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Carbon and Nitrogen Dynamics in Agroforestry Systems

Temporal patterns of some important soil processes

Gert Nyberg

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Abstract

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The ameliorative effects of different tree species on soils in some agroforestry systems were studied. The temporal pattern of nutrient release from tree organic material is important to achieve synchrony with crop uptake. When, as in many tropical agroforestry systems, trees (C_3-plants) are planted on C_4-carbon dominated soils, the difference of around 12-16‰ in natural abundance of ^{13}C between C_3 and C_4 plants makes the natural abundance of ^{13}C a particularly sensitive indicator of the influence of trees on the soil. An increase of 3-5% of the percentage C was proven to derive from trees by this method, only five years after planting.

By using the difference of around 10‰ in natural abundance of ^{13}C between the endogenous soil C (mainly C_4) and the applied C (C_3) in green manure experiments, the contributions of the two C sources to soil respiration can be calculated. The microbial response to the additions of leaves was an immediate increase in respiration. This non-destructive method allows repeated measurements of the actual rate of C mineralisation and facilitates decomposition studies with high temporal resolution in the field. The mineralisation of N was also very rapid and the concentration of NH_4^+ in the soil correlated well with respiration of added C. In our studies, 3-4% of the added C was respired daily, for the first 10 days after addition of *Sesbania sesban* leaves. Although respiration rates decline with time, we estimated 70-90% to be respired in as short time as 40 days. Weight losses of around 80% after 52 days, from high quality residues in litterbags, also indicate substantial C losses. Measurable build-up of soil organic matter is, hence, unlikely. For immediate soil fertility, addition of high quality green manure may, however, be a viable management option. To achieve synchrony with crop demand, caution is needed in management as large amounts of N are mineralised within a few days after application, inducing the risk of nutrient losses before the nutrient demand of crops is high. Green manure of poorer quality mineralised slower and may have the potential to build up SOM, but not to meet the short-term nutrient requirements of crops.

In improved fallow systems there is a mixture of qualities of organic material added to the soil, as there are differences in quality between, e.g., leaves and roots, thereby reducing the risk of nutrient losses. Sesbania fallows added 280-360 kg N ha^{-1} by N_2-fixation, resulting in a positive N-balance, after wood export and two residual maize crops, of 170-250 kg N ha^{-1}. The *Sesbania* fallows also produce considerable amounts of firewood and, most importantly, increase the residual maize yields.

Key words: agroforestry, ^{13}C, green manure, improved fallow, mineralisation, soil respiration, stable isotopes

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Preface

Once upon a time – decades, centuries, a thousand years ago – I left Kenya for studies in Sweden with the intention to get the best education in tropical agroforestry possible in Sweden. Well, I've done that, been there, got that; shortcomings are not due to the education but to latitude and myself.

In one of the first courses I took in biology, we should write a report on a chosen subject. In the instructions for the work the teacher informed us on how this report should be written. It should start with an abstract in English (the rest we could write in Swedish) and this abstract should very shortly describe what we did, how we did it, what we observed and the conclusions we draw from our work. As the subject of my group was to be forest soils, I jokingly wrote:

WE WENT TO THE FOREST
WE DUG INTO THE SOIL
WE SAW WHAT GREW ON IT
WE SAW WHAT WAS IN IT
AND DRAW THE CONCLUSION:
SOIL IS GOOD FOR LIVING THINGS

With that knowledge I entered the university. Many, many years later I could sum up the knowledge gained in university by adding three words to the verse:

AND VICE VERSA

Similarly, I can now sum up my long time as a PhD-student by adding another line.

WE WENT TO THE FOREST
WE DUG INTO THE SOIL
WE SAW WHAT GREW ON IT
WE SAW WHAT WAS IN IT
AND DRAW THE CONCLUSION:
SOIL IS GOOD FOR LIVING THINGS
AND VICE VERSA,
NOW I START TO KNOW WHY

Contents

Appendix

Papers I-IV

This doctoral thesis is based on studies reported in the following papers, which will be referred to in the text by the corresponding Roman numerals.

I. Nyberg, G. and P. Högberg. 1995. Effects of young agroforestry trees on soils in on-farm situations in Western Kenya. *Agroforestry Systems 32*, 45-52.

II. Nyberg, G., A. Ekblad, R. J. Buresh and P. Högberg. 2000. Respiration from C3-plant green manure added to a C4-plant carbon dominated soil. *Plant and Soil 218*, 83-89.

III. Nyberg, G., A. Ekblad, R. Buresh and P. Högberg. Temporal patterns of C and N mineralisation of green manure. (Manuscript.)

IV. Ståhl, L., G. Nyberg, P. Högberg and R. Buresh. Soil nitrogen dynamics and biomass production in short-duration planted tree fallows and subsequent maize crops. (Manuscript.)

Papers **I** and **II** are reprinted with kind permissions from the publishers.

Introduction

Soil fertility depletion on small farms is the fundamental biophysical root cause of declining per capita food production in sub-Saharan Africa, for which rapid population growth and the breakdown of traditional agricultural practises (e.g., long-term fallowing) are some of the main reasons (Sanchez et al., 1997). Soil fertility may be improved by short-term fallows planted with selected tree species (Kwesiga and Coe, 1994; Kwesiga et al., 1999; Szott et al., 1999) or by the use of green manure in biomass transfer systems (Mwiinga et al., 1994), which are realistic alternatives for small-scale farmers, who can not afford to buy inorganic fertilisers.

Agroforestry is the use of trees/shrubs in an agricultural setting; this may be crop cultivation or animal husbandry. The aspect of agroforestry dealt with in this thesis is soil fertility, which may be improved by some agroforestry methods, provided that management and species selection is appropriate. It should be kept in mind though, that even when soil fertility is the prime object of the agroforestry management, agroforestry simultaneously provides additional advantages for the farmer, e.g., the production of firewood, fodder, food, timber, shelter etc., which may be the short-term priority of the farmer.

Soil organic matter (SOM) plays a pivotal role in crop production systems. Mineralisation of decomposing residues is the major source of plant nutrients in highly weathered soils with little inherent fertility (Sanchez et al., 1989; Woomer et al., 1994). The importance of SOM is, almost poetically, described by Allison (1973): "Soil organic matter has over the centuries been considered by many as an elixir of life - in this case plant life. Ever since the dawn of history, some eight thousand or more years ago, man has appreciated the fact that dark soils, commonly found chiefly in the river valleys and broad level plains, are usually (but not always) productive soils. He also realised at a very early date that colour and productivity are commonly associated with organic matter derived chiefly from decaying plant materials."

Maintaining or improving the quantity and quality of SOM should be a guiding principle when management practices are developed (e.g., Syers, 1997). Amounts and qualities of SOM can be manipulated by various management practices, e.g., in agroforestry, in order to increase soil fertility. On management Allison (1973) states "Ever since man first experienced decreases in soil productivity he has waged a constant warfare against the degrading agents in his attempts to maintain or increase the productivity of his soils." In this battle agroforestry methods are formidable and widely applicable arms, not only available to the rich of the world, but also to small-scale farmers throughout the third world. Increased SOM content results in increased water holding capacity, increased erosion resistance, increased N and P availability to crops, increased cation exchange capacity of soils and reduced leaching of nutrients (Young, 1997).

The quality of SOM can be manipulated by choosing different sources of organic material inputs (e.g., Palm et al., 1997). Organic inputs can influence nutrient availability (i) by the total amounts of nutrients added, (ii) by controlling the mineralisation-immobilisation patterns, (iii) as a source of C and energy to drive microbial activities, (iv) as a precursor of stable SOM fractions and (v) through interactions with the mineral soil in complexing toxic cations and reducing the P sorption capacity of the soil. In addition to these direct effects on nutrient availability, organic materials can affect root growth, pests, and soil physical properties that in turn influence nutrient acquisition and plant growth. The net effect of these different mechanisms on nutrient availability and plant growth differ with climatic regime, soil type, and the quality of organic inputs (Palm et al., 1997)

Nutrients are released to the soil matrix as micro-organisms use organic material (OM) primarily as a carbon source. The higher the availability of energy rich C-bonds in OM to micro-organisms – the faster the decomposition. Should nutrient supply be a larger constraint than energy, micro-organisms utilise nutrients from the soil matrix to decompose the OM, i.e., immobilisation occurs. Hence, the quality of OM depends not only on its availability as energy supply for micro-organisms, but also on its nutrient content. Several indices are used to describe the quality of OM and relate it to the net nutrient mineralisation, typically the net N mineralisation (i.e., a plant nutritional perspective on quality). The higher the polyphenol and lignin content of the mulch, the slower the decomposition. The ratios of lignin:N (Mugendi and Nair, 1997; Ibewero et al., 2000; paper **III**), polyphenols:N (Palm and Sanchez, 1991; Oglesby and Fownes, 1992) or (polyphenols+lignin):N (Fox et al., 1990; Handayanto et al., 1995; Jonsson et al., 1996; Mafongoya et al., 1998a; 1998b; Ibewero et al., 2000; paper **III**) are negatively correlated with nutrient (e.g., N) release in mulches from trees. In different words, the higher the quality of the OM (i.e., the lower these ratios), the faster the nutrient release. If nutrients are released too rapidly during the cropping season, they might become plant available before the crop demand for nutrients is high. Too low quality, on the other hand, might not supply enough (or even immobilise) nutrients when crop demand is high. Timing of nutrient release from OM, to be in synchrony with nutrient demands by the crop (Myers et al., 1994), is an intricate and crucial management task, which demands good understanding of the regulating factors and temporal patterns of the processes involved (Fig. 1).

The studies in this thesis were conducted in Kenya with the objective to compare the ameliorative effects of some different agroforestry systems and tree species on soils, and especially to attend to the temporal aspects of C and N dynamics in this context.

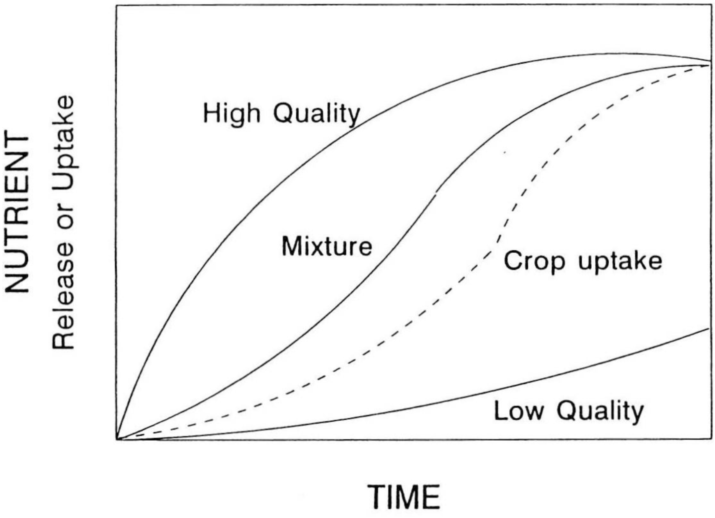

Fig. 1. *Hypothetical nutrient release patterns of different quality plant materials compared with nutrient uptake patterns (adapted from Swift [1987]; from Palm et al., 1995).*

Systems studied

Solitary trees

Solitary trees are often left in the field to improve soil fertility and/or for other benefits. Solitary trees are also commonly grown on compounds or pastures for shade or other protection and as a valuable source for firewood, fodder, fruit, medicine etc.

It has frequently been shown that soil under solitary trees left in agricultural fields (e.g., Kater et al., 1992; Tomlinson et al., 1995; 1998; Jonsson et al., 1999) or present in open savanna ecosystems (Belsky et al., 1989; 1993) is more fertile than the soil in the surroundings. There may be many reasons for this – more efficient nutrient re-cycling and nutrient enrichment through import of nutrients through animals (e.g., Vetaas, 1992), changes in micro-climate (e.g., Jonsson et al., 1999), root exploitation of surrounding soils (Tomlinson et al., 1995; 1998) and nutrient uptake from deeper soil layers and redistribution of these nutrients to the surface soil under the tree (Rhoades, 1997). Hence, changes in the soil under solitary trees may reflect changes in *in situ* biogeochemistry as well as changes in the inflow-outflow budget of the tree micro-site.

Biomass transfer

Plant biomass from outside the crop field may be transferred into the field to improve the soil fertility and/or the SOM status of the soil (e.g., Mwiinga et al., 1994; Palm et al., 1997; Nziguheba et al., 2000). The transferred biomass is typically leaves and twigs from trees in the surroundings. The term green manure is here used for such biomass incorporated into the soil (by hoeing or ploughing). Advantages with using leaves of trees/shrubs from outside the field as green manure are that these resources may be easily available, they represent a true addition of nutrients to the field (although at the expense of some other part of the farm), and the possible positive effects on SOM build-up (especially with low quality green manure). Appropriate mulching with high quality leaves may provide means to synchronise the timing of nutrient mineralisation with that of crop demand (Myers et al., 1994), a critically important issue in agriculture (Fig. 1). This may be achieved by mixing organic material of different qualities (Handayanto et al., 1997a; 1997b) or by manipulating the timing of application of high quality green manure. Biomass transfer also reflects specifically the above ground contribution in improved fallow systems, and could, by comparison, help to improve our understanding of below ground processes in improved fallow systems, where there is also a contribution of roots. A major disadvantage is that biomass transfer systems may be very labour-intensive and thus not always economically feasible.

Improved fallows

Shifting cultivation with extended periods of naturally re-growing fallows and shorter cropping periods has been a major traditional agricultural practice in the tropics to maintain soil fertility (Nye and Greenland, 1960). As a result of increasing human population and thereby increased demands for land, fallow periods have been shortened or the system completely abandoned. Improved fallows are the deliberate planting of fast-growing species – usually legumes – for rapid replenishment of soil fertility. Improved fallows are rapidly spreading in several regions of the tropics as a sensible way for *in situ* accumulation of large quantities of N in vegetation and soil (Sanchez, 1999). The most important effect of improved fallows is that it may, through the improvement in soil fertility, enhance agricultural crop production (Kwesiga and Coe, 1994; Jama et al., 1998; Maroko et al., 1998; Kwesiga, 1999; Mafongoya and Dzowela, 1999; Maroko et al., 1999; Szott et al., 1999; paper **IV**), an effect that compensates for the loss of one or more cropping seasons.

In improved fallow systems, the mixing of OM qualities, as discussed above, is integrated in the system as above- and below-ground biomass have different qualities (Lehmann et al., 1995). When N_2-fixing species are used during the fallow period, there is a substantial true addition of N to the system, sometimes up to 100-300 kg ha^{-1} yr^{-1} (Sanginga et al., 1995; Giller et al., 1997; paper **IV**). Improved fallows may also increase P in labile fractions (Maroko et al., 1999) and increase crop yield on P-deficient soils (Jama et al., 1998). Some improved fallow species may also have access to deeper nutrient pools than the crops and return nutrients from the subsoil to the surface soil (Hartemink et al., 1996; Mekkonen et al., 1997), hence adding nutrients otherwise lost from the cropping system. Improved fallows may also improve soil physical properties (Torquebiau and Kwesiga, 1996) and reduce the occurrence of weeds in the subsequent crop (Kwesiga et al., 1999). In addition to these advantages, fuel-wood, the main source of energy for cooking in most of rural Africa, is produced on the fallows (e.g., 30-40 Mg ha^{-1} DW after 22 months of *Sesbania* fallow; paper **IV**).

Methodological aspects

As one of the hypothesis underlying the work in papers **I-III** is that temporal resolution in studies of C dynamics can be improved by the use of natural ^{13}C abundance methods, and as ^{15}N was used as a tracer in paper **IV**, these isotopic methods merit some further explanation here. In paper **I**, we calculated the contribution to soil C derived from trees, and in **II** and **III** we calculated the proportions and amounts of respired CO_2 derived from organic material from trees added to the soil by studying natural ^{13}C abundance. In paper **IV** we estimated the N_2-fixation by N_2-fixing trees by the ^{15}N dilution method.

Soil organic matter (SOM)

In tropical Africa, most grasses, i.e., the crops maize (which is in fact from America), sorghum, fodder grasses and many "wild" grasses, have the C_4 carbon (C) assimilation pathway, whilst most trees and herbs and all legumes have the C_3 carbon assimilation pathway. The two carbon assimilation pathways discriminate differently against ^{13}C in CO_2 and result in differences in the ratio of the two stable C isotopes, $^{13}C/^{12}C$, of the plant matter produced. Hence, the influence on SOM of, for example, C_3 plants on a soil previously dominated by C_4 plants can be seen as a change of the isotopic ratio $^{13}C/^{12}C$ in the soil.

Isotope ratios are expressed in δ-units:

$$\delta = (R_{sample} / R_{standard} - 1) \bullet 1000\ (‰), \qquad \text{(Eq. 1)}$$

where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The unit $\delta^{13}C$ expresses the ratio of $^{13}C/^{12}C$ in per mil (‰) in a substance (Eq. 1), in relation to the international standard, Vienna Pee Dee Belemnite (V-PDB), a marine limestone, which has been decided to represent 0‰. About 1.1% of the carbon atoms is of the heavier C isotope ^{13}C. Today, the average $\delta^{13}C$ values of CO_2 in the atmosphere is about -8‰.

Plants discriminate against the heavier isotope during photosynthesis, and C_3 plants discriminate more than C_4 plants (O'Leary, 1981; Ehleringer, 1991). Hence, there are differences in the ratio of $^{13}C/^{12}C$ between C_3 plants, range -33 to -22‰, and C_4 plants, range -16 to -9‰, (Deines, 1980). This difference is generally in the order of 14‰ (O'Leary, 1988). When there has been a change in soil cover from C_3 to C_4 vegetation, or *vice versa*, changes in $\delta^{13}C$ value of the SOM can be used to quantify the respective contributions from new and old plant-cover to SOM. This has been demonstrated in earlier studies, where C_4 plants were planted on C_3-dominated soil (Balesdent et al., 1987; Vitorello et al., 1989), and where C_3 plants have been planted on C_4-dominated soil (Balesdent et al., 1988; Martin et al., 1990; Trouve et al., 1994; Jonsson et al., 1996; Eshetu and Högberg, 2000). Natural abundance of ^{13}C has also been used to describe dynamics of shifting forest-savanna boundaries (Mariotti and Peterschmitt, 1994).

In paper **I** the natural abundance of ^{13}C of plant material was taken from literature data. The natural ^{13}C abundance for woody C_3-plants on similar altitudes and precipitation in Kenya is approximately -28‰, while it is approximately -12‰ in C_4 grasses in low and medium elevation grasslands (Tieszen and Boutton, 1989). The fractions of total soil C (Ct), i.e., $Ct = 1$, derived from C_3-plants (C_3) and from C_4-plants (C_4) is calculated as follows (Vitorello et al., 1989; Trouve et al., 1994):

$$Ct = C_4 + C_3, \qquad \text{(Eq. 2)}$$

and

$$Ct \bullet \delta^{13}Ct = C_4 \bullet \delta^{13}C_4 + C_3 \bullet \delta^{13}C_3 \qquad \text{(Eq. 3)}$$

where $\delta^{13}Ct$ = the measured $\delta^{13}C$ value of soil, $\delta^{13}C_4 = \delta^{13}C$ value of C_4-plants (approximately -12; O'Leary, 1988) and $\delta^{13}C_3$ = the $\delta^{13}C$ value of C_3-plants (approximately -28; O'Leary, 1988). Thus, inserting (Eq. 2) into (Eq. 3) and rearranging, C_3 and C_4 can be calculated:

$$C_3 = (\delta^{13}Ct - \delta^{13}C_4) / (\delta^{13}C_3 - \delta^{13}C_4), \qquad \text{(Eq. 4)}$$

and

$$C_4 = (\delta^{13}Ct - \delta^{13}C_3) / (\delta^{13}C_4 - \delta^{13}C_3). \qquad \text{(Eq. 5)}$$

Soil respiration

Soil microbial biomass is an important pool of plant available nitrogen (N), phosphorus (P) and sulphur (S), and regulates the cycling of organic matter and nutrients. Because of its high turnover rate, microbial biomass reacts quickly to changes in management and is a sensitive indicator for monitoring and predicting qualitative and quantitative changes in SOM (Syers, 1997).

Basal respiration rate is the rate of soil respiration of the unamended soil, e.g., preceding the addition of a substrate (Nordgren et al., 1988). Substrate induced respiration (SIR) is the respiration rate shortly after application of a substrate, which should be a C source large enough to induce maximal respiration (before microbial growth is stimulated), and is a relative measure of microbial biomass (Anderson and Domsch, 1978). Most often glucose is used as substrate, but sucrose of different isotopic origin, deriverd from C_3- and C_4-plants respectively, has also been used (Högberg and Ekblad, 1996; Ekblad and Högberg, 2000; paper **II**). The magnitude of the microbial response to substrate addition was similar if sucrose or a high quality green manure was applied to the soil (paper **II**).

When two C pools of different isotopic composition, i.e., from added substrate and old SOM, are mixed, it is possible to distinguish between the mineralisation from the two pools by isotopic analyses of the respired CO_2. This has been done with both ^{14}C-labelled substrates (e.g., Jenkinson, 1971) and with naturally ^{13}C labelled substrate (Mary et al., 1992; Högberg and Ekblad, 1996; Ekblad and Högberg, 2000; papers **II** and **III**).

Cylindrical polyvinyl chloride (PVC) collars (equipped with water seals to ensure gas tight enclosure) were inserted 20 mm into the soil and left in the soil throughout the studies. To collect samples of CO_2, PVC cylinders with sealed tops and open bottoms were placed in the collars. The cylinders had a head-space volume of 5.4-6.0 L. One gas sample of 12 ml was drawn from the cylinder every two minutes for ten minutes with a syringe through a rubber membrane stopper in the top. The samples were directly transferred to 12 ml evacuated glass vials for later determination of concentration and isotopic composition of CO_2. The cylinders were removed after the ten minutes of gas sampling.

Inside the cylinders there is a linear increase in CO_2 concentration (Fig. 2), and a non-linear decrease in $\delta^{13}C$ since the respired CO_2 is depleted compared to the air but asymptotically approaches the isotopic signature of the respired CO_2. The bases for our calculations are mixing models of CO_2 sources with known or calculated isotope compositions. Basal respiration rates are measured before any treatment, and hence derived only from endogenous C. The separation of the $\delta^{13}C$ of the CO_2 evolved from endogenous SOM (δ_E) at basal respiration (Fig. 2b) from the atmospheric CO_2 ($\delta^{13}C \approx -8‰$), was calculated by using variable substitution and ordinary linear regression analysis according to Ekblad and Högberg (2000). Note that equations 6, 8 and 9 were printed incorrectly in paper **II**.

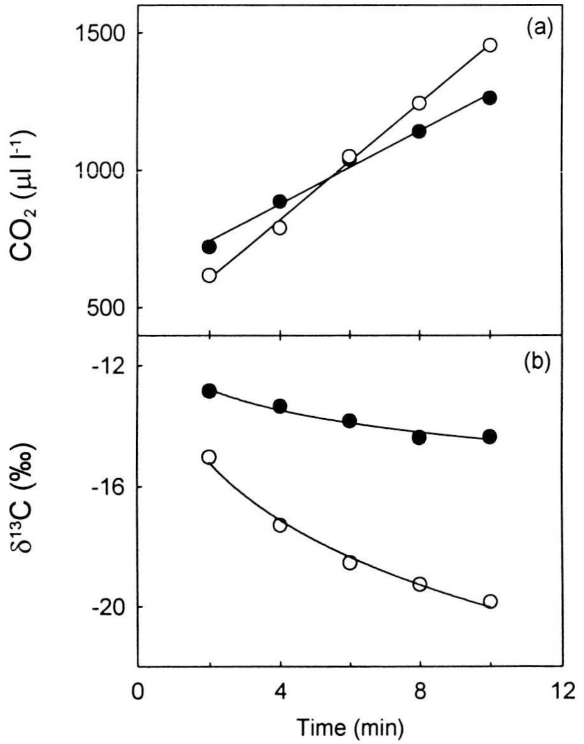

Fig. 2. *Concentration of CO_2 (a) and $\delta^{13}C$ of CO_2 (b) in gas sampled at intervals from the headspace under soil cover.* (•) *basal respiration (before treatment),* (o) *soils treated with C_3-C source (example from the addition of 320 g DW m^{-2} of Sesbania sesban leaves). This example shows data from before and five days after treatment.*

$$\delta_S = (\delta_0 C_0 + \delta_E R_E t) / (C_0 + R_E t), \qquad \text{(Eq. 6)}$$

where δ_S is the C isotopic composition of the gas-samples at time t, δ_0 is the estimated $\delta^{13}C$ value and C_0 is the estimated CO_2 concentration at time $t = 0$ and R_E is the evolution rate of (endogenous) CO_2.

The mixing model applied after the addition of C_3 sugar or C_3 leaves to a C_4 dominated soil is:

$$R_{tot} = R_E + R_3, \qquad \text{(Eq. 7)}$$

where R_{tot} (Fig. 2a) is the total CO_2 evolution rate and R_3 the evolution rate of the CO_2 from mineralisation of the added C_3-C (sugar or leaves).

The following model was applied for calculations of R_E and R_3 after addition of C_3-C:

$$\delta_S = (\delta_0 C_0 + \delta_3 R_3 t + \delta_E R_E t) / (C_0 + R_{tot} t), \qquad \text{(Eq. 8)}$$

where δ_3 is the known $\delta^{13}C$ value of the added C_3-C and δ_E is known from (Eq. 6). Thereafter, inserting (Eq. 7) into (Eq. 8) gives:

$$\delta_S = (\delta_0 C_0 + \delta_3 (R_{tot} - R_E) t + \delta_E R_E t) / (C_0 + R_{tot} t), \qquad \text{(Eq. 9)}$$

where R_E was estimated using ordinary linear regression analysis as for basal respiration. Then, R_3 was calculated by using equation 7.

Theoretical constraints of the soil respiration methodology

The isotope ratio of the basal respiration in both papers **II** and **III**, indicated that soil C before the treatments contained 25-30% C_3 derived C from previous vegetation. In general, soil C in deeper horizons usually contains more ^{13}C (Nadelhoffer and Fry, 1988; Balesdent et al., 1993) and hence has higher (less negative) $\delta^{13}C$ values. A contribution from respiration of SOM in deeper horizons with higher $\delta^{13}C$ than the surface soil, could thus, in theory, lead to a slight underestimation of the C_3 contribution to soil respiration. However, the emitted CO_2 and its $\delta^{13}C$ is an integration of the respiration from the total soil profile, and hence independent of any gradients within the soil profile.

The separation of respired CO_2 from endogenous respective exogenous sources, as outlined above, could be questioned if there is a strong microbial discrimination against ^{13}C during decomposition, as has been argued (Blair et al., 1985; Mary et al., 1992; Schweizer et al., 1999; Henn and Chapela, 2000). However, there are some more or less serious methodological problems behind those arguments, e.g., additions of C of unknown isotopic ratio, either as an additional substrate (Henn and Chapela, 2000) or as inoculum (Mary et al., 1992; Schweizer et al., 1999).

Cheng (1996) also points out that static alkali traps might potentially cause isotope fractionation (Mary et al., 1992; Schweizer et al., 1999). Cheng (1996) concluded that there was no microbial isotopic discrimination in his short-term growth chamber experiment. Recent *in situ* studies of soil respiration in Sweden (Högberg and Ekblad, 1996; Ekblad and Högberg, 2000) and the studies **II** and **III** of this thesis do not indicate any microbial discrimination against ^{13}C during decomposition. Recently, we also carried out a study to establish whether or not microbial discrimination against ^{13}C is important during the initial decomposition of a substrate (Ekblad A., G. Nyberg and P Högberg, manuscript). This was done *in situ* in a boreal forest with the soil respiration methodology described above, by adding, for SIR qualitatively identical C-sources, but with contrasting isotopic signatures (C_3-glucose, -23.4‰; C_4-sucrose, -10.8‰ and labelled glucose, +103.7‰) to a C_3-C dominated soil. If discrimination was significant, this would be detected as a difference in the calculated contribution from the two carbon sources, added C and endogenous C_3-C, to total soil respiration, when a C_4-sucrose and ^{13}C-labelled glucose was added. Substrate induced respiration was similar between the three treatments, and the calculated endogenous and exogenous contributions were similar for C_4-sucrose and for ^{13}C labelled glucose. We concluded that any ^{13}C-discrimination during microbial respiration of glucose and sucrose must be minor.

There is a slight initial increase in endogenous respiration of C in the studies in papers **II** and **III** after addition of new substrate. However, the magnitude and short duration of the increased endogenous respiration does not suggest a true priming effect, i.e., increased decomposition of endogenous SOM, but is more likely an effect of accelerated turnover of C within microbial biomass (Dalenberg and Jager, 1981; 1989; Högberg and Ekblad, 1996; Ekblad and Högberg, 2000).

Measurements of nitrogen fixation

In paper **IV** we used the ^{15}N isotopic dilution technique to estimate the per cent N derived from air by N_2-fixation (%Ndfa), i.e., the proportion of plant N that is fixed from the atmosphere through symbiosis with *Rhizobium*. A small amount of ^{15}N enriched N is applied to the soils of the plots, and atom% ^{15}N of N in N_2-fixing species and non-N_2-fixing reference species is compared. Atmospheric N_2 contains 0.3663% ^{15}N, which is the defined international standard for $\delta^{15}N = 0‰$. %Ndfa is calculated from the atom% ^{15}N in excess (AE) of the atmospheric ^{15}N content:

$$Atom\%\ of\ sample - 0.3663 = AE. \qquad \text{(Eq. 10)}$$

We calculated %Ndfa in two ways; from the AE of leaves (FAE):

$$\%Ndfa = (1 - FAE^{fix} / FAE^{ref}) \bullet 100, \qquad \text{(Eq. 11)}$$

where *fix* stands for N_2-fixing species and *ref* for the non-N_2-fixing-reference species, and from the weighted average AE of the whole tree (WAE) (Parotta et al., 1996):

$$\%Ndfa = (1 - WAE^{fix} / WAE^{ref}) \bullet 100, \qquad \text{(Eq. 12)}$$

and

$$WAE = \frac{AE_1 \bullet TN_1 + AE_2 \bullet TN_2 + AE_3 \bullet TN_3 + AE_n \bullet TN_n}{TN_1 + TN_2 + TN_3 + TN_n} \qquad \text{(Eq. 13)}$$

where TN is total nitrogen and *1* to *n* is different plant parts, e.g., foliage, branches, stem, roots etc. (Danso et al., 1995).

The ^{15}N enrichment in various plant parts frequently differs and measurements of AE from only one plant part may, therefore, not be representative for the whole plant (Danso et al., 1993). However, %Ndfa calculated from WAE in paper **IV** correlated with %Ndfa calculated from FAE ($r^2 = 0.91$-0.99), which was also found by Parotta et al. (1994; 1996).

Root sampling

The root sampling methodology used in paper **IV** needs to be mentioned here, as it differs from many other root studies (e.g., Jonsson et al., 1988; Schroth et al., 1996; Torquebiau and Kwesiga, 1996; Livesley et al., 2000). Our method includes very coarse roots, e.g., the tap-root, (Fig. 3) which might not be important for nutrient uptake or short-term nutrient dynamics, but influence the long-term dynamics of SOM. Although large roots have slower turnover rates than fine roots, they represent a substantial pool of soil C and N (40-95 kg N ha^{-1} in paper **IV**) and are, hence, relevant for quantitative measures of N_2-fixation.

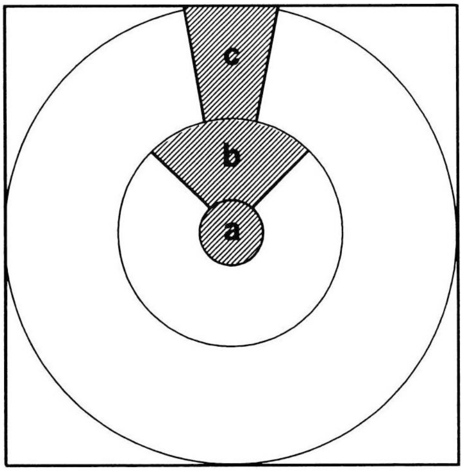

Fig. 3. *Root sampling sections in fallow/woodlot plots, within the 1 by 1 m area surrounding the tree. In sections "a-c" all roots down to 60 cm soil depth are sampled.*

A summary of results of studies in papers I - IV

Paper I

In this study, we investigated how different tree species influence the soil by comparing soil samples from under the canopy with soil samples from outside the canopy cover in on-farm grassland settings. We also studied a fenced *Prosopis juliflora* plantation in a semi-arid area. The tree species were *Acacia tortilis*, *Cordia africana*, *Croton megalocarpoides*, *Grevillea robusta*, *Prosopis juliflora* and *Sesbania sesban*. Soil parameters studied were pH, soil C, soil N, extractable soil P and natural abundance of ^{13}C and ^{15}N.

All species, except *Sesbania* and *Prosopis* in the fenced plantation, lowered the soil ^{13}C abundance by 0.5-1 δ-units in a period of five years (Fig. 4). This was equivalent to an increase of 3-5% of the percentage of soil C contributed by C_3 species. *Prosopis* trees did not decrease the soil ^{13}C abundance in the fenced plantation, presumably because of the abundant grass-growth around them in this particular setting, which excluded grazers. *Cordia* trees, which had pronounced effects on most parameters, raised the C%, N% and extractable P by 27%, 26% and 55%, respectively. Nitrogen and carbon were well correlated ($r^2 = 0.97$) in the whole material. Effects on soil pH were in both directions, e.g., it was raised under the *Prosopis* plantation by 0.33 units, while it was lowered under *Acacia* by 0.21 units.

It was concluded that effects of solitary agroforestry trees on soil could be seen within as short time as five years in practical on-farm situations. The most sensitive indicator was ^{13}C abundance, which generally reflected a shift in inputs of C from C_4 grasses to C from C_3 trees. Therefore, ^{13}C abundance is recommended as a particularly sensitive indicator of the influence of trees on sites previously dominated by C_4 crops and grasses. However, one should be cautious to note that profuse grass growth under trees may cause anomalies.

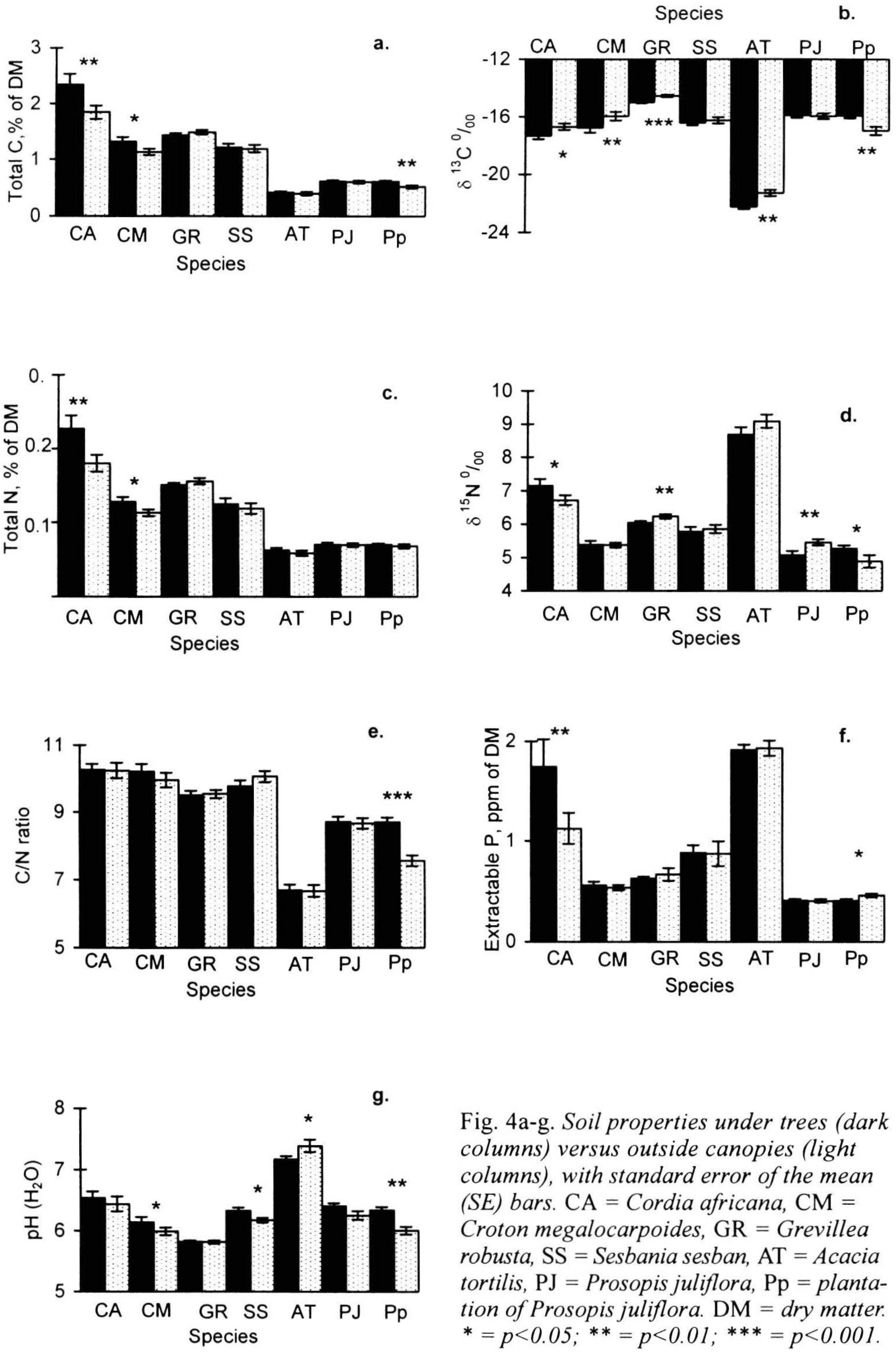

Fig. 4a-g. *Soil properties under trees (dark columns) versus outside canopies (light columns), with standard error of the mean (SE) bars.* CA = *Cordia africana,* CM = *Croton megalocarpoides,* GR = *Grevillea robusta,* SS = *Sesbania sesban,* AT = *Acacia tortilis,* PJ = *Prosopis juliflora,* Pp = *plantation of Prosopis juliflora.* DM = *dry matter.* * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.

Paper II

In this paper, we present a method to directly study the mineralisation of carbon (C) applied as green manure by measurements of the ^{13}C natural abundance of CO_2 respired from the soil.

In situ decomposition of *Sesbania sesban* leaves or C_3 sugar was studied for four to eight days after application to a field in Kenya. Using the difference of around 10‰ in natural abundance of ^{13}C between the endogenous soil C (mainly C_4) and the applied C (C_3), we could calculate the contributions of the two C sources to soil respiration. The $\delta^{13}C$ value of the basal respiration was from -15.9 to -16.7‰. The microbial response to the additions of leaves and sugar to this tropical soil was immediate. Application of *Sesbania* leaves gave an initial peak in respiration rates that lasted from one to less than six days, after which it levelled off and remained about 2 to 3 times higher (230-270 mg C m^{-2} h^{-1}) than the control respiration rates throughout the rest of the experiment (Fig. 5). In the sugar treatment, there was no initial peak in respiration rate. The respiration rate was 170 mg C m^{-2} h^{-1} after four days. At the end of the experiments, after four to eight days, as much as 14-17% of the added C had been respired and about 60% of the total respiration was from the added *Sesbania* leaves or C_3 sugar.

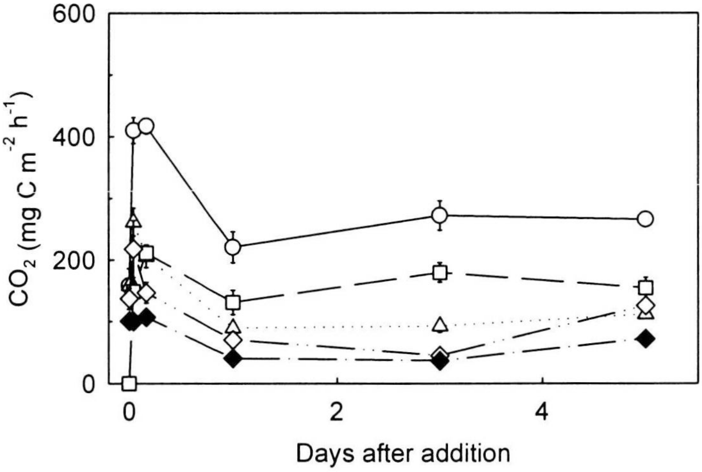

Fig. 5. *Respiration rates after addition of exogenous C_3-carbon. Example from addition of 320 g DW m^{-2} (144 g C DW m^{-2}) of Sesbania sesban leaves,* (o) *total respiration,* (❑) *respiration of added C_3-C,* (Δ) *respiration of endogenous C (mainly C_4),* (◊) *respiration from control plots (soil mixed) and* (♦) *respiration from the "blank" treatment (soil not mixed). Error bars ±SE.*

This non-destructive method allows repeated measurements of the actual rate of C mineralisation and facilitates decomposition studies with high temporal resolution in the field when there are differences in ^{13}C signature between SOM and the added material. Combined with studies of nutrient mineralisation/immobilsation patterns, this method could evidently improve time resolution in studies of decomposition and nutrient dynamics.

Paper III

In this study different *in situ* methods were used to study mineralisation of C and N after additions of fresh leaves of *Crotolaria grahamiana*, *Grevillea robusta*, *Lantana camara*, *Markhamia lutea* and *Sesbania sesban*. The initial (polyphenol+ lignin):N and lignin:N ratios of leaves had the highest positive correlation with biomass remaining in litterbags (r = 0.88 and 0.87, respectively) and the strongest negative correlation with total inorganic N in the soil at the end of the experiment (r = -0.87). Net N mineralisation was high and very rapid from residues with high quality (e.g., low ratios of (polyphenol+lignin):N) and low and slow from low quality residues.

Respiration of exogenous C from the added green manure, separated from respiration of old soil C by the isotopic ratio of ${}^{13}C/{}^{12}C$ in the respired CO_2, correlated positively with KCl extractable ammonium in the soil (r = 0.75) (Fig. 6). Carbon added with the green manure mineralised very rapidly from *Sesbania sesban* (high quality), but more slowly from *Grevillea robusta* (low quality). Ten days after application, 37% and 8% of the added C had been respired from *Sesbania* and *Grevillea*, respectively. According to our estimates, as much as 70-90% of the added C was lost in 40 days from high quality green manure (Fig. 7). Hence, it is unlikely that high-quality green manure will cause a significant build-up of soil organic matter, and thereby increased CEC and erosion resistance. For immediate effects on soil fertility, application of high quality green manure may, though, be a viable management option. The high mineralisation rates of both C and N from high quality residues, i.e., *Sesbania* or *Crotolaria* leaves, suggest that green manure may fill the N requirements of a crop, but not likely increase SOM. However, to achieve synchrony with crop demand careful management is needed as large amounts of N are mineralised within days after applications.

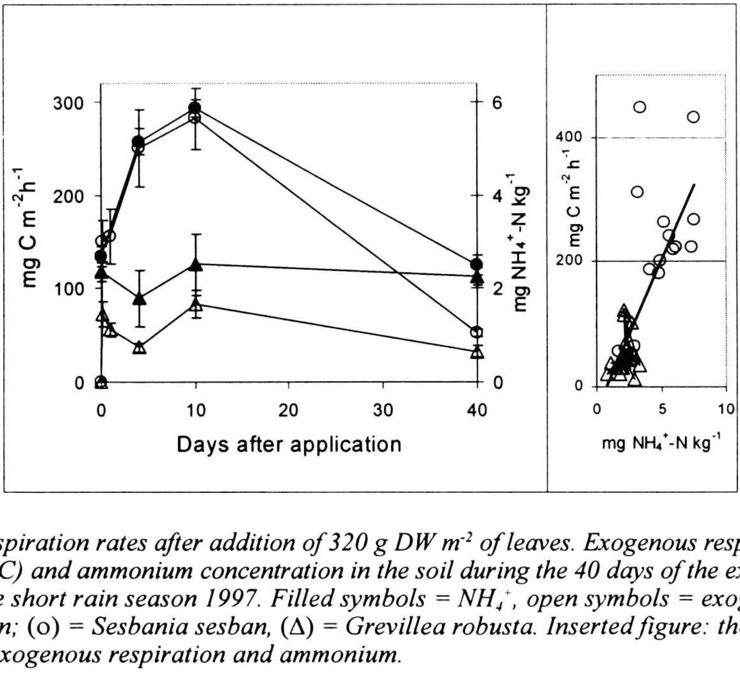

Fig. 6. *Respiration rates after addition of 320 g DW m^{-2} of leaves. Exogenous respiration (of added C_3-C) and ammonium concentration in the soil during the 40 days of the experiment during the short rain season 1997. Filled symbols = NH_4^+, open symbols = exogenous respiration;* (o) = *Sesbania sesban,* (Δ) = *Grevillea robusta. Inserted figure: the relation between exogenous respiration and ammonium.*

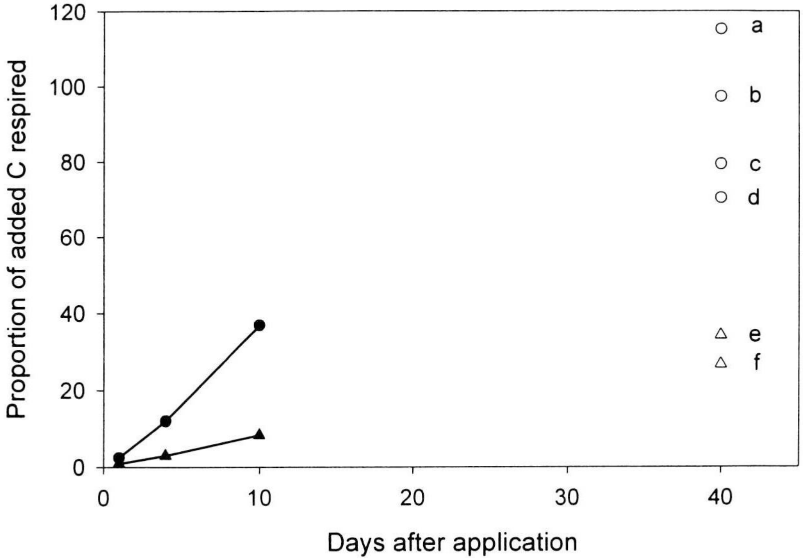

Fig. 7. *Cumulative proportion of added C respired. Respiration rates increased up to day 10. Thereafter, "a-f" are scenarios of a linear decrease in respiration rates to the level at the end of the experiment (day 40). Scenarios "a-d" reach that level at day 40, 30, 20 and 15, respectively for Sesbania. For Grevillea, scenarios "e" and "f" reach that level at day 40 and 20, respectively.* (o) = *Sesbania,* (Δ) = *Grevillea. Filled symbols = calculated on measured values, open symbols = "predicted values".*

Paper IV

Above- and below-ground biomass and N content was examined from four different fallow/wood-lot species, *Calliandra calothyrsus*, *Eucalyptus saligna*, *Grevillea robusta* and *Sesbania sesban* two years after planting. Both the foliar atom excess (FAE) and weighted whole tree atom excess (WAE) version of the ^{15}N dilution method were used to estimate the proportion of N from symbiotic N_2-fixation in the two legumes (*Calliandra* and *Sesbania*), with the other two species as reference plants. Effects on production by management for fodder (*Calliandra*) and for poles (*Sesbania*) were also monitored.

Top soil inorganic N was studied in five treatments, *Calliandra*, *Sesbania*, continuous maize cropping, maize/bean rotation and a natural weed fallow, during the fallow phase and for two consecutive cropping seasons. Maize production was monitored for two seasons after the five treatments and an additional treatment of 60 kg N ha^{-1} applied to continuous maize as urea during the first cropping season.

Above-ground biomass at tree harvest was 31.5 Mg ha^{-1} for *Sesbania*, 24.5 Mg ha^{-1} for *Calliandra*, 32.5 Mg ha^{-1} for *Grevillea* and 43.5 Mg ha^{-1} for *Eucalyptus*. Stem/branch production was 1.7 times higher in the managed treatment of *Sesbania* and fodder production was 4.5 times higher in managed *Calliandra* as compared to the unmanaged treatment. Total below-ground biomass was 11.1 Mg ha^{-1} for *Sesbania*, 15.5 Mg ha^{-1} for *Calliandra*, 17.7 Mg ha^{-1} for *Grevillea* and 19.1 Mg ha^{-1} for *Eucalyptus*, with 70-90% as coarse roots (>2 mm). This is considerably higher than in other studies, which do not include the coarsest roots, e.g., tap-roots. Of the total N incorporated into the soil after fallows/woodlots, 31-54% was from roots, with 22-37% from coarse roots. Based on our results, it is obvious that total root biomass is important in C and N budgets for different land use systems.

About 70-90% of the N in *Sesbania*, and 50-70% in *Calliandra*, was derived from N_2-fixation. The two methods to estimate %Ndfa, FAE and WAE, were well correlated ($r^2 = 0.91$-0.99; $p<0.01$) and, hence, FAE may be adequate to estimate N_2-fixation. The addition by N_2-fixation after two years of fallow was 280-360 kg N ha^{-1} for *Sesbania* and 120-170 kg N ha^{-1} for *Calliandra*. This resulted in a positive N balance (input from N_2-fixation minus export with fallow harvest and maize crop) after two maize cropping seasons of 170-250 kg N ha^{-1} and 90-140 kg N ha^{-1}, for *Sesbania* and *Calliandra*, respectively. All the other treatments had negative N balances after two cropping seasons.

Inorganic N in the topsoil was significantly higher after the fallow harvest in the *Sesbania* than in the other treatments and more N was mineralised during rain seasons in this treatment than in other treatments. None of the other treatments differed from the continuous maize treatment.

Moisture stress was not seriously affecting the fallows, but crop yields were very low the first season after fallow harvest, probably due to unusually low and erratic rainfall. Maize yield was significantly higher after addition of mineral N, in both seasons, and after the *Sesbania* fallow the second season, than in continuous maize cultivation without N addition (Fig. 8).

We conclude that *Sesbania* 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, symbiotically, fix large amounts of N_2 from the atmosphere. It also produces considerable quantities of firewood, which is a valuable asset to small-scale farmers.

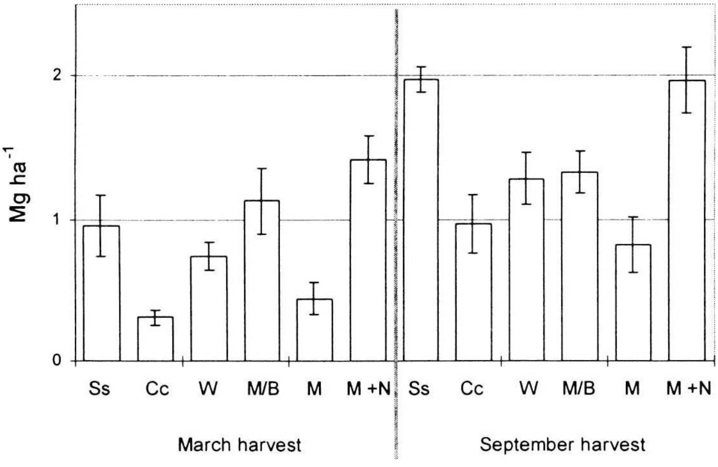

Fig. 8. *Total grain yield of maize for March and September harvests. Error bars are ±1 SE. Ss = Sesbania sesban, Cc = Calliandra calothyrsus, W = weed fallow, M/B = maize/beans rotation, M = continous unfertilized maize, M+N = continous maize + 60kg/ha first season.*

Discussion

Solitary trees

As said above, effects of trees on soils could reflect changes in *in situ* biogeochemistry as well as in the inflow-outflow budget of the tree micro-site. The common decrease in soil $\delta^{13}C$ under trees in paper **I** is clear evidence of input of C from C_3 plants, i.e., *in situ* changes under the studied tree species. However, as regards the fenced *Prosopis* plantation, there was a higher $\delta^{13}C$ in the soil inside the plantation than outside, due to the very dense undergrowth of grasses observed there. This means that fencing, and hence exclosure of grazers, had a larger effect on soil amelioration than the trees in that case.

In the soil under *Cordia* trees, the increase in C% was larger than expected from the decrease in $\delta^{13}C$, which may be due to increased growth of C_4 grasses under the trees and/or import of such C with grazing animals or birds, which may also explain the increased P and N levels. Other possible explanations may be nutrient capture from deep soil sources and/or extended lateral root system depleting the surroundings. As N and P are crucial factors in agriculture, these results suggest that *Cordia* deserves more attention by researchers.

The rates of change in soil $\delta^{13}C$ under trees observed in paper **I** are comparable to results of other studies on the $\delta^{13}C$ signature in soils with vegetation changes from C_3 to C_4 plants (e.g., Trouve et al., 1994; Jonsson et al., 1996). The differences in soil $\delta^{15}N$ between under and outside canopy cover were, although not always significant, in the expected direction, i.e., a lower $\delta^{15}N$ was found under potentially N_2-fixing trees (van Kessel et al., 1994), indicating an input of fixed N_2 with a $\delta^{15}N$ close to zero.

Biomass transfer systems

As suggested in paper **II**, measures of soil respiration were combined with other methods to study decomposition in paper **III**. There was a rapid initial net N mineralisation for the high quality residues, i.e., *Sesbania* and *Crotolaria* in study **III**. The first ten days, the increase in inorganic N consisted almost exclusively of NH_4^+. Thereafter, nitrification took off and NO_3^- reached maximum levels at day 40. This emphasises the need to measure both inorganic N species in short-term studies. Neither NH_4^+, NO_3^-, nor total inorganic N in the *Grevillea* treatment differed from the control. Total and exogenous respiration was higher from *Sesbania* than from *Grevillea* green manure, as could be expected from the higher quality of *Sesbania* green manure. Mafongoya et al. (2000) report good correlation between soil respiration and quality parameters of the green manure (C/N ratio and lignin/N). In our study NH_4^+ and exogenous respiration were well correlated (Fig. 6), indicating that these two parameters are appropriate to describe short-term, i.e., hours to weeks, dynamics of soil C and N. Mineralisation of the added C_3-C from *Sesbania* was very rapid and respiration rates increased up to day 10. In the study in paper **II**, 14% of the added C was respired within five days, while 37% of the added C had been respired after ten days from the same *Sesbania* treatment in paper **III**, as compared to 8% from the *Grevillea* treatment after ten days. Aulakh et al. (2000) reported that 36–48% of added C had been mineralised within 16 days in a green manure experiment with *Sesbania acuelata*.

The decrease in exogenous respiration rates (Fig. 6) from the peak value at day 10 (**III**) to the value at the end of the experiment (day 40) is probably negatively exponential. However, if we for simplicity assume it to be linear (not speculating on the curvature of an exponential curve), 115% and 34% of the added C would have been respired at day 40 in the *Sesbania* and *Grevillea* treatments, respectively (scenarios "a" and "e" in Fig. 7). If respiration rates are hypothesised not to fall below the levels at day 40, and to reach that level at day 20, 79% and 27% would have been respired at the end of the experiments in the *Sesbania* and *Grevillea* treatments, respectively (scenarios "c" and "f" in Fig. 7, scenarios "b" and "d" are similar for *Sesbania*, but reaching the final respiration rates at 30 and 15 days respectively). According to the calculations, as much as 70-90% of the added C is lost in respiration in the Ss treatment, and hence not available for long-term SOM build-up. The lack of significant effects on soil C and N under *Sesbania* trees in paper **I** may be explained by the rapid mineralisation of C and N of leaf litter from this species.

Weight loss from litterbags in the long rain season follows two patterns (**III**), one for the high quality residues and one for the residues with lower qualities. Per cent material remaining in litterbags at day 52 correlated well with all quality parameters used, notably with the ratio (polyphenol+lignin):N and lignin:N. Note, however, that litterbags and soil respiration data are from different seasons (long rain season and short rain season, respectively) and can hence not be correlated. However, in the *Sesbania* treatments, around 80% of the added C was respired within 40 days in the short rain season and around 20% remained in the litterbags after 52 days of decomposition in the long rain season. Both these figures suggest that most C is mineralised and that not much C is incorporated in SOM from high quality green manure. This also agrees well with C losses of 57% after 26-29 days and 81% after 70 days from a litterbag experiment with *Gliricidia sepium*, reported by Zahara and Bah (1999). For *Grevillea* residues, there is a discrepancy in estimated C losses between the two methods; only 35% of the added C had been respired in the short rain season, while 65% had been lost from the litterbags in the long rain season. This discrepancy indicates that some of the C lost from the litterbags may not have been respired. A substantial proportion of the missing C might have been incorporated into soil fauna, e.g., in termites, which can pass in and out of litterbags with this mesh size.

A total of 62-127 kg N ha^{-1} was added as green manure (**III**). For high quality residues, where 70-90% of the added C is lost in respiration in 40 days, it is reasonable to believe that similar proportions of N is mineralised (Handayanto et al., 1994). Nitrogen recovery by the first crop is typically around 10-40% of the N from additions with green manure (Giller and Cadish, 1995; Gachengo et al., 1998). Leaching of inorganic N was not significant in the studies in papers **III** and **IV**, i.e., concentrations of inorganic N did not change significantly below 50 cm depth during the sampling periods. In the presence of decomposing tree roots and active maize roots (**IV**) the risk of nutrient losses might be reduced. However, if crop uptake is not in synchrony with mineralisation and rainfall is excessive, the risk of leaching could be substantial after application of high quality residues, especially in the later phase of mineralisation, when NO_3^- has been produced from the added material. High quality residues contains large proportions of easily accessible C, available for microbial consumption, which may deplete soil O_2 (creating locally anaerobic conditions) and thereby enhance denitrification (Aulakh et al., 2000). However, even with active maize roots, those risks could be substantial in biomass transfer systems if nutrient uptake is not in synchrony with mineralisation. Without a substantial build-up of SOM, and thereby no increased CEC and erosion resistance (Young, 1997), the risk of losses of the remaining N through leaching, volatilisation and erosion is high. This would be especially true for high quality green manure from *Sesbania* and *Crotolaria*.

The high mineralisation rates of both C and N from high quality residues, i.e., *Sesbania* or *Crotolaria* leaves, show that green manure may fill the N requirements of a crop, but not likely increase SOM. When both immediate soil fertility and maintenance/improvement of SOM quality and quantity is the concern of management, other management methods may be opted for. These can be mixtures of residues of different qualities (Handayanto et al., 1997a; 1997b) or improved fallow systems (Barrios et al., 1997), where the roots may have qualities different from leaves (Lehmann et al., 1995) and affect SOM and nutrient release in another way than above ground plant material does.

Improved fallow systems

Aboveground biomass production of *Sesbania* after 22 months (paper **IV**) agrees well with a study by Jama et al. (1998), who reports 28.4 Mg ha^{-1} after a *Sesbania* fallow of the same duration, the same planting density and from the same area. High biomass production of the non-legumes *Eucalyptus* and *Grevillea* is well known and agrees with other studies (NAS, 1980).

Torquebiau and Kwesiga (1996) reports aboveground biomass of a 2-year *Sesbania* fallow of 16.4-19.6 Mg ha^{-1}, from an area in Zambia with only one rain season per year and a mortality of around 30% in the experiment. Two rainy seasons and almost no mortality may explain the higher production in paper **IV**. Root fraction levels as well as root nitrogen content reported here are in accordance with Young (1997) and Mekkonnen et al. (1997), who reported 10.9 Mg ha^{-1} root biomass and a root/shoot ratio of 0.36 in 15 months old *Sesbania* in western Kenya. In contrast, Torquebiau and Kwesiga (1996) found only 1.7-2.9 Mg ha^{-1} total root biomass (0-150 cm) resulting in a root/shoot ratio of 0.10-0.15. However, they did root sampling by coring, a technique that might underestimate root biomass and easily misses the substantial tap-root located directly below the stem. Dhyani et al. (1990) presented a root study of 28 month old *Eucalyptus tereticornis* with values of fine root biomass and root/shoot ratio agreeing with the *Eucalyptus* in this study. Actually, many root studies (e.g., Schroth et al., 1996; Torquebiau and Kwesiga, 1996; Jonsson et al., 1988; Livesley et al., 2000) do not include the coarsest roots, e.g., tap-roots. This may be appropriate for estimates of short-term root turnover and nutrient dynamics, but will seriously bias studies of total biomass C and N, and may lead to erroneous conclusions in discussions on e.g., long-term SOM dynamics and C sequestration.

Calliandra did not commence N_2-fixation until the third growing season, after which it acquired 50-70% of its nitrogen from N_2-fixation. *Sesbania* got 70-90% of its N from fixation already from the second season.

Only after the *Sesbania* fallow there was substantially more inorganic N in the topsoil than in the continuous maize treatment. This was true for both seasons. The decomposition of the lower quality litters (above and below ground) in the *Calliandra* fallow may positively influence long-term SOM dynamics. However, this was not seen during the two cropping seasons (paper **IV**).

Maize harvest was significantly higher after addition of mineral N in both seasons and after *Sesbania* fallow the second season. None of the other treatments was significantly different from the continuous maize treatment. More N was exported with crops from the *Sesbania* treatment than from any of the other treatments. Nevertheless, *Sesbania* had the highest positive net N balance after two cropping seasons. *Calliandra* also had a positive net N balance, while all other treatments had negative N balances.

Based on these results, and a substantial amount of other studies of *Sesbania* fallows (e.g., Szott et al., 1999), we conclude that *Sesbania* fallows is a viable management option for improved soil fertility, fuel-wood production and increased crop production.

Conclusions and future prospects

A fundamental basic assumption in agroforestry is that trees can ameliorate soil fertility in agricultural systems. This is confirmed in papers **I**, **II** and **IV**, but is also the base for one of the oldest existing agricultural practises, shifting cultivation, and can hardly be considered as novel or revolutionary results. However, the major conclusions (of which some are more novel) of this work are:

- The influence of trees on soil C and SOM differs between species and effects are, at least partly, due to *in situ* changes (papers **I** and **IV**). The ameliorative effects depends largely on the quality of the litter produced by the trees, e.g., (lignin+polyphenol):N (papers **III** and **IV**).

- The isotopic signature of SOM (paper **I**) and respired CO_2 (papers **II** and **III**) are useful tools to better understand the temporal resolution of decomposition. We show that the isotopic signature of SOM is a useful tool for time-scales of a few years, while the isotopic signature of respired CO_2 is applicable on time-scales of hours to weeks. For the temporal pattern of N mineralisation, NH_4^+ reflects the initial dynamics, on a time-scale of days to weeks, while NO_3^- and total inorganic N describes longer-term dynamics, e.g., over seasons. Ammonium is also well correlated to exogenous respiration. It is essential to understand both short-term and long-term temporal dynamics of mineralisation in order to develop management system with synchrony between nutrient release and crop uptake.

- Mineralisation of C and N is very rapid from high quality litter (papers **II**, **III** and **IV**). This N has to be kept in the system, in available forms, by management to achieve synchrony. In fallow systems this seems to be the case, possibly achieved by the natural mixture of litter qualities, i.e., above and below ground residues. Managing N release for synchrony may be a more delicate task in biomass transfer systems.

- Substantial amounts of N may be added to the soil by N_2-fixing leguminous fallow species. *Sesbania* fallows may increase crop production through improved soil fertility on N deficient soils (paper **IV**). In addition, substantial amounts of much needed fuel-wood is produced.

Thus, in this thesis, and elsewhere, it is shown that mineralisation of C and N of above ground biomass of high quality is very fast. Roots are important for the nutrient cycling both when they grow and when they decay, but little is known about root growth and decomposition in fallow systems. Decaying roots are likely to mineralise nutrients at a slower rate as they have different (lower) qualities compared to the above ground biomass (Lehmann et al., 1995), which may lead to an initial immobilisation of the nutrients released from aboveground OM by micro-organisms associated with the root litter. The net effect of this mineralisation/ immobilisation is what is available for the crop. Root exudates, roots and fungal mycelia bind soil particles and SOM into aggregates and, hence, gives a structure which is readily penetrated by roots, allows water to pass through larger pores and retain water in smaller pores, available for utilisation by plants. SOM also improves the cation exchange capacity (CEC) through clay-humus complexes (Oorts et al., 2000). This is especially important in soils dominated by kaolinite clay (with low CEC), which are common in the humid tropics. Organic compounds might also block fixation sites for phosphorus (P) on sesquioxides and hence make more P plant available. Many tropical soils are rich in sesquioxides and therefore P limited (Young, 1997). The role of root exudation from fallow species is poorly known, as is the rate of soil aggregate formation.

There is a need for improving the understanding of mineralisation/immobilisation patterns of decaying roots, root turnover and of the underlying processes in soil aggregate formation and its temporal and spatial resolution. With this knowledge, the management of fallow systems may be improved, enabling more productive agricultural systems for resource-poor tropical farmers. Isotopic methods using ^{13}C could be applied to address some of these research questions, e.g., in a C_4 dominated soil the C flux from C_3 fallow trees into soil aggregates could be followed both temporally and spatially by studying the change in isotopic signature of soil aggregates. Trees may also be stem-labelled (into the phloem sap) with enriched ^{13}C and/or ^{15}N to further boost the difference in isotopic signature between the trees and the other compartments studied.

Carbon sequestration is a globally important subject also in agricultural soils. Increased knowledge on aggregate formation and root respiration may improve our understanding of C sequestration into soils. Recently it was shown, in a large scale girdling experiment in a Swedish pine forest that more than 50% of the total soil respiration was root-mycorrhizal respiration (Högberg P., A. Nordgren, N. Buchmann, A. F. S. Taylor, A. Ekblad, M. Högberg, G. Nyberg, M. Ottosson Löfvenius and D. J. Read, manuscript). A similar approach in a fallow system, with C_3 trees growing on a C_4 dominated soil, would increase our knowledge of this system as a source or sink of atmospheric CO_2. The level of detection would be high in such an experiment, as there are difference between old soil organic carbon and the trees in the natural abundance of ^{13}C.

Although improved fallow systems may influence carbon sequestration into the soil, this can never be the major reason for its adoption in tropical agriculture. To resource-poor tropical farmers, the only justification of improved fallow systems would be that they can increase the agricultural production - and they definitely can.

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Acknowledgements

Welcome. As this is the first page for most people (and only for many) to read, I want to welcome You to the thesis. Here, one is supposed to show gratitude, linguistic elegance and humour. However, as I am grateful to too many to mention and as those talents has not befallen upon me, I humbly express:

Asante yote

Merci tous

Thank you, all

Tack alla

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