

Modelling carbon sequestration

With a focus on grasslands, effects of climate and management

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1. Introduction

The global terrestrial soil carbon pool has been estimated at 2200 Pg carbon and the atmospheric carbon pool at 750 Pg carbon. Global models on carbon cycle modeling suggest that the terrestrial carbon sink is a significant factor (flux: ca 60 Pg/year) in the control of atmospheric carbon dioxide levels. This sink is probably larger than current estimates indicate. Data are available suggesting that grasslands are particularly important as net carbon sinks (Van Ginkel 1999), i.e. for the sequestration of carbon into soil.

According to Boone *et a*. (1998) the temperature sensitivity of soil respiration will largely determine the effects of a warmer world on net carbon flux from soils to the atmosphere. The CO_2 flux from soils to the atmosphere is estimated to be 50-70 Pg of carbon per year and makes up 20-38% of the annual carbon to the atmosphere from terrestrial and marine sources.

In the present literature review, we give a quick scan of models describing carbon dynamics with special reference to grasslands and effects of climate and management (chapter 2). We present experimental data available for model parameters (chapter 3), and discuss information on interactions between factors affecting soil carbon sequestration.

Some notes on terminology

- Residue, i.c. plant residue: this refers to plant debris, including all plant parts, like leaves and roots (e.g. Paul & Clark 1988; Facelli & Pickett 1991).
- Litter: plant debris, also including root exudates and roots or other below-ground parts. Here, quality of litter is defined as the physical and/or chemical characteristics of plant litter (Paustian *et al.* 1997).
- Plant Organic Matter (POM): organic matter originating from plants.
- Soil Organic Matter (SOM): this originates from (higher) plant debris, but most of it has been passed through decomposer organisms, especially fungi and bacteria.
- Organic matter fractions (e.g., macro-organic matter, microbial biomass, mineralizable C, etc) describe the quality of SOM (e.g. Carter 2002).
- Sequestration: Decomposition of organic matter is the negative of sequestration (~storage); it is therefore relevant as a process, also while it is widely studied in the literature, be it often in relation to soil fertility (sustaining soil functions) rather than climate change (sustaining biosphere functions).

Problem

To what extent may agricultural management of arable and in particular grassland contribute to decrease the rise of atmospheric carbon dioxide? Are current carbon cycle models sufficiently up-to-date with modern insight in the prime processes involved in such a way that they are capable of predicting carbon sequestration in grasslands? Which experimental data are available that can be used in such modeling?

Goal

The objective of the present study is to provide a review of the state-of-the-art in the modeling of carbon sequestration in grasslands as the central item and to provide parameters values for such models, with a focus on experimental studies dealing with the influence of climate and management on carbon sequestration in soils.

2. Models of plant organic matter decomposition

During the last decades, various soil organic matter models have been developed. Some of these models have been specifically developed for grasslands, such as the Verberne/MOTOR model and the Hurley Pasture model. However, the basic processes in grassland soils probably do not differ essentially from those in other ecosystems. Here, we distinguish two main forms: continuous and discontinuous. The discontinuous models can be further separated into single- and multi-compartment models:

2.1 Continuous models

Q-theory (Bosatta & Ågren, 1999).

This theory uses element cycles as to determine the systems dynamics. In this system organic matter quality is defined as the number of steps required to break down a carbon molecule.

2.2 Discontinuous models (multi-compartment)

2.2.1 Computer language-based models

Verberne/MOTOR model (Whitmore et al., 1997);

3 added Soil Organic Matter (SOM) pools: Dissolved Plant Matter (DPM); protected structural microbial biomass (SMB), unprotected SMB, protected SOM, unprotected SOM, stable SOM.

Hurley Pasture model (Thornley & Cannell, 1997);

3 added SOM pools (metabolic, cellulose, lignin), SMB, soluble, protected SOM, unprotected SOM, stable SOM.

Century model (Parton et al., 1993);

2 added SOM pools (metabolic, structural), smb, 3 SOM fractions (active SOM, slow, SOM, passive SOM); submodels for water, temperature, mineral nitrogen;

Century model with size-density fractions (Sitompul et al., 2000)

A som submodule for the CENTURY model was based on Ludox particle size density fractions. The turnover rates of these easily measurable fractions were determined by assessing their C-13 isotope. The 'slow' (SOM2) pool in Century was divided into L, I, H and R fractions, where the R (resistant) fraction represents the 50-150 mu m size fraction.

Daisy model (Hansen et al., 1990);

3 organic matter pools (added OM; SMB; native SOM); all 3 pools subdivided into a faster and a slower pool; a separate recalcitrant pool of added om directly enters som; submodels for water, temperature, mineral nitrogen;

SOMKO (Gignoux et al., 2001)

is a new simulation model of som dynamics aimed at predicting long-term and short-term som dynamics based on a mechanistic approach focusing on smb as the key agent of decomposition. Som is partitioned into cohorts and chemical quality pools (classified by age and chemical composition).

CESAR (Vleeshouwers & Verhagen, 2002) model (Carbon Emission and Sequestration by AgRicultural land use) was developed to simulate changes in the carbon content of plant production systems using four carbon pools (living biomass, harvested dry matter, crop residues, soil organic matter (humus)).

2.2.2 Spreadsheet-based models

CAMFor (Carbon Accounting Model for Forests) (Brack & Richards, 2002)

is a sophisticated spreadsheet model developed to assist in carbon accounting. Carbon is tracked in the following pools: biomass (stem wood, branches, bark, fine and coarse roots, leaves and twigs), soil (organic matter and inert charcoal), debris (coarse and fine litter, slash, below ground dead material), products (waste wood, sawn timber, paper, biofuel, reconstituted wood products).

ICBM models (Katterer & Andren, 2001)

A model family of analytically solved models of soil carbon, nitrogen and microbial biomass dynamics. The original ICBM comprises 'Young' and 'Old' soil C, two decay constants and parameters for litter input, 'humification' and external influences - in all five parameters. The new models describe soil C (and N) balances more in detail, but they are built around the same core concepts such as first-order decomposition kinetics and a minimum number of soil C and N pools. More complex processes, such as plant growth and mortality as well as weather influence are not explicitly included.

Listed according to increasing complexity, the models are: (1) ICBM/N, which is ICBM with nitrogen added. It calculates net N-mineralisation and adds parameters for C-to-N ratios and soil organisms as well as organism efficiency - nine parameters in all; (2) ICBM/2N, which gives a more precise description of the initial stages of decomposition by splitting the 'Young' pool into two. (3) ICBM/2BN, where organism biomass C and N is explicitly modelled. The models are easily programmed in spreadsheets and can be found at http://www.mv.slu.se/vaxtnaring/olle/ICBM.html.

Mathematical models (Alvarez & Alvarez, 2000)

Objectives: (i) to establish the relationships between carbon in soil density fractions with carbon mineralisation and the microbial biomass under contrasting conditions, (ii) to compare the goodness of fit of different mathematical models to describe carbon mineralisation, and (iii) to evaluate the relationships of the SOM pools and the mineralisation parameters estimated by the best kinetic model. Microbial biomass was highly correlated with total carbon (r(2) = 0.777, P < 0.001) and carbon in the SOM light density fraction (density < 1.59 g mL⁻¹) but less strongly correlated to medium (density 1.59 - 2.0 g mL⁻¹) and heavy (density > 2.0 g mL⁻¹) soil fractions.

2.3 General remarks

Most models for the turnover of soil organic matter (SOM) include a compartment that is either considered inert, or has a very slow turnover time (refractory SOM; RSOM), The RSOM content of soils varies markedly between sites, and knowledge of its size and variability are essential for determining whether soils behave as sources or sinks of atmospheric CO₂. It has also been suggested that the accurate specification of RSOM pools is essential to modelling studies, and that uncertainty in estimates of the size of RSOM pool could be a major source of error in modelling soil organic C. Falloon & Smith (2000) review most current SOM models and approaches to modelling the refractory SOM. They conclude that only models that account for the protection of SOM (see Hassink & Whitmore, 1997) are able to give insight into stabilisation of SOM. Since it is the slow SOM pools that determine C-sequestration, it is important to experimentally identify this pool. Also the collection and critical analyses of long-term ¹⁴C and ¹³C data are essential for the development of better models, by linking measured pools to the conceptual pools in the models.

In general, modelling carbon cycles in terrestrial ecosystems requires sufficient knowledge about the interactions with nutrient cycles. For example, Gifford *et al.* (1996) present a model of the interacting global carbon and nitrogen cycles (CQUESTN). It is developed to explore the possible history of C-sequestration into the terrestrial biosphere in response to the global increases in atmospheric CO_2 concentration, temperature and N-deposition. As for all such simulation models, uncertainties in both data and functional relationships render it more useful for qualitative evaluation than for quantitative prediction (Gifford *et al.* 1996). Given the disparity of plant and microbial C-to-N, the modelled impact of anthropogenic N-deposition on C-sequestration depends substantially on whether the deposited N is initially taken up by plants or by soil microorganisms. Assuming the latter, standard-model net sequestration in 1995 was 0.2 Gt C in 1995 from the N-deposition effect alone.

Combining the effects of the historic courses of CO_2 , temperature and N-deposition, the standard-model gave C-sequestration of 3.5 Gt in 1995. This involved an assumed weak response of biological N-fixation to the increased carbon status of the ecosystem. For N-fixation to track ecosystem C-fixation in the long term however, more phosphorus must enter the biological cycle. New experimental evidence shows that plants in elevated CO_2 have the capacity to mobilise more phosphorus from so-called 'unavailable' sources using mechanisms involving exudation of organic acids and phosphatases (Gifford *et al.* 1996).

3.

Experimental data on Plant LITTER decomposition: a literature overview

Terrestrial carbon sequestration is regarded as an essential element in sustainable soil (quality) management (Carter 2002) as well as in climate (change) management (Arp *et al.* 1997; Heal *et al.* 1997). Climate is defined as the overall average of long-term (>30 yr) weather conditions. The general opinion (IPCC 2000) is that the current rise in global CO_2 and temperature has - at least partially - an anthropogenic cause. Therefore, one would expect to find long-term (ca 30 yr) studies on factors involved in terrestrial carbon sequestration. Surprisingly, very few long-term studies have been found in the literature (35 yr; Hyvönen *et al.* 1996), some having a duration of 5-10 years (e.g. Breland & Eltun 1999; Jastrow *et al.* 2000; Niklaus *et al.* 2001; Six *et al.* 2001).

3.1 Litter quality: Its Influence on decomposition and C sequestration

Definitions of terms

'Litter' is generally used for above-ground plant residues, but here it is also used for below-ground plant residues including exudates and dead roots.

'Quality' is a many-sided term, it depends on function [e.g. increasing soil fertility or soil C-sequestration] and in this sense is subjective (Whitmore and Handayanto 1997). Here, quality of litter is defined as the physical and/or chemical characteristics of plant litter (Paustian et al. 1997), which includes all dead plant material, also roots and root exudates. Typically, the contents of water- or ethanol-soluble components of litters are used as measures of easily degradable material, while the fibre fractions are considered to be more difficult to decompose or to have decomposition-modifying properties (Marstorp 1997).

3.1.1 Effect of quality

Quality component	Quality attribute	Process affected	Model Parameter
Chemical	Bond strength/energy	Growth rate, energy yield	μ, e
	Bond complexity	Exoenzyme efficacy	k _s
Physical	Particle size	Soil resources, abiotic	μ,
	Physical occlusion	Enzyme accessibility	k _s , e
Inhibitory	Interference	Exoenzyme efficacy	k _s
	Antibiotic	Growth rate	μ

Table 3.1.1. Categories of litter quality components and possible interpretation in terms of microbial growth kinetics (Paustian et al. 1997).

Model parameters: relative growth rate, µ; energy yield, e; enzyme efficacy, ks

Especially through the use of state-of-the-art labelling (e.g. ¹³C/¹⁴C steady-state labelling) and detection techniques (Isotope ratio mass spectroscopy, IRMS and nuclear magnetic resonance, NMR) more knowledge is now available not only on the (net) fluxes of litter decomposition and C-sequestration in soils, but also on the gross fluxes of the component processes (e.g. Lin *et al.* 2001; Loiseau & Soussana 1999; several contributions in Cadisch & Giller 1997). This increased our understanding of the effects of global climate and other factors on terrestrial carbon sinks.

For instance, in search of the chemical nature of stable soil carbon fractions, Hopkins & Chudek (1997) have shown by the use of NMR that the main type of C found in slowly degrading soil fractions is methyl-C and alkyl-C.

Terrestrial carbon sequestration is affected by: i) litter quality and quantity (Paustian *et al.* 1997; Arp *et al.* 1997), ii) N fertilisation (Paustian *et al.* 1997) and iii) the rate of litter production or application. The decomposition of litter is mainly governed by the rate of lignin decomposition, and this rate, in turn, is increased by a high cellulose content and decreased by a high N content (Heal *et al.* 1997). This is the case for most types of litter, including forest-litter, wood, straw, and many other substances. The effects of atmospheric CO_2 level and temperature are less clear, as will be shown below.

Studies on litter quality and decomposition and stability of the residues all confirm their strong relation (Heal *et al.* 1997; Magid *et al.* 1997; Sinsabaugh & Moorhead 1997; Whitmore & Handayanto 1997). However, ecological interactions between decomposing organisms (microbial biomass) and the physico-chemical environment (N, CO₂, temperature) are essential for understanding the effects of litter quality. In decomposition modelling studies, various litter quality parameters have been proposed and evaluated.

Table 3.1.2. The main factors determining litter decomposition rates, from a compilation of data in the literature (Paustian et al. 1997).

Main factors in litter decomposition

1. Litter quality and quantity (see Table 3.1)

2. Interaction with microorganisms

3. Interaction with physico-chemical environment

Soil C-sequestration is – in contrast to 'primary' short-term decomposition - only studied in some of the models on litter decomposition (Paustian *et al.* 1997). These authors describe and discuss three models that do so: the Rothamsted model, the Century model, and the Q-model. Litter quality in these models is expressed as:

- a) the proportion of total litter in the resistant fraction (Rothamsted),
- b) the lignin and N contents (Century), and
- c) fractions of soluble extractives, acid solubles and acid insolubles (Q).

It is important to notice that physical and inhibitory aspects affecting decomposition are not included in these models. In the following paragraphs the results of a literature search for data on the parameters used by Verberne *et al.* (1990) in their decomposition model is presented, i.c. the main input parameters (after Van Veen & Paul 1981):

- DPM (Decomposable Plant Material, e.g. solutes like proteins, amino acids, carbohydrates, etc.)

- SPM (Structural Plant Material, e.g. (hemi-)cellulose),

- RPM (Resistant Plant Material, e.g. lignified structural material).

These materials are degraded to various extents, releasing CO₂, and the residues transforming into the pools: POM, Protected Organic Matter, and NOM, Non-protected Organic Matter, and SOM, Stabilised Organic Matter (Verberne *et al.* 1990).

The ratio of N-to-lignin and other secondary compounds is a widely used as a measure of decomposability of litter (Arp *et al.* 1997).

Carbon sequestered in soils may occur in the soil C pools POM and SOM.

The relationship between model parameters and available literature data will be indicated in the following overview (underlining parameters in the text). Data are included on effects of temperature and atmospheric CO_2 partial pressure as these are the main abiotic factors influencing litter decomposition and soil C-sequestration (or long-term soil C balance).

Table 3.1.3 shows a clear example of the effect of the quality of organic matter amendments to the soil on carbon sequestration in a long-term field experiment in Uppsala, Sweden, started in 1956.

Table 3.1.3.	Effect of residue quality on soil C sequestration. Data are from a long-term (35 yr) field experiment in
	Uppsala, Sweden, showing the effect of plant residue quality (twice a year added at 185 g C m^2 yr ¹)
	on soil carbon sequestration (modified after Paustian et al. 1997; data from Hyvönen et al. 1996).
	Modelling data are based on the Q-model.

Residue Quality	Soil Carbon Sequestration (kg C m ² yr ⁻¹)		
	Experimental	Modelled	
Straw	0.04	0.04	
Green manure	0.03	0.03	
Farmyard manure	0.06	0.05	
Sawdust	0.05	0.04	
Sewage sludge	0.13	0.10	
Peat	0.13	0.13	

Giardina *et al.* (2001) argue that terrestrial ecosystem models assume that high quality litter leads to the formation of high quality organic C and N in mineral soil, and that increased soil clay content decreases soil C and N mineralization rates. According to the authors, few studies in forests, however, have examined the effects of initial litter quality and clay content on C mineralization rates (g C kg⁻¹ soil C) and net N mineralization rates (g N kg⁻¹ soil N) in soil. They used 16-months laboratory incubations of mineral soil sampled from stands of lodgepole pine (*Pinus contorta* Dougl. ex loud ssp. *latifolia*) and aspen (*Populus tremuloides* Michx.) that varied in clay content (70 to 390 g kg⁻¹ soil) to examine how soil C and N mineralization rates relate to initial litter quality and soil texture. Aspen litter quality (C-to-N = 52-71; lignin-to-N = 26) was higher than pine litter quality (C-to-N = 82-111; lignin-to-N = 40-57), but pine soils released an average of 238 g C kg⁻¹ soil C over 16 months compared with 103 g C kg⁻¹ soil C for aspen soils. Higher microbial biomass (mg kg⁻¹ soil C) under pine also indicates that pine soil C was of higher quality than aspen soil C. Net N mineralization rates did not relate to species or to soil C mineralisation rates.

Litter quality and decomposition rate: methodology

Several attempts have been made to quantify residue quality and its relationship with residue decomposition, mostly in terms of N-mineralisation (Vanlauwe *et al.* 1997), clearly from the viewpoint of application of plant residues as a source of nutrients.

It is still questionable whether a decomposition rate, defined in terms of N-mineralisation, may also be used as an estimate of C-mineralisation.

The aim of the present study is focussed on the opposite of mineralisation of nutrients -i.c. immobilisation of residues. Thus, from the viewpoint of C sequestration of soils under a changing climate, the focus is on C-mineralisation as a measure of immobilisation.

Litter quality, decomposer biota and decomposition rate

According to Arp *et al.* (1997) three aspects relate soil and decomposer functioning (at an elevated CO₂ concentration): i). The amount of nutrients in litter and the availability to microbes during microbial production and decomposition; ii). The quality of the soil organic matter produced or used as substrate by microbes and; iii). The composition of the decomposer community. Tian *et al.* (1997) provide some information showing that there is an interaction of carbon decomposition with presence of decomposer biota; sweet chestnut litter (data by Coûteaux *et al.* 1991) with a C-to-N ratio of 40 was decomposed at a rate 2.5 times the rate of litter with C-to-N of 75, in the presence of

microflora + protozoa (MP), but this difference was absent in the presence of MP + nematodes +/-collembola +/- isopods.

This role of decomposer biota may be one explanation of the observation that litter C-to-N ratio is not an appropriate general indicator for the quality and decomposition rate of litter (Gorissen & Cotrufo 2000, Sowerby *et al.* 2000; Van Ginkel *et al.* 2000; Ross *et al.* 2002). Similar data for grassland systems are not available in the literature, to our knowledge.

Table 3.1.4.	A compilation of data from the literature (Tian et al. 1997; Coûteaux et al. 1991) showing the effect
	of decomposer biota on decomposition.

Sweet chestnut litter C-Decomposer biota to-N		Carbon Total CO ₂ released (% of initial content)	Decomposition Total CO ₂ released (mg per unit)	Faunal contribution (%)	
High (75)	Р	10	196	_	
	NP	20	411	52	
	CNP	26	536	63	
	ICNP	31	643	69	
Low (40)	Р	24	491	-	
	NP	23	470	-5	
	CNP	22	450	-9	
	ICNP	24	483	-2	

P, microflora + protozoa; NP, P + nematodes; CNP, NP + collembola; ICNP, CNP + isopods.

3.1.2 Effects of elevated atmospheric CO₂ and temperature

Note on terminology

Whereas in modelling studies the term SOM (Soil Organic Matter) is used because this term also includes the nutrient content ('quality') of the organic matter, SOC (Soil Organic Carbon) is more often used in the context of experimental sequestration studies. SOC and SOM both refer to the same soil organic compounds, but their units differ in the sense that the weight of either carbon (C; SOC) or total organic matter (SOM) is expressed per kg of soil. SOC is generally about 40-50% of SOM, but it varies with SOM type. Thus, SOC is not necessarily a fixed fraction of SOM.

The effect of atmospheric CO_2 level on soil organic carbon content (SOC) in the long term is not clear in the literature, mainly due to uncertainty about the effects of elevated CO_2 on plant residue quality, which is of prime importance for carbon decomposition and thus carbon sequestration. Some authors report changes in plant residue quality under elevated CO_2 , while others don't. Traditionally, plant residue quality has been described by the terms 'primary' and 'secondary metabolites' (or compounds), where the term 'secondary' implies that such compounds are only of minor importance to the plant. Examples are alkaloids, lignin, polyphenols, terpenes. However, in recent years this opinion has been gradually replaced by the view that, for instance, many phenolic compounds play an essential role in the regulation of plant growth, development, and interaction with other organisms (Raskin 1995; Heal *et al.* 1997).

Arp *et al.* (1997) conclude that elevated CO_2 has little effect on C-to-N ratio and level of secondary metabolites (SM), resulting in minor changes of litter decomposability (based on N to SM ratio) under elevated CO_2 . This conclusion is supported by Hirschel *et al.* (1997) for alpine, temperate and tropical systems (short-term, i.e. 61-day exposure period).

However, Van Ginkel *et al.* (2000) report a lower decomposition rate of SOM under elevated CO_2 , which in their system was not caused by a lower substrate use efficiency of the micro-organisms. Torbert *et al.* (1998) conclude

that, although changes to both plant residue quality and quantity caused by elevated CO_2 concentration affected C cycling in soil, residue quality may be more important for determining C storage. They argue that understanding N cycling in soils is fundamental to understanding potential C sequestration in terrestrial ecosystems. However, little information is available in the literature, even more so regarding long-term studies.

In one relatively 'long-term' (8 yr) study, Jastrow *et al.* (2000), report significant changes in grassland N dynamics in response to CO_2 enrichment, which were –however- too small to lead to changes in plant growth. The mostly root-like, light POM (density < 1.8 Mg m³) appeared to turn over more rapidly, while the more amorphous and rendered heavy POM (density >1.8 Mg m³) accumulated under elevated (CO_2). Overall, rhizome and root C-to-N ratios were not greatly affected by CO_2 enrichment. However, elevated CO_2 increased the C-to-N ratios of root litter and POM in the surface 5 cm and induced a small but significant increase in the C-to-N ratio of the silt/clay fraction to a depth of 15 cm. Their data suggest that 8 years of CO_2 enrichment may have affected elements of the N cycle (including mineralisation, immobilisation, and asymbiotic fixation) but that any changes in N dynamics were insufficient to lead to significant plant growth responses.

Niklaus *et al.* (2001a) report no increase in SOC after six years of growth of a calcareous grassland under CO_2 enrichment, while newly fixed C did not enter the stable micro-aggregate fractions. Niklaus *et al.* (2001b) report conflicting results of labelling vs C-exchange studies; CO_2 enrichment leads to a shift towards more small, stable aggregates in the SOC, without affecting total SOC.

Gorissen & Cotrufo (2000) provided evidence that elevated CO_2 has the potential to increase soil C stores in grassland via increasing C uptake and shifting C allocation towards the roots, with an inherent slower decomposition rate than the leaves. An overall increase of 15% in ¹⁴C remaining after 222 days was estimated for the combined tissues, i.e., the whole plants; the leaves made a much smaller contribution to the C remaining (+ 6%) than the roots (+ 26%). This shows the importance of clarifying the contribution of roots and leaves with respect to the question whether grassland soils act as a sink or source for atmospheric CO_2 (See also: Conant *et al.* 2001).

Berntson & Bazzaz (1996) present a conceptual model of integrated plant-soil interactions which illustrates the importance of identifying the primary below-ground feed-backs, both positive and negative, which can simultaneously affect plant growth responses to elevated CO₂.

The primary negative feed-backs share the common feature of reducing the amount of nutrients available to plants. These negative feed-backs include

- 1. increased litter C-to-N ratios, and therefore
- 2. reduced mineralisation rates,
- 3. increased immobilisation of available nutrients by a larger soil microbial pool, and
- 4. increased storage of nutrients in plant biomass and detritus due to increases in net primary productivity (NPP).

Most of the primary positive feedbacks share the common feature of being plant mediated feedbacks, the only exception being Zak *et al.*'s hypothesis that

- 1. increased microbial biomass will be accompanied by increased mineralisation rates.
- 2. plant nutrient uptake may be increased through alterations in root architecture, physiology, or mycorrhizal symbioses. Further,
- 3. the increased C-to-N ratios of plant tissue mean that a given level of NPP can be achieved with a smaller supply of nitrogen.

Identification of the plant-soil feedbacks to enhanced productivity with elevated CO_2 are a critical first step for any ecosystem. It is necessary, however, that they first identify how universally applicable the results are from one study or one ecosystem before ecosystem models incorporate this information. The effect of elevated CO_2 on plant growth (including NPP, tissue quality, root architecture, mycorrhizal symbioses) can vary greatly for different species and environmental conditions. Therefore it is reasonable to expect that different ecosystems will show different patterns of interacting positive and negative feedbacks within the plant-soil system. This inter-ecosystem variability in the potential for long-term growth responses to rising CO_2 levels implies that we need to parameterise mechanistic models of the impact of elevated CO_2 on ecosystem productivity using a detailed understanding of each ecosystem of interest. Ross *et al.* (1996) investigated the effects of elevated CO₂ (525 and 700 uL L⁻¹), and a control (350 uL L⁻¹ CO₂), on biochemical properties of a Mollic Psammaquent soil in a well-established pasture of C3 and C4 grasses and clover, with continuously moist turves in growth chambers over four consecutive seasonal temperature regimes from spring to winter inclusive. The continuously moist turves were then pulse-labelled with ¹⁴CO₂ to follow C pathways in the plant/soil system during 35 days. Below-ground net productivity at the end of these seasons' averaged 465, 800 and 824 g m⁻² in the controls, 525 and 700 uL L⁻¹ treatments, respectively (an increase by about 70%). In continuously moist soil, elevated CO₂ had no overall effects on total, extractable or microbial C and N, or invertase activity, but resulted in increased CO₂ production from soil, and from added herbage during the initial stages of decomposition over 21 days; rates of root decomposition were unaffected. CO₂ produced h⁻¹ mg⁻¹ microbial C was about 10% higher in the 700 uL L⁻¹ CO₂ treatment than in the other two treatments. Combined, these data suggest an increase in C sequestration at elevated CO₂.

Elevated CO_2 had no clearly defined effects on N availability, or on the net N mineralisation of added herbage. In the labelling experiment, relatively more ¹⁴C in the plant/soil system occurred below ground under elevated CO_2 , with enhanced turnover of ¹⁴C also being suggested. Drying increased levels of extractable C and organic-N, but decreased mineral-N concentrations; it had no effect on microbial C, but resulted in lowered microbial N in the control only. In soil that had been previously 'summer'-dried, CO_2 production was again higher, but net N mineralisation was lower, under elevated CO_2 than in the control after 'autumn' pasture growth. Over the trial period of 422 days, elevated CO_2 generally appears to have had a greater effect on soil C turnover than on soil C pools in this pasture ecosystem.

Elevated concentrations of atmospheric CO_2 can influence the relative proportions, biomass and chemical composition of plant species in an ecosystem and, thereby, the input of litter nutrients to soil.

Plant growth under elevated CO_2 appears to have no consistent effect on rates of litter decomposition; decomposition can, however, differ in C3 and C4 plant material from the same CO_2 environment. We here describe the decomposability of leaf litter of two grass species - the C3 *Holcus lanatus* L. and C4 *Pennisetum clandestinum* Hochst. - from an unfertilised, ungrased grassland at a cold CO_2 spring in Northland, New Zealand. Decomposability was measured by net CO_2 -C production from litter incubated for 56 days at 25°C in a gley soil from the site; net mineral-N production from litter was also determined. Both litter and soils were sampled under 'low' and 'high' concentrations of atmospheric CO_2 . Decomposition of *H. lanatus* litter was greater than that of *P. clandestinum* litter throughout the 56-day incubation. Decomposition tended to be greater in 'high- CO_2 ' than in 'low- CO_2 ' *H.* lanatus litter, but lower in 'high- CO_2 ' than 'low- CO_2 ' *P. clandestinum* litter; differences were, however, non-significant after 28 days. Overall, litter decomposition was greater in the 'low- CO_2 ' than 'high- CO_2 ' soil.

Differences in decomposition rates were related negatively to litter N concentrations and positively to C-to-N ratios, but were not predictable from lignin-to-total N ratios. Net mineral-N production from litter decomposition did not differ significantly in 'high- CO_2 ' and 'low- CO_2 ' samples incubated in 'low- CO_2 ' soil; in 'high- CO_2 ' soil some net immobilisation was observed. Overall, the results of Ross *et al.* (2002) indicate the likely complexity of litter decomposition in the field but, nevertheless, strongly suggest that rates of decomposition will not necessarily decline in a 'high- CO_2 ' environment.

Temperature rise increased death rates of roots in a 1.5-year study with an upland grassland system in UK (Fitter *et al.* 1999). Root production is not affected, but is closely related to PAR (Photosynthetic Active Radiation). Thus, root production acclimates to temperature, while root death rate does not. As a result, SOC may increase or decrease with temperature, depending on the quality of the root litter and PAR.

Very few experimental data are available in the literature on SOC fluxes in relation to temperature (Breymeyer *et al.*, 1995). Studies generally concern forest soils or conversions of forest soil to arable land or pasture (e.g. Golchin *et al.* 1995). Thus, the few data available, dealing with other agro-ecosystems than grasslands, suggest that the various components of SOC flux respond differently to elevated CO_2 and temperature. Therefore, in view of the large global grassland area and recent data on the C sequestration potential of grasslands (Van Ginkel 1999), it seems important to study these SOC fluxes in grasslands. However, studies on other agro-ecosystems than grasslands may yield some indication of effects to be expected for grasslands.

Edwards and Norby (1998) studied below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO_2 enrichment and elevated air temperature, during a period of three years. Mineral soil respiration in root-exclusion zones averaged 12% higher in the high temperature treatments than at ambient temperature, but was not affected by CO_2 treatments.

The fraction of total efflux attributable to root + rhizosphere respiration ranged from 14 to 61% in measurements made around red maple plants, and from 35 to 62% around sugar maple plants. In both 1995 and 1996 root respiration rates of red maple were highest in high-CO₂ treatments and lowest in high temperature treatments. Specific red maple root respiration rates of excised roots from near the soil surface in 1996 were also highest under CO₂ enrichment and lowest in high temperature treatments. In sugar maple the highest rates of CO₂ efflux were from around the base of plants exposed to both high temperature and high-CO₂, even though specific respiration rates were lowest for this species under the high temperature and CO₂ enrichment regime. In both species, patterns of response to treatments were similar in root respiration and root mass, indicating that the root respiration responses were due in part to differences in root mass. The results underscore the need for separating the processes occurring in the roots from those in the forest floor and mineral soil in order to increase our understanding of the effects of global climate change on carbon sequestration and cycling in the below-ground systems of forests.

Many studies show that plants and soil processes can respond to altered climates in a transient way. During 2 years, Lin *et al.* (2001) studied time-dependent responses of soil CO_2 efflux components to elevated atmospheric (CO_2) and temperature in experimental forest mesocosms in Arizona using stable isotope techniques. They found contrasting effects on soil CO_2 effluxes in the two successive years. They partitioned soil CO_2 efflux into three source components (rhizosphere respiration, litter decomposition, and soil organic matter (SOM) oxidation) using experimental chambers planted with Douglas-fir seedlings. The components responded differently to elevated CO_2 (ambient + 200 umol mol⁻¹) and elevated temperature (ambient + 4 °C) treatments during the first year.

Rhizosphere respiration increased most under elevated CO_2 , and SOM oxidation increased most under elevated temperature. Total soil CO_2 efflux increased significantly under elevated CO_2 and elevated temperature in both years (1994 and 1995), but the enhancement was much less in 1995. Rhizosphere respiration increased less under elevated temperature in 1995 compared with 1994. Litter decomposition also tended to increase comparatively less in 1995 under elevated CO_2 , but was unresponsive to elevated temperature between years. In contrast, SOM oxidation was similar under elevated CO_2 in the 2 years. Less SOM oxidation occurred under elevated temperature in 1995 compared with 1994. The results indicate that temporal variations can occur in CO_2 production by the sources. The variations likely involve responses to antecedent physical disruption of the soil and physiological processes.

Owensby (1993) studied potential impacts of elevated CO_2 on above- and belowground litter quality of a tallgrass prairie. Data from a tallgrass prairie which was subjected to increased CO_2 for a 4-year period on above- and belowground biomass accumulation, litter and forage quality, water relations and microbial biomass and respiration were analysed. Only C4 plants are limited by elevated CO_2 levels and as tallgrass prairie has a high C3 component, increased CO_2 should increase biomass production. When water was limiting C3 plants still increased their productivity and water use efficiency. N use efficiency was also increased as there was a reduced requirement for N. As CO_2 increased and plant tissue N content reduced, soil OM had reduced N concentrations. Increased plant fibre contents led to higher C-to-N ratios and higher microbial biomass C and N and soil respiration. Digestibility of forage from CO_2 enriched crops was lower than in ambient CO_2 plots.

3.1.3 Effect of management on decomposition and litter quality

Soil organic matter (SOM) is considered as a key indicator of sustainability (Whitbread *et al.* 2000; Carter 2002). The terrestrial carbon pool has been identified as a significant controlling factor of atmospheric CO_2 level and the global carbon cycle (Arp *et al.* 1997; Heal *et al.* 1997). Increasing terrestrial carbon sequestration in arable soils may therefore be expected to contribute both to sustainable agriculture and to diminishing atmospheric CO_2 levels. Management measures such as nitrogen fertilisation and tillage may have large effects on litter quality and decomposition processes and carbon fluxes in soil (e.g. see Table 3.1.5).

Nitrogen fertilizing and soil carbon sequestration

An enhanced sequestration of soil organic matter (SOM) which would counteract the increasing CO_2 concentration in the atmosphere, requires a simultaneous net input of N into the system or a shift (increase) in the C-to-N ratio of SOM (Arp *et al.* 1997). Few studies appear to be dealing with all these aspects. It seems clear, however, that N supply rate will affect turnover rates of soil C pools. Fertilising (adding nitrogen) various types/qualities of organic materials increased SOC in a long-term field experiment in Uppsala, Sweden (Table 3.1.5; Paustian *et al.* 1997). This increase in SOC (as % of C added) over 35 years decreased in the following order: peat (75%), sewage sludge (65%), farmyard manure or sawdust (30%), straw or green manure (20%).

Residue	Soil carbon sequestration (kg C m ⁻² yr ⁻¹)			
_	Expe	rimental	Мо	delled
	0 N	N fertiliser	0 N	N fertiliser
None	-0.03	-0.03	-0.03	-0.03
Straw	0.00	0.02	0.02	0.03
Green manure	0.01	n.d.	0.02	n.d.
Farmyard manure	0.03	n.d.	0.03	n.d.
Sawdust	0.01	0.03	0.01	0.03

 Table 3.1.5.
 Effect of residue quality on soil C sequestration. Data are from a long-term (35 yr) field experiment in Uppsala, Sweden, showing the effect of plant residue quality (twice a year added at 185 g C m² yr¹) and N fertiliser supply (no data provided) on soil carbon sequestration (modified after Paustian et al. 1997). Modelling data are based on the Century-model. n.d., no data.

Loiseau and Soussana (1999) report the effects of N supply on the turnover of below-ground carbon in a 2.5 year experiment with a temperate grassland ecosystem exposed to elevated CO_2 and temperature. There were two N fertiliser supplies, 160 (N-) and 530 (N+) kg N ha-1 y-1. Elevated CO_2 stimulated the turnover of organic C in the roots and stubble and in the macro-organic matter >200 um (MOM) at N+, but not at N-. At the high N supply, the mean replacement time of 'old' C by 'new' C declined in elevated, compared to ambient (CO_2), from 18 to 7 months for the roots and stubble and from 25 to 17 months for the MOM. This resulted from increased rates of 'new' C accumulation and of 'old' C decay. By contrast, at the low N supply, despite an increase in the rate of accumulation of 'new' C, the soil C pools did not turnover faster in elevated CO_2 , as the rate of 'old' C decomposition was reduced. A 3°C temperature increase in elevated CO_2 decreased the input of fresh C to the roots and stubble and enhanced significantly the exponential rate for the 'old' C decomposition in the roots and stubble. An increased fertiliser N supply reduced the carbon turnover in the roots and stubble and in the roots and stubble and enhanced

Root exudation has been hypothesised as one possible mechanism that may lead to increased inputs of organic C into the soil under elevated atmospheric CO_2 , which could lead to greater long-term soil C storage (Uselman *et al.* 2000). These authors studied effects of increased atmospheric CO_2 , temperature, and soil N availability on root exudation of dissolved organic carbon by the N-fixing tree *Robinia pseudoacacia* L. They report that elevated CO_2 did not affect root exudation of organic C. A 4°C increase in temperature and N fertilisation did, however, significantly increase organic C exudation rates. Approximately 60% of the exudate decomposed relatively rapidly, with a turnover rate of less than one day, while the remaining 40% decomposed more slowly. The results suggest that warmer climates, as predicted for the next century, may accelerate root exudation of organic C, which will probably stimulate rapid C cycling and may make a minor contribution to intermediate to more long-term soil C storage. However, as these losses to root exudation did not exceed 1.2% of the net C fixed by *Robinia pseudoacacia* (Uselman *et al.* 2000), root exudation of organic C appears to have little potential to contribute to long-term soil C sequestration.

Tillage and soil carbon sequestration

Organic matter decomposition rates can be greatly affected by soil management according to Reicosky (1997) who reports a three-fold reduction of C-mineralisation (measured as CO_2 loss from the soil) by conservation tillage as compared to the traditional moldboard plow. In a review, Lal (1997) concludes that conservation tillage (any form of tillage that maintains at least 30% of the soil surface covered by residue) is an important tool for crop residue management and for enhancing C sequestration in soil. This author estimates SOC to increase by 0.01% yr¹ by conservation tillage.

No tillage systems increase C sequestration and size of the labile SOC pool (Franzluebbers *et al.* (1998), caused by a lower rate of soil C evolution. Sequestration of crop derived C into SOC was about 22% under no tillage, compared to 9% under conventional tillage. However, in contrast to these findings, Campbell *et al.* (1999) report no difference in total SOC after a 12-yr experiment comparing no tillage with conventional tillage.

3.1.4 Conclusions

Some conclusions on the potential role of litter quality and litter quantity (as affected by elevated CO_2) on soil organic carbon (SOC) sequestration and microbial biomass:

- 1. Litter quality (although not expressed as C-to-N ratio) is often significantly affected by CO₂ level leading to increased sequestration (Van Ginkel *et al.* 2000; Gorissen & Cotrufo 2000), but this varies with plant species and is not the general rule (Ross *et al.* 2002).
- Litter quality is little affected by CO₂ level (Arp *et al.* 1997; Hirschel *et al.* 1997); its digestibility is decreased (Owensby 1993). Litter quality might be more important than litter quantity (Torbert *et al.* 1998; Jastrow *et al.* 2000), but: litter quantity is more important for C sequestration than litter quality (Burket & Dick 1997; Van Ginkel, 1999)
- 3. SOC turnover is more affected by CO₂ level than SOC pool size (Ross *et al.* 1996; Niklaus *et al.* 2001ab)
- 4. Knowledge of soil N cycling is the key to understanding C sequestration in soils (Torbert *et al.* 1998, Jastrow *et al.* 2000).
- Microbial biomass is increased by elevated CO₂ (Berntson & Bazzaz 1996; but negative feedback through nutrient immobilization; Diaz *et al.* 1993) or is not affected (Ross *et al.* 1996; Heal 2001; Frederiksen *et al.* 2001; Kandeler *et al.* 1998).

3.2 Microbial activity: its role in organic matter decomposition in relation to temperature, elevated CO₂, and soil factors

'Microbial activity' (MA) may be defined in various ways. Respiration (CO_2 evolution) can be used as a measure of MA and amounts decomposed, although part of the decomposed substrate is also used for microbial synthesis. Alternatively, MA is measured as mass loss or change in chemical composition, as in the litterbag method (Marstorp 1997), where –however- soil fauna and leaching also contribute to 'MA'.

The contribution of MA to decomposition of deciduous leaf material may vary widely, e.g. between 70% on a dry site, and 18% on a wet site of alder (Wachendorf *et al.* 1997). For ryegrass shoots, respiration rate (or MA) increases linearly with the content of carbohydrates and amino acids in the shoots.

3.2.1 Effects of increased temperature

In CO_2 efflux in a planted soil that is equilibrium equals the C input by litter and roots. An increase in temperature stimulates decomposition of organic matter (Lundegårdh 1927, Kirschbaum 1995). Jenkinson *et al.* (1991) & Thornley *et al.* (1991) showed that this will lead to lower soil organic matter levels when the higher decomposition is not compensated by extra input though litter fall or rhizosphere deposition. When there is an extra carbon input e.g.

caused by stimulated photosynthesis and increased carbon allocation to the soil, the soil may turn from a source into a sink, especially when decomposition rates of this extra carbon input decrease through changes in quality (Van Ginkel *et al.* 1999).

An increased decomposition at higher temperatures can often not be described by a simple relationship. There is no consensus about the relationship between decomposition of soil organic carbon pools and temperature. In literature we find:

- linear functions (Gupta & Singh, 1981; Van der Linden *et al.*, 1987; Whitmore *et al.*, 1997)
- power functions (Kucera & Kirkham, 1971)
- s-shaped functions (De Neve et al. 1996)
- Arrhenius-functions (Lloyd & Taylor, 1994; Fang & Moncrieff, 2001)
- Q₁₀-relations. A Q₁₀-relation of 2 means that a process rate doubles when the temperature is increased by 10°C. This Q₁₀-relation is often used in model studies.

Kirschbaum (1995) has reviewed this Q10-relation and presented the following data:

Temperature (°C)	Q_{10}
8	4.5
20	2.5

Kätterer et al. (1998) came with other results after analyses of literature data:

Temperature (°C)	Q ₁₀
5-35	2

The underlying causes of these differences are not clear. Kätterer *et al.* (1998) indicate that this Q_{10} may strongly diverge depending on the substrate (or litter quality). The value 2 is according to these authors not reliable below 5°C and above 35°C.

Boone *et al.* (1998) suggest that the sensitivity to temperature (e.g. Q_{10}) of soil respiration is much affected by roots. They determine that the Q_{10} value (the coefficient for the exponential relationship between soil respiration and temperature, multiplied by 10) is 4.6 for autotrophic root respiration plus rhizosphere decomposition, 2.5 for respiration by soil lacking roots and 3.5 for respiration by bulk soil. If plants in a higher-CO₂ atmosphere increase their allocation of photosynthate to roots, these findings suggest that soil respiration should be more sensitive to elevated temperatures, thus limiting carbon sequestration by soils.

According to Kätterer *et al.* (1998) lignin decomposers would have a different temperature dependence than other functional microbial groups. Bardgett *et al.* (1999) found an increased number of fast-growing Gram-positive bacteria using PLFA-analyses (fatty acids) after 3 months growth at a 2°C increased temperature. After 9 months, these

Conclusions:

- Between 15-30°C a Q₁₀-value of 2-2.5 is well established
- Outside this range, the Q₁₀-value becomes more uncertain, but is presumably greater between 0-15°C.

This variation in Q₁₀-value is linked with differences in temperature dependence of the soil microbial population.

Besides these intrinsic differences in response of the soil microbial population to increased temperature, external factors may cause interactions with temperature.

Bardgett *et al.* (1999) did not find effects of increased temperature on respiration and N mineralisation in low nutrient soils and ascribed this to the limiting effect of nutrients on soil microbial activity. Similar effects may be expected from other external factors like soil moisture and pH.

differences had disappeared. Slower growing species did not respond, according to the authors, due to the low soil nutrient status.

On the other hand, Zogg *et al.* (1997) reported a clear shift in population composition using PLFA-analyses, but they applied a higher temperature in their experiment (25°C). Klironimos *et al.* (1996) also found a shift in the functional composition microbial population using Biolog plates. Nutrients were not limiting in their experiments.

Despite some reports on changes in the microbial population at a higher temperature, Tinker & Ineson (1990) and Bardgett *et al.* (1999) argue that the composition of the microbial population, in contrast to its activity (see above), doesn't change dramatically with small changes in temperature because of the wide temperature spectre of most species and a broad temperature optimum.

3.2.2 Effects of elevated CO₂

Decomposition of organic matter and microbial activity and in relation to elevated CO₂

Elevated CO_2 often decreases decomposition of plant litter. Usually, this effect is ascribed to an increase in C-to-N ratio of the plant materials involved (Norby *et al.*, 1986; Coûteaux *et al.*, 1991; Cotrufo *et al.*, 1998). Changes in litter quality have led to the hypothesis that decomposition rates of plant litter may subsequently change (Strain & Bazzaz, 1983). Although some studies confirmed this hypothesis (Cotrufo *et al.*, 1994; 1996), the majority seems to dismiss it at present (Norby and Cotrufo, 1998). Although decomposition of roots is often decreased by elevated CO_2 (Gorissen *et al.*, 1995; Van Ginkel *et al.*, 1996; Van Ginkel & Gorissen, 1998), without any relationship with C-to-N ratios, Loiseau & Soussana (1999) reported that elevated CO_2 increased the C-to-N-ratio of the roots and macro-organic matter (undecomposed or partly decomposed roots. They were also able to reduce the C-to-N-ratio again through fertilisation.

Kandeler *et al.* (1998) conclude that overall, their studies suggest that the effects of climate change on the soil microbial community and processes are likely to be minimal and largely unpredictable in soils of low nutrient availability. Heal (2001) argues that soil microbial biomass will show little change following warming, but decomposition rates are likely to change most in mesic soils; computer models at 3 spatial scales show how different microbial strategies respond to changing litter quality.

Frederiksen *et al.* (2001) confirm the above conclusions: Bacterial biomass was not significantly affected by the CO_2 induced changes in the litter quality, but the lower decomposition rate and fewer bacterial grazers in the straw from plants grown at elevated CO_2 together indicate reduced microbial activity and turnover.

Notwithstanding this, these data show that growth at elevated atmospheric CO_2 concentration results in slower decomposition of wheat straw, but the effect is of minor importance compared to the effect of varying crops, agricultural practice or changing land use.

Six *et al.* (2001) studied the effects of an increased atmospheric CO_2 concentration on organic matter dynamics in grass/clover leys and found no increase in carbon content after 6 years. Elevated CO_2 did increase the aggregate formation (+54%) as found by Loiseau & Soussana (1999) and the carbon content in the POM fraction (+40%), possibly caused by changes in the residue quality.

Such changes can easier be implemented in models based on size-fractions than in models based on chemical fractions (see below). Elevated CO_2 seems to exert a different effect on old and new organic pools in soil (Cardon *et al.*, 2001). The higher input under elevated CO_2 causes the microbial biomass to leave aside the older substrates (longer residence times) and stimulates decomposition of the fresh substrate. This is in accordance with results obtained by Lekkerkerk *et al.* (1990) and the so-called 'preferential substrate use theory' (Van Veen *et al.* 1993). Adding fresh substrates can – in theory – lead to a priming or a conserving effect on soil organic matter fractions (Dormaar, 1990). From studies by Zak *et al.* (1993) with N-measurements and Körner and Arnone (1992) with C-measurements it could be derived that priming had occurred. However, in sensitive ¹⁴C-labelling experiments with elevated CO_2 and grass by Van Ginkel *et al.* (1996) and in a study with ¹⁵N-labelling (Gorissen & Cotrufo, 1999), no priming or conserving effects on soil organic matter were found.

Elevated CO_2 stimulates the activity of the microbial population through the supply of easily decomposable substrate (Lekkerkerk *et al.*, 1990; Zak *et al.* 1993; Díaz *et al.* 1993; Cotrufo & Gorissen, 1997). Under elevated CO_2 , the increased carbon input into soil will stimulate the pool sizes of the microbial population, the amount of soluble C in soil and soil residue (Cotrufo & Gorissen, 1997; Van Ginkel & Gorissen, 1998; Van Ginkel *et al.*, 2000). Data on the increase in pool sizes of carbon in roots, soluble carbon, microbial biomass and soil residue for grasslands can be found in these papers. However, some authors report that C turnover in soil is increased in response to elevated CO2, rather than soil C pool size (Ross *et al.* 1996).

Decomposition and C-to-N-ratios of microbial population

Bacterial and fungal C-to-N-ratios are not constant. Bacterial ratios range from 3 - 5 and fungal ratios between 4.5 - 15 (Paul & Clark, 1988). An average value for the C-to-N-ratio of the microbial population is 5 - 8 (Merckx & Van der Linder, 1988).

Changes from a bacterial to a fungal dominated population or vice versa are not well documented, but the composition of the microbial population and its C-to-N-ratio probably do not change very fast. On the longer term, soil management can change the ratio between bacterial and fungal biomass and thus the C-to-N ratio. In no-till systems fungi are usually favoured because ploughing damages fungal hyphae (Beare *et al.*, 1997; Frey *et al.*, 1999). Changes in soil management (no-tillage *versus* conventional) often cause little change in C-storage, except that the carbon distribution among the soil profile changes (Doran, 1980; Campbell *et al.*, 1999; Angers *et al.*, 1997).

Decomposition of organic matter is performed by the microbial population. Depending on the C-to-N-ratio of the substrate (organic matter), mineral nitrogen is mineralised or immobilised. Decomposition of organic residues with a C-to-N-ratio of about 25 usually result in a net mineralisation/immobilisation of 0. Higher C-to-N-ratios require extra nitrogen, whereas at lower C-to-N-ratios mineral nitrogen is released.

Most models that simulate soil organic matter decomposition use several pools in plant residues and soil organic matter with different C-to-N-ratios.

Decomposition in relation to organic matter pools, k-values and efficiencies

The rate constants for decomposition (k-values) depend on the nature of the pool, with the highest values for sugarlike substances and the lowest for old organic matter pools. The efficiency by with carbon is taken up by the microbial population also depends on the nature of the pool. Sugars are converted with the highest growth efficiency, whereas lignin has an extremely low growth efficiency.

Table 3.2.1 gives an impression of pool sizes, k-values and efficiencies of different organic fractions for decomposition of straw.

	С (µg)	k-value	Efficiency
Sugars etc	150	0.2	60
(Hemi-)cellulose	650	0.08	40
Lignin	200	0.01	10
Microbial products	6	0.8	40
Active protected SOM	5000	3 x 10 ⁻⁴	20
Old organic matter	7000	8 x 10 ⁻⁷	20

Table 3.2.1. Pool sizes, k-values and efficiency during decomposition (Paul & Clark, 1988).

This type of data is commonly used in models (Van Veen *et al.*, 1984; Parton *et al.*, 1987; Verberne *et al.*, 1990, Whitmore *et al.*, 1997). The disadvantage of this method is that many pools can not be described adequately. E.g.,

the microbial biomass can be measured with a certain accuracy, but not the distinction between the protected and the unprotected fraction as used in the Verberne model. The most important methods for measuring the soil microbial biomass are the chloroform-extraction method (Vance *et al.*, 1989) and the chloroform-centrifugation method (Van Ginkel *et al.*, 1994). More data about pools, decomposition rates, and efficiencies can be found in Van Veen & Paul (1981), Van Veen *et al.* (1984), Verberne *et al.* (1990) and Whitmore *et al.* (1997). Decomposition rate is usually thought to depend on soil texture, but the effect of soil texture on measured decomposition rates is not always the same. Merckx *et al.* (1985) reported a faster turnover in a soil with a lower clay content (2%) than in a soil with 37% clay. Franzluebbers *et al.* (1996) also recovered a higher proportion of soil carbon in the microbial biomass at a higher clay content. The ascribed this to physical protection and smaller variations in moisture conditions. On the other hand, Gregorich *et al.* (1991) did not observe differences in decomposition of glucose in 10 soils with a different texture (19-38% clay), although more sandy soils were apparently lacking in this study. Physical protection of soil organic matter or soil miicrobial biomass is sometimes incorporated in models describing organic matter decomposition (e.g Verberne *et al.*, 1990).

Besides differences in texture, different size or size-density fractions in the soil organic matter play an important role in decomposition and Meijboom *et al.* (1995) developed a size-density fractionation technique that distinguishes physical fractions in stead of chemical fractions. This type of fractionation techniques is less destructive than chemical fractionation and seems more related to the structure and function of soil organic matter fractions (Christensen, 1992). The size-density fractions can be separated using substances like Ludox or polytungstate and subsequently, decomposition rates can be determined. Hassink (1995) has applied the Ludox-technique to obtain *k*-values for different size-densities of organic matter (Table 3.2.2).

Organic matter fraction	Turnover	
	k-value (d ⁻¹)	
> 150 µm, light	0.002390	
> 150 µm, intermediair	0.000984	
> 150 µm, heavy	0.000394	
20 – 150 µm	0.000052	
< 20 μm	0.000071	

Table 3.2.2. Turnover of organic matter fractions after size-density fractionation.

Decomposition rates of the macro-organic fraction, the least decomposed and youngest material, are highest. Carbon in the smaller fractions is much more stabile. (Dalal & Mayer, 1986). Hassink (1995) proposed to implement these fractions in future models. The concept of protected and non-protected organic matter fractions, which cannot be separated experimentally, is not necessary using this approach.

Decomposition rates are according to Hassink (1995) not dependent on soil texture - a factor that plays an important role in the protection concept. With this approach, models get a structure with pools that can be actually measured, an important advantage compared with the 'old' approach (Bonde *et al.* 1992).

Some problems still have to be resolved, because when the fractions have been obtained with polytungstate, determination of decomposition rates suffer from the toxicity of this fractionation substance. Ludox is not toxic, but seems to stimulate decomposition of the obtained fractions. Magid *et al.* (1996) ascribed this to changes in pH of the fractions due to Ludox.

Conclusion:

The decomposition of plant material grown under eleveted CO_2 by the soil microbial biomass is often decreased, probably through changes in the quality of the plant material. The relationship between decomposition and C-to-N ratio is often weak, other 'quality factors' are probably responsible. Under elevated CO_2 , evidence was found that soil carbon input is increased, decomposition retarded and the formation of aggregates stimulated, thus affecting soil structure and physical protection of organic matter and microbial biomass. Future research should focus on plant 'quality factors' in relation to decomposition and fractionation techniques of soil organic matter in order to supply models with adequate data.

3.2.3 Manipulation of microbial activity (MA) by management

C sequestration in relation to management

General

Several reviews have been published on the subject, e.g. by the Food and Agriculture Organization. The FAO presents a review of carbon dynamics and the fundamental role of organic matter in soil, and proposes a method for monitoring and verifying the changes both in carbon sequestration and in the degree of degradation, based on a soil monitoring network (FAO; Anonymous 2001).

Soil C-sequestration is affected by a number of management measures on different scales from farmer's measures (e.g. crop choice, fertilization, tillage; Ma *et al.* 2001) to regional/national changes (e.g. changes in land use). Several options for management on a small scale aiming at high carbon sequestration have been proposed. In general, management practices for increasing C sequestration in soils are considered to have the following characteristics: they are soil specific (Batjes 1998), require innovative technology (Metting *et al.* 2001), and may include fertilizer application (e.g. N, S, Nyborg *et al.* 1998; Kucharik *et al.* 2001), or reduced or no soil tillage (Torbert *et al.* 1999; Doran *et al.* 1999; Kessavalou *et al.* 1998; Cihacek *et al.* 1998; Kucharik *et al.* 2001). Some data indicate interaction between soil type and management practice with regard to C sequestration (Potter *et al.* 2001). E.g carbon storage in soil and the crop (*Panicum virgatum*) was higher at wide row spacing and increased with N application rates up to 224 kg N ha⁻¹ yr⁻¹ (Ma *et al.* 2001), although several years of switchgrass culture were required before soil C sequestration could be measured: only after 10 years SOC was 45% and 28% higher at depths of 0-15 and 15-30 cm, respectively, compared with fallow soil in an adjacent area.

The effect of tillage is not clear, changes in soil management (e.g. no-tillage *versus* conventional) often cause little change in C-storage, except that the carbon distribution among the soil profile changes (Doran, 1980; Campbell *et al.*, 1999; Angers *et al.*, 1997). In no-tillage systems most of the carbon will be recovered nearer to the surface compared with conventional systems.

On the other hand, Watts *et al.* (2000) found an increase in soil respiration during a week after ploughing. Minimising the physical changes in soils therefore seem to have a positive effect on carbon stabilisation, because aggregates are less disrupted in no-tillage systems and the formation of aggregates plays an important role in stabilising carbon in soil (Denef *et al.* 2001a; 2001b).

On a global scale, land use changes have a major impact on C exchange between soil and atmosphere. Land use changes from forest or grassland to arable agriculture have been and still are a significant source for the release of former plant and soil carbon into the atmosphere. The reasons for decreasing soil carbon contents are a reduced input of plant biomass into cropland on one hand, and an accelerated decomposition of the existing organic matter in agricultural soils on the other for example introduced by ploughing or changing water tables. The combined losses from the earth's biomass and from soil organic matter due to cultivation between the year 1700 and today amount to approximately 170 Gt carbon, which is now largely present in the atmosphere. A further CO_2 emission in the range of 1.2 Gt C per year is still going on due to additional land clearing for agriculture in the tropics.

The only way to escape from this forest conversion is a more sustainable use by balancing the C-fluxes and improved productivity of the already existing farmland (Sauerbeck *et al.* 2001). Improved soil management is capable of increasing carbon levels in existing agricultural soils, both in temperate (e.g. Wright *et al.* 2001) and tropical regions of the world (e.g. in monsoon east Asia, Koizumi *et al.* 2000; Silver *et al.* 2000). However, the ultimate potential for terrestrial C sequestration is not known, due to lack of adequate understanding of (1) the biogeochemical mechanisms responsible for C fluxes and storage potential on the molecular, regional, and global scales, and (2) the complex genetic and physiological processes controlling key biological and ecological phenomena (Metting *et al.* 2001). Nevertheless, authors seem to agree on the temporary increase of C sequestration through management: after 50 to 100 years this increase vapourizes to nil (Sauerbeck *et al.* 2001; Silver *et al.* 2000). Wright *et al.* (2001) suggest that maize cropping systems are the most efficient in sequestering C, but the global maize production would have to increase by a factor five to balance excess CO₂ accumulation in the atmosphere. Obviously, the conversion of arable land to grassland and agroforestry has been identified as a possible option to offset rising CO₂ levels by increasing C sequestration (e.g. Wright *et al.* 2001) and agroforestry appears to be the only agricultural system that could realistically be implemented to reduce global CO₂ levels.

Microbial biomass/ activity:

Larionova *et al.* (2001) report that conversion of old arable land to grassland resulted in significant C sequestration in soil organic matter and soil microbial biomass. Silver *et al.* (2000) conclude from a literature review that tropical reforestation has the potential to serve as a carbon offset mechanism both above- and belowground for at least 40 to 80 years, and possibly much longer (cf. Table 3.2.3). The estimated net productivity for temperate forests is significantly greater than the productivity of maize, rice, or wheat cropping systems (Table 3.2.3). Increasing land area for agricultural production such as maize may thus not be the answer to the global C dilemma, but intensive management systems that result in increased soil organic matter will be a significant part of the solution (Wright *et al.* 2001), although efforts should be made to determine the stability of the stored C. Larionova *et al.* (2001) reported that the stored C was not very stable, since a six-month incubation of soil sampled on young grasslands that had replaced arable soil showed high C losses. How this applies to forest systems is not clear.

Option	Productivity (Mg C ha ⁻¹ yr ⁻¹)	Increase of world wide area (ha x 10 ⁸)	Increase of area (%)	Ref.
Agroforestry (temperate)	6.7 – 7.1	3.6 - 4.6	52 – 66	a
maize, rice or wheat cropping systems forest grassland reforestation (tropics) 0-20 vr	2.7 – 4.3 0.34 0.33	6.7 – 7.6 - -	477 – 543 - -	a b b
20-100 yr	1.2 veg, 0.4 soil	-	-	С

Table 3.2.3.	Agricultural systems options for carbon sequestration balancing global excess CO ₂ accumulation of
	3.3 Pg year ¹ (references: a, Wright et al. 2001; b, Post and Kwon 2000; c, Silver et al. 2000,
	review).

There is a large variation in the length of time for (and the rate at) which carbon may accumulate in soil, related to the productivity of the recovering vegetation, physical and biological conditions in the soil, and the past history of soil organic carbon inputs and physical disturbance. Maximum rates of C accumulation during the early aggrading stage of perennial vegetation growth, while substantial, are usually much less than 100 g C/m² per year. Average rates of accumulation are similar for forest or grassland establishment: 33.8 g C/m² per year (0.34 Mg C/ha.yr) and 33.2 g C/m² per year (0.33 Mg C/ha.yr), respectively (Post and Kwon 2000; Table 3.2.3).

3.2.4 Conclusions

Summarizing, the maintenance of soil organic matter (SOM) can be strongly influenced by management. Many management techniques (fertilising, crop choice, tillage) may increase primary production and may potentially increase SOM, thus sequestering atmospheric carbon.

A valid general conclusion is, that conversion of soils from arable crop production into grassland and forest has the highest potential to sequester atmospheric carbon. However, direct effects of management on microbial activity have not been studied sufficiently to reliably incorporate them in modelling studies.

3.3 Interactions between soil management, litter quality and microbial activity

Any management measure affecting soil properties like aeration will affect microbial activity (Paul & Clarck, 1989). Adding fertilisers and changing ploughing regimes will thus affect soil carbon and nutrient dynamics. Fisk and Fahey (2001) tested the hypothesis that higher soil nutrient availability stimulates microbial activity. Respiration quotients (qCO₂, respiration per unit biomass) were indeed higher in fertilized plots (56 μ g CO₂-C mg C⁻¹ d⁻¹) than control (48 μ g CO₂-C mg C⁻¹ d⁻¹) or litter removal (45 μ g CO₂-C mg C⁻¹ d⁻¹). The results of effects of urban land use on chemistry and decomposability of *Quercus rubra* (red oak) leaf litter in forests suggest that microbial activity in forests near large cities may also be affected by antropogenic induced changes in the biotic, chemical and physical environment (Carreiro *et al.* 1999).

King *et al.* (2001) investigated the effect of N-availability and CO_2 on sugar maple (*Acer saccharum*) litter quality and microbial activity (as measured by microbial respiration or DOC production). They found that elevated CO_2 and low soil nitrogen resulted in higher litter concentrations of non-structural carbohydrates and condensed tannins, higher C-to-N ratios and lower N concentrations. Soil N availability appears to have had a greater effect on litter quality than did atmospheric CO_2 , although the treatments were additive, with highest concentrations of non-structural carbohydrates and condensed tannins occurring under elevated CO_2 -low soil N. Rates of microbial respiration and the production of DOC (dissolved organic carbon) were insensitive to differences in litter quality. They conclude that the chemical composition of sugar maple litter will change in the future in response to rising atmospheric CO_2 , and that soil N availability e.g. via N-fertilisation) will exert a major control.

A critical note was made by Burket and Dick (1997) with respect to C accumulation in soils, litter quality seems often of less importance than litter amount. They discuss long-term vegetation management, be it largely in relation to N accumulation rather than C accumulation in soils. They argue that the amount of organic C that accumulates in aerobic agricultural soils appears to have less to do with the type of organic residue than with the amount of C that is returned to the soil. Also, N accumulation does not depend totally on litter quality (i.c. N content), since N fertilizer application can complement added litter with low N content. They suggest that –similarly - microbial biomass N accumulation in soil depends more on the total amount of N (organic or inorganic) than on the plant residue quality (N content). In conclusion, these authors find from their literature review that the increase of soil organic C is much more related to the rate of N-application than to the type or quality of the (plant or organic) residue.

No tillage favoured aerobic bacteria bacteria, nitrifying bacteria, and fungi in the upper 7.5 cm compared with a soil layer between 7.5 - 15 cm under no tillage compared with conventional tillage (Doran, 1980; Table 3.3.1).

Microbial group	Ratio	NT/CT
	0-7.5 cm	7.5-15 cm
Aerobic bacteria	1.41	0.68
Facultative aerobes	1.57	1.23
Nitrifying bacteria	1.58	0.75
Fungi	1.57	1.23

Table 3.3.1. Average ratio of microbial populations between no-till (NT) and conventional tillage (CT) at two soil depths.

Ploughing causes disruption of aggregates and stimulates the release of easily decomposable carbon compounds. This change will transform protected organic matter (POM-fraction in Verberne's model *et al.*, 1993) into nonprotected organic matter (NOM fraction) that will be subject to decomposition (Hassink *et al.*, 1993). For example, breaking native prairie to cropland resulted in significant losses of C and N in the top 5 cm as reported by Follett *et al.* (2001). The C losses were not related to changes in soil texture or pH. The decline in C storage at the top 5 cm of soil were attributed to lower organic inputs, to increased SOM losses by decay and erosion, and to dilution effects by ploughing. Carter MR (2002) discusses Canadian studies on soil quality which were initiated in the early 1980s and showed that loss of SOM and soil aggregate stability were standard features of non-sustainable land use. Organic matter fractions (e.g., macro-organic matter, light fraction, microbial biomass, and mineralizable C) describe the quality of SOM. These fractions have biological significance for several soil functions and processes and are sensitive indicators of changes in total SOM.

Doran et al. (1999) established two experiments in 1969 and 1970 near Sidney, Australia, to determine the effect of mouldboard plow (plow), sub-tillage (sub-till), and no-tillage (no-till) fallow management on soil properties, biological activities, and carbon and nitrogen cycling. The first experiment was conducted on land which had been broken from sod in 1920, seeded to crested wheatgrass (Agropyron cristatum) from 1957-67, and cultivated for wheat again in 1967 (previously cultivated site). The second experiment was established on land that was in native mixed prairie sod until 1969 (Native Sod site), and compared the three tillage management practices listed above in a winter wheat-fallow system as well as replicated plots remaining in sod. Soil samples taken 10-12 years after the initiation of the experiments, indicated that the biological environment near the soil surface (0-30 cm) with no-till was often cooler and wetter than that with conventional tillage management practices, especially mouldboard plowing. Biological activity and organic C and N reserves were concentrated nearer to the soil surface (0-7.6 cm) with notillage, resulting in greater potential for tie-up of plant available N in organic forms. However, regardless of tillage practice with wheat-fallow management at either site, long-term (22-27 years) losses of soil organic C from surface soil (0-30 cm) ranged from 12 to 32% (320-530 kg C/ha per year), respectively, for no-till and plowing. These soil C losses were closely approximated by losses measured to a depth of 122 cm, indicating that under the cropping, tillage, and climatic conditions of this study, soil C changes were adequately monitored by sampling to a depth of 30 cm within which most C loss occurs. No-till management maintained a protective surface cover of residue and partially decomposed materials near the soil surface. However, the decline in soil organic matter, and associated degradation in soil quality, will likely only be slowed by increasing C inputs to soil through the use of a more intensive cropping system which increases the time of cropping and reduces the time in fallow.

Wagener and Schimel (1998) noted that in the forest floor of Alaskan taiga, annual layers of *Equisetum* (horsetail) litter demarcate cohorts of birch (*Betula papyrifera*) litter. Overall, respiration potential decreased with depth of litter (litter age) and over the growing season. N mineralization potential increased with depth, and fluctuated over time. Microbial biomass did not vary with depth, but did increase greatly in September in conjunction with increased litter moisture. Litter C-to-N ratio decreased with time and varied with depth according to the year-to-year variation in litter chemistry. A conceptual model of the forest floor_describing microbial activity on a litter cohort as controlled primarily by litter chemistry is presented, but modified by the vertical position in the forest floor and seasonal climatic variation.

These authors conclude that litter quality was the main factor associated with changes in microbial activity with season and down the soil profile.

Vance & Chapin III (2001) conclude that respiration and N immobilization responded more strongly to substrate additions than did microbial biomass, suggesting that the nature of resource limitation depends on the particular microbial parameter considered. The response of microbial respiration to added C and N also depended on the quality of native soil organic matter.

Some data are available on microbial biomass (bacterial vs fungal) residues in soils as affected by management measures. Bailey et al. (2002) show that fungal activity is affected by management. Fungi and bacteria govern most of the transformations and ensuing long-term storage of organic C in soils. Thus, in a small set of diverse soils in their study, increased fungal activities, more than F-to-B ratios, were associated with increased soil C. These authors conclude that practices that involved invasive land management decreased fungal activity and stored soil C compared to similar soils that were less intrusively managed. In a comparative study on bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems, Guggenberger et al. (1999) argue that agricultural management practices have been shown to influence the decomposer community in soils, with no-tillage (NT) systems favoring fungi as compared with conventional tillage (CT) systems. They used total amino sugar contents to estimate living and decomposing microbial cell-wall mass in soil and the contents of glucosamine and muramic acid to separate fungal and bacterial contributions to microbial-derived soil organic matter (SOM). At three sites, the ratios of glucosamine to muramic acid in NT soils (32.0, 30.0, 42.2) significantly exceeded those in the respective CT soils (18.8, 22.1, 23.0) because of a higher enrichment of glucosamine. This coincided with higher values for fungal biomass, particulate organic matter carbon (POM-C), mean weight diameter of water-stable aggregates (MWD), and total organic carbon (TOC). Analysis of aggregate-size classes showed that the additional glucosamine accumulated in >53-mm aggregates but not in smaller particles. The enrichment of SOM in fungal-derived glucosamine suggests that the accrual of hyphal cell-wall residues is an important process in the three NT agroecosystems which leads to higher SOM storage in surface soil concurrent with an increase in aggregate stability. The other soils, having a lower clay plus silt content, exhibited no significant differences in POM-C, MWD, and total amino sugars between NT and CT management systems. They suggest that at lower clay plus silt contents the beneficial potential for NT to sequester microbial-derived SOM is lower because of limited physical stabilization.

Field data and modelling by Kucharik *et al.* (2001) suggest that agricultural land management – conversion of prairie to agricultural land near Arlington between 1860 and 1950 caused SOC to be depleted by as much as 63% (native SOC was approximately 25.1 kg C m²). This depletion was possibly related increased aeration and destruction of aggregated by ploughing and was correlated to reductions in microbial biomass and N-mineralisation. Prairy restoration after 1976 appears to have done little to increase SOC over the past 24 years. Measurements show that the prairie contained between 28% and 42% less SOC (in the top 1 m) than the no-tillage maize plots and 40% - 47% less than simulated potential SOC for the site in 1999. The study indicates that high-productivity C4 grasslands (NPP = 0.63 kg C m⁻² y⁻¹) and high-yield maize agroecosystems (10 Mg ha⁻¹) have a potential to sequester C at a rate of 74.5 g C m⁻² y⁻¹) and 86.3 g C m⁻² y⁻¹), respectively.

Breland & Eltun (1999) report on a cropping systems experiment in southeastern Norway, where ecological (ECO), integrated (INT) and conventional (CON) forage (FORAGE) and arable (ARABLE) model farms were compared. After 5 experimental years, topsoil was sampled in spring from spring grain plots and incubated for 449 days at controlled temperature (15°C) and moisture content (50% water-holding capacity). There were no detectable differences between model farms in terms of total soil C or N. For INT and CON, however, values of microbial biomass C and N, microbial quotient (C(mic)/C(org)), and C and N mineralization were, or tended to be, higher for FORAGE than for ARABLE. For the ECO treatment, values were similar for FORAGE and ARABLE and did not differ significantly from that of CON-FORAGE. For INT and CON, the metabolic quotient (qCO₂) was lower for FORAGE than for ARABLE. Again, for the ECO treatment, values were similar for FORAGE and ARABLE and did not differ significantly from that of CON-FORAGE. They estimated the sizes of conceptual soil organic matter pools by fitting a decomposition model to biomass and mineralization data. This resulted in a 48% larger estimate for CON-FORAGE than for CON-ARABLE of physically protected biomass C. For physically protected organic C the difference was 42%.

The relationship between litter quality and microbial biomass (and/or activity) has been studied in conjunction with a range of factors, including vegetation management, climate change, nutrient availability, water relations and other parameters like forage digestibility. The views in the - relatively scarce - literature vary widely on the (potential) interactions between litter quality and microbial biomass and/or microbial activity in relation to climate change. Changes in the microbial biomass (activity and/or composition) will affect litter quality through changes in litter turnover processes and the subsequent availability of nutrients for plant growth (Berendse, 1994). This ecosystem response may be evoked by land use changes or changes in fertilisation strategies. Systems with lower nutrient inputs will have a lower net primary production, resulting in lower carbon input into soil and litter with lower 'quality' which is more difficult to decompose, resulting in less available nitrogen, subsequently affecting the plant composition of the vegetation. Fertilising effects on decomposition of soil carbon was found after application of NPK fertilisers and cutting in Russian grasslands: newly formed soil organic matter appeared to be less resistant to decomposition than in unfertilised soil (Larionova, 2003). Apparently, the fertilised fields yielded soil organic matter with a 'higher quality' in terms of decomposability. In this study, the impact of land use change and management on soil C sequestration was investigated during the 1980s-1990s on gray forest soils in Pushchino, and on the soddypodzolic soil in a region near Moscow. Mean annual rates of C sequestration after establishment of perennials (layer 0-60 cm) were 63-182 g C m² and 22-43 g C m² for gray forest and soddy-podzolic soils, respectively. Establishing grasslands resulted in higher soil C accumulation than afforestation.

Under normal conditions, soil fauna and microflora form an integrated system for decomposition of organic residues. Tian *et al.* (1997) discuss soil fauna-mediated decomposition of plant residues under constrained environmental and residue quality conditions. They examined the effects of the decomposer community on the decomposition of litters of various qualities. They conclude that soil fauna contributed relatively more to the decomposition of low-quality (high C-to-N ratio) residues, probably because they stimulated microbial activity.

3.3.1 Conclusions

- Chemical composition of litter will change in the future in response to rising atmospheric CO₂, and soil N availability e.g. via N-fertilisation can largely affect this response. Fertilising effects on decomposition of soil carbon showed that newly formed soil organic matter appeared to be less resistant to decomposition than in unfertilised soil
- Tillage regime affects the ratio fungal-to-bacterial activity and aggregation status of soil organic matter. Ploughing causes disruption of aggregates and stimulates the release of easily decomposable carbon compounds. C depletion after ploughing is possibly related to increased aeration and destruction of aggregated by ploughing. No-till management maintains a protective surface cover of residue and partially decomposed materials near the soil surface.

The general view in the literature is that it is important that only models that account for the protection of SOM are able to give insight into stabilisation of SOM, since it is the slow SOM pools that determine C-sequestration (Falloon and Smith, 2000). It is therefore important to identify this pool and to identify the protection mechanisms that preclude this pool from decomposition. For this purpose it is necessary to further develop experimental methodologies, based on state-of-the-art technology, e.g. stable or radioactive isotopes (De Visser *et al* 1997; Falloon and Smith, 2000; Richnow *et al.* 1999; Schnyder 1992). Also physicochemical techniques like GCMS, PyMS and NMR (Heal *et al.* 1997; Chefetz *et al.* 2002), together with size-density fractionation techniques (Meijboom *et al.*, 1995; Magid *et al.*, 1996). determination methods for microbial biomass (Vance *et al.*, 1987; Van Ginkel *et al.*, 1994) and composition of the microbial population using PCR-DGGE should be further developed. These technologies should be used in long-term studies (decades). However, long-term studies are rare and mostly related to soil fertility and seldom to climate change.

Especially the role of the microbial biomass should be in focus, as microbial decomposition processes play a central role in soil nutrient cycles (Van Veen *et al.*, 1989). Although much (often contradicting) information is available on the relation between litter quality and decomposition, the microbial biomass as the motor of these transformations is often regarded as a black box. In study with grasses (Van Ginkel *et al.*, 2000) and sugar maple leaf litter (King *et al.*, (2001) was concluded that microbial metabolism will not be intrinsically affected by changes in litter quality.

However, precise mechanisms describing decomposition of litter with different qualities by the microbial biomass need still to be described and possibly need to include more levels of the soil food web (Coûteaux *et al.*, 1991, King *et al.*, 2001).

Depending on the model to be used, more precise information is necessary on the size of the different soil organic matter pools and exchange rates between these pools as governed by the soil microbial biomass and soil properties like protection of organic matter by aggregates or clay particles.

4. General conclusion

To increase our understanding of C-sequestration processes in relation to climate change, long-term studies are essential, i.e. with a duration of several decades. This is precisely the weak point in the currently available literature, where even 5-10 yr studies are rare. Knowledge of C exchange fluxes is essential for understanding the long-term dynamics of C sequestration in agro-ecosystems in general and grasslands in particular.

Despite the fundamental importance of rhizosphere C-flow in managed and natural systems, reliable measurement/ resolution of C-flow and assessment of its consequences have largely remained elusive to soil biologists. Techniques involving both radioactive (¹⁴C) and stable (¹³C) isotopes of carbon have made some progress in terms of studying rhizosphere C-flow. However, these fluxes are poorly understood, mainly due to inadequate methodology. An example is the use of pulse-chase labelling while steady-state labelling is the method of choice.

It seems that insufficient experimental data of the required quality are available for modelling management effects on the size, activity, and composition of the soil microbial population and subsequent implications for carbon sequestration under elevated CO_2 , in grasslands or in any other agro-ecosystem. New and further developed experimental techniques to determine carbon and nutrient fluxes, together with size-density fractionation techniques and sensitive methods to determine microbial populations are needed to sufficiently feed these modelling activities.

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6. Glossary

Modelling

SOC, soil organic carbon (g C kg⁻¹ soil); **SOM**, soil organic matter (g organic matter kg⁻¹ soil); **PSOM**, protected **SOM**; **USOM**, unprotected **SOM**; SSOM, stable SOM; RSOM, refractory SOM; OM, organic matter, e.g., macro-organic matter, light fraction, microbial biomass, and mineralizable C (Carter 2002) **POM**, particulate organic matter POM, protected organic matter NOM, non-protected organic matter SOM, stabilized organic matter DPM, dissolved plant matter **DPM**, decomposable plant material, e.g. solutes like proteins, amino acids, carbohydrates, etc.); SPM, structural plant material, e.g. (hemi-)cellulose); RPM, resistant plant material, e.g. lignified structural material); MB, microbial biomass SMB, structural microbial biomass PSMB, protected structural microbial biomass **USMB**, unprotected **SMB** NPP, net primary productivity C-to-N, carbon to nitrogen ratio μ , relative growth rate; e, energy yield; k_s, enzyme efficacy;

Other

POM-C, particulate organic matter carbon;
MWD, mean weight diameter of water-stable aggregates;
TOC, total organic carbon
[NT, no-tillage
CT, conventional tillage]
HA, humic acid
DOC, dissolved organic carbon
[CNB, carbon-nutrient balance
GDB, growth differentiation balance]
GCMS, gas chromatography mass spectrometry
Py(GC)MS, pyrolysis (gas chromatography) mass spectrometry
NMR, nuclear magnetic resonance
SM, secondary metabolites