

Planted Tree Fallows and Their Influence on Soil Fertility and Maize Production in East Africa

Nitrogen Fixation and Soil Nitrogen Dynamics

Lena Ståhl

*Faculty of Forest Sciences
Department of Forest Ecology
Umeå*

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Abstract

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Soil fertility depletion is a main constraint to food production in sub-Saharan Africa. This thesis concerns the potential of N₂-fixing trees to increase nitrogen inputs to agroforestry systems and accordingly to improve crop production. The suitability of five tropical tree species (including two N₂-fixing species, *Leucaena leucocephala* and *Prosopis chilensis*) for tree fallows in Tanzania were evaluated by comparing their leaf chemistry, their effects on soil properties and on maize growth. After five years fallow, the per cent total soil N was higher under *Prosopis* compared to under other tree species. Maize biomass production was higher on soils from *Leucaena* or *Prosopis* compared to grass fallow. *Prosopis* contributed 11% to the total soil C over a period of 8 years.

Field experiments in Kenya were performed to test a low-level ¹⁵N-tracer technique to estimate biological nitrogen fixation in *Sesbania sesban* over an 18-months period, and to compare the effects of short-duration tree fallows on two subsequent maize harvests with natural fallow and continuous cropping. We estimated the N derived from atmosphere by *Sesbania* after 18 months to between 500 and 600 kg ha⁻¹, depending on which plant parts were used for ¹⁵N data and on the choice of reference species. We consider the ¹⁵N dilution method to be appropriate for quantifying N₂ fixation in improved fallows in studies of young trees with high N₂-fixing ability.

In an experiment examining the effects of tree fallows on subsequent maize crops approximately 70-90% of the N in *Sesbania*, and 50-70% in *Calliandra calothyrsus*, was derived from N₂-fixation. The quantity of N added by N₂-fixation, 280-360 kg N ha⁻¹ for *Sesbania* and 120-170 kg N ha⁻¹ for *Calliandra*, resulted in a positive N balance after two cropping seasons of 170-250 kg N ha⁻¹ and 90-140 kg N ha⁻¹ respectively. Both the content of inorganic N in the topsoil and the quantity of N mineralised during rainy seasons were higher after the *Sesbania* fallows than after the other treatments. The substantial accumulation of N in planted *Sesbania* demonstrated its potential to increase the sustainability of crop production on N-limited soils.

Key words: agroforestry, improved fallow, ¹⁵N, N₂-fixation, *Sesbania sesban*, woody legumes

Author's address: Lena Ståhl, Department of Forest Ecology, SLU, S-90183 Umeå, Sweden.

Contents

Introduction, 7

Agroforestry, 7

N₂ fixation in legumes, 9

Quantifying BNF using ¹⁵N, 10

Soil organic matter and soil N cycling, 11

Objectives, 12

Material and methods, 13

Experimental sites and plant material, 13

Sampling, analyses and design, 13

Site Mafiga, Tanzania (paper I), 13

Site Machakos, Kenya (papers II and III), 14

Results, 15

Effects of tree species on soils and maize growth after woody fallows in Mafiga, Tanzania. (Paper I), 15

Nitrogen fixation by Sesbania fallows in the highlands of eastern Kenya. (Paper II), 16

Effects of tree fallows on biomass production, N₂ fixation, nitrogen dynamics and subsequent maize production. (Paper III), 19

Discussion, 22

Paper (I), 22

Paper (II), 23

Paper(III), 25

Concluding remarks, 26

References, 28

Acknowledgements, 33

Appendix

Papers I-III

This thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Jonsson K, Ståhl L and Högberg P. 1996. Tree fallows: A comparison between five tropical tree species. *Biology and Fertility of Soils* 23: 50-56.
- II. Ståhl L, Högberg P, Sellstedt A and Buresh RJ. 2005. Measuring nitrogen fixation by *Sesbania sesban* planted fallows using ¹⁵N tracer technique in Kenya. *Agroforestry Systems* 65: 67-79.
- III. Ståhl L, Nyberg G, Högberg P and Buresh RJ. 2002. Effects of planted tree fallows on soil nitrogen dynamics, above-ground and root biomass, N₂-fixation and subsequent maize crop productivity in Kenya. *Plant and Soil* 243: 103-117.

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Introduction

In sub-Saharan Africa, small farms of less than five hectares account for over 90% of agricultural production (IFPRI 2002). These farmers are trying to make the best use of their resources, but the vast majority is very poor resulting in food security being one of their main concerns. The low and decreasing per-capita food production (World Bank 2004) is basically caused by soil fertility depletion (Sanchez 2002). It is fundamental for sustainable crop production that nutrients removed in crops are replenished. The lack of access to inorganic fertilisers has made the interest in alternative solutions, e.g., agroforestry, a necessity (Giller & Cadisch 1995). A major contribution of agroforestry to soil fertility is the capacity to maintain or increase soil organic matter (SOM) through the supply of above-ground litter and root residues (Young 1997). Concerning nitrogen, the main input options are animal manure, biomass transfer or biological nitrogen fixation (BNF). Agroforestry, BNF and SOM are further treated below.

Agroforestry

Agroforestry is defined as “a dynamic, ecologically based natural resources management system that, through the integration of trees in farmland and rangeland, diversifies and sustains production for increased social, economic and environmental benefits for land users at all levels” (Leakey 1996). It is a collective name for land-use systems in which woody perennials (trees, shrubs etc.) are grown in association with herbaceous plants (crops, pastures) and/or livestock in a spatial arrangement, a rotation, or both; there are usually both ecological and economic interactions between the trees and other components of the system (Young 1997).

Farmers have been growing trees on their farms for ages for the many benefits they provide (Nye & Greenland 1960), e.g. for both products and services. Products are for example fuelwood, poles, construction wood, fodder, food, medicine and chemicals (insecticides, dye, tannins). Examples of services provided are erosion control, soil fertility improvement, fencing, windbreaks, shade and weed control. Woody perennials have the potential to improve soil fertility by processes which

- a) increase additions to the soil (build-up of SOM, N₂ fixation, uptake of nutrients from the subsoil)
- b) reduce losses from the soil (erosion, leaching)
- c) improve soil physical, chemical and biological conditions

The effects may also be secondary through fauna: animals resting in the shade of the trees and birds provide droppings under the trees. In dry environments, however, competition for water is a serious problem of trees in crop production systems (Young 1997).

The oldest agroforestry practice, shifting cultivation, is still widely spread. It is generally considered sustainable as long as the fallow periods are sufficient to restore soil fertility. When fallow periods are shortened this practice results in degraded land and low crop production. Examples of agroforestry practices are shown in Table 1.

Table 1. Brief description of some agroforestry practices including main utilities

Agroforestry practice	Description	Main utilities
Alley cropping	Crops grown between hedges of woody species	Soil fertility, crop and tree products
Trees on croplands/rangelands	Scattered or systematically arranged multipurpose trees	Fodder, shelter, tree and crop products
Shade trees for plantation crops	Multipurpose trees scattered in for instance coffee or tea plantations	Shade, tree products
Home gardens	Intensively managed small areas with high species diversity	A large number of products
Live hedges and boundary plantings	Trees around farmlands	Fencing, boundary, tree products
Fodder banks and biomass transfer	Trees are grown as separate blocks and managed for fodder or mulch production	Fodder or mulch
Trees in soil conservation	Trees on terraces, banks, grass strips etc used for soil and water conservation	Soil conservation, tree products
Improved fallow	Rotation of planted, mainly N ₂ -fixing, trees with crops	Soil fertility, tree products

There are many ways of classifying agroforestry systems. One of them is based on arrangements of components in time resulting in two main groups, simultaneous and sequential agroforestry systems. In a simultaneous system, trees and crops or animals are present together, at the same time on the same piece of land. Competition for light, water and nutrients has to be considered in the design for instance by choosing appropriate tree species. Good qualities of woody species might be small canopies, not shading out too much light from the crops, and roots reaching deeper than the crop roots. In sequential systems, crops and trees take turns in occupying the same space. The time sequence keeps competition to a minimum. Trees in a sequential system should grow rapidly when crops are not growing, recycle nutrients from deep layers, fix N and have a large canopy to help suppress weeds. For soil fertility management improved fallow (short rotation planted tree/shrub fallow) has become a land use system in focus for a lot of research with promising results (e.g., Chikowo et al. 2004; Gathumbi et al. 2004; paper III this thesis). Improved fallow implies restoring soil fertility by using fast growing, N₂-fixing woody perennials on agricultural land for a period of 6 months to 3 years, planted or as a result of selective cutting. The trees may be partially

harvested during the fallow period. The main purpose is to maintain or enhance crop production, which is made through improved soil fertility as an effect of:

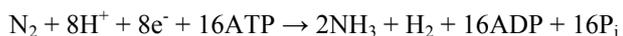
- addition of N from N₂-fixing species (e.g., Sanginga et al. 1995; Giller et al. 1997; papers I-III this thesis)
- increased P in labile fractions as high-quality organic matter can give rise to a net release of P from the plant material and a decrease in the soil P adsorption capacity (Nziguheba et al 1998)
- access to sub-soil nutrient pools through deeper rooting (Hartemink et al. 1996; Mekkonen et al. 1997)
- improved soil physical properties due to organic-matter maintenance and the effect of tree roots (Young 1997; Chirwa et al. 2004)
- weed suppression (natural seed bank decline, reduced impact of Striga (parasitic weed) infestations) (Gallagher et al. 1999)

Additionally, fuel wood, fodder, stakes etc. are produced. Even if research on improved fallow species is encouraging, there is still a lack of information regarding their growth characteristics and productivity as well as inter- and intraspecies interactions (Gathumbi et al. 2004). Further work is needed to identify more species that are easily established, are less prone to pests and diseases, provide a range of fallow by-products, and coppice on fallow clearance (Buresh and Cooper 1999; Niang et al. 2002).

Practising agroforestry on small farms can, furthermore, result in a positive impact on food and income security (WAC 2005) through increased food supply and fewer periods of shortage, and income from sales of tree products and surplus crops. In the context of global climate change and accumulation of carbon dioxide in the atmosphere, the potential of agroforestry systems for restoration of degraded soils and ecosystems is being increasingly recognized (Vågen et al. 2005). Through agroforestry, both C storage in biomass and soil (C sequestration) and decreased pressure on natural forests (C conservation) can be achieved (Montagnini & Nair 2004). Nitrogen is of importance in C sequestration and soils under N₂-fixing trees accumulate more C compared to soils under non-N₂-fixing trees (Resh et al. 2002). The influence of management regime of agroforestry systems on C sequestration potential is of interest for future research (Sierra & Nygren 2005).

N₂ fixation in legumes

Already in 1883, when studying the effect of N fertiliser on plants, Helriegel & Wilfart found that peas often seemed to get N from some non-identified source. In a control experiment they got both yellow and green plants and after inoculation with sand from outside the experiment all plants grew well. Good growth could be correlated to the presence of root nodules. More than a century later the mechanisms of N₂ fixation in legume/rhizobia symbiosis are fairly well elucidated. The equation for the energetically costly reaction carried out by the enzyme nitrogenase is as follows:



The ability of legumes to fix atmospheric dinitrogen, available everywhere free of charge, is a quality of great value to small-scale farmers with limited financial means. The use of legumes in crop production to improve sustainability and restore soil fertility as an alternative to inorganic fertilisers is gaining ground. Good growth conditions for both legume and rhizobia are fundamental to obtain effective BNF. Limiting factors are for instance unfavourable temperature or soil pH, drought, water logging, salinity, high levels of combined N, pathogenic nematodes and nutrient deficiencies. Especially phosphorous deficiency, a frequent characteristic of soils in sub-Saharan Africa, is a serious constraint to BNF (Buresh & Tian 1998). Additional factors influencing fixation are for example survival and persistence of rhizobia in the soil, management regimes i.e., pruning (Nygren & Cruz 1998) and competition from intercropped species.

Quantifying BNF using ^{15}N

Sustainability of a land use system requires the replacement, via N fertilisation or BNF, of any N that is removed or lost. Consequently, the N input via BNF must be quantified to judge if it balances the N exported. Various methods for estimating BNF have been developed, e.g., the acetylene reduction assay, N-difference procedures, xylem-solute techniques, and ^{15}N isotope methods (e.g. Peoples et al. 1989; Binkley & Giardina 1997). In the studies presented here, isotope-based methods were selected as they account for temporal variations and are appropriate for quantifying BNF under field conditions (Hardarson & Atkins 2003). Isotopic methods exploit differences in $^{15}\text{N}/^{14}\text{N}$ ratio between soil N and atmospheric N_2 , either natural variations (natural abundance method) or ratios extended by addition of the stable isotope ^{15}N to the soil (^{15}N dilution method). The natural abundance of ^{15}N in atmospheric N_2 is constant at 0.3663 atom%. The ^{15}N abundance in plant-available soil N is obtained by analysing a non-fixing reference plant, which explores the same soil N pool as the N_2 -fixing plant. With increasing N_2 fixation, the abundance of ^{15}N in the legume declines, due to N with higher ^{15}N abundance from plant-available soil N (natural or enriched) being diluted by fixed atmospheric N_2 of lower ^{15}N abundance. An estimation of BNF is calculated from ^{15}N abundance values in legumes and reference plants.

The first soil based experiment for measuring N_2 fixation using ^{15}N labelling was reported by McAuliffe et al. (1958), who used the isotope to show that fixation was reduced in clover and alfalfa when N fertiliser was applied. The technique has been frequently used for quantifying BNF in various annual legumes but applying it on deep-rooted trees is an extra challenge because of their perennial nature of growth, which involves seasonality in N dynamics, and because of the problem of labelling uniformly a deep soil profile (Chalk & Ladha 1999). Several studies have been made aiming at minimising both temporal and spatial isotopic non-uniformity in the soil N (e.g., Viera-Vargas et al. 1995; Sanginga et al. 1996). As long as isotopic uniformity is not obtained, selecting an appropriate reference plant for each experiment is crucial (Chalk & Ladha 1999). For a reference plant to accumulate N from the same soil N pool as the N_2 -fixing plant, it should mimic both its root architecture and N assimilation pattern with time. Moreover, in studies of older trees, the reference species must grow in close

proximity to the legume to account for N recycling (Parrotta et al 1996). The use of several reference species in field trials has been proposed as one way to reduce the problems with mismatched reference plants (Boddey et al. 1990; Viera-Vargas et al. 1995), the use of models (which do not require a reference plant) based on soil extracts, as another (Chalk & Ladha 1999). However, the ^{15}N dilution method is insensitive to reference plant selection when %Ndfa (nitrogen derived from atmosphere) is high (e.g., Danso et al. 1993). In order not to perturb the studied system and also to avoid high costs, the quantity of added ^{15}N should be kept low. More data on the effects of low to moderate rates of ^{15}N labelling is needed to judge the isotope dilution method for quantifying N_2 fixation by field grown trees (Chalk & Ladha 1999).

The ^{15}N natural abundance method is increasingly being used to estimate %Ndfa in agroforestry systems (e.g., Gathumbi et al. 2002; Dulormne et al. 2003; Chikowo et al. 2004). The main advantage with the method is that no ^{15}N tracer is added and consequently the system is not disturbed (Shearer & Kohl 1986, Högberg 1997, Boddey et al. 2000). Disadvantages are that it is potentially more susceptible to errors associated with recycling of fixed N and to isotopic discrimination processes during N transformations, particularly in established ecosystems (Shearer & Kohl 1986; Hairiah et al. 2000). As the method is based on minute differences in $^{15}\text{N}/^{14}\text{N}$ ratios, sampling, sample preparation and analysis require great care. In paper I, when natural abundance was used to trace N and C from different tree species in the soil, a considerable variability in ^{15}N natural abundance was found among the non- N_2 -fixing tree species (cf. Högberg 1990). In the remaining work (II and III) isotope dilution technique was, therefore, used for estimating BNF.

Soil organic matter and soil N cycling

SOM consists of plant, animal and microbial residues at various stages of decay. The decomposition process is driven by the need for energy “locked-up” in the carbon – hydrogen bond of organic molecules. Mineralisation refers to release of organically bound nutrients and immobilisation to the opposite, use of nutrients by decomposers (Killham 1994).

Nutrient cycles of mature natural forest are quite closed in contrast to high-input agricultural system, where inputs through fertiliser are balanced by large losses through accelerated natural processes (leaching, gaseous losses, erosion) and removals in harvests. Agroforestry systems, including trees, can achieve a condition intermediate between these extremes, by reducing losses and increasing nutrient input and plant uptake (Young 1997).

Crop production is worldwide often limited by the supply of available N. Uptake of organic N forms has been demonstrated in high-latitude systems (Chapin et al. 1993, Näsholm et al. 1998) and in natural woody ecosystems in Australia (Schmidt et al. 1996). There is currently little information on the significance of this process in tropical agriculture. I have thus chosen here to study the N forms conventionally discussed as the forms available in tropical agriculture, ammonium and nitrate. Mineralisation converts organic N to inorganic N, ammonium (NH_4^+)

and, after nitrification, nitrate (NO_3^-), forms readily available to plants. The N cycle is complex with reversible reactions in abundance (Figure 1).

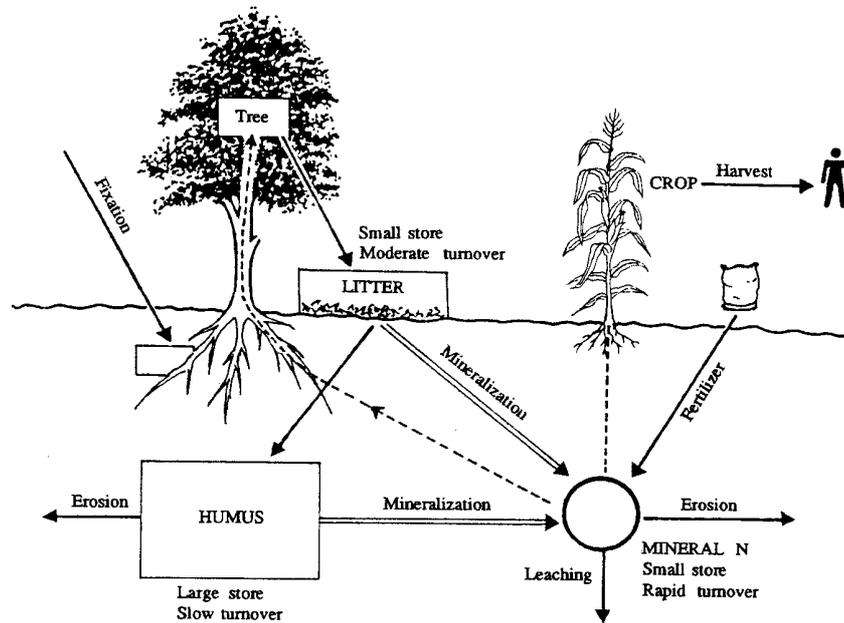


Figure 1. A simplified nitrogen cycle under agroforestry (from Young 1989).

Temperature is the main factor behind the differences in N cycling between the tropics and the temperate zone. Faster decay rates result in N immobilization being much less of a problem in the tropics. Additional factors influencing decay rates are for example water availability, quality of organic residues and soil microbial biomass (Giller et al 1997). Nutrient recycling between plant and soil occurs through two different paths; the short-term path via mineralisation and the long-term path via humification and storage as SOM (Figure 1). The half-life of the stored organic molecules has been suggested to be of the order of 10 years in the tropics and up to 50 years in the temperate zone (Young 1997). The quality of tree leaves is one of the factors influencing N mineralisation. The (lignin+polyphenol):N ratio has been found to be a good predictor of N release (Fox et al 1990), and is often discussed when different tree species are compared in the context of agroforestry (e.g., Mafongoya et al. 1998a, paper I)

Objectives

The overall objective of this thesis was to evaluate potential tree fallow species, to estimate BNF in symbiotic trees and to evaluate the effects of fallows on subsequent maize crop production. The work was based on field studies conducted in sub-humid areas of Kenya and Tanzania.

The specific objectives were (1) to evaluate the effect of different tree species on soil properties (paper **I**) and their suitability for planted tree fallows (papers **I** and **III**), (2) to test a low-level ^{15}N -tracer technique, under field conditions, for estimating BNF in trees (papers **II** and **III**), and (3) to compare planted tree fallows with traditional land-use systems regarding the effects on biomass production (paper **III**), soil inorganic N dynamics and subsequent maize harvests (papers **I** and **III**).

Material and methods

Experimental sites and plant material

The fieldwork for this thesis was carried out in East Africa. Study **I** was performed at Mafiga near Morogoro in Tanzania ($6^{\circ} 50'S$, $37^{\circ} 38'E$, 500 m altitude) on fine loamy sand soil. The site receives a mean annual rainfall of 870 mm that is unimodal in distribution. Sampling was performed in a woodlot experiment (plot size 10 x 10 m, 1800 stems ha^{-1}) with five tree species (*Leucaena leucocephala* (Lam.), *Prosopis chilensis* (Mol.) Stuntz (both N_2 -fixing), *Eucalyptus camaldulensis* (Dehnh), *E. tereticornis* (Sm.), *Senna siamea* (Lam.) Irwin & Barneby (syn. *Cassia siamea*)) and a grass fallow dominated by *Panicum maximum* (Stapf). The plots had been weeded regularly and no fertilisers were used.

The remaining two studies (**II** and **III**) were performed in a farmer's field outside Machakos in Kenya ($1^{\circ} 31'S$, $37^{\circ} 19'E$, 1920 m altitude) on soils with sandy clay loam to sandy loam structure. Rainfall at the site is bimodal with an annual mean of 900 mm. The area was uniformly cropped with unfertilised maize for the two preceding growing seasons and then ploughed with a tractor. The trees were established by planting seedlings at 1 x 1 m spacing. Paper **II** was based on an experiment including the N_2 -fixing species *Sesbania sesban* (L.) Merr. and as reference species the non-fixing *Eucalyptus saligna* (Sm.), *Grevillea robusta* (A. Cunn) and *Senna spectabilis* (D.C.) Irwin and Barneby (syn. *Cassia spectabilis*). In the experiment reported in paper **III** one further legume, *Calliandra calothyrsus* (Meissner) and the control treatments weed fallow (natural regrowth of native vegetation), maize-bean (*Phaseolus vulgaris* L., common bean) rotation (maize during the short rains and beans during the long rains) and continuous maize (*Zea mays* L.) were included, while *S. spectabilis* was excluded. The control treatments were chosen because they represent the realistic land-use alternatives in the area. When the fallow period was completed, maize was grown on all plots for two seasons.

All the tree species used in these studies are known to be fast-growing and to produce large quantities of biomass.

Sampling, analyses and design

Site Mafiga, Tanzania (paper I)

In order to evaluate the suitability of different tree species for fallows, their influence on SOM and soil fertility was compared and related to a grass fallow. Tree leaves were analysed for lignins, polyphenols, N, C and the stable isotopes ^{13}C and ^{15}N . Soil analyses of N, P, C, pH ^{13}C and ^{15}N were made, 4 and 8 years after planting. Samples of the major understorey species, *P. maximum*, were analysed for N, C, ^{13}C and ^{15}N . As C_3 (trees, legumes) and C_4 (tropical grasses, e.g., maize) plants have different C assimilation pathways and these pathways discriminate differently against ^{13}C in CO_2 , the natural abundance ($\delta^{13}\text{C}$) in biomass produced will differ. C_3 plants generally vary from $\delta = -33$ to -22% and C_4 plants from $\delta = -16$ to -9% (Deines 1980). This makes it possible to distinguish between these two origins of organic C input to the soil and thus calculate the fractions of organic C derived from trees. The ^{15}N natural abundance was used, as discussed above, to indicate input of N from BNF. In addition, a maize bioassay experiment was carried out, where maize plants were grown in 5 l polyethylene bags drained by numerous small holes. The bags were filled with topsoil, collected from the tree and grass plots, grown with one seedling per bag, kept in a nursery and watered daily. After 100 days, the maize was harvested, dried and weighed.

Site Machakos, Kenya (papers II and III)

For N_2 fixation estimation, ^{15}N labelling of the soil with a single dose of ammonium sulphate dissolved in water was done inside galvanized iron barriers prior to planting. The allocation of biomass was determined after 6, 12 and 18 months (paper II) and 12, 18 and 22 months (paper III) by whole tree harvests of both N_2 -fixing tree legumes and non- N_2 -fixing reference trees. Above-ground biomass was separated into stem, branches, dead branches, leaves and pods. Root sampling to 0.60 m soil depth was carried out with a modified monolith sampling method, described in paper III, using locally constructed metal samplers. Root sampling from 0.60 to 2.10 m (paper III) was done with an auger. The root samples were hand sorted to remove organic debris and to separate fine roots (< 2 mm), coarse roots (> 2 mm) and root nodules. All samples were dried, ground and analysed for total N and ^{15}N . N_2 fixation was estimated based on foliar ^{15}N atom excess (FAE), above-ground ^{15}N atom excess (AAE, only in paper II) or whole tree ^{15}N atom excess (WAE) data and using different reference trees. Soil sampling was done with a 7-cm diameter Edelman auger to 0.60 m depth (paper II) or to 1.50 m depth (paper III) at the same times as biomass sampling. Total N and ^{15}N was analysed.

To assess fallow effects on soil N and maize production (paper III), total soil inorganic N was measured monthly from five months before harvest of the fallows to after the second subsequent maize crop. During the first growing season following the fallows, 21- m^2 areas within each plot of the N_2 -fixing trees, maize-bean, continuous maize and weed fallow treatments were kept free of vegetation. Topsoil samples from these areas were analysed for inorganic N. The effects of the different fallows on two subsequent maize crops were evaluated.

All three experiments had a randomised complete block design with four replicate plots of each treatment.

Results

Effects of tree species on soils and maize growth after woody fallows in Mafiga, Tanzania. Paper (I)

The tree species studied had significantly different impacts on soils and on maize growth. Already after 4 years there were significant differences between the studied soils in N ($P<0.001$), C ($P<0.01$), C:N ratio ($P<0.001$), and pH ($P<0.001$). *Prosopis* contributed more C to the soil than the other four tree species, 11% to the total C of the soil over a period of 8 years. N% was higher and the natural abundance of ^{15}N of soil total N was lower under *Prosopis* as compared to in soil collected under the other tree species. This indicated an input of fixed N. The three non- N_2 -fixing species in this study showed a considerable variation in $\delta^{15}\text{N}$, which resulted in substantial differences in estimates of N_2 fixation using ^{15}N natural abundance method depending on reference species used.

There were large differences between tree species in (lignin+polyphenol):N ratio in leaves (Table 2). The leaves of the N_2 -fixing species had a low ratio of (lignin+polyphenol):N, a parameter negatively correlated with maize growth. Maize biomass production was highest when grown in soil from the *Leucaena* plots followed by *Prosopis*, *Senna*, *E. camaldulensis*, *E. tereticornis* and grass fallow in that order.

Table 2. Chemical properties of leaves of five tropical tree species

Species	Lignin (%)	Polyphenols (%)	N (%)	(l+p):N
<i>Senna siamea</i>	24.8±0.5	2.7±0.5	2.01±0.02	13.7±0.3
<i>E. camaldulensis</i>	24.9±1.5	10.1±1.2	2.17±0.54	18.2±4.5
<i>E. tereticornis</i>	31.7±3.0	10.4±1.1	1.48±0.07	28.6±2.9
<i>L. leucocephala</i>	29.3±1.3	5.4±0.7	2.97±0.19	11.8±0.7
<i>Prosopis chilensis</i>	14.9±1.0	1.5±0.3	4.18±0.20	3.9±0.3

Data are means ± SEM, n=4 except for the two *Eucalyptus* spp., where n=3.

(l+p)=lignin+polyphenol, the ratio (l+p):N was calculated from individual values not means.

L=*Leucaena*, E=*Eucalyptus*.

Nitrogen fixation by *Sesbania sesban* fallows in the highlands of eastern Kenya. Paper (II)

The early growth patterns differed considerably among species. *Grevillea* exhibited the lowest early growth rate, while *Sesbania* grew fast throughout the study (Figure 2). The other tree species never exceeded the rate of biomass production of *Sesbania*, which, however, showed a substantial variation. Eighteen months after planting, *Grevillea* and *Eucalyptus* were similar in size, but their periods of rapid growth did not coincide (Figure 2). Leaves constituted a higher fraction of total biomass in *Eucalyptus* and *Grevillea* than in *Sesbania* and *Senna*. *Eucalyptus* and *Grevillea* maintained leaf cover all through the year, while *Sesbania* and *Senna* dropped a large portion of their leaves in the dry seasons. *Eucalyptus* and *Sesbania* were the species with the highest total fine root biomass and more than half of that was located in the top 15 cm of the soil at 12 to 18 months after planting (Figure 3). The fine root biomass of *Senna* and *Grevillea* were more homogeneously distributed with depth all through the experimental period.

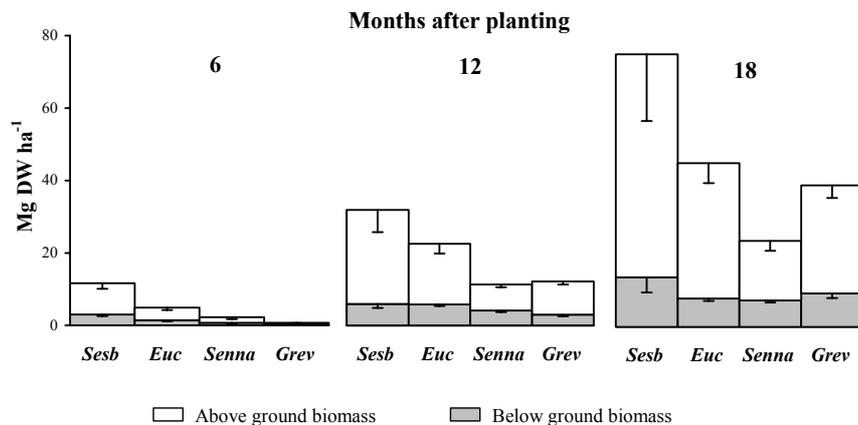


Figure 2. Allocation of the biomass in four tree species after 6, 12 and 18 months. DW=dry weight. Error bars represent 1 SE.

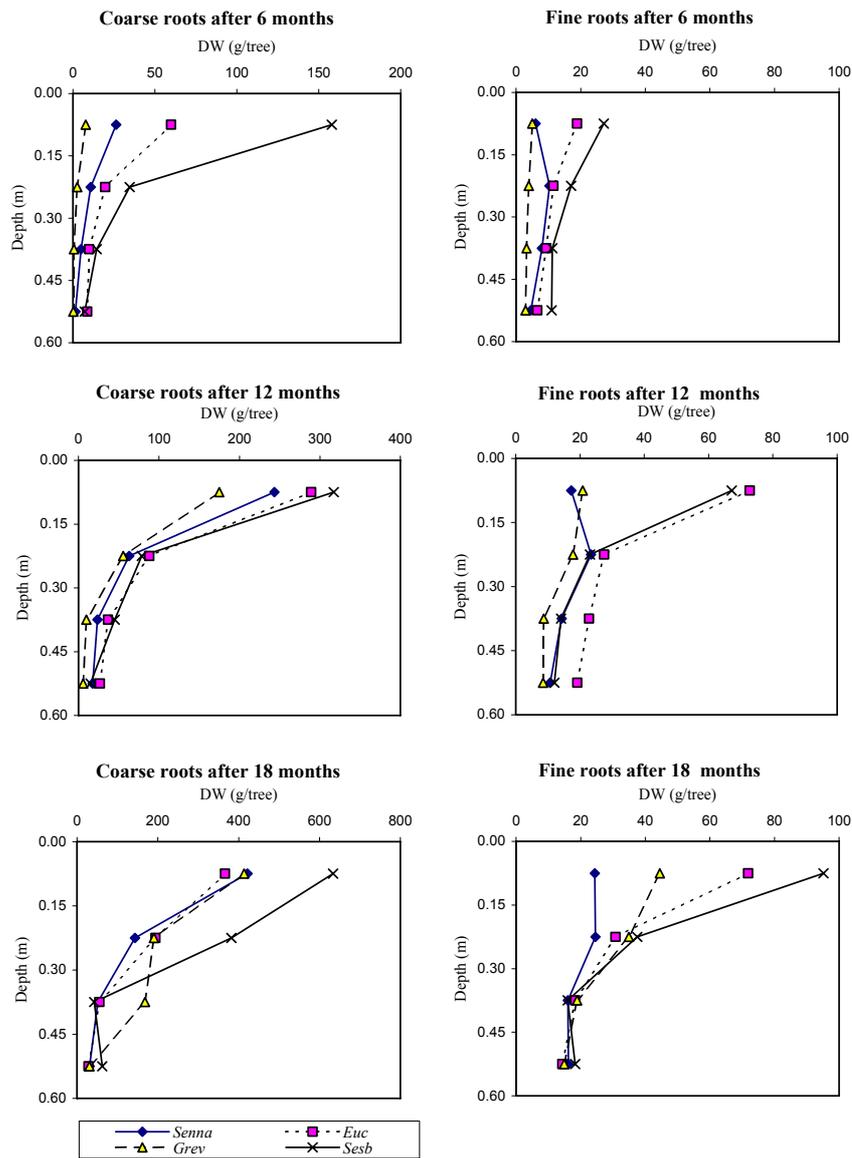


Figure 3. Depth distribution of the coarse and fine root biomass of four tree species after 6, 12 and 18 months at Muange Farm, eastern Kenya. Error bars represent \pm SE.

Sesbania and *Senna* had higher N concentrations in the different plant parts than *Eucalyptus* and *Grevillea*, and more than 20% of their total N was found in roots throughout the study. After 18 months, none of the reference species accumulated even 40% of the total N within above- plus below-ground biomass of *Sesbania*. In *Sesbania*, the N concentration in the different plant parts was fairly constant throughout the study, while it decreased over time in the non-N₂-fixing species.

After ¹⁵N labelling, ¹⁵N enrichment of the soil declined for a period of 12 months. During the remaining time of the experiment, there were only minor changes in soil atom % ¹⁵N excess. In accordance with soil data, ¹⁵N enrichment in all plant parts decreased over time in all species. The correlation between atom% ¹⁵N excess in total biomass and in leaves was significant for all species and at all times. *Grevillea* was the reference species with the lowest atom % ¹⁵N excess at both 6 and 12 months. Atom % ¹⁵N excess in *Sesbania* biomass was significantly lower than in all the reference species. In contrast to atom% ¹⁵N excess in the soil, fine root ¹⁵N increased with depth.

After 6 months, %Ndfa calculated on the basis of FAE, AAE, and WAE were similar for a given reference species. After 12 and 18 months, higher fixation estimates were obtained using FAE as compared to AAE or WAE. Calculations based on the different reference species, however, resulted in distinct differences in estimates of %Ndfa in *Sesbania* at 6 months, when fixation was still low. After 12 and 18 months the influence of choice of reference tree on %Ndfa was substantially reduced and calculations based on the various reference species resulted in similar N₂ fixation estimates.

In this study, *Senna* was the most suitable of the three reference species because its N uptake pattern and phenology were very similar to those of *Sesbania*. When well established, the amount of N fixed by *Sesbania* accounted for more than 80% of its total N content, according to FAE-based estimates. We estimated the quantity of N fixed from the atmosphere by *Sesbania* to range from roughly 200 (WAE) to 250 (FAE) kg N ha⁻¹ after 12 months and from 500 (WAE) to 600 (FAE) kg N ha⁻¹ after 18 months (Table 3).

Table 3. Estimates of total N fixed and %Ndfa in *Sesbania sesban* using different reference species 6, 12 and 18 months after planting.

Age (months)	Reference species	Plant parts used for calculations					
		Leaves		Above-ground biomass		Whole tree	
		% Ndfa	N fixed (kg ha ⁻¹)	% Ndfa	N fixed (kg ha ⁻¹)	% Ndfa	N fixed (kg ha ⁻¹)
6	<i>Eucalyptus</i>	32	60	32	61	34	63
	<i>Grevillea</i>	16	30	17	33	16	31
	<i>Senna</i>	41	77	43	80	43	80
	<i>Euc+Senna</i>	37	69	38	71	39	72
12	<i>Eucalyptus</i>	76	264	64	223	60	210
	<i>Grevillea</i>	70	245	55	194	50	174
	<i>Senna</i>	73	255	67	236	66	229
	<i>Euc+Senna</i>	74	260	66	231	63	221
18	<i>Eucalyptus</i>	82	622	63	476	61	465
	<i>Grevillea</i>	85	639	66	497	62	472
	<i>Senna</i>	82	622	70	529	71	534
	<i>Euc+Senna</i>	82	622	67	505	67	506

Effects of tree fallows on biomass production, N₂ fixation, nitrogen dynamics and subsequent maize productivity. Paper (III)

The allocation of biomass and N in *Sesbania*, *Calliandra*, *Grevillea* and *Eucalyptus* after 12, 18 and 22 months is shown in Figure 4. Noteworthy, twelve months after planting, the total biomass of *Grevillea* was only 60% of that for *Sesbania* or *Eucalyptus* while after 22 months, total biomass was highest for *Eucalyptus* followed by *Grevillea*, *Sesbania* and *Calliandra* (Figure 4a). Below-ground biomass consisted of 70-90% coarse roots (>2 mm). Fine root biomass was fairly constant throughout the period investigated. Approximately 90% of the total root dry matter in the soil profiles sampled was found in the top 60 cm for all species.

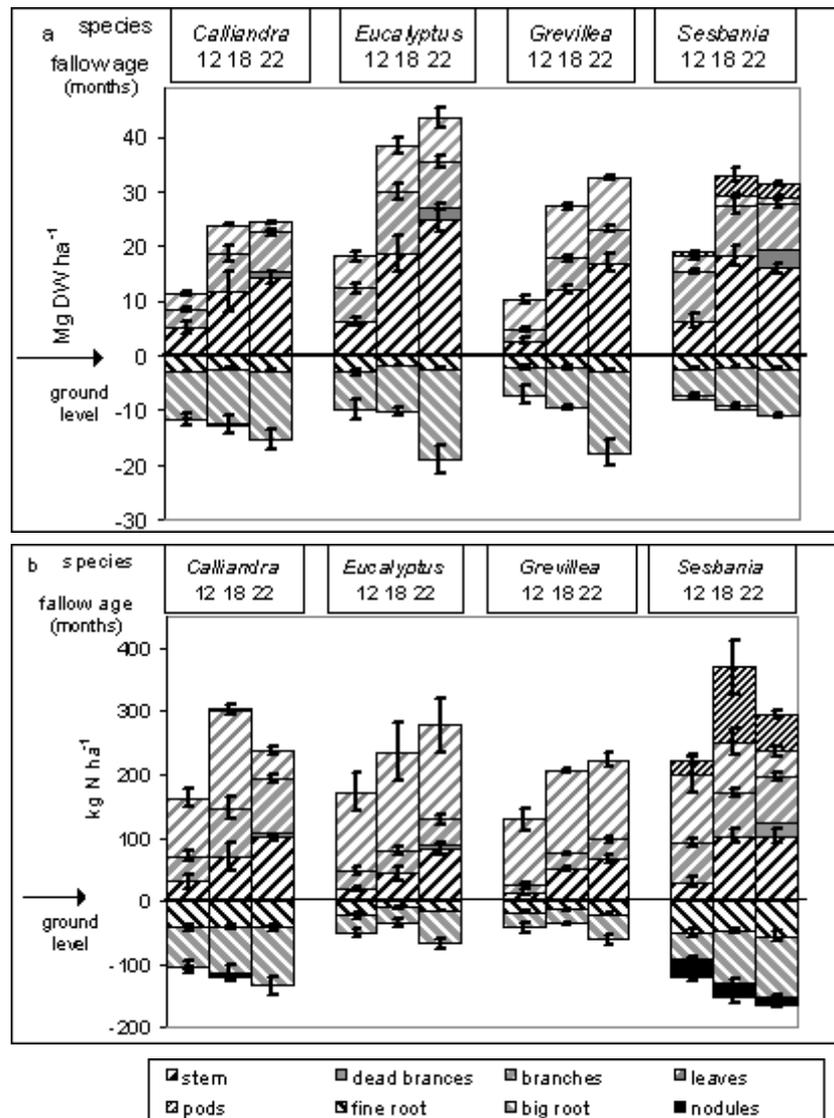


Figure 4. Total biomass (a) and nitrogen (b) in different plant parts at different tree ages. Data are means \pm SE.

Sesbania had the highest total N content all through the study. The tree species examined differed greatly in N concentration in their plant parts. The two leguminous tree species, *Calliandra* and *Sesbania*, had higher N percentage levels in their plant parts than the non-leguminous species, *Eucalyptus* and *Grevillea*. For example, the N concentration in leaves was significantly higher in N₂-fixing than in non-fixing species. Because of the high N concentration in the roots of the N₂-fixing species, the total N contents of their roots were double those of *Eucalyptus* and *Grevillea* even though the root biomass in the non-fixing species was greater (Figure 4).

Dinitrogen fixation in *Calliandra* was weak or absent during the first growing season and did not attain substantial levels until the third season, while *Sesbania* was fixing at a high rate from the second season onwards. One and a half years after planting, the proportion of plant N derived from N₂ fixation was 70-90% in *Sesbania* and 50-70% in *Calliandra*, and these levels persisted until the final harvest. These intervals were based on whether FAE or WAE based estimates were used. Dinitrogen fixation calculated from whole plants and leaves correlated well ($r = 0.95-0.99$ for the different tree species), with whole plant values being slightly lower. In the control treatment maize-bean rotation only dead or inactive nodules were found on the beans and no N₂ fixation could be verified from atom% ¹⁵N excess data.

The N added by N₂ fixation amounted to 280-360 kg N ha⁻¹ for *Sesbania* and 120-170 kg N ha⁻¹ for *Calliandra* (Table 4). This resulted in a positive N balance after two maize cropping seasons of 170-250 kg N ha⁻¹ for the *Sesbania* fallow and 90-140 kg N ha⁻¹ for the *Calliandra* fallow. All the other treatments gave rise to negative N balances after two cropping seasons (Table 4). The differences in N concentrations in the maize grown after the different types of previous land use had major consequences for the amount of N exported with the maize at harvest. For example, maize grown following *Sesbania* fallow had significantly higher N concentrations in its total biomass (1.0% N) compared to other treatments (e.g., 0.5% N in maize following unfertilised maize).

We found a strong correlation ($r = 0.78$) between pre-season topsoil total inorganic N and maize grain yield. The content of inorganic N in the topsoil as well as the quantity of N mineralised during rainy seasons were higher after the *Sesbania* fallows than after the other treatments. Erratic rainfall distribution restricted the growth of the first residual maize crop. In the second growing season the grain yields were significantly higher following the *Sesbania* and fertilised maize treatments than following unfertilised maize (Table 4).

Table 4. Effects of trees and previous cropping history on yield and N accumulation in two successive maize crops

Treatment	First residual crop			Second residual crop			N balance for two crops	
	Grain (Mg ha ⁻¹)	Total biomass (Mg ha ⁻¹)	Total plant N (kg ha ⁻¹)	Grain (Mg ha ⁻¹)	Total biomass (Mg ha ⁻¹)	Total plant N (kg ha ⁻¹)	N added by N ₂ - fixation or as fertiliser (kg ha ⁻¹)	N removed with two crops (kg ha ⁻¹)
<i>Sesbania</i>	1.0	5.0*	43.5**	2.0**	6.8*	68.9***	282-363	112
<i>Calliandra</i>	0.3	2.0	10.3	1.0	4.8	24.7	122-171	35
Continuous maize + N	1.4**	5.1*	28.6	2.0**	7.2*	55.2**	60	84
Maize-bean rotation	1.1	4.3	25.6	1.3	4.8	26.5	0	52
Continuous maize	0.4	2.5	12.4	0.8	3.6	20.0	0	32
Weed fallow	0.7	3.0	18.6	1.3	4.3	22.3	n.d.	41

Net N additions are calculated assuming that N₂-fixation accounted for 70-90% of the N supplied in the *Sesbania* treatment, and 50-70% in the *Calliandra* treatment. Significantly different from continuous maize, * = p<0.05, ** = p<0.01, *** = p<0.001; Tukey's post hoc test. n.d. = not determined.

In these experiments, there were no visible pest problems as reported from other *Sesbania* fallow field trials (Desaeger & Rao 1999; Sileshi et al. 2000). Neither root-knot nematods (*Meloidogyne javanica*), nor defoliating beetles (*Mesoplatys ochroptera*), seems to have reduced growth of *Sesbania*. Neither was the parasitic weed *Striga* found on the maize.

Discussion

Paper (I)

The study site was deficient in N. The positive effect of N₂-fixing trees on maize growth, which was found in this study and also reported by others (e.g., Kwesiga & Coe 1994; Mafongoya & Dzowela 1999), was not associated with a major increase in %N of soil, nor was there any changes in %C and C/N ratio in this direction. One explanation to this is that a measure of total N in soil does not reflect the very small fraction of N available to plants (e.g., Binkley & Hart 1989). Attempts to estimate N₂ fixation based on ¹⁵N natural abundance technique were not very successful. The use of the technique in woody perennials is thoroughly reviewed by Boddey et al. (2000). The complexity of soil N dynamics makes the

use of ^{15}N natural abundance method for evaluating N dynamics in soils difficult, and it should be used with caution unless differences in $\delta^{15}\text{N}$ between the N_2 -fixer and reference species are substantial (Högberg 1997).

The ratio (lignin+polyphenol):N in plant material has been shown to be strongly negatively correlated with N mineralisation (Fox et al 1990; Constantinides & Fownes 1994, Handayanto et al 1994; Mafongoya et al 1998a,1998b). Our leaf data supported the contention that this ratio is a good predictor of N availability from plant residues. In this paper, chemical analyses were made on fresh but dried leaves. As the main input of organic matter to the soil was leaf litter (material in which senescence and retranslocation of nutrients had occurred) from the growing trees, the relation between the different tree species in (lignin+polyphenol):N ratio, not the absolute figures, was the main interest.

In conclusion, the two N_2 -fixing species *Prosopis* and *Leucaena* turned out to be more appropriate for soil improvement by tree fallows than the two *Eucalyptus* spp. The positive impact on soils by trees as reported above could be expected in a tree fallow system where there is no tree-crop competition.

Paper (II)

The early growth of *Sesbania* was outstanding and supports earlier findings (Kamara & Maghembe 1994, Karachi et al. 1994, Mafongoya & Dzowela 1999, Gathumbi et al. 2002). Its high production in the highlands of Kenya is also confirmed by earlier authors (Mekonnen et al. 1997, Hartemink et al. 2000). *Eucalyptus* is well known for its high productivity, a quality appreciated and exploited in many parts of the world. The initially slow, but accelerating growth of *Grevillea* was well in line with data presented by Lott et al. (2000). The main trends for all species were for the stem fraction to increase and the leaf fraction to decrease with time. The seasonal litterfall from *Sesbania* and *Senna* was of the same magnitude as the leaf fraction 12 months after planting (L. Ståhl unpubl.). Fine root distribution with depth differed between species (Figure 3). Both *Sesbania* and *Eucalyptus* could be characterised as shallow-rooted during their early growth stage, but they formed deeper roots at approximately the same time. The shape and functionality of root systems are determined by environmental factors, such as competition and availability of water and nutrients, management regime, for example pruning frequency (Schroth 1999, Livesley et al. 2000) and genetic factors. An underestimation of root biomass was made due to the omission of roots deeper than 0.60 m, but I think it is of low significance.

The differences in N content between species are striking. If harvested after 18 months, the *Sesbania* biomass left behind (below ground biomass, leaves and pods) to be incorporated into the system would contribute more than 500 kg N ha^{-1} , while the corresponding figures for *Eucalyptus* or *Grevillea* would be about 200 kg N ha^{-1} .

Temporal and spatial variations in isotope distribution in the soil due to isotopic labelling are major complicating factors when using the ^{15}N dilution technique. The decline in soil atom% ^{15}N tends to be rapid directly after labelling, which is reflected in differences in ^{15}N enrichment between tree species due to differences

in N uptake pattern. In our experiment this was exemplified by the 6-month old *Grevillea*, having lower atom% ^{15}N excess values than the other reference species due to its initially low growth rate (low N uptake). Thus, differences in N uptake patterns during early growth introduce greater errors in N_2 fixation estimates than at later growth stages (Witty 1983; Danso et al. 1993, Table 3).

Estimated N_2 fixation in *Sesbania* was very high even with low P content in the soil and moisture stress during the dry seasons. At 12 and 18 months, %Ndfa estimates based on FAE were higher than corresponding values based on WAE (Table 3), agreeing with the results Danso et al. (1995) obtained in *Robinia pseudoacacia*. Using FAE for estimating N_2 fixation in deciduous perennials will not produce fully time-integrated figures, but will reflect uptake and translocation during the lifetime of the leaves. This is clearly illustrated in our experiment in the comparisons of atom% ^{15}N excess values after 18 months between leaves and stem or below-ground plant parts (Table 3).

To identify a non- N_2 -fixing reference species, which will have access to N from the same N sources, in the same proportions, and with the same temporal and spatial patterns as any given N_2 -fixing perennial, is very difficult (Boddey et al. 2000). As there are time-related changes in soil ^{15}N levels, an appropriate reference species should start to accumulate N and reach its maximum N concentration at the same time as the related N_2 -fixing species (Peoples et al. 1989). Well-matched reference crops are crucial when rates of N_2 fixation are low and/or the $^{15}\text{N}/^{14}\text{N}$ ratio in the soil declines rapidly (e.g., Peoples et al. 1989; Sanginga et al. 1996). For highly effective symbioses a well-matched reference plant is of minor importance. We consider *Grevillea* unsuitable as a reference tree in this experiment mainly because of its very slow initial growth. Both *Senna* and *Sesbania* are known to be very effective in taking up soil N (MacLean et al., 1992; Livesley et al. 2002; Gathumbi et al. 2003). *Senna* was the most suitable of our reference species because its N uptake pattern and phenology matches that of *Sesbania*. Also in paper (I), when discussing N_2 fixation in the two leguminous tree species *Prosopis* and *Leucaena*, *Senna* was suggested to be a more appropriate reference species than *Eucalyptus*. It is important to examine the rooting patterns and the biomass and N contents in order to explain the differences in estimates of fixed N_2 associated with different reference crops. I recommend the use of several reference species since any one of them may help to elucidate and validate the results obtained.

Sesbania sesban has a very high N_2 -fixing ability. When well established, more than 80% of its N was found to originate from N_2 fixation. We estimate that over 18 months *Sesbania* fixed 500 to 600 kg N ha $^{-1}$ from the atmosphere. Furthermore, our figures should be considered underestimates, since root mortality, exudation and litter fall were not taken into account. The total N accumulation in the biomass of planted *Sesbania* after 18 months was impressive and a strong indicator of its potential as a short-term fallow species, which could contribute substantially to compensating N removed by cropping and thus to maintaining long-term productivity of the soils.

Paper (III)

The differences between species in early growth patterns agreed well with the results obtained in paper (II). *Grevillea* diverged from the other species tested in needing a longer establishment period after planting before entering a period of rapid growth. The high biomass production of the species included in the study was expected and well in line with other reports, e.g., Jama et al. (1998), NAS (1980), Duguma & Mollet (1997). Quantification of root biomass differs substantially depending on sampling techniques used. Root sampling by coring easily underestimates coarse root biomass, as taproots, located directly below the stem, are not included (e.g., Jonsson et al., 1988; Schroth et al., 1996; Torquebiau & Kwesiga, 1996; Livesley et al., 2000). The organic input through roots left in the soil at fallow harvest contributes to improve both soil physical properties and nutrient availability, which is clearly beneficial for soil fertility and plant production in the future. Accurate estimations of total biomass production are important in the discussions of long-term SOM dynamics and nutrient budgets. Also N concentrations in different tree species are characteristics to consider when selecting trees for agroforestry with the aim of improving soil fertility. We found no detectable N₂ fixation in *Calliandra* during the first growing season, and only low levels in the second season. Weak N₂ fixation in *Calliandra* during early growth was confirmed by Peoples et al. (1996). This was explained by *Calliandra* having prolific root growth and consequently an efficient capacity to scavenge soil mineral N. Failure to fix N₂ by beans under unfavourable conditions has been observed in various locations, including semi-arid areas of Kenya (Pilbeam et al. 1995). Possible reasons for this might be high soil temperatures and drought (Sangakkara et al. 1995) and/or phosphorous deficiency (e.g. Högberg 1986, 1989).

The contribution of fixed N₂ to the cropping system by *Sesbania* fallow was substantial. The effect on maize yield after the second cropping season was significant. Residual benefits of *Sesbania* fallows lasting for one to four cropping seasons have been reported (Kwesiga et al., 1999; Mafongoya & Dzowela, 1999). Nitrogen content in maize varies and is mainly dependent on environmental conditions like available soil N, soil moisture and stage of maturity. Although more N was exported with maize from the *Sesbania* treatment than from any other treatment, *Sesbania* had the highest positive net N balance after two cropping seasons. Also the *Calliandra* treatment had a positive net N balance (although much lower than *Sesbania*), while all the others had negative N balances (Table 4). Extractable inorganic N in the topsoil was high after *Sesbania*, possibly due to easily mineralised N from the high quality litter. Maroko et al. (1998) also showed that N mineralisation was higher after *Sesbania* fallow than in other land-use systems. To date, the (lignin + polyphenol):N ratio seems to be the most robust index to predict litter mass loss and N release in agroforestry systems (Mafongoya et al., 1998a). Examples of ratios reported for fresh leaves are for *Sesbania* 2.4 to 3.3 and for *Calliandra* 5.1 to 6.3 (Kwabiah et al. 2003; Mugendi et al. 1999). The initially low topsoil inorganic N after *Calliandra* might originate in high polyphenol concentration in all plant parts including roots as reported by Lehman et al. (1995) and Mugendi et al. (1999). When applying tree prunings to improve

maize yield Mafongoya et al. (1997) showed that *Calliandra* prunings released N slowly due to high protein-binding capacity. The strong correlation between maize grain yield and pre-season topsoil total inorganic N was confirmed by Maroko et al. (1998). Barrios et al. (1998) reported similar results from Zambia.

Our study showed that *Sesbania sesban* is a tree species well suited for short-duration fallows in the eastern highlands of Kenya because of its fast growth, high nutrient content in all plant parts, high litter quality and effective N₂ fixation.

Concluding remarks

- The ¹⁵N dilution method is adequate for quantifying N₂ fixation in young trees. The differences in estimates related to choice of reference species could be explained by differences in phenology and were important at an early stage – in the long run, the estimates converged. At high fixation rates, the choice of reference species is of little importance (Boddey et al 1990; Unkovich & Pate 2000).
- *Sesbania* has a very high N₂-fixing ability and can be recommended for agroforestry in east Africa. The substantial accumulation of N in *Sesbania* highlighted its potential as a species for soil fertility improvement on N limited soils in the tropics. Impressive biomass production of *Sesbania* in Kenya is confirmed by, for example, Hartemink et al. 2000, Mekonnen et al. 1997 and Niang et al. 2002. Lower, but still high, production is reported from unimodal rainfall areas in sub-Saharan Africa (e.g., Mafongoya & Dzwela 1999, Torquebiau & Kwesiga 1996). Table 5 gives an indication of quantities of nitrogen fixed by some tree species grown in the tropics. It can be concluded that *Sesbania sesban* is a tree species well suited for short duration fallows due to its fast growth, high nutrient content, high litter quality and its ability to fix large amounts of N₂ from the atmosphere.

Table 5. Examples of nitrogen fixation estimates (isotope dilution method, whole-tree ^{15}N atom excess values used) by tropical tree species in the field

Species, location	Plants ha ⁻¹	Time period	Ndfa		Ref.
			kg N ha ⁻¹ yr ⁻¹	%	
<i>Casuarina equisetifolia</i> Puerto Rico	10000	12 months	74	43	Parrotta et al. 1994
<i>Gliricidia sepium</i> Sri Lanka	5000	9 months	166/9 months	55	Liyanage et al. 1994
<i>Faidherbia albida</i> Senegal	1600	12 months	65	20.3	Gueye & Ndoyle 2000
<i>Leucaena leucocephala</i> Nigeria	10000	4 years	208-238	64-73	Sanginga et al. 1996
<i>Sesbania sesban</i> Kenya	10000	18 months	337-356	67-71	Ståhl et al. 2005

N.B. Kg ha⁻¹ is influenced by quantity and distribution of rainfall.

- There was a substantial impact of BNF on subsequent maize production as available N was limited at the study sites. The use of N₂ fixing trees resulted in improved maize production in both studies. In the Kenyan studies considerable quantities of N were fixed by leguminous trees.

When crop yields are increased through input of N from N₂ fixing trees, export of other nutrients in harvestable crops is also increased (van Noordwijk et al 1998, Giller 2001). Planted tree fallows will not eliminate the need for P inputs on P-deficient soils (Sanchez & Palm 1996; Buresh et al. 1997). When N and P are sufficient, attention must be paid to other nutrient limitations. Sustainable outputs from a land-use system will require external inputs of nutrients. Results from an on-farm trial in Zambia, reported by Kwesiga et al. (2003), indicate that application of ¼ dose of the recommended fertiliser (i.e., 112 kg N, 20 kg P and 16 kg K ha⁻¹) to maize after planted tree fallows to enhance yields and sustain the increase beyond two years of cropping, provide farmers with better returns.

There is a need of more investigation of the impact of tree fallows on long-term nutrient budgets (Kwesiga et al. 2003). Also, there is a need to adapt the production to farming systems, with due attention to farmers needs, where for instance bi-products like stakes, firewood and fodder may be vital (Giller & Cadisch 1995). The African small-scale farming systems are diverse and a “basket of choice” is required to meet the heterogeneous farm situations (Raussen 1998). Based on this research, the position of *Sesbania sesban* as an appropriate species to make part of the content of the basket has been further improved.

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