Tansley review

Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2

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Contents

Summary

The substantial stocks of carbon sequestered in temperate grassland ecosystems are located largely below ground in roots and soil. Organic C in the soil is located in discrete pools, but the characteristics of these pools are still uncertain. Carbon sequestration can be determined directly by measuring changes in C pools, indirectly by using ^{13}C as a tracer, or by simulation modelling. All these methods have their limitations, but long-term estimates rely almost exclusively on modelling. Measured and modelled rates of C sequestration range from 0 to > 8 Mg C ha^{-1} yr^{-1}. Management practices, climate and elevated CO_2 strongly influence C sequestration rates and their influence on future C stocks in grassland soils is considered. Currently there is significant potential to increase C sequestration in temperate grassland systems by changes in management, but climate change and increasing CO_2 concentrations in future will also have significant impacts. Global warming may negate any storage stimulated by changed management and elevated CO_2, although there is increasing evidence that the reverse could be the case.

I. Introduction

In recent years there has been a surge of research activity directed at improving our understanding of the global carbon (C) cycle and quantifying the pools and fluxes that constitute this cycle (Prentice *et al.*, 2001). This has come about because it is clear that human activities are perturbing the C cycle to a significant extent and that the consequence is a change in climate which could have significant negative impacts on terrestrial ecosystems (IPCC, 2001). We are still uncertain about the size and global distribution of the pools and the fluxes of C (Houghton, 2003) although it is clear that, of the terrestrial pools, the largest is in the soil. This is particularly so for grassland ecosystems, where up to 98% of the total C store can be found sequestered below ground (Hungate *et al.*, 1997). About two-thirds of terrestrial C is below ground and this pool generally has much slower turnover rates than aboveground C (Schlesinger, 1977).

In broad terms, grasslands are ecosystems in which the dominant vegetation component is comprised of herbaceous species. Global estimates of the relative amounts of C in different vegetation types suggest that grasslands probably contribute > 10% of the total biosphere store (Eswaran *et al.*, 1993; Nosberger *et al.*, 2000). There have been many approaches to the classification of grasslands of the world, but inevitably there is an element of arbitrariness about this (Coupland, 1979). The broadest division is between temperate and tropical grasslands and this review focuses on the first of these. Of the temperate grasslands of the world, some have grasslands as their natural vegetation and some are anthropogenic in origin. In areas where grasslands are the natural climax vegetation (e.g. the steppes of central Asia and the prairies of North America), the rainfall is low enough to prevent the growth of forests. Where grasslands are non-natural (e.g. north-western and central Europe, New Zealand, parts of North and South America and Australia), rainfall is normally higher and the climax vegetation is forest. These climate differences mean that the productivity of natural grasslands is generally low while that of the non-natural grasslands is significantly higher, with the result that they tend to be used more for intensive agricultural production (Whitehead, 1995).

Carbon sequestration is the process of removing CO_2 from the atmosphere and storing it in C pools of varying lifetime. While the processes of C sequestration are ultimately regulated at the molecular level, management practices, climate and atmospheric CO_2 concentration can greatly affect the way in which terrestrial ecosystems sequester C. The capacity of land to store C has particular significance now because, under Article 3.4 of the Kyoto Protocol of the United Nations Framework Convention on Climate Change, countries can count this sequestration as a contribution to reducing greenhouse gas emissions (Smith *et al.*, 1997; IPCC, 2001). There is therefore an imperative to improve our understanding of the processes regulating C sequestration in order to manage landscapes to maximize their potential to store C in the future.

This review describes the processes involved in C sequestration in temperate grassland ecosystems and assesses the influences of altered management practices, climate change and increasing atmospheric CO_2 concentration on future levels of C sequestration. Because virtually all the labile C in grassland ecosystems is in the soil, and our mechanistic understanding of processes occurring here is still relatively weak, the emphasis is on identifying approaches that will improve our knowledge at the soil process level.

II. Carbon in temperate grasslands

The roots, senescent leaves and stems from which soil organic matter (SOM) is derived differ in their rate and process of breakdown in the soil (Joffre & Ågren, 2001). In most temperate grassland ecosystems, 75–80% of the root biomass is in the top 30 cm of the soil but, because root growth, death and decomposition occur simultaneously and at different rates according to species and climatic conditions, accurate determination of C transfer from the various sources to the soil is difficult (Reeder *et al.*, 2001). Plant roots contribute to soil C not only through their death and decomposition, but also by rhizodeposition resulting from exudation, mucilage production and sloughing from living roots (van Veen *et al.*, 1991; Reeder *et al.*, 2001). Furthermore, microbial activity in the rhizosphere produces similar products to root exudates (Paul *et al.*, 1979). It is therefore also difficult to distinguish between plant-derived and microbial-derived metabolites in terms of CO_2 production and C transfer (van Veen *et al.*, 1991).

Classical descriptions of SOM have normally combined chemical extractions with the identification of specific chemical compounds, but this approach has contributed little to a functional understanding of soil processes (Collins *et al.*, 2000). As an alternative, researchers studying ecosystem functioning have tended to adopt a model where organic C is located in more-or-less discrete 'pools' in the soil. However, there is at present little agreement on the precise definition of most of these pools and they can mean different things to different researchers (Jenkinson, 1990; Jenkinson *et al.*, 1992; Smith *et al.*, 2002). To some they mean different fractions of plant residues at different stages of decomposition, in such a way that the C is associated with different soil particle size fractions (Six *et al.*, 2002). To others they are interpreted as chemical fractions containing specified chemical structures/or functional groups (Christensen, 1996; Post & Kwon, 2000).

A significant proportion of SOM is physically protected from decomposition through occlusion by clay minerals and encapsulation within soil aggregates (Fig. 1). A large amount of this SOM comprises a pool having an intermediate (10–15 yr) residence time, but this decomposes more quickly on disturbance. More active organic matter, consisting of
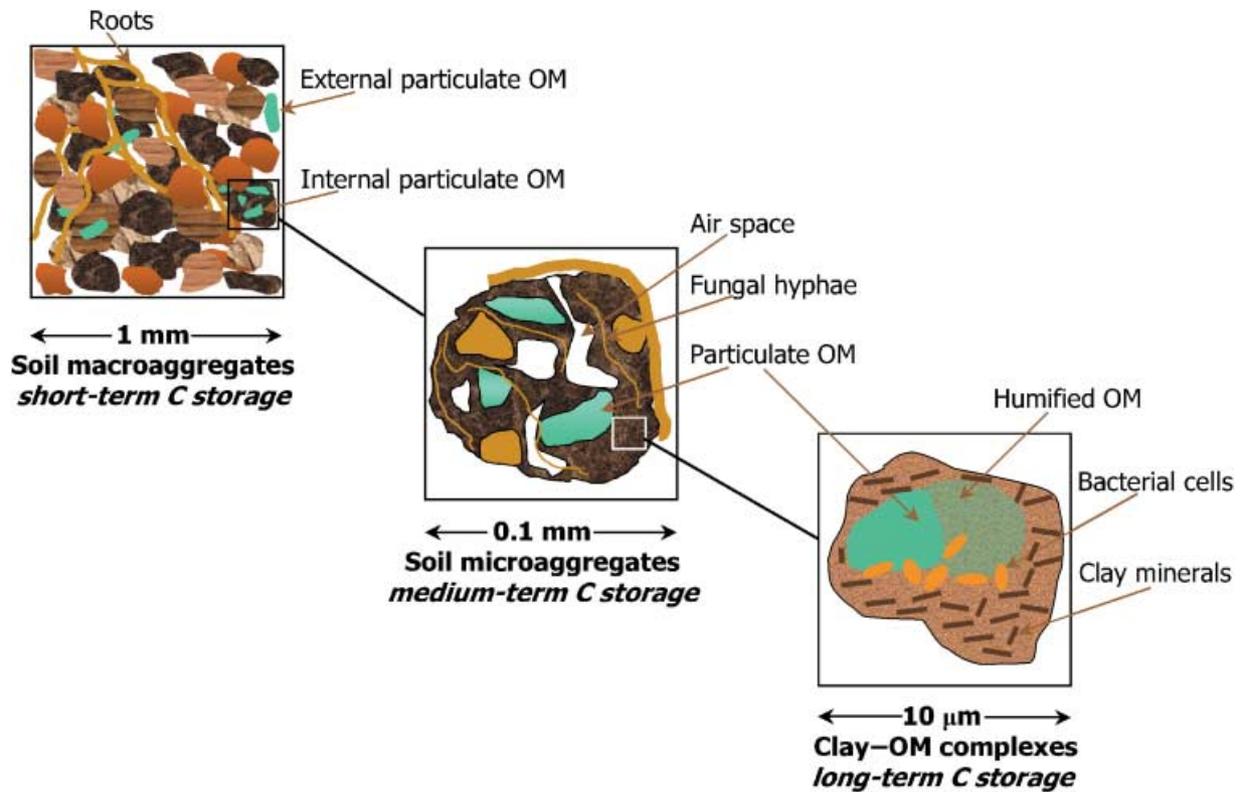
Fig. 1 Model of aggregate organization showing the location of soil organic matter (OM) within the soil matrix, with turnover times.

microbial biomass and labile organic matter, such as plant detritus, cycles more rapidly but makes up only 3–5% of total organic matter (Darrah, 1996; Joffre & Ågren, 2001). At the other extreme is very old material that is physically or biochemically protected in a passive recalcitrant form with a turnover time of hundreds to thousands of years (Jenkinson, 1990; Paul *et al.*, 1997b; Post & Kwon, 2000). According to Jastrow *et al.* (1996), C turnover time is greater in macroaggregates (> 212 µm) than in microaggregates (53–212 µm), indicating that microaggregate C is both physically and biochemically more recalcitrant. From the perspective of the impact of climate and management practices on soil C, it is the intermediate pools that are the most important and probably least well understood in terms of their composition and dynamics (Elliott *et al.*, 1996).

Most model descriptions of SOM in soils have represented the heterogeneity of SOM by defining several pools, usually three to five, which vary in their intrinsic decay rates and the factors controlling their decomposition (McGill, 1996; Six *et al.*, 2002). Unfortunately these pools are usually only loosely associated with measurable quantities which can be determined using current analytical methods (Paustian *et al.*, 1997). Attempts have been made to correlate analytical laboratory fractions with conceptual model pools (Motavalli *et al.*, 1994; Paul *et al.*, 1997a), but this has met with limited success to date (Six *et al.*, 2002). According to Smith *et al.* (2002), a measured soil organic pool is equivalent to a model pool only

when it is both unique and noncomposite, because composite fraction characteristics change in different environments as a result of changing properties in the subpools. They have defined a C pool as a compartment containing material that is chemically indistinguishable and equally accessible to both plants and the microbial population in the soil. Using this approach, when applied to the SUNDIAL (simulation of nitrogen dynamics in arable land) model they concluded that the debris, biomass and humus pools are unique, however the measured biomass (and possibly the humus fraction) is composite.

In their conceptual model, Six *et al.* (2002) distinguish the SOM that is protected either physically or biochemically against decomposition from that which is unprotected (Fig. 2). They identified four measurable pools: (i) an unprotected C pool; (ii) a biochemically protected C pool; (iii) a silt- and clay-protected C pool; and (iv) a microaggregate-protected C pool. The unprotected SOM pool consists of both the light fraction and the particulate organic matter (POM) fraction, although they are conceptually considered to be identical pools by Six *et al.* (2002). The origin of both light and POM fractions is mainly plant residues, but they may also contain microbial debris. These fractions are highly labile organic matter pools and Bremer *et al.* (1994) have shown that variation in the light fraction pool is the best indicator of management-induced changes in SOM.

Protected SOM is stabilized by three main mechanisms. First, chemical stabilization is the result of chemical binding
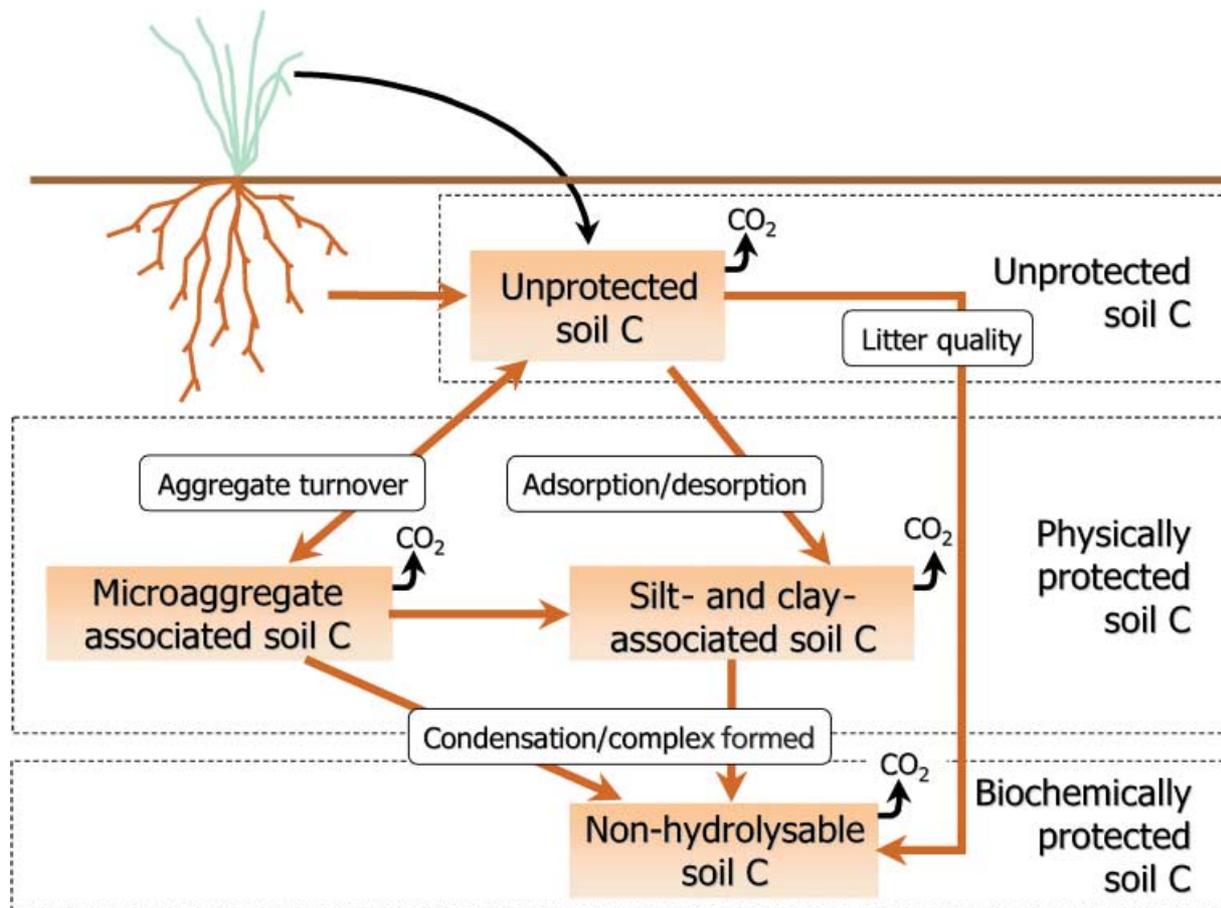
Fig. 2 Conceptual model of soil organic matter dynamics showing measurable pools. (Adapted from Six *et al.*, 2002.)

between soil minerals (clay and silt particles) and SOM. Second, biochemical stabilization is caused by the chemical-complexing processes between substrates such as lignins and polyphenols and soil particles. Finally, physical aggregates form physical barriers between microbes and enzymes and their substrates. Organic matter can be protected against decomposition when it is positioned in pores that are too small for bacteria or fungi to penetrate, or it can be inside large aggregates which become partially anaerobic because of slow O_2 diffusion through the small intra-aggregate pores (Marinissen & Hillenaar, 1997). Soil aggregates are held together by microbial debris and by fungal hyphae, roots and polysaccharides, in order that increased amounts of any of these agents will promote aggregation (Oades, 1984). Earthworms (*Lumbricidae*) are often the dominant soil-ingesting animals that mix plant residues and mineral soil, promoting aggregate stability. Marinissen (1994) found a strong correlation between macroaggregate stability and earthworm numbers.

Soil C surveys usually consider a fixed soil depth, typically 30–100 cm (Jobbágy & Jackson, 2000; Gifford & Roderick, 2003), and generally provide little information on the vertical distribution of soil organic carbon (SOC). However, Jobbágy

& Jackson (2000), in a survey of temperate grasslands, found that while 64% of SOC occurred in the top 40 cm, this depth contained as much as 87% of the roots. Possible explanations for deeper placement of SOC include: (i) decreasing SOC turnover with depth resulting in higher SOC accumulations per unit C input in lower soil layers; (ii) increasing root turn-over with depth causing higher C inputs per unit standing biomass in lower soil levels; (iii) SOC leaching from upper to lower levels; and (iv) vertical mixing by soil organisms (Jobbágy & Jackson, 2000). There is substantial support for the first explanation, including radiocarbon evidence from Paul *et al.* (1997a) from soils of the Great Plains of North America. Additionally, the observation that the nutrient content in deeper roots is lower provides a mechanistic explanation for reduced turnover rates (Gordon & Jackson, 2000), as does the fact that C residing at depth is often protected physically and/or chemically from microbial attack (Ajwa *et al.*, 1998).

III. The process of carbon sequestration in soils

The main factors determining the amount of C sequestered in soil are: (i) the rate of input of organic matter; (ii) the
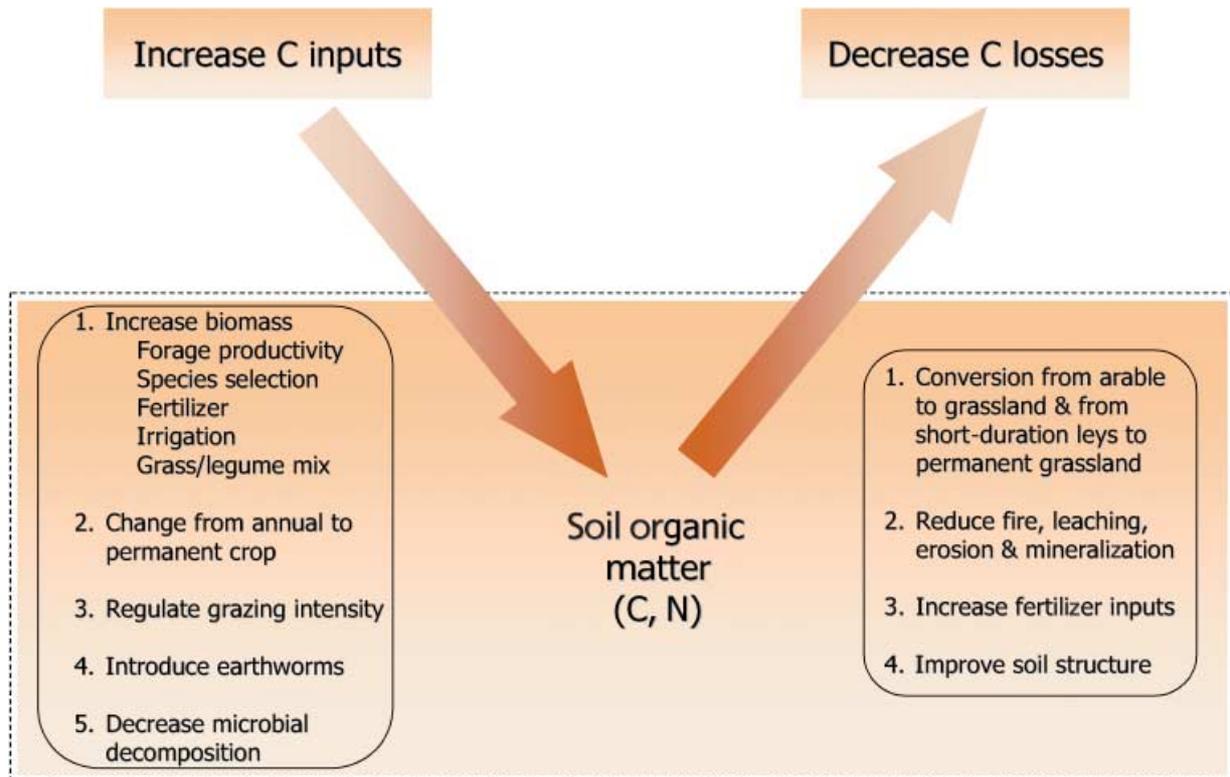
Fig. 3 Diagrammatic representation of management options to increase soil organic matter in grassland ecosystems.

decomposability of the organic matter inputs, in particular the light fraction organic C; (iii) the depth in the soil at which the organic C is placed; and (iv) the physical protection of either intra-aggregate or organomineral complexes (Fig. 3). Carbon from plants enters the SOC pool in the form of either above-ground litter or root material. Also, in grasslands a significant but variable proportion of plant material is consumed by herbivores and then enters the SOC pool from animal excretion (Bol *et al.*, 2004). Within the soil, plant fragments become reduced in size to either the light fraction or the POM fraction (Post & Kwon, 2000). In addition, plant residue leachate and microbial and plant-root exudates contribute to a more active C pool which consists of microbial biomass and microbial metabolites. The leachates and exudates from roots and microbes, together with fungal hyphae, earthworm casts and other biological binding mechanisms, effectively encase the light fraction of the plant material with clay and other mineral particles (Fig. 1). Soil microaggregates and macroaggregates are formed around the light fractions through a process of microbial and chemical binding of C to soil mineral particles to form the heavy fraction organic C (Post & Kwon, 2000). The majority of the SOC is associated with this fraction, which has a turnover time in the order of decades.

A large proportion of the C that enters the soil is returned to the atmosphere through respiration carried out by roots and soil organisms. The distinction between autotrophic and heterotrophic respiration in soils is difficult to make (Trumbore, 2000), and estimates are extremely uncertain, but the fraction of CO_2 evolution attributable to root respiration can vary between 16 and 95% (Darrah, 1996). Other significant losses of C in grasslands are through soil erosion and soil water drainage containing dissolved organic carbon (Kalbitz *et al.*, 2000).

The C sequestered by grasslands is the difference between net primary production (NPP) on one hand and hetrotrophic respiration, harvest, fire and changes in soil C stocks on the other. This difference is termed net biome productivity, and is normally taken as a measure of sink or source strength (Schulze *et al.*, 2002). Figure 4 summarizes these processes in a temperate European extensively managed grassland, and highlights the fact that the change in soil C is normally very small compared with the large fluxes into and out of the system. The options available to determine sink or source activity are to try to measure the small changes in C stocks in the soil or to determine the C balance based on a full accounting of C gains and losses. Both approaches are fraught with difficulty. The measurement of C stocks has to account for the heterogeneous nature of the distribution of C in the soil and, if significant changes are to be detected, then measurements may need to be made over timescales of, at least, decades (Hungate *et al.*, 1996; Conant *et al.*, 2001). Full C accounting depends on the reliable measurement of large fluxes of C into and out of the system.
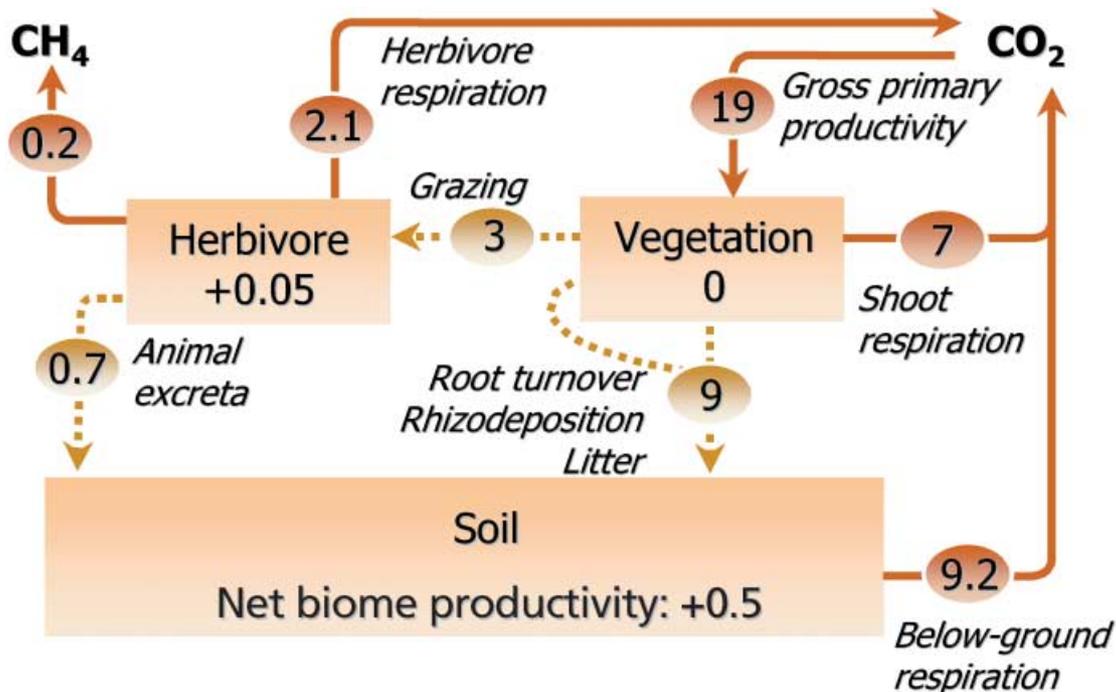
Fig. 4 The carbon cycle in a grazed grassland showing the annual net change (Mg C ha^{-1} yr^{-1}) for herbivores, vegetation and soils, where net biome productivity is equivalent to C sequestration. The C fluxes are shown for an intensively grazed grassland at an annual stocking density of 2 livestock units (LSU) ha^{-1}. (Source: Soussana *et al.*, 2004.)

Both these approaches have shown that, compared with the use of land for arable crops, temperate grasslands sequester significantly more C (Conant *et al.*, 2001). Tables 1–3 list C sequestration rates under a range of conditions, including conversion from arable to grassland, determined using a number of approaches. Carbon sequestration rates range from 0 to > 8 Mg C ha^{-1} yr^{-1}. The higher rates in grasslands compared with arable systems is explained partly by greater supply of C to the soil under grassland (Jackson *et al.*, 1996) and partly by the increased residence time of C resulting from the absence of disturbance by tilling. Additional reasons are: (i) a greater part of the input from root turnover and rhizodeposition is physically protected as POM; (ii) a large part of the POM is chemically stabilized (Gregorich *et al.*, 2001); and (iii) aggregates tend to protect native organic matter from decomposition (Tisdall & Oades, 1982; Collins *et al.*, 2000; Six *et al.*, 2002).

Under existing management conditions, most temperate grasslands worldwide are considered to be C sinks. In the USA and Canada, Bruce *et al.* (1999) estimated that North American soils sequester, on average, 0.2 Mg C ha^{-1} yr^{-1}, while Conant *et al.* (2001) produced an estimate of 0.58 Mg C ha^{-1} yr^{-1} for the same region. For Australia, Conant *et al.* (2001) give a value of 0.28 Mg C ha^{-1} yr^{-1}, while Gifford *et al.* (1992) estimated that the same soils can sequester between 0.5 and 0.6 Mg C ha^{-1} yr^{-1}. In a model prediction for Europe, under a business-as-usual scenario in 2008–12, Vleeshouwers & Verhagen (2002) propose that the majority of European grass-

lands will be sinks for C and the average sequestration could be 0.52 Mg C ha^{-1} yr^{-1}. Post & Kwon (2000) reported a mean accumulation rate of 0.33 Mg C ha^{-1} yr^{-1} for recently established permanent grasslands. Because the rate of C accumulation is strongly influenced by the productivity of the grassland systems, the range of the observations is large. For example, while a relatively productive area of the US Central Plains accumulated 1.1 Mg C ha^{-1} yr^{-1} (Gebhart *et al.*, 1994), under more arid conditions the shortgrass steppe of Colorado accumulated only 0.03 Mg C ha^{-1} yr^{-1} over a 50 yr period (Burke *et al.*, 1995).

Although there is now plenty of evidence to show that temperate grassland soils can sequester relatively large amounts of C, there is still uncertainty as to how long this can continue and whether there is an upper limit to C storage (Franck, 2002). Estimates of time to saturation range from 10 yr (Janzen *et al.*, 1998) to 100 yr (Potter *et al.*, 1999), but many models of SOC dynamics predict that soil C stocks can, in theory, be increased without limit (Six *et al.*, 2002). These models, however, are generally best at representing SOM dynamics in soils with low-to-moderate C levels (< 5%) and there are doubts as to their validity as C content increases because of the observational evidence that at higher soil C levels the storage capacity of soils becomes saturated with respect to C (Paul *et al.*, 1997a; Solberg *et al.*, 1997). Hassink (1997) investigated the relationship between SOM fractions and soil texture, and proposed that the capacity of the soil to preserve C is directly related to the proportion of silt plus clay in the

Table 1 Measured carbon sequestration (accumulation) rates of temperate grasslands

Location	Grassland system	Management	Technique	Climate	CO_2 sequestration (Mg C ha^{-1} yr^{-1})	Reference
Switzerland	Semi-natural calcareous grassland	2 cuts yr^{-1} (low nutrient)	^{13}C labelling in open-top chambers (OTC)	600 ppm CO_2	< 0.8	Niklaus *et al*. (2001a)
Switzerland	Sown *Trifolium repens*	4 cuts yr^{-1}	^{13}C labelling in free-air CO_2 enrichment (FACE)	600 ppm CO_2	4.6 ± 2.2	van Kessel *et al*. (2000b)
	Sown *Lolium perenne*			600 ppm CO_2	6.3 ± 3.6	
	Sown *T. repens*	4 cuts yr^{-1}	^{13}C-enriched soil (C$_4$) in FACE	Ambient CO_2	1.9	Nitschelm *et al*. (1997)
				600 ppm CO_2	3.1	
Netherlands	Sown *L. perenne*	10 cuts yr^{-1} High N (800 kg ha^{-1} yr^{-1})	C balance	Ambient CO_2	2.29	Schapendonk *et al*. (1997)
				2 × ambient CO_2	3.90	
France	Sown *L. perenne*	5 cuts yr^{-1} Low N (160 kg ha^{-1} yr^{-1}) (LN) and high N (530 kg ha^{-1} yr^{-1}) (HN)	Soil C analysis	Ambient CO_2	0.6 (LN), 0.8 (HN)	Loiseau & Soussana (1999)
				2 × ambient CO_2	1.4 (LN), 1.9 (HN)	
UK	Species-rich grassland on limestone soil in solardome	4–5 cuts yr^{-1}	C balance	Ambient CO_2 ambient CO_2 + 250 ppm CO_2	1.2 ± 0.5 2.6 ± 0.3	Fitter *et al*. (1997)
	Species-poor community on peaty gley in solardome	No cutting/grazing	C balance	Ambient CO_2 ambient CO_2 + 250 ppm CO_2	6.4 ± 0.6 8.7 ± 0.2	
USA California	Annual grassland on serpentine	No cutting/grazing	^{13}C labelling in OTC	2 × ambient CO_2	2.66 ± 0.6	Hungate *et al*. (1996)
	Annual grassland on sandstone	No cutting/grazing	^{13}C labelling in OTC	2 × ambient CO_2	3.03 ± 0.4	
USA Central Texas	Perennial grassland	Converted from arable to grassland for 6–60 yr	Soil C analysis	Ambient	0.45	Potter *et al*. (1999)

Table 2 Modelled carbon sequestration (accumulation) rates of temperate grasslands

Model	Location	Grassland system	Management	Climate	CO_2 sequestration (Mg C ha^{-1} yr^{-1})	Reference
CESAR	Europe	European grasslands	European grasslands average	Commitment period (2008–12)*	0.52	Vleeshouwers & Verhagen (2002)
			Conversion of all arable land to grassland		1.44	
			Application of farmyard manure		1.50	
Simple statistical model‡	France	Managed grasslands	Reduction in N-fertilizer inputs in intensive leys	Ambient	0.3	Soussana *et al.* (2004)
			Conversion of arable land to grass/legume		0.3−0.5	
			Intensification of permanent grassland		0.2	
			Intensification of nutrient-poor grassland		−0.9−1.1	
			Permanent grassland to medium-duration leys		−0.2	
			Increasing duration of leys		0.2−0.5	
			Short-duration leys to permanent grassland		0.3−0.4	
CENTURY	Global	Temperate steppe (C_3/C_4)	Unfertilized	350 ppm CO_2	0.002	Parton *et al.* (1995)
				+CC§	0.030	
				$2 \times$ ambient CO_2 + CC§	−0.029	
		Humid temperate (C_4)		+CC¶	−0.030	
				$2 \times$ ambient CO_2 + CC¶	−0.029	
				350 ppm CO_2	0.031	
				+CC§	−0.060	
				$2 \times$ ambient CO_2 + CC§	−0.028	
				+CC¶	−0.056	
				$2 \times$ ambient CO_2 + CC¶	−0.030	
Hurley pasture model (HPM)	UK	UK temperate	N input, 20 (upland site, US) and 50 (lowland site, LS) kg N ha^{-1} yr^{-1}	Standard conditions, US	0.08	Thornley & Cannell (1997)
			Continuous grazing of five (US) and 10 (LS) sheep ha^{-1}	Standard conditions, LS	0.05	
				+5°C +700 ppm CO_2, US	0.09	
				+5°C +700 ppm CO_2, LS	0.15	
HPM	UK	UK temperate	Range from low (5) to high (100 kg N ha^{-1} yr^{-1}) atmospheric fixed N flux	280 ppm CO_2	9200−12000†	Thornley *et al.* (1991)
				280 ppm CO_2 +2°C	7800−10000†	
			Grazing consisted of 10 sheep ha^{-1}	350 ppm CO_2	11900−16100†	
				350 ppm CO_2 +2°C	10100−13500†	
				600 ppm CO_2	17300−27100†	
				600 ppm CO_2 +2°C	14600−22200†	

*Business-as-usual scenario: 1°C increase in temperature and 0.2% increase in CO_2 yr^{-1}.
†Mg C yr^{-1} for UK total above- and below-ground C sequestered by the temperate grassland system.
Note that the HPM presents C sequestration rates for the grassland system whereas the other models present soil C sequestration rates.
‡After Hénin & Dupuis (1945); see Soussana *et al.* (2004).
Climate change (CC) according to §Canadian Climate Change scenario; ¶Geophysical Fluid Dynamics Laboratory High scenario.

Table 3 Measured and modelled carbon sequestration (accumulation) rates of temperate grasslands: summaries from literature reviews

Location	Grassland system	Management	Climate	CO_2 sequestration (Mg C ha^{-1} yr^{-1})	Reference
Worldwide	Global (primarily temperate) grasslands	Fertilization	Ambient	0.30	Conant *et al.* (2001)
		Improved grazing		0.35	
		Conversion from arable to permanent grassland		1.01	
		Conversion from native vegetation to grassland		0.35	
		Introduction of legumes		0.75	
		Earthworm introduction		2.35	
		Improved grass species		3.04	
Europe	European grasslands	Conversion from arable land to 1 : 3 yr ley : arable rotation	Ambient	1.6	Smith *et al.* (1997)
USA	Cool temperate grassland	Conversion from arable land to permanent pasture	Ambient	0.27	Post & Kwon (2000)
USA	Rangelands	Poorly managed	Ambient	0.1	Schuman *et al.* (2002)
		Well managed		0.3	
		Conservation Reserve Program (CRP) grasslands		0.6	
USA	US grazing lands	Grazed grassland	Ambient	$29.5 \times 10^6 - 110 \times 10^6$†	Follett *et al.* (2001)
		Land conversion and restoration		$17.6 \times 10^6 - 45.7 \times 10^6$†	
		Low-input grassland		$-4.1 \times 10^6 - 13.9 \times 10^6$†	
		'Improved' management and intensification		$16.0 \times 10^6 - 50.4 \times 10^6$†	
		Emissions from grazing lands		$-12.0 \times 10^6 - 19.5 \times 10^6$†	
		Net gain		**$17.5 \times 10^6 - 90.5 \times 10^6$†**	

†Mg C yr^{-1} for US total grazing lands.

soil. This relationship is different for different types of land use and different clay types, although it has been suggested that grassland-derived soils have a higher potential for C stabilization because of their higher base saturation (Collins *et al.*, 2000).

IV. Tracking carbon movement

Because of the relatively large amount of C already present in most soils, it has usually proven extremely difficult to identify the new C present in different fractions in the soil. Measurements are complicated because of the spatial and temporal heterogeneity of soil C, which shows large field-scale variability caused by varying topography and parent material as well as past differences in vegetation and management. Furthermore, although the release of organic compounds from roots of growing grassland plants have substantial effects on organic matter dynamics, the fundamental mechanisms involved are not yet fully understood and there is still no proper quantification of the release of organic C compounds from roots or the assessment of seasonal dynamics (Cardon, 1996; Darrah, 1996; Saggar & Hedley, 2001).

As we have seen, most currently available data on soil C changes have been obtained from long-term field experiments of bulk C content. When sampling and analyses were well designed and treatments fully randomized (Bowman *et al.*,

2002), it has been possible to demonstrate significant differences in soil C (Schulze *et al.*, 1996; Potter *et al.*, 1999; Schulze *et al.*, 2002; Martens *et al.*, 2003). An alternative and/or complementary approach developed in recent years is to use stable C-isotope analysis to track C in the soil (Schimel, 1993; Ehleringer *et al.*, 2000; Schimel *et al.*, 2000). This type of analysis has been shown to provide a more sensitive method for determining C gains and losses in soil than direct measurements of total C (Balesdent *et al.*, 1987), although Ehleringer *et al.* (2000) argue that stable isotopes are best viewed as a tool for constraining magnitudes of different processes and for source identification, not as a tool for directly assessing flux rates.

It has long been known that the major photosynthetic pathways (C_3 and C_4) discriminate against $^{13}CO_2$ to different degrees, and this is reflected in the soil that forms under either C_3 or C_4 vegetation. Consequently, growing plants of photosynthetic types different from those plants with which the soil developed provides a natural tracer experiment and a sensitive method for tracking C sequestration (Balesdent *et al.*, 1988; Wedin *et al.*, 1995). A simple isotopic mixing model can be used to calculate the proportion of new C input to the soil (Balesdent *et al.*, 1987).

Experiments where grasses have been grown at elevated CO_2 also provide an opportunity to track changes in C storage, because the additional CO_2 is usually derived from fossil

fuel which is depleted in ^{13}C ($\delta^{13}C$ typically −35‰) compared with atmospheric CO_2 ($\delta^{13}C$ −8‰) (Hungate *et al.*, 1996; Nitschelm *et al.*, 1997; van Kessel *et al.*, 2000b). The isotopic composition of CO_2 in the elevated CO_2 treatment is determined by the proportions of atmospheric and fossil fuel-derived CO_2, and provides a continuous C-isotope tracer in the elevated treatments. Plants grown in the elevated CO_2 atmosphere are depleted in $\delta^{13}C$ and, as the litter from these plants decomposes and becomes incorporated into the SOM, the $\delta^{13}C$ of the soil C will decrease. To track C in ecosystems at ambient CO_2 concentrations is more difficult, but by using enclosed mesocosms it is possible to pulse $^{13}CO_2$ tracers that can induce a 10–12‰ ^{13}C enrichment in bulk plant isotopic composition relative to untreated plants (Leavitt *et al.*, 2001). This ^{13}C signal can then be tracked in the plant–root–soil system.

Using these methods, van Kessel *et al.* (2000a) investigated the effects on clover (*Trifolium repens*) and ryegrass (*Lolium perenne*) pastures of exposure to ambient and elevated CO_2 conditions over a 6 yr period. They found large differences in productivity which led to differences in below-ground C input, but this did not lead to a significant increase in total soil C sequestration. Carbon associated with the sand and light fractions of the soil organic pool showed the largest change in ^{13}C content, indicating that these C fractions are the most labile of the C pools. Their results indicate a sharp discontinuity between the turnover rates of labile C and other more stable pools in grassland soils (van Kessel *et al.*, 2000b).

Balesdent *et al.* (1987) were among the first to track the ^{13}C signals into different particle-size fractions of soils and found that in their soils most C was associated with fractions in the 0–20 μm range (fine clay through fine silt). This combination of SOM fractionation with the ^{13}C natural abundance technique is now recognized as offering a very useful approach to estimating small shifts in soil C stores that might be significant in the long term, but that cannot be detected by conventional methodologies (del Galdo *et al.*, 2003).

Another method of tracking C in soils is to measure the content of the radioactive isotope ^{14}C (Schimel, 1993). Natural radiocarbon ^{14}C has an abundance in the atmosphere of ≈1 atom ^{14}C per 10^{12} atoms ^{12}C, with a half-life of 5730 yr. ^{14}C is also produced during nuclear weapons testing which, in the two decades after 1950, released large quantities of ^{14}C into the atmosphere: so-called bomb ^{14}C. Living plants exchange ^{14}C with the atmosphere through photosynthesis and respiration and have about the same ^{14}C content as the contemporary atmosphere. When plants die they no longer absorb ^{14}C from the atmosphere and the ^{14}C content declines as a result of radioactive decay. The ^{14}C content of organic matter can therefore serve as a clock to measure how long C has resided in soils and the average rate of C flux into soils on different timescales (Trumbore, 2000; Wang & Hsieh, 2002). A widely used method of determining the turnover time of SOC has been to examine the uptake of bomb ^{14}C in SOM.

This ^{14}C-tracer technique has proved useful in estimating the rate of soil C turnover on timescales of years and decades (Jenkinson, 1990; Paul *et al.*, 1997a; Wang *et al.*, 2000; Wang & Hsieh, 2002; Wang *et al.*, 2002). However, this approach does require that both archived and present-day samples of the same soil are available for C and ^{14}C analysis, and also assumes that turnover time is constant and independent of changes in climate and management conditions. On a shorter timescale, measurements of the ^{14}C isotopic content of soil-respired CO_2 offers the opportunity of investigating the seasonal and annual dynamics of the soil C cycle (Wang & Hsieh, 2002; Wang *et al.*, 2002).

V. Models of soil carbon dynamics

An alternative approach to complex, direct measures of soil C dynamics is to model these processes. Models are not substitutes for direct measurements, but they do allow integration of the various factors controlling decomposition processes and SOM dynamics. Most importantly, they can be used to predict changes in SOM under the different management and climatic conditions that may occur in the future. Table 2 compares the outputs of a selection of models that have been used to predict C sequestration rates in temperate grasslands. The applications of simulation models range across scales from field or plot level (Jenkinson *et al.*, 1987) to regional (Parton *et al.*, 1987) and global scale (King *et al.*, 1996; Cao & Woodward, 1998). Many soil C models have been relatively successful in simulating C dynamics at the field and regional scale, but they generally need some site-specific calibration to provide reliable predictions (Paustian *et al.*, 1997). Most of the models describe SOC turnover as a sum of multiple and parallel compartments or pools, with each compartment having its own turnover rate. These pools are, in effect, simplifications of the complex chemical, biological and physical characteristics of SOM (see Section II). An example of a widely used compartmental model is the Rothamsted SOC model (RothC), which has five compartments: decomposable plant material; resistant plant material; microbial biomass; humus; and inert organic matter (Jenkinson & Rayner, 1977; Jenkinson, 1990). Using the Rothamsted long-term agricultural experimental data and ^{14}C radiocarbon dating of the archived soil samples, Jenkinson & Rayner (1977) calibrated their SOC-turnover model and estimated the sizes and turnover times of the five SOC compartments.

Another, well developed compartment SOC model with similarities to RothC is the CENTURY model (Parton *et al.*, 1987; Parton *et al.*, 1988). This is an ecosystem model that simulates soil C, N, P and S dynamics, primary productivity and water balance at monthly time steps. It was originally designed to analyse SOM dynamics in grassland soils for periods up to several thousand years (Parton *et al.*, 1987). It includes two litter fractions (metabolic and structural) and three organic matter fractions (active, slow and passive). All

such compartment models have the disadvantage that they require reliable field information on the size and turnover rates of each compartment, which is difficult to obtain, especially if the characteristics of the components are ill-defined (Smith *et al.*, 2002; del Galdo *et al.*, 2003).

Both the RothC and CENTURY models are classified as ecosystem-level models by Paustian *et al.* (1997) to distinguish them from another group, classified as macro-scale models. A macro-scale model such as the Terrestrial Ecosystem Model (Melillo *et al.*, 1993) assesses soil C change at very large spatial resolutions, typically thousands of square kilometres. Compared with the ecosystem models they have a simple structure (fewer plant, litter and soil components) and employ more general rate-controlling factors.

More recent developments by Falloon *et al.* (1998) have used RothC on a scale closer to the macro-scale models to estimate C sequestration at the regional level using the simulation model linked to spatially explicit data. By linking geographical information systems that contain detailed information on soils, land use and climate to dynamic simulation models such as RothC for the turnover of organic C, it is possible to estimate the impacts of land use and climatic changes on C stocks in soil at the macro-scale.

VI. Management effects on carbon sequestration

The amount of SOM retained by grassland soils is strongly influenced by management (Fig. 3; Barnwell *et al.*, 1992; Conant *et al.*, 2001; Zan *et al.*, 2001; Schuman *et al.*, 2002). Management practices which eliminate disturbance to soil C in established pastures, and conversion from cultivation to well managed permanent grasslands, have the greatest impact on C sequestration. Guo & Gifford (2002) demonstrated in their meta-analysis that conversion from crop to pasture leads to large increases in soil C of up to nearly 30%, although this was very dependent on soil depth, the topsoil being more active in sequestering C after land-use change. Unsurprisingly, the reverse process of transition of grassland to arable land resulted in a decrease in soil C averaging close to 60% from 97 observations (Guo & Gifford, 2002), and also occurred mainly in the upper horizons (Wang *et al.*, 1999). In addition, management methods that increase forage production, such as fertilization, irrigation, intersowing of grasses and legumes, intensification of grazing, and introducing earthworms, also have the potential to increase SOM (Conant *et al.*, 2001). The introduction of productive forage grasses also increases sequestration. For example, sowing tall fescue (*Festuca arundinacea*) and smooth bromegrass (*Bromus inermis*) has been shown to increase the soil C pool by 17.2%, equivalent to a C sequestration of ≈3 Mg C ha^{-1} yr^{-1} over a 6 yr period (Lal *et al.*, 1998). Other high-yielding grasses, such as switchgrass (*Panicum virgatum*) and miscanthus (*Miscanthus × giganteus*), will also increase the soil C pool as a consequence of their high biomass production rates, deep rooting systems and perennial

nature. For example, over 10 yr under switchgrass soil, organic C was 45 and 28% higher at depths of 1–15 and 15–30 cm, respectively, compared with fallow soil in an adjacent area (Ma *et al.*, 2000).

Post & Kwon (2000) summarized the most significant factors that might determine the direction and rate of change in SOC in response to management. Those factors that may lead to an increase in C storage include: (i) increasing the input rates of organic matter; (ii) changing the decomposability of organic matter inputs to increase the light fraction organic C; (iii) placing organic matter deeper in the soil; and (iv) enhancing physical protection through either intra-aggregate or organomineral complexes.

In general, grasslands with the greatest potential for soil C increase are those that have been depleted in the past by poor management. On intensively managed grasslands, improved practices such as rotational grazing and fertilizer application have the greatest potential, while on extensively managed grassland, grazing intensity and frequency are the main management practices to affect soil C levels. Reeder & Schuman (2002) have shown that soil C content was highest in US mixed-grass and short-grass rangelands at the highest stocking density, while excluding grazing caused immobilization of C in excessive above-ground plant litter or an increase in annuals which lack the dense fibrous rooting systems conducive to SOM formation and accumulation. They concluded that soil C was increased by grazing, caused by a higher annual shoot turnover and a redistribution of C within the plant–soil system as a result of changes in plant species composition. Both LeCain *et al.* (2002) and Reeder & Schuman (2002) recommended a light-to-moderate stocking density to maintain a diverse plant community with a dense rooting system, enabling a greater degree of C sequestration in the soil. According to Schuman *et al.* (1999), livestock grazing, both heavy and light, resulted in an increase in soil carbon and nitrogen in the top 30 cm of a soil profile after 12 yr as compared with an ungrazed control. They attributed these increases to a redistribution of C and N within the plant–soil system, an increase in C and N cycling rates between the system components, and reduced losses of C and N from the plant–soil system. However, in this study the total mass of C in the plant–soil system to 60 cm depth was unaffected, suggesting that this form of management simply leads to a redistribution of C in the soil profile. Bruce *et al.* (1999) have proposed that, over the next two decades, intensively managed pastures in North America have the potential for further C gains of 0.2 Mg ha^{-1} yr^{-1} through the use of improved grazing regimes, fertilization practices and irrigation management as well as the introduction of more productive species. However, they also suggest that most extensively managed rangelands and long-term (> 50 yr) pasture are probably near equilibrium with respect to C and will not be significant sinks without some additional inputs such as fertilizer.

Soussana *et al.* (2004) recently used a simple single-pool model to determine the effects of grassland management on

C accumulation in French grassland soils. They show that moderately enhanced N fertilization increases the organic matter input to the soil proportionally more than it increases the process of C mineralization. Furthermore, although intensive N fertilization increases production, it is also shown to stimulate mineralization and therefore enhance C losses. Consequently the practices that most favour C sequestration are those that involve a reduction in the intensification of highly fertilized grasslands and a moderate intensification of poor grasslands (Tables 1–3). Also, grazing that stimulates primary production increases C accumulation when compared with cutting.

It is clear that there is still some uncertainty about the impact of changed management practices on the ability of grassland soils to sequester C, particularly in the long term. For example, in an analysis of changes in SOC storage resulting from land-use and management practices employed in US agriculture, Ogle *et al.* (2003) were unable to conclude with 95% confidence that US agricultural soils were a net sink for atmospheric CO_2 for the period 1982–97. Also Soussana *et al.* (2004) found that uncertainties concerning the estimated values of C storage or release after a change in grassland management are in the order of 0.25 Mg C ha^{-1} yr^{-1}, which falls within their range of estimates of C sequestration (0.2–0.5 Mg C ha^{-1} yr^{-1}).

VII. Climate-change effects on carbon sequestration

Climate influences both the above- and below-ground processes which drive the C cycle and ultimately determine how much C is sequestered in grassland soils. Joffre & Ågren (2001) have made a useful distinction between climate-driven changes that are either quantitative or qualitative, where the former are those in which the basic structure of the ecosystem remains unchanged and only the rates of processes change, while in the latter there are compositional changes in the ecosystem. The components of the climate that are most important for soil processes are temperature and rainfall.

According to IPCC (2001), the global average surface temperature increased over the 20th century by $\approx 0.6°C$ and is projected to increase between 1.4 and 5.8°C over the period 1990–2100. Winter rainfall is also expected to increase in regions occupied by temperate grasslands (IPCC, 2001). Using the CENTURY model, Ojima *et al.* (1993) and Parton *et al.* (1995) assessed grassland production and soil C worldwide in response to temperature increases of 2–5°C and predicted a substantial loss (3–4 Pg C after 50 yr) of SOC for all grassland areas. The losses from soil C were caused by higher decomposition rates which were increased by as much as 25% in temperate grasslands. However, in contrast Thornley & Cannell (1997) and Cao & Woodward (1998) predicted net increases in the C sink of temperate grasslands with increases in temperature.

Recent model predictions from Riedo *et al.* (2000, 2001) using a more detailed simulation model (PaSim), applied over smaller spatial areas of cool temperate grasslands in Switzerland, suggest that an increase in temperature of 2°C will have small and variable effects on the labile SOC content. According to this model, SOC content declines at some highly productive low-altitude valley sites with an increase in temperature, but at higher altitudes with a high soil clay content and where the relative temperature response of NPP is largest, SOC content increases by up to 10%. At these sites, C loss caused by faster decomposition rates at higher temperatures was more than compensated for by increased C input to the soil resulting from a higher NPP. According to Riedo *et al.* (2000), management practices such as cutting or grazing had less effect than temperature increases on NPP. Overall, with increasing temperature the effect of grazing on C balance may be both positive and negative. For example, while at a warmer site a 4°C increase in temperature combined with increased precipitation resulted in C loss from grazed swards, at a cooler site a 2°C rise in temperature resulted in greater C storage.

In response to evidence based on experimental observations that soil C pools may be much less depleted at elevated temperatures than predicted by most ecosystem models, Giardina & Ryan (2000) and Thornley & Cannell (2001) hypothesize that increasing temperatures may have a larger effect on the rate of physicochemical processes relative to biological processes, thus transferring increased amounts of organic C to 'protected', more stable soil C pools. They suggest that, in the short term, accelerated microbial respiration caused by warming results in an increase in soil C loss, but in the long term more C is sequestered because of higher NPP combined with accelerated physicochemical 'stabilization' reactions. Thus in the long term rising temperature tends to induce a negative feedback, enabling greater amounts of C to be sequestered at higher temperatures.

Experimental treatments that have exposed grassland monoliths to elevated temperatures have tended to support the more recent model predictions of Thornley & Cannell (2001). For example, Loiseau & Soussana (1999) found no effect of a 3°C increase in temperature (under elevated CO_2) on soil C accumulation in organic matter fractions above 50 μm. Fitter *et al.* (1999) also recorded no change in soil C storage in an upland grass ecosystem soil warmed by 3°C, presumably because root production and death rates increased by equivalent amounts. Evidence from global patterns of C stocks along gradients of mean annual temperature is mixed. In a survey of > 2700 soil profiles from around the globe, Jobbágy & Jackson (2000) concluded that SOC decreased with increasing temperature and increased with higher rainfall and clay content. Their analysis also showed that the importance of these controls switches with soil depth so that climate dominates in shallow layers and clay content dominates in deeper layers. On the other hand, Kirschbaum (2000) found

no clear trend when global patterns of soil C were plotted against mean annual temperature as long as very wet and very dry locations were excluded. Liski *et al.* (1999) also showed that soil respiration along a Scandinavian temperature gradient had low sensitivity to temperature.

VIII. Response to elevated CO_2

The continuous increase in atmospheric CO_2 is well documented (IPCC, 2001), and the response of ecosystems to elevated CO_2 provides important feedback to the global C cycle. Direct effects of elevated atmospheric CO_2 on soil processes are unlikely to occur because of the already high CO_2 concentration (> 10^3 μmol mol^{-1}) present in soil (van Veen *et al.*, 1991). However, a large number of experimental studies have demonstrated the direct effects of elevated CO_2 on the C balance of grassland species as a result of an increase in NPP at elevated CO_2 and a preferential allocation of additional fixed C to the roots and subsequently to the soil.

Exposure of grassland to elevated CO_2 has been shown to affect soil aggregate size, but the response appears to be restricted to drier soils. Consequently, whereas Rillig *et al.* (1999) found elevated CO_2 increased aggregate size in two Mediterranean grassland systems, possibly because of increased mycorrhizal secretion of glomalin promoting soil aggregation, Niklaus *et al.* (2001a) reported the opposite for an alpine species-rich calcareous grassland. The explanation for the reduction in aggregate size was that at elevated CO_2 there was an increase in soil moisture, caused by reduced evapotranspiration, resulting from partial stomatal closure induced by high CO_2 (Niklaus *et al.*, 2001a). Under these conditions, aggregate formation was restricted in the wetter soils. Elevated CO_2 has also recently been shown to cause a reduction in the water repellency or hydrophobicity of soils at field capacity, a characteristic that influences aggregation of soil particles and C sequestration (Spaccini *et al.*, 2002; Newton *et al.*, 2003).

Long-term studies on *L. perenne* swards grown in free-air CO_2 enrichment (FACE) have shown that the significant stimulation of leaf photosynthesis by elevated CO_2 was maintained for as long as 10 yr (Ainsworth *et al.*, 2003). The stimulation was maximal following harvest, at the warmest times of the year and with a high supply of N, and decreased progressively during the regrowth following harvests. Two frequently observed additional effects of growing plants in elevated CO_2 are increases in the leaf concentration of total nonstructural carbohydrates and the C : N ratio of plant litter (Körner, 2000). Although it has been suggested that both effects could influence the rate of mineralization in the soil, observed differences in decomposition rates between plants grown at ambient and elevated CO_2 concentrations are not as large as first hypothesized, and the effects on mineralization rates appear to be minimal (O'Neill & Norby, 1996). A more important response appears to be greater below-ground C inputs through root exudation and turnover, leading to

increased soil microbial biomass (Diaz *et al.*, 1993; Cotrufo & Gorissen, 1997; Williams *et al.*, 2000). Also in dry periods, microbial activity in soil may increase because of greater moisture content resulting from higher water-use efficiency of plants in response to elevated CO_2 (Williams *et al.*, 2000). As a result of greater microbial activity, N availability may increase because of the more rapid recycling of microbial N. In contradiction to this, Hu *et al.* (2001), Jongen *et al.* (1995), van Ginkel & Gorissen (1998) and van Ginkel *et al.* (2000) have demonstrated a reduction in microbial decomposition in grassland after exposure to elevated CO_2, and Hu *et al.* (2001) suggested that elevated CO_2 reduces the amount of N available to microbes through enhanced plant growth. This could result in enhanced C accumulation in grassland soils at elevated CO_2. The response of nutrient-limited grasslands to elevated CO_2 therefore depends on the availability of N in the soil, the N-use efficiency of the plant, and uptake and loss of nutrients by the plant. Consequently, it is likely that any initial stimulation in growth rate cannot be sustained because the required nutrients are tied up in the decomposition process and the longer-term responses to elevated CO_2 will be dominated by slow changes in turnover of soil C and N pools.

Several experiments where grasses have been exposed to elevated CO_2 have now demonstrated that C sequestration is increased under these conditions. Schapendonk *et al.* (1997), using a C-balance approach, found that in regularly cut swards of *L. perenne* in a 2 yr experiment, the total amount of C sequestered by the system was 458 and 779 g m^{-2} in the ambient and twice ambient treatments, respectively. Casella & Soussana (1997) showed that a large part of the additional photosynthetic C assimilated at elevated CO_2 by a sward of *L. perenne* was stored below ground as root biomass. Cotrufo & Gorissen (1997) have shown an increase in C input to the soil by up to 26% from three grass species grown at different levels of N availability under elevated CO_2. Experiments at the Swiss FACE site using stable isotopes to determine soil C sequestration potential of *T. repens* at ambient and elevated CO_2 also found that soil C input and storage was greater under elevated than ambient CO_2, probably because of enhanced plant biomass production (Nitschelm *et al.*, 1997) (Table 1). Owensby *et al.* (1996) showed increased C accumulation in soil under tallgrass prairie in response to elevated CO_2 and suggested that, even in the absence of increased N availability, it is likely that these soils will become a substantial sink for C as atmospheric CO_2 continues to rise. Finally, Fitter *et al.* (1999) showed an increased root biomass in both species-poor and species-rich grassland vegetation at elevated CO_2. Both grasslands acted as C sinks under present-day CO_2 concentrations, but more C was sequestered by the species-poor community on a peaty gley soil compared with the species-rich grassland on a brown earth soil over limestone in elevated CO_2.

Körner (2000, 2003) has argued that, for low-input temperate grasslands that are phosphorus-deficient, nutrient

feedbacks are central to understanding responses to CO_2 enrichment and therefore the regulation of C sequestration in soils. Here the crucial issue for grassland responses will be the effect of elevated CO_2 on legume content. If legume content increases, larger quantities of N will potentially be allocated to the soil (Soussana & Hartwig, 1996), although the legume response will also depend on the availability of P (Körner, 2003). There is therefore a complicated interaction between elevated CO_2, legume presence and phosphate availability. Additionally, there is now substantial evidence that the variable responses of different species at elevated CO_2 result in changes in species composition favouring broadleaved species and legumes (Byrne & Jones, 2002). This will have consequences for the N dynamics of grasslands and may reduce N limitation enough to result in larger than anticipated responses to elevated CO_2.

Hungate *et al.* (1997), working with naturally occurring grasslands in central coastal California, also found that elevated CO_2 enhanced C partitioning to the roots, but they suggest that most of the additional C ends up in increased root respiration and exudation. Hungate *et al.* (1997) and Robles & Burke (1998) concluded that short-term CO_2-enrichment experiments tended to overestimate the potential for grasslands to sequester C in the long term. Niklaus *et al.* (2001b) also argue that, although elevated CO_2 leads to more biomass production, both above and below ground in their nutrient-poor and species-rich calcareous grasslands, high rates of long-term sequestration of C in soils is unlikely because most short-term C sequestration is in plants and detritus with a rapid turnover. Experiments where plants have been grown on soils that have developed under elevated CO_2 for at least 20 yr have shown that plant growth response to elevated CO_2 is reduced compared with plants grown on unmodified soils (Edwards *et al.*, 2003). This is further evidence that it may be impossible to extrapolate from short-term experiments at elevated CO_2 (< 5 yr) to long-term responses in the soil (> 50 yr) because of the slow changes in soil characteristics that occur during exposure to elevated CO_2.

IX. Conclusions

This review summarizes current knowledge on how temperate grasslands operate as C sinks and identifies the factors that are most important in regulating their C sequestration potential. Some outstanding questions to be answered by future research are: (i) what are the mechanisms for entry of C into the 'labile', 'active' and 'recalcitrant' pools; (ii) what are the roles of heterotrophic and autotrophic respiration in returning C to the atmosphere; and (iii) what are the roles of soil temperature, moisture, elevated CO_2, and soil texture and structure in the distribution and turnover of C? A shortage of suitable techniques to follow C flows through the plant–root–soil system are largely responsible for the current lack of information, but labelling with ^{14}C or ^{13}C is increasingly used

to provide quantitative information on below-ground inputs and decomposition rates of newly formed root material. Suitable isotope techniques combined with physical fractionation have the potential to improve greatly our understanding of the kinetic fractions of SOM, as there is little doubt that the partitioning of C inputs among soil pools with varying turnover times is a critical controller of the potential of grassland to increase C storage. As only a small percentage of the C added to soil becomes stabilized, it is important to understand those soil physicochemical reactions that stabilize soil C and protect it from microbial respiration in more detail. In particular, it is crucial to understand how management processes and climate factors such as global warming and increases in atmospheric CO_2 concentration regulate these processes, which have the potential to sequester substantial amounts of C in grassland soils in the future.

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