



Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems



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ABSTRACT

The C sequestration capacity of grassland soils depends on both the net primary production of the ecosystem that determines the C flows from atmosphere to vegetation and soil, and on the mean residence time of C within the different compartments. Within grassland ecosystems, C and N cycles are strongly coupled by elemental stoichiometry of plant autotrophy and of soil microbial heterotrophy. Plasticity in plant form and function, plant species diversity and regulation of biological N fixation all contribute to stabilize the C:N ratio of organic matter inputs to soil. Soil processes such as the priming effect and nitrate leaching tend to restore stoichiometry by releasing elements in excess. Nevertheless, domestic herbivores tend to uncouple the C and N cycles, by releasing digestible C as CO₂ and CH₄, and by returning digestible N at high concentrations in urine patches. At low stocking density, herbivores enhance soil N cycling and net primary productivity, leading to an increased soil C sequestration, which however declines at high stocking density. Assuming no overgrazing, the environmental impacts of grassland intensification are therefore controlled by a trade-off between increased C–N coupling by vegetation and increased C–N decoupling by animals. Stimulation of vegetation by adequate N and P fertilizer applications increases the C flows from the atmosphere to the soil, while increasing stocking density reduces mean C residence time within the system.

Intensification of grassland productivity by manipulation of both primary production and stocking density leads to complex responses in terms of environmental impacts: as intensification increases, positive impacts, such as C sequestration are progressively impaired by negative impacts linked to excessive active N forms. Hence, in each unique environmental setting, a threshold level of grassland intensification can be determined above which any additional animal production would be associated with unacceptable environmental risks. Improved grassland management and integration with crop systems may help minimize the harmful environmental effects of C–N decoupling by domestic herbivores, thereby enhancing synergies among food production, biodiversity and various other ecosystem services.

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1. Introduction

The grassland biome, which corresponds to permanent herbaceous vegetation used by wild and domestic herbivores, covers about one-quarter of the earth's land area (Ojima et al., 1993). Grasslands are estimated to currently contribute to the livelihoods of over 800 million people (Reynolds et al., 2005) and provide a range of goods and services to support flora, fauna and human populations. Except within eco-geographical regions where vegetation is climatically maintained at herbaceous stage, most of

the grasslands around the world are the result of livestock management avoiding encroachment by shrubs and trees (Lauenroth, 1979; Lemaire et al., 2005). The co-evolution between grassland plant species and wild herbivores has framed the structure and balance of grassland plant communities (Harper, 1977).

Herbivore domestication, livestock management systems, and animal and plant breeding have contributed to shift the balance towards increased animal productivity, leading to increased environmental impacts (White and Vannaselt, 2001; FAO, 2006). Ruminant grazing intensity in rangelands and extensive grasslands is projected to further increase, resulting in considerable intensification of livestock production in the humid and sub-humid grazing systems of the world (Thornton, 2010), while intensification is likely to be severely constrained by increased droughts and heat waves in some arid and semi-arid regions (Tubiello et al., 2007; Soussana et al., 2013).

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A key question for grassland management systems is how far can the intensification of animal production be increased without deteriorating other ecosystem services? Grassland ecosystems play a key role in the dynamics of atmosphere, hydrosphere and land interactions that drive global changes and environmental hazards, as well as contribute to the preservation of biodiversity and to the production of safe food (Lemaire et al., 2011). Most of the ecosystem services provided by grasslands, such as protection of soil quality, preservation of ground and surface water quality and regulation of climate through soil carbon sequestration are linked to ecosystem processes (such as photosynthesis, respiration and soil organic matter decomposition), which are part of the global C and N cycles. The large biodiversity hosted by grasslands (vegetation, soil biota, fauna and microbes) plays an important role in controlling these biogeochemical cycles and in the adaptive capacity of these ecosystems to disturbance and to global environmental change (Soussana and Duru, 2007). Further intensification of grasslands will be confronted with the need to reduce greenhouse gas (GHG) emissions, to better control impacts on water quality and eutrophication, and to preserve ecosystem services (Lemaire et al., 2011).

The objective of this paper is to review our understanding of grassland ecosystem processes and of their contribution to the C and N cycles and to GHG emissions. We show that the C and N cycles are locally strongly coupled in extensive pastures, but become progressively uncoupled as intensification of grassland management increases. We argue that re-coupling the C and N cycles by improving grassland management and by better integrating crop and livestock systems would create synergies between food production, biodiversity and ecosystem services. Finally, we discuss limits to grassland intensification and practical options to achieve an environmentally sustainable intensification.

2. The carbon cycle in grasslands

As underlined by Parsons et al. (2011), the relative distribution of C between atmosphere and biosphere is proportional to the relative mean residence time of C in each compartment. Hence, the C sequestration capacity of grasslands depends (i) on net C flows from atmosphere to vegetation and soil (*how much?*), and (ii) on mean residence time of C within the ecosystem (*how long?*). Under grazing conditions, the residence time of above-ground C is very short (e.g. 10–50 days). It varies according to the probability of defoliation and digestion of leaf tissues and to the associated release of C to the atmosphere. In contrast, the residence time of below-ground C is long (from about 1 to >1000 years) in grassland ecosystems.

Grassland soils are typically rich in organic matter, partly owing to active rhizodeposition (Jones and Donnelly, 2004) and partly to the activity of earthworms and other fauna that promote macro-aggregate formation into which micro-aggregates form that stabilize soil organic carbon (SOC) for extended periods (Six et al., 2002; Bossuyt et al., 2005). Rhizodeposition favours C storage (Balesdent and Balabane, 1996), because direct incorporation into the soil matrix allows a high degree of physical stabilization of the SOC. Root litter transformation is also an important determinant of the C cycle in grassland ecosystems, which is affected both by the root litter quality and by the rhizosphere activity (Personeni and Loiseau, 2004, 2005; Rasse et al., 2005). Mean residence time of coarse organic carbon (>0.2 mm) is determined by the C:N ratio of plant litter, which can be high under extensive management leading to long residence time (Klumpp et al., 2007). Intensive grassland management lowers C:N ratio of plant litter, leading to rapid degradation and short residence time. Soil organic C may persist because it is bound to soil minerals in forms that microbial decomposers cannot access (Baldock and Skjemstad, 2000). Six et al. (2002) suggested that physicochemical characteristics (i.e. the silt and clay

fractions) inherent to soils define the maximum protective capacity of these pools, thereby limiting soil C sequestration with increased organic residue inputs. Carbon saturation may happen in top soil layers (Six et al., 2002), but is unlikely in deep soil, given the low density of roots and of fresh organic matter inputs in deep soil layers. Sequestered SOC can, if undisturbed, remain in the soil for centuries. In native prairie sites in the US, where SOC was ¹⁴C-dated (Follett et al., 2004), substantial amounts of SOC remained at depth even after several millennia (Fontaine et al., 2007). The lack of energy supply from fresh organic matter protects ancient buried organic C from microbial decomposition (Fontaine et al., 2007). Therefore, agricultural practices like ploughing, which mix soil layers and break soil aggregates, accelerate top soil organic C decomposition (Paustian et al., 1998; Conant et al., 2007).

While there has been steady C accumulation in soils of many ecosystems over millennia (Schlesinger, 1990), it is usually thought that soil C accumulation capacity is limited (Six et al., 2002). Therefore, in a steady-state, non-disturbed soils should have attained C balance after several centuries (Lal, 2004). However, net primary productivity and soil respiration are currently affected by climate change in most regions of the world (Nemani et al., 2003), which implies that soil C stocks are unlikely to have reached equilibrium (Soussana et al., 2010). Despite low C concentration in soil layers below 30 cm, sub-soil C may account for >50% of total soil C stored. Moreover, the residence time of C within deep soil horizons is much greater than within top soil layers, since as discussed above (i) less fresh and degradable organic matter accumulates within these horizons, (ii) microbial activity is low, and (iii) sites for protection of organic matter by mineral bounds are not saturated. Therefore, the potential for sequestering C in deep soil layers is considered large (long residence time), but owing to the low influx of C within these horizons this process remains slow.

Soil C sequestration is reversible and C can be rapidly lost through a number of processes such as soil disturbance, vegetation degradation, fire, erosion, nutrient shortage and water deficit. Changes in SOC with time are often non-linear after a change in land use or in grassland management. A simple two parameter exponential model has been used to estimate the magnitude of soil C stock change, whereby C is lost more rapidly than it is gained after a change in land use (Soussana et al., 2004). As a result of periodic tillage and re-sowing, short-duration grasslands tend to have a potential for soil C storage intermediate between crops and permanent grasslands. Part of the additional C stored in soil during the grassland phase is released when the grassland is ploughed. Mean SOC storage increases proportional to the lifespan of perennial cover, i.e., less frequent ploughing (Soussana et al., 2004).

Under intensive grazing, up to 60% of above-ground dry-matter production is ingested by domestic herbivores (Lemaire and Chapman, 1996). However, this percentage can be much lower under extensive grazing. The largest part of ingested C is digestible and, hence, is respired shortly after intake. The non-digestible C (25–40% of the intake according to the digestibility of the grazed herbage) is returned to the pasture in excreta, mainly as faeces. In most productive husbandry systems, herbage digestibility tends to be maximized by agricultural practices such as frequent grazing and use of highly digestible forage cultivars. Consequently, in these systems the primary factor that modifies C returned to the soil by excreta is grazing pressure, which varies with the stocking rate (mean number of livestock units per unit area) (Soussana et al., 2004). Secondary effects of grazing on the C cycle of a pasture include: (i) the role of excretal returns, which, at a moderate rate of grazing intensity, could favour nutrient cycling and increase primary production, especially in nutrient-poor grasslands (De Mazancourt et al., 1998); (ii) the role of defoliation intensity and frequency, and of treading by animals, all of which reduce leaf area and capacity to capture atmospheric CO₂.

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