such an equilibrium is transient and long term stability is only reached as one of the two species prevail. It is intended that the Silvopastoral system remains functional for at least longer than the traditional pasture mono-crop. The definition of equilibrium in the *Brachiaria decumbens* - leguminous trees inter-crop requires further investigation, and the Silvopastoral model can be of much value in this regard.

One of the more constraining factors in establishing such an innovative system is the lack of knowledge, both from the researchers and the local participants, as to the ecological interactions between species and the management of the experiment. Training of technicians and deliberating with the farm owner in order to set the plot in agreement with his future necessities take an enormous part of the time and effort of the field work.

The final result of the establishment of the experiment was one of a fairly well developed sward of *Brachiaria decumbens* with small zones invaded by tussocks of native grass and a tree population which was not fully successfully established. The trees varied in their capability to set off and to remain in good shape during the experiment, especially after pruning. Factors such as the proper management of the

nursery and preventing light competition from the grass in the following months after transplanting, as well as the control of pests and diseases are crucial if the effective establishment of the tree population is to be achieved.

The aim of this study was to provide insights into the potential of such an inter-crop for sustaining grass production, rather than the disavow of any species, thus no specific tests were performed for this purpose. Instead, progress was made on the characterisation of potentialities of each species and identifying the areas where more research resources should be concentrated.

8.3 Potential of *Brachiaria decumbens* in the Silvopastoral system

Brachiaria decumbens possesses attributes that make it qualify for tree - grass inter-cropping. These attributes are basically the same as in mono-crop, i.e. high productivity and nutritive value, adaptability to poor soils and the partial fulfilment of nitrogen demand by the development of symbiotic association with bacteria for nitrogen fixation (Reis *et al*., 1999). In addition, *Brachiaria decumbens* can grow under moderate shade (Stür and Shelton, 1991).

Paradoxically, these characteristics set the sustainability of the grazing system in jeopardy as the increased uptake of soil nutrients leads to an accelerated degradation of soil if no fertility amendments are considered. The need for additional sources of nutrients to soil in improved tropical pastures has been well demonstrated (Myers and Robbins, 1991). The present work tested one method consisting of mulching with leaves of leguminous trees in inter-crop since this method has been proven successful in some agroforestry systems with annual crops (e.g. Kass *et al*, 1989).

8.4 Potential of selected trees in the Silvopastoral system

Delonix regia

D. regia suffered the highest mortality among the four species after the first pruning. Also, according to root excavations and mini-rhizotron observations, this species was particularly susceptible to the attack of rodents, which proliferated during the wet season. These two events combined to undermine *D. regia* population to a greater extent than grass competition did. Forage biomass production in plots under *D. regia* was relatively free to grow after the first pruning, thus it is difficult to explain grass yield as a result of the accompanying tree. However in the sampling period before

pruning (dry season), grass growing under *D. regia* produced within the *medium* category (Table 4.13), the same as the Control plot. Similarly, *D. regia* associations, at the tree density used, did not alter the crude protein content, NDF and ADF of the grass.

Lysiloma auritum

L. auritum survival in inter-cropping is less clear. Of the two plots originally planted, one presented high survival rate (plot 2) but the other suffered the death of almost all trees (plot 11; this plot was further designated Control of grass mono-crop). *L. auritum* did not suffer pest attacks or poor re-sprout as a result of pruning but the re-growth was very slow. It is not clear whether this species has the potential for mulch production at the plant density used.

L. auritum may not be advisable as mulch producer because of its low re-growth rate, but its leaves share many similar (anatomical and chemical) characteristics with *L. leucocephala*. The short size of the trees and its positive effect on pasture (high yield in rains and medium yield in dry season, Sections 4.3.1 and 4.4.1) and soil (increases in soil organic matter, total nitrogen and nitrates, Section 6.3.3) suggest that this species deserves further consideration for its potential as a shade tree in grazing pastures.

Leucaena leucocephala

With respect to *L. leucocephala*, all plots presented more than 50% survival, but the re-growth rate after pruning was as low as in *L. auritum* (Table 4.3). No sign of nodulation for symbiotic fixation of nitrogen was found and the attempt to induce nodulation with natural strains from a neighbouring beans crop failed. Despite rodents severing some roots, the survival of the population was not endangered.

L. leucocephala leaves present desirable characteristics for green manuring (Section 4.4.5), and despite the low re-growth rate observed in this work, most authors report higher yields (Yamoah *et al*., 1986; Grewal *et al*., 1993; Avery and Rhodes, 1990). Decomposition in *L. leucocephala* leaves appears to be strongly restricted by its high (petiole + rachis) to lamina ratio and the particular arrangement of tissues in the leaf, that protects the nitrogen rich parts under the cuticle or other resistant tissues (Section 6.4.1).

Low decomposition rate of mulch can be beneficial, depending on the requirements of the system. High quality and slow decomposing mulch, in combination with the low light attenuation coefficient of the canopy (Harrington and Fownes, 1995) allow for longer pruning intervals since the nutrients are gradually released along the pruning interval, and transmitted light through the upper storey is not limiting for pasture growth. The slow release of nutrients is also valuable to prevent leaching in rainy environment and sandy soils.

Gliricidia sepium

G. sepium survival was good in plots established vegetatively but inconsistent in those of nursery trees. This suggest that the grass competition for light and soil resources is deleterious for small saplings but tolerable for pole-stands. On the other hand, this species was associated with lower organic matter and nitrogen in soil. This, in addition to its healthier rooting system could support the hypothesis that *Gliricidia sepium* competition caused the low to medium grass yields in plots 3 and 8 in the driest part of the year (Table 4.13). Re-growth rate in surviving trees was the highest among the species in this experiment (Table 4.3) but lower than other similar trials reported (e.g. Nygren and Cruz, 1998). No symbiotic fixation of nitrogen was present nor successfully induced.

G. sepium is a species of high potential for green manuring in tropical pastures. Its adaptability to inter-cropping, particularly when the stand is planted with poles, together with its high re-growth rate (Table 4.3) and high nitrogen foliage (Table 4.11) combine to produce a fertiliser of low cost and easy management. Species such as *Gliricidia sepium* might attenuate the detrimental effect of high yielding pasture on livestock systems (Section 8.3) by reducing the growth of grass and producing inputs for the balance of nutrients in the system. This hypothesis requires to be tested at tree densities higher than used in this work.

The rapid decomposition of *G. sepium* mulch (Section 6.3.1) may lead to a temporary excess in soil mineral nitrogen if the volume of mulch is high. However, absolute mineralisation can be brought down if pruning events are scattered in smaller volumes and shorter periods by applying partial pruning. This method is also compatible with the more regular demand of nutrients of a permanent pasture, and boosts the re-growth of the tree foliage.

8.5 Nutrient cycling

Roots perform an active role in nitrogen cycling by absorbing and releasing this nutrient. On the other hand, leaves and branches play a more passive role at modifying the chemical structure of organic matter and providing N rich substrate for microbial activity, determining the rate of decomposition/mineralisation of SOM. Prunings constitute an important pool of nutrients to the system because they decompose at a rate that can be synchronised with crop demand and because they are deposited near the area of higher concentration of roots. In summary, prunings are a useful tool for the management of the fertility status of the inter-crop.

Rising tree density from that used in this study to 2000 - 4000 trees ha^{-1} is suggested to increase mulch biomass yield, and the pools of metabolic and cellulose litter, thus improving soil fertility in the long term. By keeping more shade and more root competition, grass production can be restricted (as suggested by results in *G. sepium* - *B. decumbens*, Chapter 4), thus retarding the degradation of the pasture. Cannell *et al*. (1996) defined the potential benefit to the crop in agroforestry as the difference between those resources captured by the tree that the crop could not acquire itself and the fraction of the resources the crop was deprived of and are not later recycled (e.g. prunings of the next cycle). The Silvopastoral system aims at minimising this un re-cycled fraction. Nevertheless, since no symbiotic activity was detected in the tree roots and they occupied mainly the top soil, the role of the trees as sources of nutrients can hardly be claimed. This situation suggests the presence of trees as necessarily deleterious to the crop. I suggest that provided such negative effect is moderate and under the control of the farmer, it is beneficial for the sustainability of the system when dealing with pastures with the potential for rapid soil degradation. Sanchez (1995), however, elaborated on beneficial effects the trees provide other than resource capture, such as improving soil microbial activity and nitrogen mineralisation, as stated above.

The nitrogen that entered the soil derived mainly from root turnover, tree prunings and grass BFN. Even though no quantification of tree root longevity was performed, it is likely that pollarding effectively increases root turnover. This effect has been demonstrated for other tropical leguminous species (Nygren, 1995). The ratio of nitrogen entering soil organic matter from below and above ground (c 3:1) suggest

that more attention should be drawn to the role of the roots in nutrient cycling. Whether leguminous tree roots retranslocate nutrients after pruning, as well as the rate of root turnover and how this is affected by management and by the crop is an area that deserves investigation if the tree species is candidate for agroforestry systems.

8.6 Simulation analysis

In a broad sense, the Silvopastoral model performed within reasonable bounds if compared with this research and with independent datasets. Much work is still required in order to parameterise and validate the model. However, some general uses were described, such as the comparison of mono-crop and inter-crop on grass yields and soil organic matter. Although no conclusive results can be drawn, insights were given into the role of each source of interaction (shade, mulch and nutrient competition). I believe that these comparisons are useful even if they are not completely accurate, because they allow to evaluate whether the solutions produced by model prototype are in agreement with real data. Consequently, they constitute a tool in the improvement of the model.

8.7 Concluding remarks

Introducing an improved grass species that requires to be further attenuated in its growth may sounds contradictory. This working hypothesis was conceived in the light of the need for overcoming soil deficiencies with the use of germplasm adapted to local soil conditions, so as to prevent land degradation and to attain sustainability. It is important to state that favouring that, relies on means other than the use of chemical fertilisers, such as enhancing soil microbial activity and optimising nutrient cycling (Sanchez, 1994).

Silvopastures at low tree density (< 900 trees ha^{-1}) may not be beneficial for the pasture in the short term, but they are not detrimental when taken over a full year. Meanwhile, they provide shade for the animals, retain nutrients for recycling (both in plant and soil organic matter) and incorporate environmental services, such as soil stability and reduced chemical fertilisation and act as niche for birds and other fauna.

The results presented suggest that *Delonix regia* and *Lysiloma auritum* may be less suitable for a silvopastoral system in the fashion proposed in this study, mainly

because of their poor re-growth after pruning (i.e. because of intrinsic, rather than grass competition derived limitations). *L. leucocephala* and *G. sepium*, on the other hand, appear to have better performance under the prescribed management. However, the number of trees in each plot seemed to be insufficient to provide enough mulch to fulfil the grass demand. Whether a higher tree density would counteract the deleterious effects of *B. decumbens* is not certain. Simulation analysis indicated a reduction in grass growth when the upper storey canopy is fully developed, perhaps in association with nitrogen uptake.

8.8 Suggestions for farmers.

Introducing germplasm [in low input farming systems] is inevitably bound to changing management and, at some point, the rundown of initial production (Myers and Robbins, 1991; Burrows, 1991). Apart from the need for a plan to tackle the technical and economic requirements of the new scenario, awareness of the environmental impact caused must be gathered. Burrows (1991) suggest that meanwhile the dynamics of introduced species are not fully understood, the advice should be only to introduce small changes, so that it is possible to stay within grounds in which sustainability is not in risk.

Care must be taken of the nutritional status of silvopastures in the humid tropics as it is unlikely that trees develop deep rooting system, thus high competition with grass should be expected. The main reasons for shallow rooting of trees could be: pruning, short periods of hydric stress (i.e. there is plenty of moist in the top soil most of time); forest soils are usually infertile, thus nutrient availability depends on mineralisation of new soil organic matter, biological nitrogen fixation and chemical fertilisation, many of which are inherent to the top layer of soil.

Green manure from pruning of nitrogen fixing trees should be laid (or buried) in lines several metres apart from each other in order to prevent damage to the pasture and to reduce losses of volatile nutriments during decomposition. Also, by limiting the fertilised area in rows, the uncovered area remains low in mineral nitrogen, minimising the negative effect on the nitrogen fixing activity, which is already affected by frequent pruning (Nygren, 1995). Rotating the place for deposition of

mulch every pruning period will compensate for the uneven distribution of the organic amendments.

8.9 Research needs

Brachiaria decumbens was shown to be a species with potential for inter-cropping because of its adaptability to shade, suppression of weeds and deep rooting system. However, some disadvantages were detected as to the negative effect on the survival and development of associated trees. New research is needed in order to determine whether such problems can be solved by selecting better accompanying species or favouring the establishment of the tree stand or, if there are factors in *Brachiaria decumbens* such as allelopathy or antibiotic secretions (Davidson, 1978) or otherwise that will prevent normal growth of the trees.

Once nitrogen demand of grass and trees is solved by combining mineralisation of soil organic matter, mineral fertilisation and biologically fixed nitrogen, it is likely that phosphorus becomes the most limiting nutrient for grass production. The understanding of other nutrients and mainly phosphorus uptake is crucial for the appropriate management of the fertility status of soil. Likewise, water balance explains much of the cycle of nutrients in the plant soil interface, thus no complete description of fate of nutrients in inter-cropping is possible whilst its water relations are not included.

Some steps were taken into the characterisation of species adapted to the particular conditions of Valle Nacional, and I suggest that the further investigation of potential species for introduction in this zone should be guided toward the use of species that withstand the natural fertility of the site, and may accompanying crops be introduced in order to restore soil nutrients. Special attention should be paid to seeking local provenances of leguminous tree species, which match the nutritional requirements of the system by maximising biological fixation of nitrogen.

Bio-physic as well as socio-economic factors will alter the suitability of different tree-grass combination and must therefore be considered when formulating new research projects.

APPENDICES

I. Analytical Methods
II. The Silvopastoral Model program code for ModelMaker 3.0.3

I

Analytical Methods

1 Total nitrogen (Kjeldahl):

Reagents

15 ml Sulphuric Acid analytical reagent grade
6 Kjeldahl tablets
70 ml 40% Sodium Hydroxide
50 ml distilled water
60 ml 2% Boric Acid
6 drops indicator
0.1 M Sulphuric Acid

Apparatus

Buchi Digestion Unit 435
Buchi Distillation Unit B-323
10 ml Burette

Procedure

500 mg sample plus duplicate were weighed into digestion tubes, 15 ml sulphuric c. and 6 Kjeldahl tablets added and the mix digest to maximum temperature for 2 hr. Leave to cool down until fumes disappear and add 70 ml 40% Sodium Hydroxide and 50 ml distilled water. Distil for 4 minutes collecting the distilled into 60 ml 2% Boric Acid plus 6 drops indicator in a conic flask. Titrate the distilled with 0.1 M Sulphuric Acid. Calculate total nitrogen with the following equation:

$\%N_2 = ((V1 - V2) * N * f * 1400) / Wt$

Where:

V1 and V2 are the volumes of 2% Boric Ac. used for titring the sample and the control respectively
N = 0.5 (normality)
f = 0.95 (factor of the acid)
Wt is the weight of the sample (mg DM)

2 Neutral Detergent Fibre.

Reagents (adapted from Van Soest and Wine, 1967)

Neutral-detergent solution:
- sodium lauryl sulphate
- disodium dihydrogen ethylenediaminetetraacetic acid (EDTA)
- sodium borate decahydrate
- disodium hydrogen phosphate
- 2-ethoxy-ethanol used for starch removal (Triethylene glycol)

Acetone
Sodium sulphite (dissolved in the ND solution)

Procedure

0.5 g samples and replicates were sealed into filter bags (Ankom technologies, Inc.) and heat to boiling in 1500ml beakers with ND solution in batches of 15-20 filter bags per beakers. Heat was reduced immediately after boiling to prevent foaming but maintained hot enough to simmer for one hour, replacing water lose after 30 min. We suspended the use of Decahydronaphtalene (Decalin) which involves health risk. Bags with NDF residue were immersed in acetone to extract water and residual reagents and dry weight determined before and after further analysis.

3 Acid Detergent Fibre (adapted from Van Soest, 1963b).

Reagents

Cetyltrimethylammonium bromide (CTAB) diluted (2%) in 1.0 N sulphuric acid
Acetone

The procedure is identical to NDF determination (see above).

4 Lignin (adapted from Van Soest, 1963b).

Reagents

Sulphuric acid
Acetone

Procedure

NDF-ADF residues in filter bags were immersed for 3 hr in %72 standardised sulphuric acid. Residue in the bags was repeatedly rinsed with boiling hot distilled water, to wash the sulphuric acid, until pH 5. Finally residue was treated in acetone to eliminate water and dry weigh determined before and after ignition.

5 Total Phenolics (Folin-Ciocalteau)

Materials

1 lt. round bottom flask
Reflux apparatus
Glass beads
Glass wool

20 100 ml volumetric flasks w/stopper
Spectrophotometer

Reagents

80% ethanol (extractant)
17.5 lt. deionized water
100g sodium tungstate
25g phosphomolybdic acid
100 ml concentrated hydrochloric acid
50 ml 85% orthophosphoric acid
150 g lithium sulphate
drops of liquid bromide
300g anhydrous sodium carbonate
sodium carbonate decahydrate

Procedure

500 mg were weighed out for extraction and analysis. 80% Ethanol was used as extraction solvent. Samples were extracted in an shaking bath for 24 hr at 60°C before two replicates of 1.0 ml were taken for analysis. Total phenolics in the extract were estimated with the Folin-Ciocalteau method (Folin & Ciocalteau, 1927) slightly modified by Waterman and Mole (1994). The method consists of an extraction and further oxidation of phenolate ions, which were measured colourimetrically with an spectrophotometer. A 1.000 ml aliquot was poured into a 100 ml volumetric flask containing c. 65 ml distilled water, 5 ml Folin-Ciocalteau reagent were added. After thoroughly mixing and before 8 min, 15 ml of 20% $CaCO_3$ were stirred in the flask and distilled water was used to fill 100 up. After exactly 2 hours of the $CaCO_3$ addition with eventual shaking half the way, 1 ml aliquot was used for determination. Absorvance was measured at 760 nm, using water as a blank and 80% Ethanol assayed aliquot as control. A duplicate of gallic acid dissolved in extraction solvent was used as a standard for the assay.

6 Decomposition rate

Procedure

100 g of fresh prunings were weighed (p_0) and deposited on bare soil spots in the corresponding plot into litter bags (0.7 mm mesh in the bottom and 7 mm in the top) in triplicate for a set period of time, namely 15, 30, 45, 60 and 75 days. Corresponding litter bags were collected at every period and the content dried into a chamber of incandescent bulbs and weighed (p_t). Sub-samples of decomposing mulch were freeze dried for dry matter determination (%DM_t). N extra set of fresh prunings was used for dry matter determination (%DM_0).

7 Available N (NO_3) in Soil

Procedure

Soil samples were air dried and sieved trough a 1 mm mesh and then analysed for available nitrates. Separate set of sub-samples of sun dried soil were used for dry matter determination using an oven at 60oC for 24 hr. 10 l of 1.0 M KCl were prepared by adding 745.6 g of Potassium chloride to 10 lt distilled water. 5.0000 gr not oven-dried soil samples were weighed into 250 ml plastic bottles and 100 ml 1 M KCl were added and the bottles lidded and shaken for 2 hr. After 20 min settle, 15 ml were taken and centrifuged at 7500 rpm for 15 min. The extract was then analysed for nitrates in the auto-analyser.

8 Determination of Mineralisation rate (Nitrachek® meter, adapted from Rees *et al*. 1996).

Procedure

50 g fresh soil samples with replicates were incubated at room temperature (25°C) with N free purified water (less than 7 ppm NO_3) 2:1 v/w for four days. After incubation, samples transferred to plastic glasses and 120 ml purified water stirred into the glass. After 15 min the soil was filtered (Whatman No. 1). Mineralised nitrates were determined colourimetrically with Nitrachek® strips (Merckoquant Nitra test strips, MERCK Co.) before and after incubation. Colour was measured with a Nitrachek® meter (Nitrachek 404, Challenge Agriculture, UK). The Nitrachek® meter is calibrated for every reading (this triggers the countdown for the reading), the strip sensitive end (pad) is immersed in the leachate for two seconds and shaken to remove any unwanted water. One minute after calibration the strip is replaced in the Nitrachek® meter for automatic determination of NO_3 (mg l^{-1}).

II

The Silvopastoral model program Code for ModelMaker 3.0.3

TOP-LEVEL MODEL

Variables:

Definition	**Equation**
Air temperature	Tair = 23 + 2.5 * sin(2 * 3.1415926 * (t - 55) / 365)
Air temperature function	fTair = ((Tair-T0)*(2*Tmax-T0-Tair))/((Tref-T0)*(2*Tmax-T0-Tref))
Soil temperature in Kelvin degrees	ToK = Tsoil + 273.15
Soil surface temperature function	fTsoil = ((Tsoil-T0)*(2*Tmax-T0-Tsoil))/((Tref-T0)*(2*Tmax-T0-Tref))
Soil upper layer temperature function	Tsoil = 30 + 1 * sin(2 * 3.1415926 * (t - 56) / 365)
Soil upper layer moisture potential function	fPSI = (exp(18 * psi_s / (R * ToK))) ^ q_psi_s
Day lenght function	H = 43200 + 3600 * sin(2 * 3.1415926 * (t - 21) / 365)
PAR receipt on the i-th day function (J m^{-2} d^{-1})	PAR = 11.64e6 + 0.5e6 * sin(2 * 3.1415926 * (t - 81) / 365)
Transmitted PAR	PARtransmited = PAR - fshz * (n_stems * (1.7 * PAR * ((1 - 0.08) * (1 - exp(-k_tree * OutOutLAI_tree)) + 0.08)))
Carbon dioxide concentration in air, CO2air (kg CO_2 m^{-3}):	CO2air = CO2vpm * $1.0e^{-6}$ * (273.15 / (Tair + 273.15)) * 101325 * $9.86923e^{-6}$ * 1.9636

ANIMAL

Variables:

Definition	Equation
C flux retained by the animal (kg C m^{-2} d^{-1})	DMCan = rCNan * DMNan
Retained N flux	DMNan = fNret * INpl_an
Nitrogen flux to faeces	fNfaeces = 1 - fNurine
Fraction of total excreted N which appears in the urine	fNurine = 0.5 - 0.00769231 * (rCNtotsh - 12.0)
Total C flux into the animal (kg C m^{-2} day^{-1})	ICpl_an = InCtotsh * IDMpl_an_gnd
Dry matter (DM) intake per unit ground area (kg total DM m^{-2} day^{-1})	IDMpl_an_gnd = (IDMpl_anmax / (1.0 + 1.0 / zKLAIan)) * n_anim
Total N fluxes into the animal (kg N m^{-2} day^{-1})	INpl_an = InNtotsh * IDMpl_an_gnd
C flux from the animal to faeces	OC_an_so_fa = OCan_exc - OCan_so_ur
Animal growth respiration rate (kg C m^{-2} d^{-1})	OCan_en_G = DMCan * (1 - Yan) / Yan
fraction of the C intake is taken for maintenance, and given off to the environment as CO2 (kg C m^{-2} day^{-1})	OCan_en_mai = fCan_mai * ICpl_an
fraction of the C intake given off as methane (kg C m^{-2} day^{-1})	OCan_en_met = fCan_met * ICpl_an
Total excreted C (kg C m^{-2} day^{-1})	OCan_exc = ICpl_an - OCan_en_mai - OCan_en_met - DMCan - OCan_en_G
C flux to urine (kg C m^{-2} d^{-1})	OCan_so_ur = (12 / 28) * ONan_so_ur
Total excreted flux of N (kg N m^{-2} day^{-1})	ONan_exc = INpl_an - DMNan
N flux to faeces (kg N m^{-2} d^{-1})	ONan_so_fa = ONan_exc * fNfaeces
N flux to urine (kg N m^{-2} d^{-1})	ONan_so_ur = fNurine * ONan_exc
Carbon:nitrogen ratio in the ingested dry matter	rCNtotsh = InCtotsh / InNtotsh
Intake function	zKLAIan = (InLAIgrass / KLAIan) ^ qLAIan

GRASS

Variables:

Definition	Equation
Lamina structure removed from Wlam1 (kg structural dry matter m^{-2} day^{-1})	FClam1_an = clam1_an * L1 * InOXlam_an / zlam_an
Lamina structure removed from Wlam2 (kg structural dry matter m^{-2} day^{-1})	FClam2_an = clam2_an * L2 * InOXlam_an / zlam_an
Lamina structure removed from Wlam3 (kg structural dry matter m^{-2} day^{-1})	FClam3_an = clam3_an * L3 * InOXlam_an / zlam_an
Lamina structure removed from Wlam4 (kg structural dry matter m^{-2} day^{-1})	FClam4_an = clam4_an * L4 * InOXlam_an / zlam_an
Sheath and stem structure removed from Wss1 (kg structural dry matter m^{-2} day^{-1})	FCss1_an = clam1_an * L1 * InOXss_an / zlam_an
Sheath and stem structure removed from Wss2 (kg structural dry matter m^{-2} day^{-1})	FCss2_an = clam2_an * L2 * InOXss_an / zlam_an
Sheath and stem structure removed from Wss3 (kg structural dry matter m^{-2} day^{-1})	FCss3_an = clam3_an * L3 * InOXss_an / zlam_an
Sheath and stem structure removed from Wss4 (kg structural dry matter m^{-2} day^{-1})	FCss4_an = clam4_an * L4 * InOXss_an / zlam_an
Rate of grass leaf appearance	gamma_sh = gamma_sh20 * Tair / fPSI
Rate of synthesis of shoot structural dm (kg X dm m^{-2} d^{-1})	Gsh = mu20 * Csh * Nsh * MXsh * fTair * fPSI
Leaf area removed from L1 by grazing [m^{-2} leaf (m^{-2} ground)$^{-1}$ day^{-1}]	L1_an = FClam1_an * L1 / Mlam1
Leaf area removed from L2 by grazing [m^{-2} leaf (m^{-2} ground)$^{-1}$ day^{-1}]	L2_an = FClam2_an * L2 / Mlam2
Leaf area removed from L3 by grazing [m^{-2} leaf (m^{-2} ground)$^{-1}$ day^{-1}]	L3_an = FClam3_an * L3 / Mlam3
Leaf area removed from L4 by grazing [m^{-2} leaf (m^{-2} ground)$^{-1}$ day^{-1}]	L4_an = FClam4_an * L4 / Mlam4
Grass canopy LAI	LAIgrass = L1 + L2 + L3 + L4

Shoot structural dm (kg C m^{-2})	MXsh = Mlam1 + Mlam2 + Mlam3 + Mlam4 + Mss1 + Mss2 + Mss3 + Mss4
Specific leaf area of newly synthetised grass lamina	SLA = ISLAmax_grass * (1 - ISLAgrass * Csh)
Potential leaf area removed by grazing	zlam_an = clam1_an * L1 + clam2_an * L2 + clam3_an * L3 + clam4_an * L4
Root turnover rate	Gamma_rt = gamma_rt20 * fTsoil * fPSI Rate of synthesis of new structural dm in grass roots (kg X dm m^{-2} d^{-1})
Grt = mu20 * Crt * Nrt * MXrt * fTair * fPSI	
Root structural dm (kg C m^{-2})	MXrt = Wrt1 + Wrt2 + Wrt3 + Wrt4
Sustrate C concentration of grass structure	Cgrass = (MCSsh + MCSrt) / MXpl
Substrate C concentration in root [kg C (kg structural DM)$^{-1}$]	Crt = MCSrt / OutMXrt
Substrate C concentration in shoots [kg C (kg structural DM)$^{-1}$]	Csh = MCSsh / OutMXsh
Total (storage + structure) C concentrations in the shoot {kg total C [kg total DM]$^{-1}$}	Ctotsh = (MCSsh + fCplX * OutMXsh) / Msh
Fraction of structural DM in roots	f_rt = OutMXrt / MXpl
Fraction of structural DM in shoots	f_sh = OutMXsh / MXpl
Substrate N loss to litter in dead grass shoots	FCsh_lit = OXsh4_li * fCplX - ICSresh
Fraction of the flux of N to shoot litter which is re-supplied to the N substrate pool.	fNrtli_re = 1.0 / (1.0 + Nrt / KNrec_grass)
Substrate N loss to litter in dead grass shoots	FNsh_lit = OXsh4_li * fNplX - INSresh
Fraction of the flux of N to shoot litter which is re-supplied to the N substrate pool.	fNshli_re = 1.0 / (1.0 + Nsh / KNrec_grass)
Fraction of Nitrogen Uptake corresponding to the flow from Namm	fuNamm = Namm / NeffuN
fraction of N input corresponding to Nnit uptake	fuNnit = 1.0 - fuNamm
Fraction of structural DM removal to grazing from the lamina (kg structural DM m^{-2} d^{-1})	fXlam_an = MXlam / (MXlam + MXss * css_an)
Substrate N loss to litter in dead grass shoots	ICSrert = INSrert * roCNrec
Substrate N loss to litter in dead grass shoots	ICSresh = INSresh * roCNrec
Re-supply of substrate N (and C) from root litter structural DM	INSrert = fNplX * fNrtli_re * OXrt4_li

re-cycling (kg N m^{-2} day^{-1}).	
Substrate N in dead grass shoots which is recycled	INSresh = OXsh4_li * fNplX * fNshli_re
Maintenance coefficient for its age categories	kmai_rt1 = kmai_rt120 * fTsoil * fPSI
Maintenance coefficient for its age categories	kmai_rt2 = kmai_rt220 * fTsoil * fPSI
Maintenance coefficient for its age categories	kmai_rt3 = kmai_rt320 * fTsoil * fPSI
Maintenance coefficient for its age categories	kmai_rt4 = kmai_rt420 * fTsoil * fPSI
Maintenance coefficient for its age categories	kmai_sh1 = kmai_sh120 * fTair * fPSI
Maintenance coefficient for its age categories	kmai_sh2 = kmai_sh220 * fTair * fPSI
Maintenance coefficient for its age categories	kmai_sh3 = kmai_sh320 * fTair * fPSI
Maintenance coefficient for its age categories	kmai_sh4 = kmai_sh420 * fTair * fPSI
Partitioning fraction leading to a maximum grass root growth rate	lamda_rt = 1 / (1 + Pgrass)
Partitioning fraction leading to maximum grass shoot growth rate	lamda_sh = Pgrass / (1 + Pgrass)
Leaf as a proportion of stem DM	LS = MXlam / (MXlam + WXgrass)
Leaf photosynthetic efficiency	alpha_grass = alpha_max_grass * (1 - (beta_grass / (tau_grass * CO2air))) * fTair * fPSI
Effect of shoot N concentration on Pmax	0.5 for InNshlamA <= 0.001
	0.5 * (1 + (InNshlamA - 0.001) / 0.001) for InNshlamA < 0.002
	1 for 0.002 <= InNshlamA
dx factor of exponential function for P_CO2	Fx0grass = PHSYNsh1 + Pmax_grass * ln((PHSYNsh1 + PHSYNsh2) / (Pmax_grass * (PHSYNsh1 + (1 - 2 * ksi_ph) * x0grass + Pmax_grass))) - 2 * ksi_ph * Pmax_grass * ln(2 * (PHSYNsh1 + PHSYNsh2))
dy factor of exponential function for P_CO2	Fx1grass = PHSYNsh3 + Pmax_grass * ln((PHSYNsh3 + PHSYNsh4) / (Pmax_grass * (PHSYNsh3 + (1 - 2 * ksi_ph) * x1grass + Pmax_grass))) - 2 * ksi_ph * Pmax_grass * ln(2 * (PHSYNsh3 + PHSYNsh4))
Instantaneous light flux density	I0grass = InInPARtransmited/h
Canopy gross photosynthetic rate	P_CO2grass = (x0grass - x1grass - Fx0grass + Fx1grass) / (2 * ksi_ph * k_grass)
Carbon input via grass photosynthesis [kg C m^{-2} d^{-1}]	Pcarb_grass = (12 / 44) * h * P_CO2grass
common factor 1 0 in grass photosynthesis calculation	PHSYNsh1 = (x0grass ^ 2 + 2 * Pmax_grass * (1 - 2 * ksi_ph) *

	x0grass + (Pmax_grass ^ 2)) ^ 0.5
common factor 2 0 in grass photosynthesis calculation	PHSYNsh2 = x0grass + Pmax_grass * (1 - 2 * ksi_ph)
common factor 1 1 in grass photosynthesis calculation	PHSYNsh3 = (x1grass ^ 2 + 2 * Pmax_grass * (1 - 2 * ksi_ph) * x1grass + (Pmax_grass ^ 2)) ^ 0.5
common factor 2 1 in grass photosynthesis calculation	PHSYNsh4 = x1grass + Pmax_grass * (1 - 2 * ksi_ph)
Light-saturated value of grass photosynthetic rate	Pmax_grass = ksi_ph * CO2air * Ntotsh / 0.04 for InNshlamA >= 1
	Pmax_grass20 * (1 / 1 + (KCO2_Pmax / CO2air)) * fN_Pmax * fTair * fPSI by default
min value for integration	x0grass = alpha_grass * k_grass * I0grass / (1 - LeafTransgrass)
max value for integration	x1grass = (alpha_grass * k_grass* I0grass / (1 - LeafTransgrass)) * exp(-k_grass * max(1e^{-6},InLAIgrass))
Proportion of dead DM in total DM	propDead = Wdead / (MXlam + WXgrass + Wdead)
Live leaf as a proportion of total DM	propL = MXlam / (MXlam + WXgrass + Wdead)
Proportion of stem in tot. DM	propS = WXgrass / (MXlam + WXgrass + Wdead)
Shoots DM per hectare (kg shoot DM ha^{-1})	shoot_ha = Msh * 10000
Grass root activity (m2/(kg root structural DM) * d^{-1})	sigmaUN_grass = sigmaUN_grass20 * fTsoil * fPSI
Dead shoot material	Wdead = OutMlam4 + OutMss4
Grass stem structural DM	WXgrass = OutMXsh - MXlam
Michaelis-Menten term for N uptake	zNeffuN = NeffuN / (NeffuN + KNeffuN)
N uptake by grass roots	UNgrass = sigmaUN_grass * zNeffuN * (OutMrt1 +c_uN2 *OutMrt2 + c_uN3 * OutMrt3 + c_uN4 * OutMrt4) / (1 + (KCgrass / Crt) * (1 + Nrt / KNgrass))
Total Dry Matter of grass roots (kg dm m^{-2})	Mrt = MSrt + OutMXrt
Total Dry Matter of grass shoots (kg dm m^{-2})	Msh = MSsh + OutMXsh
The roots storage Dry Matter	MSrt = ((rmmCS / 12) * MCSrt) + ((rmmNS / 14) * MNSrt)
Shoots storage Dry Matter	MSsh = ((rmmCS / 12) * MCSsh) + ((rmmNS / 14) * MNSsh)
Total lamina structure (kg structural dm m^{-2})	MXlam = OutMlam1 + OutMlam2 + OutMlam3 + OutMlam4
Total grass structural dm (kg m^{-2})	MXpl = OutMXsh + OutMXrt
Total sheat and stem structure (kg structural DM m^{-2})	MXss = OutMss1 + OutMss2 + OutMss3 + OutMss4

Sustrate N concentration of grass structure	Ngrass = (MNSsh + MNSrt) / MXpl
Substrate nitrogen concentration in root kg N (kg structure)$^{-1}$.	Nrt = MNSrt / OutMXrt
Substrate N concentration of grass structure (kg N [structural dm]$^{-1}$)	Nsh = MNSsh / OutMXsh
Effect of N concentration in lamina (on area basis) on Photosynthesis	NshlamA = Ntotsh / OutLAIgrass / MXlam
Total (storage + structure) N concentrations in the root {kg total N [kg total DM]$^{-1}$}	Ntotrt = (MNSrt + fNplX * OutMXrt) / Mrt
Total (storage + structure) N concentrations in the shoot {kg total N [kg total DM]$^{-1}$}	Ntotsh = (MNSsh + fNplX * OutMXsh) / Msh
Flux of C from root to litter	OCrt_so = OXrt4_li * fCplX - ICSrert
Grass maintenance respiration	OCSrt_mai = fCplX * (Crt / (Crt + KCmai)) * (kmai_rt1 * OutMrt1 + kmai_rt2 * OutMrt2 + kmai_rt3 * OutMrt3 + kmai_rt4 * OutMrt4)
Respiration of root C substrate associated with plant uptake of N (kg C respired m^{-2} day^{-1}).	OCSrt_uN = cuNamm_grass * InuNamm_grass + cuNnit_grass * InUNnit_grass
Utilization of C substrate for shoot growth (kg C m^{-2} day^{-1})	OCSrtG = fCplX * OutGrt / Ygrass
Grass maintenance respiration	OCSsh_mai = fCplX * (Csh / (Csh + KCmai)) * (kmai_sh1 * (OutMlam1 + OutMss1) + kmai_sh2 * (OutMlam2 + OutMss2) + kmai_sh3 * (OutMlam3 + OutMss3) + kmai_sh4 * (OutMlam4 + OutMss4))
Utilization of C substrate for growth of shoot (kg C m^{-2} day^{-1})	OCSshG = fCplX * OutGsh / Ygrass
Substrate N loss to litter in dead grass shoots	ONrt_so = OXrt4_li * fNplX - INSrert
Structural DM removal flux from lamina to grazing	OXlam_an = fXlam_an * OXpl_an
Total structural DM removal to grazing (kg structural DM m^{-2} d^{-1})	OXpl_an = InIDMpl_an_gnd * OutMXsh / Msh
Grass shoots total litter (kg structural DM m^{-2})	OXsh4_li = OutFlam4 + OutFss4
Removal of structural DM from sheat and stem to grazing	OXss_an = (1 - fXlam_an) * OXpl_an
Teleonomic partitioning function for maximum grass growth rate	Pgrass = (f_rt * Ngrass / (Ngrass + fNplX)) / (f_sh * Cgrass / (Cgrass + fCplX))

Compartments:

Definition	**Equation**	**Initial Value**
Leaf area index of growing shoots	dL1/dt = SLA * fLgrass * Gsh - FLAI1 - L1_an	0.5
Leaf area index of 1st. fully expanded shoots	dL2/dt = FLAI1 - FLAI2 - L2_an	1
Leaf area index of 2nd fully expanded shoots	dL3/dt = FLAI2 - FLAI3 - L3_an	1
Leaf area index of senescing shoots	dL4/dt = FLAI3 - gamma_sh * L4 - L4_an	1
Growing grass leaves lamina	dMlam1/dt = fLgrass * Gsh - Flam1 - FClam1_an	0.01
1st fully expanded grass leaf lamina	dMlam2/dt = Flam1 - Flam2 - FClam2_an	0.01
2nd fully expanded grass leaf lamina	dMlam3/dt = Flam2 - Flam3 - FClam3_an	0.01
Senescent grass leaves lamina	dMlam4/dt = Flam3 - Flam4 - FClam4_an	0.01
Growing sheath and stem	dMss1/dt = (1 - fLgrass) * Gsh - Fss1 - FCss1_an	0.01
sheath and stem ist full expended	dMss2/dt = Fss1 - Fss2 - FCss2_an	0.01
sheath and stem 2nd full expended	dMss3/dt = Fss2 - Fss3 - FCss3_an	0.01
senescent sheath and stems	dMss4/dt = Fss3 - Fss4 - FCss4_an	0.01
Growing grass roots	dWrt1/dt = Grt - Frt1	0.01
1st full expanded grass roots	dWrt2/dt = Frt1 - Frt2	0.01
2nd full expanded grass roots	dWrt3/dt = Frt2 - Frt3	0.01
Senescent roots	dWrt4/dt = Frt3 - Frt4	0.01
Root carbon substrate pool (kg substrate C m^{-2})	dMCSrt/dt = OCSshrt + ICSrert - OCSrtG - OCSrt_mai - OCSrt_uN - OCSrt_ex	0.05
Substrate C in grass shoots (kg C m^{-2})	dMCSsh/dt = OutPcarb_grass + ICSresh - OCSshG - OCSsh_mai - OCSshrt - OCSsh_an_gr	0.016
Substrate N in grass shoots (kg N m^{-2})	dMNSrt/dt = uNamm + uNnit + INSrert - fNplX * OutGrt - ONSrtsh - ONSrt_ex	0.004
Shoot nitrogen substrate pool (kg substrate N m^{-2} day^{-1}).	dMNSsh/dt = ONSrtsh + INSresh - fNplX * OutGsh - ONSsh_an_gr	0.001

Flows:

Definition	Equation
L1 to L2	FLAI1 = 2*gamma_sh * L1
L2 to L3	FLAI2 = gamma_sh * L2
L3 to L4	FLAI3 = gamma_sh * L3
Mlam1 to Mlam2	Flam1 = 2*gamma_sh * Mlam1
Wlam2 to Wlam3	Flam2 = gamma_sh * Mlam2
Mlam3 to Mlam4	Flam3 = gamma_sh * Mlam3
Wlam4 to OutFlam4	Flam4 = gamma_sh * Mlam4
Mss1 to Mss2	Fss1 = 2 * gamma_sh * Mss1
Mss2 to Mss3	Fss2 = gamma_sh * Mss2
Mss3 to Mss4	Fss3 = gamma_sh * Mss3
Wss4 to OutFss4	Fss4 = gamma_sh * Mss4
InuNamm_grass to MNSrt	uNamm = fuNamm * UNgrass + 0.0001
MCSrt to OutOCSrt_ex	OCSrt_ex = kCSrt_ex20 * fTsoil * fPSI * Crt
MCSsh to OutOCSsh_an_gr	OCSsh_an_gr = InIDMpl_an_gnd * MCSsh / Msh
MCSsh to MCSrt	OCSshrt = OutPcarb_grass * lamda_rt
Wrt1 to Wrt2	Frt1 = 2*Gamma_rt * Wrt1
Wrt2 to Wrt3	Frt2 = Gamma_rt * Wrt2
Wrt3 to Wrt4	Frt3 = Gamma_rt * Wrt3
Wrt4 to OutFrt	Frt4 = gamma_rt * Wrt4
MNSrt to OutONSrt_ex	ONSrt_ex = kNSrt_ex20 * fTsoil * fPSI * Nrt
MNSrt to MNSsh	ONSrtsh = (uNamm + uNnit) * lamda_sh
MNSsh to OutONSsh_an_gr	ONSsh_an_gr = InIDMpl_an_gnd * MNSsh / MSsh
InUNnit_grass to MNSrt	uNnit = fuNnit * UNgrass

LITTER AND MULCH

Variables:

Definition	**Equation**
Structural C which is recycled after branches dead	Cb_rec = L_MbXlit * Nb_rec * lamdaCNrec Structural C which is recycled after coarse roots dead
Cc_rec = L_McXlit * Nc_rec * lamdaCNrec Structural C which is recycled after fine roots dead	Cf_rec = L_MfXlit * Nf_rec * lamdaCNrec
Structural C which is recycled after leaves dead	Cl_rec = L_MlXlit * Nl_rec * lamdaCNrec
Substrate C to dead branches (kg C m^{-2} d^{-1})	FCdead_b = L_MbXlit * fCbX - Cb_rec * n_stems
Substrate C to dead coarse roots (kg C m^{-2} d^{-1})	FCdead_c = L_McXlit * fCcX - Cc_rec * n_stems
Substrate C to dead fine roots (kg C m^{-2} d^{-1})	FCdead_f = L_MfXlit * fCfX - Cf_rec * n_stems
Substrate C to dead leaves (kg C m^{-2} d^{-1})	FCdead_l = L_MlXlit * fClX - Cl_rec * n_stems
Substrate C to mulch from branches (kgC m^{-2} d^{-1})	FCprun_b = ((L_MbXmulch * fCbX) + (L_MbMmulch * fCbM)) * n_stems
Substrate C to mulch from leaves (kg C m^{-2} d^{-1})	FCprun_l = ((L_MlXmulch * fClX) + (L_MlMmulch * fClM)) * n_stems
Fraction of senecent degradable branches structure which is recycled	fi_rec_b = 1/(1+InNb/KNrec_tree)
Fraction f senecent degradable coarse root structure which is recycled	fi_rec_c = 1/(1+InNc/KNrec_tree)
Fraction of senecent degradable fine roots structure which is recycled	fi_rec_f = 1/(1+InNf/KNrec_tree)
Senecent degradable leaves structure which is recycled	fi_rec_l = 1 / (1 + InNl / KNrec_tree)
Lignin fraction function for litter on soil surface	fLIG_a = exp(-m_lig * (C_Mlig_a / (C_Mcel_a + C_Mlig_a)))
Lignin fraction function for litter in soil upper layer	fLIG_s = exp(-m_lig * (C_Mlig_s / (C_Mcel_s + C_Mlig_s)))
Substrate N to dead branches (kg N m^{-2} d^{-1})	FNdead_b = L_MbXlit * fNbX * (1 - fi_rec_b) * n_stems
Substrate N to dead coarse roots (kg N m^{-2} d^{-1})	FNdead_c = L_McXlit*fNcX*(1-fi_rec_c) * n_stems
Substrate N to dead fine roots (kg N m^{-2} d^{-1})	FNdead_f = L_MfXlit * fNfX * (1-fi_rec_f) * n_stems
Substrate N to dead leaves (kg N m^{-2} d^{-1})	FNdead_l = L_MlXlit * fNlX * (1 - fi_rec_l) * n_stems
Substrate N to mulch from leaves (kg N m^{-2} d^{-1}))	FNprun_b = L_MbXmulch * fNlX * n_stems

Substrate N to mulch from leaves (kg N m_2 d^{-1})	FNprun_l = L_MlXmulch * fNlX * n_stems
Dependence of litter decay on lignin litter C:N ratio on soil surface	fRO_a = m_ro / RO_lit_a
Dependence of litter decay on lignin litter C:N ratio	fRO_s = m_ro / RO_lit_s
Litter rate of branches (d^{-1})	k_bXlit = k_bXlit20 * fTair * fPSI
Decomposition rate function of cellulose litter in soil surface	k_cel_a = k_cel20 * (fTair + fTsoil)/2 * fPSI * fRO_a * fLIG_a
Decomposition rate function of cellulose litter in soil upper layer	k_cel_s = k_cel20 * fTsoil * fPSI * fRO_s * fLIG_s
Litter rate of coarse roots (d^{-1})	k_cXlit = k_cXlit20 * fTsoil * fPSI
Litter rate of fine roots (d^{-1})	k_fXlit = k_fXlit20 * fTsoil * fPSI
lignin litter decomposition rate in soil surface	k_lig_a = k_lig20 * (fTair + fTsoil) / 2 * fPSI * fRO_a * fLIG_a
lignin litter decomposition rate in soil upper layer	k_lig_s = k_lig20 * fTsoil * fPSI * fRO_s * fLIG_s
Litter rate of leaves (d^{-1})	k_lXlit = k_lXlit20 * fTair * fPSI
Decomposition rate function of metabolic litter in soil surface	k_met_a = k_met20 * (fTair + fTsoil)/2 * fPSI * fRO_a
Decomposition rate function of metabolic litter in soil upper layer	k_met_s = k_met20 * fTsoil * fPSI * fRO_s
Fraction of branches meristem lost to mulch	L_MbMmulch = InMbM * f_pruning
Losses of branches structure to litter in soil surface	L_MbXlit = k_bXlit*InMbX
Fraction of leaves lost to mulch	L_MbXmulch = InMbX * f_pruning
Losses of coarse roots structure to litter in upper soil layer	L_McXlit = k_cXlit*InMcX
Losses of fine roots structure to litter in upper soil layer	L_MfXlit = k_fXlit * InMfX
Fraction of leaves meristem lost to mulch	L_MlMmulch = InMlM * f_pruning
Losses of leaves structure to litter in soil surface	L_MlXlit = k_lXlit * InMlX
Fraction of leaves lost to mulch	L_MlXmulch = InMlX * f_pruning
Substrate N recycled from dying branches structure	Nb_rec = fNbX * fi_rec_b
Substrate N recycled from dying coarse roots structure	Nc_rec = fNcX * fi_rec_c
Nitrogen from cellulose mulch and litter in upper layer	Ncel_a = C_Mcel_a / roCNcel
Cellulose C transfer to SOM from soil upper layer	Ncel_s = C_Mcel_s / roCNcel
Substrate N recycled from dying fine roots structure	Nf_rec = fNfX * fi_rec_f
Substrate N recycled from dying leaves structure	Nl_rec = fNlX * fi_rec_l
Nitrogen from lignin mulch and litter in upper layer	Nlig_a = C_Mlig_a / roCNlig
Cellulose C transfer to SOM from soil upper layer	Nlig_s = C_Mlig_s / roCNlig
Carbon to Nitrogen ratio of soil surface litter	RO_lit_a = (C_Mmet_a + C_Mcel_a + C_Mlig_a) / (Nmet_a + Ncel_a + Nlig_a)

Carbon to Nitrogen ratio of soil upper layer litter	RO_lit_s = (C_Mmet_s + C_Mcel_s + C_Mlig_s) / (Nmet_s + Ncel_s + Nlig_s)
Cellulose litter above ground	V1 = Fa_cel + Fb_cel_lit + Fl_cel_lit + Fsh_cel
Cellulose litter below ground	V2 = Fa_lig + Fb_lig_lit + Fl_lig_lit + Fsh_lig
Lignin litter above ground	V3 = Fc_cel + Ff_cel + Frt_cel
Lignin litter below ground	V4 = Fc_lig + Ff_lig + Frt_lig
N metabolic mulch and litter pool in soil surface	dNmet_a/dt = Nfaeces + FNdead_b + FNdead_l + InFNdead_sh - (V1 / roCNcel + V2 / roCNlig) - FNsol1

Compartments:

Definition	**Equation**	**Initial Value**
N mulch and litter pool in soil surface	dNmet_a/dt = FNdead_sh + FNdead_l + InFNfaeces - (V1 / roCNcel + V2 / roCNlig) - Fnsol1	0.0005
N mulch and litter pool in upper soil layer	dNmet_s/dt = FNdead_f + FNdead_c + InFNdead_rt - (V3 / roCNcel + V4 / roCNlig) - FNsol2	0.0005
cellulose mulch and litter in soil surface	dC_Mcel_a/dt = Fa_cel + Fsh_cel+Fb_cel_lit+Fl_cel_lit - FCsol2	0.1
cellulose litter in soil upper layer	dC_Mcel_s/dt = Ff_cel + Frt_cel + Fc_cel - FCsol4	0.1
lignin mulch and litter in soil surface	dC_Mlig_a/dt = Fa_lig + Fsh_lig + Fb_lig_lit + Fl_lig_lit - Flig1	0.15
Lignin litter in soil upper layer	dC_Mlig_s/dt = Ff_lig + Frt_lig + Fc_lig - FClig2	0.15
Metabolic mulch and litter in soil surface	dC_Mmet_a/dt = Fa_met + Fsh_met + Fb_met_lit + Fl_met_lit - FCsol1	0.0025
Metabolic litter in soil upper layer	dC_Mmet_s/dt = Ff_met + Frt_met + Fc_met - FCsol3	0.0025

Flows:

Definition	Equation
C_Mlig_s to OutFClig2	FClig2 = k_lig_s * C_Mlig_s
InCfaeces to C_Mcel_a	Fa_cel = lamda_cel_fa * InCfaeces
InCfaeces to C_Mlig_a	Fa_lig = lamda_lig_fa * InCfaeces
InCfaeces to C_Mmet_a	Fa_met = InCfaeces * lamda_met_fa
InMbXdead to C_Mcel_a	Fb_cel_lit = FCdead_b * lamda_cel_b
InMbXdead to C_Mlig_a	Fb_lig_lit = FCdead_b * lamda_lig_b
InMbXdead to C_Mmet_a	Fb_met_lit = FCdead_b * lamda_met_b
InMcXdead to C_Mcel_s	Fc_cel = FCdead_c * lamda_cel_c
InMcXdead to C_Mlig_s	Fc_lig = FCdead_c * lamda_lig_c
InMcXdead to C_Mmet_s	Fc_met = FCdead_c * lamda_met_c
C_Mmet_a to OutFCsol1	FCsol1 = k_met_a * C_Mmet_a
C_Mcel_a to OutFCsol2	FCsol2 = k_cel_a * C_Mcel_a
C_Mmet_s to OutDCsol3	FCsol3 = k_met_s * C_Mmet_s
C_Mcel_s to OutFCsol4	FCsol4 = k_cel_s * C_Mcel_s
InMfXdead to C_Mcel_s	Ff_cel = FCdead_f * lamda_cel_f
InMfXdead to C_Mlig_s	Ff_lig = FCdead_f * lamda_lig_f
InMfXdead to C_Mmet_s	Ff_met = FCdead_f * lamda_met_c
InMlXdead to C_Mcel_a	Fl_cel_lit = FCdead_l * lamda_cel_l
InMlXdead to C_Mlig_a	Fl_lig_lit = FCdead_l * lamda_lig_l
InMlXdead to C_Mmet_a	Fl_met_lit = FCdead_l * lamda_met_l
C_Mlig_a to OutFlig1	Flig1 = k_lig_a * C_Mlig_a
Nmet_a to OutFnsol1	FNsol1 = k_met_a * Nmet_a
Nmet_s to OutFNsol2	FNsol2 = k_met_s * Nmet_s
InFCrt_lit to C_Mcel_s	Frt_cel = InFCrt_lit * lamda_cel_sh
InFCrt_lit to C_Mlig_s	Frt_lig = InFCrt_lit * lamda_lig_sh
InFCrt_lit to C_Mmet_s	Frt_met = InFCrt_lit * lamda_met_sh
InFCsh_lit to C_Mcel_a	Fsh_cel = InFCsh_lit * lamda_cel_sh
InFCsh_lit to C_Mlig_a	Fsh_lig = InFCsh_lit * lamda_lig_sh
InFCsh_lit to C_Mmet_a	Fsh_met = InFCsh_lit * lamda_met_sh

component event: Pruning

Definition	Actions
Pruning event triggers pruning and mulching Trigger: Al >= LAIprun Tolerance = 0.1	C_Mmet_a = C_Mmet_a + FCprun_l * mulch_met_l * z_mulch + FCprun_b * lamda_met_b * z_mulch
	C_Mcel_a = C_Mcel_a + FCprun_l * mulch_cel_l * z_mulch + FCprun_b * lamda_cel_b * z_mulch
	C_Mlig_a = C_Mlig_a + FCprun_l * mulch_lig_l * z_mulch + FCprun_b * lamda_lig_b * z_mulch
	Nmet_a = Nmet_a + FNprun_l * z_mulch + FNprun_b * z_mulch - (z_mulch * (FCprun_l * mulch_cel_l + FCprun_b * lamda_cel_b) / roCNcel + (FCprun_l * mulch_lig_l + FCprun_b * lamda_lig_b) / roCNlig)
	Al = Al * (1 - f_pruning)
	MlX = MlX - L_MlXmulch
	MlM = MlM - L_MlMmulch
	MbX = MbX - L_MbXmulch
	MbM = MbM - L_MbMmulch
	MlN = MlN * (1 - f_pruning)
	MbN = MbN * (1 - f_pruning)

SOIL

Variables:

Definition	**Equation**
N application (kg N m^{-2})	AppN = N_ha/10000
Fraction of Namm taken to attain C:N ratio in SOM in upper layer	fNamm_bio_s = Namm / Neff_bio_s
Flux of Nitrate N away from upper layer by denitrification	FNdenit = k_denit * InCbio_s * Nnit
Flux of ammonium N lost to the environment by volatilisation	FNenv = fNenv_amm * Namm
Fraction of Nnit taken to attain C:N ratio in SOM in upper layer	fNnit_bio_s = 1 - fNamm_bio_s
Losses of nitrate N to environment during nitrification	FNnitrif_env = 0 for Namm < 0.001
	Famm_nit * fnitrif by default
Lower limit for fTuNmin	fTuNmin = max (0.0,fTuNmin1)
N availability parameter	fTuNmin0 = fTuN20 - (fTuN20 - fTuN10) * ((20 - Tsoil) / (20 - 10))
Upper limit for fTuNmin0	fTuNmin1 = min (1.0,fTuNmin0)

Nitrate N denitrification rate function	k_denit = k_denit20 * fTsoil * fPSI for Nnit > 0.02
	k_denit20 * fTsoil * fPSI * 0.1 by default
nitrification function in upper layer	k_nit_s = k_nit20 * fTsoil * fPSI
Ammonium N volatilisation rate function	k_vol = k_vol20 * fTsoil * fPSI
Biological N fixation rate function	kNfix = kNfix20 * fTsoil * fPSI
Effective N substrate concentration in soil upper layer	Neff_bio_s = Namm + cNbio * Nnit
Effectivie (to plant) soil N (kg N/m2 ground)	NeffuN = Namm + fTuNmin * Nnit
Biological N fixation funtion	Nfix = kNfix * InCbio_s / (1 + Neff_bio_s / JNfix)
Flux of nitrate N away due to leaching	Nleach = Nnit * k_leach * fPSI
Flux of N from dying microbes to Namm	FNbio_min = ((fCbioDR * Dbio_s) + Fbio1) / ro_bio
Flux of N out from dying microbes in soil upper layer	FNbioD_s = Dbio_s / ro_bio
Total flux of nitrogen from dying microbes to SOM	FNbioSOM_s = FNbioD_s - FNbio_min
Flux of N from dying microbes into Namm when balancing fixed C:N ratio of u and pSOM in upper layer	FNbioSOMmin_s = FNbioSOM_s - ReqFNbioSOM_s
Flux of N from lignin litter to SOM in soil surface	FNligSOM_a = InInFClig1 / roCNlig
Flux of N from lignin litter to SOM in soil upper layer	FNligSOM_s = InInFClig2 / roCNlig
N requeriments for microbial growth in upper layer	FNmin_bio_s = Fsol1 / ro_bio
Flux of min Nitrogen to attain C:N ratio of stabilised SOM	FNmin_stSOM = ReqNu_stSOM - FNu_stSOM + ReqNp_stSOM - FNp_stSOM
Flux of N from mineral pools to attain C:N ratios in both u and pSOM pools	FNminSOM = NReqSOM_a + NReqSOM_s - FNligSOM_a - FNligSOM_s
Flux of N when pSOM stabilisation	FNp_stSOM = FSOM2 / ro_pSOM
Freed of N when mineralisation of SOM	FNSOMmin = (FSOM3 + RuSOMst_s) / ro_uSOM + (FSOM4 + RpSOMst_s) / ro_pSOM + (FSOM5 / ro_stSOM)
Flux of N when uSOM stabilisation	FNu_stSOM = FSOM1 / ro_uSOM
Microbial biomass growth rate constant	k_bioG = k_bioG20 * fTsoil * fPSI * fCNbio_s*f_bio_s_max
microbial death rate constant in upper layer	k_dead_s = k_dead20 * fTsoil * fPSI * f_bio_min_s
Rate constant for mineralisation of pSOM in upper layer	k_pSOMmin_s = k_pSOMmin20 * fTsoil * fPSI
Rate constant for stabilisation of pSOM in upper layer	k_pSOMst_s = k_pSOMst20 * fTsoil * fPSI
Mineralisation rate of stabilised SOM	k_stSOMmin = k_stSOMmin20 * fTsoil * fPSI
Rate constant for stabilisation of uSOM in upper layer	k_uSOMmin_s = k_uSOMmin20 * fTsoil * fPSI
Rate constant for stabilisation of uSOM in upper layer	k_uSOMst_s = k_uSOMst20 * fTsoil * fPSI

Total mineral nitrogen	Nmin = Namm + Nnit
N requeriments to attain C:N ratio in both SOM pools from soil surface litter	NReqSOM_a = Flig1_pSOM / ro_pSOM + Flig1_uSOM / ro_uSOM
N requeriments to attain C:N ratio in both SOM pools from upper layer litter	NReqSOM_s = Flig2_pSOM / ro_pSOM + Flig2_uSOM / ro_uSOM
Microbes grouth respiration	RbioG = Fsol1 * ((1 / Ybio) - 1)
Respiratory costs of celluloselitter mineralization in soil surface	RCcel_lit_min_a = FCsol2 * fCcelR_a
Respiratory costs of cellulose litter mineralization in soil upper layer	RCcel_lit_min_s = FCsol4 * fCcelR_s
Respiratory costs of metabolic litter mineralization in soil surface	RCmet_lit_min_a = FCsol1 * fCmetR_a
Respiratory costs of metabolic litter mineralization in soil upper layer	RCmet_lit_min_s = FCsol3 * fCmetR_s
Requirements of N to attain C:N ratio in u and pSOM when microbes death	ReqFNbioSOM_s = (Fbio2 * (1 - fCbioDR)) / ro_uSOM + (Fbio3 * (1 - fCbioDR)) / ro_pSOM
Flux of N when pSOM stabilisation	ReqNp_stSOM = (FSOM2 - RpSOMst_s) / ro_stSOM
Flux of N when uSOM stabilisation	ReqNu_stSOM = (FSOM1 - RuSOMst_s) / ro_stSOM
Respiratory costs of lignin litter decay in soil surf.	RfClig_a = fCligR_a * InInFClig1
Respiratory costs of lignin litter decay in upper layer	RfClig_s = fCligR_s * InInFClig2
C:N ratio of pSOM	ro_pSOM = ro_pSOMmax - (ro_pSOMmin - ro_pSOMmin) * Nmin/ (KpSOM + Nmin)
C:N ratio of stabilised SOM	ro_stSOM = ro_stSOMmax - (ro_stSOMmin - ro_stSOMmin) * Nmin/ (KstSOM + Nmin)
C:N ratio max limit of the stabilised pool	ro_stSOMmax = 20 - 10 * mc * fclay_s
C:N ratio min limit of the stabilised pool	ro_stSOMmin = ro_stSOMmax / 2
C:N ratio of pSOM	ro_uSOM = ro_uSOMmax - (ro_uSOMmin - ro_uSOMmin) * Nmin/ (KuSOM + Nmin)
Respiratory costs of pSOM decay in upper layer	RpSOMmin = fCpSOMminR * FSOM4
Respiratory costs of pSOM stabilisation in upper layer	RpSOMst_s = fCpSOMstR * FSOM2
Respiratory costs of decay of stSOM in upper layer	RstSOM = fCstSOMminR * FSOM5
Respiratory costs of uSOM decay in upper layer	RuSOMmin = fCuSOMminR * FSOM3
Respiratory costs of pSOM stabilisation in upper layer	RuSOMst_s = fCuSOMstR * FSOM1
see info	zf_bio_s_max = 1.0-(Cbio_s/(fSOMbio*CSOM_s))

Volatilisation of ammonium N rate	Nvol = k_vol * Namm
C losses to leaching	CsolLeach = k_leach * Csol
Total C in SOM at upper layer	CSOM_s = CuSOM+CpSOM+CstSOM_s
microbial absolute death rate	Dbio_s = k_dead_s * Cbio_s
see info	f_bio_min_s = max (0.0 , (1.0 - (Cbio_min / Cbio_s)))
see info	f_bio_s_max = max(0.0,zf_bio_s_max)
Fraction of litter decaying that gets protected by the effect of clay	fClit_prot = c_lit_prot * fclay_s
Bisubstrate Michaelis-Menten dependence on C and N	fCNbio_s= ((1.0+KCbioG/Csol)*(1.0+KNbioG/InNeff_bio_s))

Compartments:

Definition	**Equation**	**Initial values**
Ammonium N in soil solution upper layer	dNamm/dt = Nfix + InInFNurine + InInSNf_ex_s + ONSrt_ex + FNsol1 + FNsol2 + (InfCcel_a + InfCcel_s) / roCNcel + InFNSOMmin + InFNbio_min_s + InFNbioSOMmin_s + FNenv - (Famm_f * n_stems) - (InFNminSOM + InFNmin_stSOM_s + InFNmin_bio_s) * fNamm_bio_s - Famm_nit - Nvol-UNamm_grass	0.015
Nitrate N in soil solution upper layer	dNnit/dt = (Famm_nit - FNnitrif_env) - (Fnit_f * n_stems) - uNnit - (InFNminSOM + InFNmin_stSOM_s + InFNmin_bio_s) * fNnit_bio_s - FNdenit - Nleach	0.005
Microbial biomass in soil upper layer	dCbio_s/dt = Fsol1- Fbio3 - Fbio2 - Fbio1	0.16
C in protected Soil Organic Matter	dCpSOM/dt = (Fbio3 * (1 - fCbioDR)) + Flig1_pSOM * (1 - RfClig_a) + Flig2_pSOM * (1 - RfClig_s) - FSOM4 - FSOM2	3.7
Carbon in soil solution in upper layer	dCsol/dt = FCsol1 - RCmet_lit_min_a + FCsol2 - RCcel_lit_min_a + FCsol3 - RCmet_lit_min_s + FCsol4 - RCcel_lit_min_s + (FSOM3 - RuSOMmin) + (FSOM4 - RpSOMmin) + (FSOM5 - RstSOM) + InInSCf_ex_s + OCSrt_ex + Fbio1 - (Fsol1 / Ybio) - CsolLeach	0.8
C in Stabilised Soil Organic Matter	dCstSOM_s/dt = FSOM1- RuSOMst_s + FSOM2 - RpSOMst_s - FSOM5	2.15
C in unprotected Soil Organic Matter	dCuSOM/dt = (Fbio2 * (1 - fCbioDR)) + Flig1_uSOM * (1 - RfClig_a) + Flig2_uSOM * (1 - RfClig_s) - FSOM3 - FSOM1	0.06

Flows:

Definition	Equation
Namm to Nnit	Famm_nit = InCbio_s * Namm * k_nit_s
Cbio_s to Csol	Fbio1 = Dbio_s * fCbioD_Csol
Cbio_s to CuSOM	Fbio2 = (Dbio_s - Fbio1) * (fCmic_uSOM_sandy + (c_bioDclay * fclay_s * (fCmic_uSOM_clay - fCmic_uSOM_sandy)))
Cbio_s to CpSOM	Fbio3 = Dbio_s - Fbio1 - Fbio2
InInFClig1 to CpSOM_s	Flig1_pSOM = InInFClig1 * fClit_prot
InInFClig1 to CuSOM_s	Flig1_uSOM = InInFClig1 - Flig1_pSOM
InInFClig2 to CuSOM	Flig2_uSOM = InInFClig2 - Flig2_pSOM
InInOCSrt_ex to Csol	OCSrt_ex = InInOCSrt_ex
Csol to Cbio_s	Fsol1 = (Cbio_s ^ q_bio) * k_bioG
CuSOM to CstSOM_s	FSOM1 = k_uSOMst_s * CuSOM
CpSOM_s to CstSOM_s	FSOM2 = k_pSOMst_s*CpSOM
CuSOM to Csol	FSOM3 = k_uSOMmin_s * CuSOM
CpSOM to Csol	FSOM4 = k_pSOMmin_s * Cbio_s * CpSOM
CstSOM_s to Csol	FSOM5 = k_stSOMmin * CstSOM_s

Independent event: Nappl Active Reset

Definition	Actions
Nitrogen fertiliser application Non-periodic triggers at: t = 100	Nnit = Nnit + AppN * 0.2 Namm = Namm + Appn * 0.8

TREE

Variables:

Definition	**Equation**
Branches surface area	Ab = cAb * (max($1e^{-10}$,(MbX))) ^ qAb
Substrate C concentration in branches	Cb = MbC/MbM
Activity parameter of branches meristemes	k_bM = k_bM20*fTair
maintenance respiration function for branches	mAb = mAb20 * fTair
Potential mass of branches meristemes	MbMpot = c_bMpot*Ab*Cb*Nb
Intrinsic specific growth rate of branches meristemes	mu_bM = k_bM*Cb*Nb
Branches N substrate concentration (kg substrate N (kg X DM)$^{-1}$)	Nb = MbN/MbM
Branches maintenance respiration (kg C stem^{-1} d^{-1})	RbXm = mAb * Ab * (Cb / (Cb + Km_bC))
Utilization of N for branches growth (kg N d^{-1})	U_NbG = (fNbM*Fb6)+(fNbX*Fb7)
partitioning ratio between structure and meristem in branches	z_b = min((MbMpot-MbM)/MbM,0.9999)
Incremental specific leaf area	c_sla = c_sla_max_tree * fSLAC
Coarse roots surface area	Ac = cAc * (max($1e^{-10}$,(McX))) ^ qAc
Substrate C concentration in coarse roots	Cc = McC/McM
Activity parameter of coarse root meristemes	k_cM = k_cM20 * fTsoil
maintenance respiration function for coarse roots	mAc = mAc20 * fTsoil
Potential mass of coarse root meristemes	McMpot = c_cMpot*Ac*Cc*Nc
Intrinsic specific growth rate of coarse root meristemes	mu_cM = k_cM*Cc*Nc
coarse roots N substrate concentration kg substrate N (kg X DM)$^{-1}$)	Nc = McN/McM
Coarse roots maintenance respiration (kg C stem^{-1} d^{-1})	RcXm = mAc * Ac * (Cc / (Cc + Km_cC))
Utilization of N for coarse root growth (kg N d^{-1})	U_NcG = (fNcM*Fc6)+(fNcX*Fc7)
partitioning ratio between structure and meristem in coarse roots	z_c = min((McMpot-McM)/McM,0.9999)
C tran coefficient from branches to stem (d^{-1})	cTCbs = cTCp20 * fTair
C tran coefficient from coarse to fine roots (d^{-1})	cTCcf = cTCp20 * fTsoil
C tran coefficient from leaves to branches (d^{-1})	cTClb = cTCp20 * fTair

C tran coefficient from stem to coarse roots (d^{-1})	cTCsc = cTCp20 * fTsoil
N transport coefficient from branches to leaves(d^{-1})	cTNbl = cTNp20 * fTair
N transport coefficient from coarse root to stem (d^{-1})	cTNcs = cTNp20 * fTsoil
N transport coefficient from fine to coarse roots (d^{-1})	cTNfc = cTNp20 * fTsoil
N transport coefficient from stem to branches (d^{-1})	cTNsb = cTNp20 * fTair
Substrate C conc. in fine root	Cf = MfC/(MfM+MfX)
Activity parameter of fine root meristemes	k_fM = k_fM20 * fTsoil
Potential mass of fine root meristemes	MfMpot = c_fMpot*InAc*Cf*Nf
Maintenance coefficient for fine roots (d^{-1})	mMfX = mMfX20 * fTsoil
Intrinsic specific growth rate of fine root meristemes	mu_fM = k_fM*Cf*Nf
Substrate N conc. in fine root	Nf = MfN/(MfM+MfX)
Fine roots maintenance respiration (kg C $stem^{-1}$ d^{-1})	RfXm = mMfX*fCfX*MfX*(Cf/(Cf+Km_fC))
Utilization of N for fine root growth (kg N d^{-1})	U_NfG = (fNfM*Ff6)+(fNfX*Ff7)
partitioning ratio between structure and meristem in fine roots	z_f = min((MfMpot-MfM)/MfM,0.9999)
Incremental SLA limiting function	fSLAC = 1 - c_slaC * OutCl
Leaf area growth rate	G_Al = c_sla * OutFl7
C substrate trans conductance frombranches to stem (kg X dm $stem^{-1}$ d^{-1})	gCbs = cTCbs*(OutMbM*OutMsM)/(OutMbM+OutMsM)
C substrate trans conductance from coarse to fine root (kg X dm $stem^{-1}$ d^{-1})	gCcf = cTCcf*(OutMcM*(OutMfM+OutMfXdead)) / (OutMcM+OutMfM+OutMfXdead)
C substrate trans conductance from leaves to branches (kg X dm $stem^{-1}$ d^{-1})	gClb = cTClb*((OutMlM + OutMlX) * OutMbM) / (OutMlM + OutMlX + OutMbM)
C substrate trans conductance from stem to coarse root (kg X dm $stem^{-1}$ d^{-1})	gCsc = cTCsc*(OutMsM*OutMcM)/(OutMsM+OutMcM)
N substrate trans conductance from branches to leaves (kg X dm $stem^{-1}$ d^{-1})	gNbl = cTNbl*(OutMbM * (OutMlM + OutMlX)) / (OutMbM + OutMlM + OutMlX)
N substrate trans conductance from coarse root to stem (kg X dm $stem^{-1}$ d^{-1})	gNcs = cTNcs*(OutMcM * OutMsM)/(OutMcM + OutMsM)
N substrate trans conductance from fine to coarse roots (kg X dm $stem^{-1}$ d^{-1})	gNfc = cTNfc*((OutMfXdead + OutMfM) * OutMcM) / (OutMfXdead + OutMfM + OutMcM)
N substrate trans conductance from stem to branches (kg X dm $stem^{-1}$ d^{-1})	gNsb = cTNsb*(OutMsM * OutMbM)/(OutMsM + OutMbM)

Litter function for leaf area	kAl_lit = kAl_lit20 * fSLAC * fTair * fPSI
Losses of leaf area to litter	L_Al = kAl_lit * Al
Substrate C conc. in leaves	Cl = MlC / (MlM + MlX)
Activity parameter of leaves meristemes	k_lM = k_lM20 * fTair
Potential mass of leaves meristemes	MlMpot = c_lMpot * InAb * Cl * Nl
Maintenance coefficient for leaves (d^{-1})	mMlX = mMfX20*fTair
Intrinsic specific growth rate of leaves meristemes	mu_lM = k_lM * Cl * Nl
Leaves N substrate concentration (kg substrate N (kg X DM)$^{-1}$)	Nl = MlN / (MlM + MlX)
Total N concentration in foliage (kg tot N/kg X dm)	Nl_tot = (MlN + fNlX * MlX + fNlM * MlM) / (MlX + MlM)
Fine roots maintenance respiration (kg C stem^{-1} d^{-1})	RlXm = mMlX*fClX*MlX*(Cl/(Cl+Km_lC))
Utilization of N for leaves growth (kg N d^{-1})	U_NlG = (fNlM*Fl6)+(fNlX*Fl7)
Partitioning ratio between structure and meristem in leaves	z_l = min((MlMpot-MlM)/MlM,0.9999)
Canopy gross photosynthetic rate (kg C stem^{-1} d^{-1})	Pcarb = (12/44)*(h*OutP_CO2_tree / n_stems)
Leaf photosynthetic efficiency	alpha_tree = alpha_max_tree * (1 - (beta_tree / tau_tree * CO2air))
Effect of foliage N on photosynthesis	fNitph = 0.5 for Nltot < 0.02
	0.5 * (1.0 + (Nltot - 0.02) / 0.015) for Nltot < 0.035
	1.0 for Nltot > 0.035
dx factor of exponential function for P_CO2	Fx0 = PHSYNf1 + Pmax_tree * ln((PHSYNf1 + PHSYNf2) / (Pmax_tree * (PHSYNf1 + (1 - 2 * theta_tree) * x0 + Pmax_tree))) - 2 * theta_tree * Pmax_tree * ln(2 * (PHSYNf1 + PHSYNf2))
dy factor of exponential function for P_CO2	Fx1 = PHSYNf3+Pmax_tree * ln((PHSYNf3+PHSYNf4) / (Pmax_tree * (PHSYNf3 + (1 - 2 * theta_tree) * x1 + Pmax_tree))) - 2 * theta_tree * Pmax_tree * ln(2 * (PHSYNf3 + PHSYNf4))
Instantaneous light flux density (J m^{-2} sec^{-1})	I0 = InInPAR_tree / h
leaf area index m2 (leaf) m^{-2} (ground)	LAI_tree = n_stems * InAI
Canopy gross photosynthetic rate (kg CO2 m^{-2} s^{-1})	P_CO2_tree = (1/(2*theta_tree*k_tree))*(x0-x1-Fx0+Fx1)
common factor 1 0	PHSYNf1 = (x0^2+2*Pmax_tree*(1^{-2}*theta_tree)*x0+(Pmax_tree ^ 2)) ^ 0.5

common factor 2 0	PHSYNf2 = x0+Pmax_tree*(1^{-2}*theta_tree)
common factor 1 1	PHSYNf3 = (x1^2+2*Pmax_tree*(1^{-2}*theta_tree)*x1+(Pmax_tree ^ 2)) ^ 0.5
common factor 2 1	PHSYNf4 = x1+Pmax_tree*(1^{-2}*theta_tree)
Light-saturated value of photosynthetic rate	Pmax_tree = Pmax_tree20 * fTair
Light-saturated value of photosynthesis rate at 20oC	Pmax_tree20 = theta_tree * CO2air * Nltot / 0.04 for fNitph >= 1.0
	(PmxCO2 / (1 + KPmxCO / CO2air)) * fNitph by default
min value for integration	x0 = alpha_tree*k_tree*I0/(1-LeafTranstree)
max value for integration	x1 = (alpha_tree*k_tree*I0/(1-LeafTranstree))*exp(-k_tree*(max($1e^{-10}$,(LAI_tree))))
Respiratory costs of N uptake (kg C $stem^{-1}$ d^{-1})	R_UN = Ff1_2*cUNamm+Ff2_2*cUNnit
Stem surface area	As = cAs * (max($1e^{-10}$,(MsX))) ^ qAs
Substrate C concentration in stem	Cs = MsC/MsM
Activity parameter of stem meristemes	k_sM = k_sM20*fTair
maintenance respiration function for stem	mAs = mAs20 * fTair
Potential mass of stem meristemes	MsMpot = c_sMpot*As*Cs*Ns
Intrinsic specific growth rate of stem meristemes	mu_sM = k_sM*Cs*Ns
Stem N substrate concentration (kg substrate N (kg X DM)$^{-1}$)	Ns = MsN/MsM
Stem maintenance respiration (kg C $stem^{-1}$ d^{-1})	RsXm = mAs * As * (Cs / (Cs + Km_sC))
Utilization of N for stem growth (kg N d^{-1})	U_NsG = (fNsM*Fs6)+(fNsX*Fs7)
Tree root activity ((m2/kg X dm) * d^{-1})	sigmaUN_tree = sigmaUN_tree20 * fTsoil * fPSI
Carbohidrates exudation from tree fine roots	SCf_ex_s = kCSrt_ex20 * OutOutMfX * OutOutCf * fTsoil
Nitrogen exudation from tree fine roots	SNf_ex_s = kNSrt_ex20 * OutOutMfX * OutOutNf * fTsoil
Tree nitrogen uptake	U_N = (OutOutMfX * sigmaUN_tree * zNeffuN) / (1 + (K_CUN / OutOutCf) * (1 + OutOutNf / J_NUN))
partitioning ratio between structure and meristem in stem	z_s = min((MsMpot-MsM)/MsM,0.9999)

Compartments:

Definition	**Equation**	**Initial Value**
Leaf (foliage) area (m2 stem^{-1})	dAl/dt = G_Al - L_Al	0.03
Branches C substrate (kg C stem^{-1})	dMbC/dt = Fl2 - Fb2 - ((Fb6 * fCbM / YbM) + (Fb7 * fCbX / YbX)) - RbXm	0.7e^{-2}
Branches meristem (kg DM stem^{-1})	dMbM/dt = Fb6	0.01
Branches N substrate (kg N stem^{-1})	dMbN/dt = Fs3bis + InInNb_rec - Fb3bis - U_NbG	0.005
Branches structural DM (kg stem^{-1})	dMbX/dt = Fb7 - Fb8	0.1
Coarse roots C substrate (kg C stem^{-1})	dMcC/dt = Fs2- ((Fc6 * fCcM / YcM) + (Fc7 * fCcX / YcX)) - RcXm - Fc2	0.006
Coarse roots meristem in upper layer (kg DM stem^{-1})	dMcM/dt = Fc6	0.01
Coarse root N substrate (kg N stem^{-1})	dMcN/dt = Ff3bis + InInNc_rec - U_NcG - Fc3bis	0.008
Coarse roots structural DM (kg stem^{-1})	dMcX/dt = Fc7 - Fc8	0.2
Fine root C substrate (kg C stem^{-1})	dMfC/dt = Fc2 - RfXm - InR_UN - ((Ff6 * fCfM / YfM) + (Ff7 * fCfX / YfX))	0.2e^{-3}
Fine root meristem (kg dm stem^{-1})	dMfM/dt = Ff6	10e^{-6}
Fine root N substrate (kg N stem^{-1})	dMfN/dt = Ff2_2 + Ff1_2 + InInNf_rec - U_NfG - Ff3bis	0.3e^{-3}
Fine root structural dry matter (kg dm stem^{-1})	dMfX/dt = Ff7 - Ff8	0.01
Leaves C substrate (kg C stem^{-1})	dMlC/dt = InPcarb - ((Fl6 * fClM / YlM) + (Fl7 * fClX / YlX)) - RlXm - Fl2	0.4e^{-3}
Leaves meristem (kg DM stem^{-1})	dMlM/dt = Fl6	1000e^{-6}
Leaves N substrate (kg N stem^{-1})	dMlN/dt = Fb3bis + InInNl_rec - U_NlG	0.1e^{-3}
Leaves structural DM (kg stem^{-1})	dMlX/dt = Fl7 - Fl8	0.01
Stem C substrate (kg C stem^{-1})	dMsC/dt = Fb2 - Fs2 - ((Fs6 * fCsM / YsM) + (Fs7 * fCsX / YsX)) - RsXm	0.006
Stem meristem (kg DM stem^{-1})	dMsM/dt = Fs6	0.025
Stem N substrate (kg N stem^{-1})	dMsN/dt = Fc3bis - Fs3bis - U_NsG	0.028
Stem structural DM (kg stem^{-1})	dMsX/dt = Fs7	0.2

Flows:

Definition	Equation
MbC to MbM	Fb6 = mu_bM * z_b * MbM
MbC to MbX	Fb7 = mu_bM * (1 - z_b) * MbM
McC to McM	Fc6 = mu_cM * z_c * McC
McC to McX	Fc7 = mu_cM * (1 - z_c) * McM
OutMbC to InMbC	Fb2 = gCbs * (OutCb - OutCs)
OutMbN to InMbN	Fb3 = gNbl * (OutNb - OutNl)
OutMcC to InMcC	Fc2 = gCcf * (OutCc - OutCf)
OutMcN to InMcN	Fc3 = gNcs * (OutNc - OutNs)
OutMfN to InMfn	Ff3 = gNfc * (OutNf * OutNc)
MfC to MfM	Ff6 = mu_fM * z_f * MfM
MfC to MfX	Ff7 = mu_fM * (1 - z_f) * MfM
OutMlC to InMlC	Fl2 = gClb * (OutCl - OutCb)
OutMsC to InMsC	Fs2 = gCsc * (OutCs - OutCc)
OutMsN to InMsN	Fs3 = gNsb * (OutNs - OutNb)
MlC to MlM	FL6 = mu_lM * z_l * MlM
MlC to MlX	Fl7 = mu_lM * (1 - z_l) * MlM
MsC to MsM	Fs6 = mu_sM * z_s * MsM * DiamIncr for MsX > StemHeight_max
	mu_sM * z_s * MsM by default
MsC to MsX	Fs7 = (mu_sM * (1 - z_s) * MsM) * DiamIncr for MsX > StemHeight_max
	mu_sM * (1 - z_s) * MsM by default
OutOutNamm_tree to InNamm_tree	Ff1 = U_N * (Namm/NeffuN)
OutOutNnit_tree to InNnit_tree	Ff2 = U_N * (fTuNmin * Nnit / NeffuN)

PARAMETERS

alpha_max_grass	$2.5e^{-8}$
alpha_max_tree	$1e^{-8}$
beta_grass	$3e^{-7}$
beta_tree	$2e^{-7}$
c_bioDclay	3
c_bMpot	50
c_cMpot	50
c_fMpot	50
c_lit_prot	3
c_lMpot	50
c_sla_max_tree	15.1
c_slaC	2.5
c_sMpot	50
c_stSOMclay	3
c_uN2	0.5
c_uN3	0.25
c_uN4	0.1
cAb	0.16
cAc	0.16
cAs	0.16
Cbio_min	0.001
chileaf_grass	0.1
clam1_an	1
clam2_an	1
clam3_an	1
clam4_an	0.5
cNbio	1
CO2vpm	350
css_an	0.7
cTCp20	100
cTNp20	2
cUNamm	0.4
cuNamm_grass	0.4
cUNnit	0.5
cUNnit_grass	0.5
DiamIncr	0.05
dr	1.8
f_deg_grass	0.1667
f_pruning	0.99
fCan_mai	0.6
fCan_met	0.05
fCbioD_Csol	0.1
fCbioDR	0.5
fCbM	0.4
fCbX	0.4
fCcelR_a	0.4
fCcelR_s	0.4
fCcM	0.4
fCcX	0.4
fCdeg_grass	0.45
fCfM	0.4
fCfX	0.4
fclay_s	0.1
fCligR_a	0.2
fCligR_s	0.2
fClM	0.43
fClX	0.43
fCmetR_a	0.6
fCmetR_s	0.6
fCmic_uSOM_clay	0.3
fCmic_uSOM_sandy	0.7
fCplX	0.45
fCpSOMminR	0.4
fCpSOMstR	0.2
fCsM	0.4
fCstSOMminR	0.4
fCsX	0.4
fCuSOMminR	0.4
fCuSOMstR	0.2
fi_cel	0.4
fi_met	0.6
fLgrass	0.7
fNbM	0.025
fNbX	0.005
fNcM	0.025
fNcX	0.025
fNenv_amm	$1.37e^{-6}$
fNfM	0.025
fNfX	0.025
fNgrass_d	0.005
fnitrif	0.01
fNlM	0.034
fNlX	0.034
fNplX	0.016
fNret	0.01
fNsM	0.025
fNsX	0.025
fTuN10	0.5
fTuN20	1
gamma_rt20	0.11
gamma_sh20	0.11
IDMpl_anmax	13.5
ISLAgrass	2.5
ISLAmax_grass	25
J_NUN	0.005
JNfix	0.001
k_bioG20	0.1
k_bM20	10
k_bXlit20	0
k_cel20	0.01
k_cM20	10
K_CUN	0.05
k_cXlit20	0.01
k_dead_rt20	0.06
k_dead_sh20	0.08
k_dead20	0.01
k_denit20	0.01
k_dif_b20	0
k_dif_c20	0
k_dif_f20	0
k_dif_l20	0
k_dif_s20	0
k_fM20	10
k_fXlit20	0.03
k_grass	0.7
k_leach	0.0035
k_lig20	0.002
k_lM20	10
k_lXlit20	0.01
k_met20	0.05
k_nit20	0.4
k_pSOMmin20	0.00045
k_pSOMst20	$2e^{-5}$
k_sM20	10
k_stSOMmin20	$3e^{-5}$
k_sXlit20	0
k_tree	0.57
k_uSOMmin20	0.007
k_uSOMst20	0.0002
k_vol20	0.0017

kAl_lit20	0.01	KpSOM	0.002	mulch_lig_l	0.1	ro_uSOMmax	12
KCbioG	0.001	ksi_ph	0.95	mulch_met_l	0.65	ro_uSOMmin	6
KCgrass	0.05	KstSOM	0.002	m_lig	3	roCNcel	150
KCmai	0.03	KuSOM	0.002	m_ro	50	roCNlig	100
KCO2_Pmax	0.00128072	LAIprun	5.25	mAb20	0.0005	roCNrec	2.7
kCshrt20	0.5	lamda_cel_b	0.65	mAc20	0.0005	soilden	1000
kCSrt_ex20	0.02	lamda_cel_c	0.65	mAs20	0.0005	sigmaUN_grass20	0.25
kf_amm	0.1	lamda_cel_f	0.65	mc	3	sigmaUN_tree20	0.25
kf_somd	0.05	lamda_cel_fa	0.65	n_anim	0.0004	StemHeight_max	3
KLAIan	1.4	lamda_cel_l	0.65	N_ha	150	T0	8
Km_bC	0.01	lamda_cel_rt	0.65	n_stems	0.25	tau_grass	0.0015
Km_cC	0.01	lamda_cel_sh	0.65	p_atm	101325	tau_tree	0.001
Km_fC	0.01	lamda_lig_b	0.3	Pmax_grass20	0.0007	theta_tree	0.95
Km_lC	0.01	lamda_lig_c	0.3	PmxCO2	$3e^{-5}$	Tmax	35
Km_sC	0.01	lamda_lig_f	0.15	psi_s	-16.94	Tref	20
kmai_rt120	0.02	lamda_lig_fa	0.15	q_bio	0.6667	Yan	0.4
kmai_rt220	0.02	lamda_lig_l	0.15	q_psi_s	20	Ybio	0.5
kmai_rt320	0.015	lamda_lig_rt	0.15	qAb	0.66667	YbM	0.75
kmai_rt420	0.01	lamda_lig_sh	0.15	qAc	0.66667	YbX	0.75
kmai_sh120	0.02	lamda_met_b	0.05	qAs	0.66667	YcM	0.75
kmai_sh220	0.02	lamda_met_c	0.05	qLAIan	3	YcX	0.75
kmai_sh320	0.015	lamda_met_f	0.2	R	8314	YfM	0.75
kmai_sh420	0.01	lamda_met_fa	0.2	rCNan	3.5	YfX	0.75
KNbioG	0.001	lamda_met_l	0.2	rmmCS	28.5	Ygrass	0.75
KNeffuN	0.005	lamda_met_rt	0.2	rmmNS	62	YlM	0.75
kNfix20	$5e^{-5}$	lamda_met_sh	0.2	ro_bio	8	YlX	0.75
KNgrass	0.005	lamdaCNrec	2.7	ro_f_mic	3.5	YsM	0.75
KNrec_grass	0.02	LeafTransgrass	0.1	ro_pSOM	10	YsX	0.75
KNrec_tree	0.01	LeafTranstree	0.3	ro_pSOMmax	12	z_mulch	0.25
kNrtsh20	0.05	mMfX20	0.001	ro_pSOMmin	6		
kNSrt_ex20	0.005	mMlX20	0.001	ro_stSOM_clay	10		
kNtransSOM_R	0.2	mu20	500	ro_stSOM_sandy	20		
KPmxCO	0.00128072	mulch_cel_l_X	0.3149	ro_uSOM	15		