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The impact of grassland management on biogeochemical cycles involving carbon, nitrogen and phosphorus

C. Rumpel^{1,2*}, A. Crème², P.T. Ngo³, G. Velásquez³, M.L. Mora³, A. Chabbi^{2,4}

¹CNRS, IEES (UMR UPMC-CNRS-UPEC-INRA-IRD), Campus AgroParisTech, Thiverval-Grignon, France

²INRA, UR Ecosys (UMR INRA-AgroParisTech), Campus AgroParisTech, Thiverval-Grignon, France

³Universidad de La Frontera ~ Scientific and Technological Bioresource Nucleus (BIOREN-UFRO), Temuco, Chile ⁴INRA, UR 3PF, Lusignan, France *Corresponding author: cornelia.rumpel@grignon.inra.fr

Abstract

Grassland introduction into intensively managed agricultural landscapes may enhance soil organic matter (SOM) content and ecosystem services. However, the magnitude of this effect depends on grassland management practices, and their influence on the soil system. The aim of this paper is to highlight these impacts and their consequences for SOM dynamics and element cycling. We focused in particular on the effect of different grassland management practices in terms of grazing regime, fertilization, and species choice.

While carbon, nitrogen and phosphorus cycles are more strongly coupled under grassland as compared to permanent cropping, uncoupling of elemental cycles may occur through management intensification. Grazing regime, fertilization and species choice affect elemental coupling and SOM turnover via organic matter input and rhizosphere activity to different extent, thereby resulting in contrasting SOM storage. Grazing may be more beneficial for SOM contents compared to mowing up to a certain animal density depending on soil type and pedoclimatic context. SOM storage may be increased in some cases through specific fertilizer additions, whereas in others no change was observed. Species choice, e.g. high diversity or introduction of legumes, influence element budgets and soil nutrient availability through plant physiological constraints as well as intra- or interspecific interactions. The effect of different plant species mixtures on soil parameters has rarely been elucidated.

We conclude that the impact of grassland management practices on SOM of different soil types and the resulting ecosystem services, such as C and nutrient storage need further research in contrasting pedoclimatic contexts. More studies on the controls of belowground biogeochemical cycling of elements are necessary in order to fully understand and manage belowground processes via aboveground plant communities.

Keywords: Grassland management, elemental coupling, carbon, nitrogen, phosphorus, soil organic matter

1. Introduction

By now it has become evident that intensive agriculture leads to organic matter depletion of soils (Lal, 2004), threatening the ability of agroecosystems to provide ecosystem services. Replenishing soil organic matter (SOM) pools may be possible through the adaptation of land use practices, which favor permanent soil cover and high carbon (C) input belowground (Whitmore *et al.*, 2014). One option may be the establishment of grasslands into agricultural landscapes (Franzluebbers, 2012). Grassland systems include rangelands, shrublands, pastureland, and cropland sown with pasture and fodder crops. They are important in many parts of the world, contain about 20% of the world C stocks (FAOSTAT, 2009; Ramankutty *et al.*, 2008), and have multiple functions and values in terms of ecosystem services (Conant *et al.*, 2010). Grasslands may reduce soil erosion through a permanent soil cover and dense rooting systems, thus favoring soil fertility, water quality and water retention, compared with other crops (Conant *et al.*, 2010). The high organic matter (OM) content of grassland soil is beneficial to soil quality due to its positive effects on aggregation, microbial activity and diversity as well as nutrient and water availability (Kononova, 1966; Allison, 1973; Tate, 1987).

One of the most important characteristics of the SOM pool is its response towards human interventions. In grassland systems, elemental cycles are strongly coupled (Soussana and Lemaire, 2014). However, intensive grassland management may lead to uncoupling of these cycles, leading to negative environmental impacts in terms of air and water quality (Dungait *et al.*, 2012). Grassland management is therefore most important in determining if this land use system preserves its beneficial effects in terms of

closed elemental cycles. As in grasslands, the main SOM stocks are found belowground, it is crucial to understand the effect of management strategies on the coupling via plant litter input and rhizosphere processes. Grassland management concerns species choice as well as management options, such as production versus pasture, grazing type and/or intensity and type of fertilisation, which may influence OM input as well as its dynamics. In recent years it has become evident that maintenance and increase of SOM may be closely related to microbial C use efficiency (Cotrufo *et al.*, 2013) as well as the built up of microbial biomass (Miltner *et al.*, 2012). Recent studies indicated that microbial growth stimulated by plant input of low molecular weight dissolved organic compounds may contribute to SOM built up (Bradford *et al.*, 2013). It has been shown that microorganisms may be able to produce recalcitrant OM (Jiao *et al.*, 2010) and even easily decomposable microbial products may be subject of stabilisation by interaction with the mineral phase (Rumpel *et al.*, 2015). However, microbial turnover and subsequent SOM stabilisation by mineral interactions may have stoichiometric constraints requiring narrow C:N:P ratios (Kirkby *et al.*, 2014), which associates a nutrient cost to soil C sequestration (Richardson *et al.*, 2014). In addition to requiring nutrients, microbial built up of SOM may be counterbalanced or accentuated by priming effects, which are important processes in the plants rhizosphere (Merino *et al.*, this issue). Positive priming refers to mineralisation of otherwise stable C through shifts in microbial community composition (Fontaine *et al.*, 2003). However, in some cases the addition of organic matter to soil as well as rhizosphere processes may lead to a switch of the microbial communities with regards to the substrate they use preferentially, thereby protecting SOM from its decomposition (Kuz'yakov and Gavrichkova, 2010). Plant communities are main controlling factors of these processes because they can

alter the quality of their litter input as well as their rhizosphere processes. By such alterations, they influence soil microbial activity, water and labile C availability as well as pH and nutrient cycling (Peres *et al.*, 2013; Frinzi *et al.*, 2015). In this review, we support the hypothesis that for evaluation of C storage

and nutrient availability in grassland soils, knowledge about the impact of management practices such as cutting or grazing, fertilisation and species choice on belowground processes is crucial (Figure 1). We aim to review the recent literature on different grassland management practices and their impact on the forms and turnover of carbon and major nutrients (N, P).

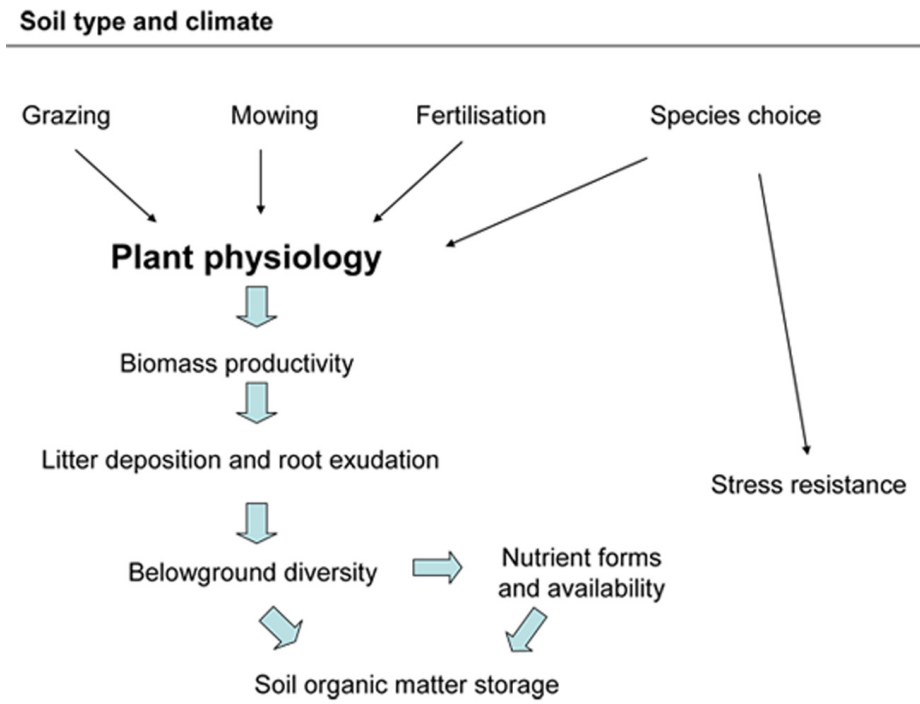


Figure 1. Grassland management effects on plant communities and potential impacts

2. Element coupling and organic matter dynamics in grassland soil

The amount of SOM stored in a given soil is determined by the balance of C, N and P entering the soil, via plant production, atmospheric deposition or fertilisation, and C, N and P leaving the soil driven by microbial processes through mineralization and leaching as CO₂, NH₄, NO₃,

PO₄ (Figure 2) as well as biomass export and erosion. Consequently, a main control on SOM storage is the PO₄ (Figure 2) as well as biomass export and erosion. Consequently, a main control on SOM storage is the amount and type of residues that are produced by plants as the primary producers in the ecosystem and the amount and type of nutrient input. In natural grassland systems, the nutrient elements N and P are coupled closely with

the C cycle through plant production via CO₂ and N and P assimilation leading to plant growth (Figure 2). After the senescence process, when plants recovered some essential nutrients, in natural systems, litter is returned to soil and microbial decomposition starts and decoupling of elemental cycles occurs through mineralisation. However, new coupling of C, N and P cycles also occurs through growth of the soil microbial biomass (Figure 2). These processes are extremely important, as they release nutrients for plant and microbial utilisation and also contribute to the accumulation of stabilized SOM (Miltner *et al.*, 2012). In general, C and N are more strongly

than C and P, due the greater limitations of plant and microbial growth by N than P and the increasing decoupling of P from N and C during SOM formation (Dungait *et al.*, 2012). This may be due to strong sorption and thus immobilization of organic and inorganic P forms to soil minerals (Cerli *et al.*, 2003). Because of its strong association with soil particles, soil erosion is one of the most important processes leading to P loss. As erosion under grassland is low due to permanent soil cover, little P loss may occur in these systems through this process (McLauchlan, 2006), while harvesting export may lead to P depletion in the long-term in unfertilised grassland soils (Pätzhold *et al.*, 2013).

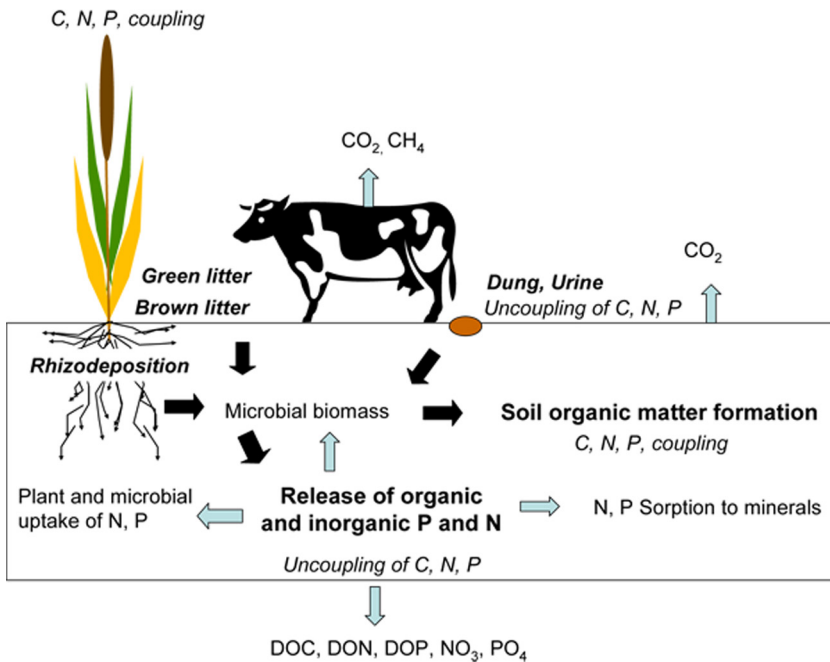


Figure 2. Processes leading to coupling and uncoupling of C, N and P cycles in grassland soil (Soussana and Lemaire, 2014; Miltner *et al.*, 2012; Sanaullah *et al.*, 2010; Dungait *et al.*, 2012; Parsons *et al.*, 2012)

In contrast, N is mobile in soil and subject to leaching losses mainly in form of nitrate if not taken up by plants and gaseous losses through denitrification and ammonia volatilization. In general nitrate leaching under grassland is greatly reduced as compared to cropland and recently it has been shown that grassland introduction into the cropping cycle reduces the amount of nitrate leached from the system (Robinson Kunrath *et al.*, 2015). However, increasingly intensive grassland management also leads to high amounts of reactive N and P present in soil, which may in some cases be released from the system through leaching and volatilisation and contribute to its negative environmental impacts (Sharpley *et al.*, 1994; Soussana and Lemaire, 2014).

Traditionally, it has been supposed that organic N and P have to be mineralised before plant uptake. In recent years it has been shown that amino acids undergo rapid mineralisation (Farrell *et al.*, 2011) as well as direct plant uptake (Hill *et al.*, 2011) in grassland soil. The turnover rates of low molecular weight organic N in grassland soils was found to be rapid, suggesting that these compounds are very important for microbial and potentially plant nutrition despite their low quantitative amounts in soil solution (Wilkinson *et al.*, 2014). Dissolved organic P also contributes in high proportion to total dissolved P losses under grassland soil especially when soils are rich in P (McDowell and Koopmans, 2006) or when they are subjected to dung input (Fuentes *et al.*, 2012). These compounds are easily available to the soil microbial biomass (Turner *et al.*, 2002) even after sorption to the mineral phase (Franson and Jones, 2007), but may also constitute a high proportion of P leached from intensively used pasture systems (McDowell and Koopmans, 2006). It is unknown, whether dissolved organic P can be taken up by plant directly from the solution. The fate of low molecular weight organic compounds containing P and N in soil is insufficiently understood (Figure 3). Studies addressing C, N and P coupling should therefore also concentrate

on dissolved organic compounds, which are a highly dynamic compartment in grassland soils constituting a link between soil, plants and microbes.

3. Effect of grassland management on OM input

Grassland management can impact coupling and decoupling of elemental cycles through regulation of plant production via fertilisation and the grazing regime. Stoichiometry of plant residues determines the intensity of microbial decomposition, and ultimately C sequestration. Under extensive management, for example, plant N nutrition status is low leading to longer residence times of plant litter, compared to intensive management where plants have higher N nutrition status (Klumpp *et al.*, 2007). Thus in extensively managed systems the resulting SOM may be constituted mainly of labile particulate organic matter protected within soil aggregates and not through strong organomineral associations it may therefore be vulnerable to loss upon disturbance (Six *et al.*, 2004). OM input into grassland soil occurs in the form of above- and belowground plant tissue (Figure 2). Aboveground litter input may occur as brown senescent litter in grazed pastures (Mazzanti *et al.*, 1994). Under mowing regime, a significant proportion of aboveground plant litter is returned as fresh litter during harvest. It has been shown, that leaf litter of grassland species may be of very different quality depending whether or not it has been affected by the senescence process (Sanaullah *et al.*, 2010). The initial litter quality determines its degradation behaviour in soil. This is true for aboveground as well as belowground litter additions (Redin *et al.*, 2014). Total soluble sugar content is an important controlling factor in the earlier phase of decomposition, whereas the later stages of decomposition may be regulated by the lignin/N ratio of initial litter. It was shown that grass litter added to soil at different stages of maturity decomposes at different rates and maintains these differences for several years (Sanaullah *et al.*, 2010).

In temperate grassland systems, more than 80% of the net primary production is diverted to root production (Swift *et al.*, 1979). Herbaceous species are less deep rooting than forest vegetation or shrubs and globally ca. 40 % of all SOC in the first meter of grassland soil is found in the uppermost 20 cm (Jobbagy and Jackson, 2000). Root carbon input into soil may occur as root cell sloughing, other root debris, mucilage and root exudation. All may contribute greatly to SOM due to preferential stabilisation within the mineral matrix (Rasse *et al.*, 2005), in addition to the root chemical composition, which makes root material more difficult to decompose compared to aboveground material (Bertrand *et al.*, 2006). Rhizosphere processes, such as root turnover, rhizodeposition, root respiration and microbial response are extremely important in grassland soil. These processes may lead to stabilisation as well as destabilisation of soil carbon and nitrogen (Cheng and Kuzyakov, 2005). Plant roots may affect SOM decomposition through (1) decreasing mineral nutrient availability to soil microorganisms due to plant uptake (Schimel *et al.*, 1989), (2) changing the physical environment in the rhizosphere (Shields and Paul, 1973), (3) increasing organic substrate supply and (4) enhancing microbial turnover due to fungal grazing. However, interactions at the rhizosphere level between soil microorganisms and roots of different plant communities are complex and remain poorly understood (Cheng and Kuzyakov, 2005). Rooting behaviour of plants and rhizosphere processes may be strongly influenced by grassland management, which can therefore impact the storage and composition of C, N and P in soil. For example, defoliation of plants by grazing and cutting stimulates root exudation, thereby increasing the quantity of rhizomicrobial communities and their activities (Paterson and Sim, 1999; Hamilton *et al.*, 2008), leading to increased availability of P and N through positive feedback mechanisms (Hamilton and Frank, 2001).

However, this effect may be transient and last only for some days (Henry *et al.*, 2008; McDonald *et al.*, 2004). Defoliation may also affect C flow and allocation within grasses (Kuzyakov *et al.*, 2002) as well as N fixation and allocation in legumes (Dahlin and Martensson, 2008). However, these effects have been studied up to now mainly in pot experiments, whereas their assessment under natural conditions is scarce. Defoliation under natural conditions has been assessed by isotopic labelling of defoliated grasses. It has been shown that defoliation under field conditions alters belowground C allocation (Holland *et al.*, 1996) and stimulates rhizospheric N mineralisation, which ultimately benefits the defoliated plants (Hamilton *et al.*, 2008). It is not known, whether defoliation by grazing induces different physiological plant responses compared to cutting. In addition to above- and belowground litter, dung can constitute an important OM source in grasslands managed by grazing (Jarvis *et al.*, 1996). On a pasture with a grazing intensity of 700 cow days ha⁻¹ a⁻¹, an average of 6.4% of the grazed area is commonly covered by dung patches which provide a C input equivalent to 22.5 t C ha⁻¹ (Bol *et al.*, 2000). By grazing and depositing dung and urine, large herbivores remove carbon and nutrients and return them by excretion, leading to cycling and redistribution, which in turn influences the structure and functioning of grassland systems (Heynes and Williams, 1993) as well as OM dynamics through carbon dioxide release and OM incorporation into soil. Dung is a source of labile C, N and P, which may increase microbial biomass (Lovell and Jarvis, 1996; Hatch *et al.*, 2000) and induce priming of native organic matter (Fontaine *et al.*, 2003). Molecular studies have shown that carbohydrates constitute part of the dung-derived C in soil (Dungait *et al.*, 2009). While dung and urine deposition occurs in well defined patches, limited information is available about the impact of this labile C on the soil biogeochemical cycles at larger scales.

Many types of grassland worldwide are managed by regular burning. Fire disrupts C, N and P cycles by releasing much C and N in gaseous form and P in mineral form. In the long-term burning tends to conserve soil P while it removes C and N (Johnston *et al.*, 2003). In addition fire-derived organic matter forms are deposited on soil. Quantification of this material in the major grassland ecosystems of the world showed a contribution between 5 and 30 % of total SOM (Rodionov *et al.*, 2010). This is high compared to agricultural soils, which do not accumulate fire-derived SOM even when subject to annual stubble burning (Rumpel, 2008). Fire-derived SOM forms are in general more difficult to degrade than plant-derived SOM due to their aromatic structure and low nitrogen content (Knicker, 2011). During fire, P is generally converted to inorganic forms, while N may be part of pyrogenic organic matter. However, the degradability of fire-derived SOM may vary according to fire conditions and chemical composition of the affected vegetation (Alexis *et al.*, 2010). Moreover, fire-derived SOM forms may influence element cycles in grassland soil through their specific nutrient adsorption and plant growth stimulating properties (Criscuoli *et al.*, 2014).

4. Impact of harvesting regime and fertilisation on soil properties and processes affecting SOM storage and nutrient forms

The SOM storage and stabilisation pathways may be influenced by grazing management of grassland ecosystems through alterations of OM input (see above) and associated soil properties. Intensive grazing leads to significantly decreased SOC stocks associated with higher bulk density in topsoils (Steffens *et al.*, 2008, 2009) and additionally to lower mean-weight diameter of water stable aggregates, lower monosaccharide contents and lower contribution of microbial-derived

sugars (Dormaer and Williams, 1998). The grazing regime (high or low intensity) greatly influences SOM dynamic (Steffens *et al.*, 2009). Intensively grazed grasslands are dominated by fast-growing species producing litter low in lignin and rich in N, which is rapidly decomposed by bacteria (Bargett *et al.*, 1998), whereas grasslands adapted to low grazing levels are dominated by slow growing species and slow litter decomposition (Michunas and Lauenroth, 1993). The two different plant communities have been reported to control SOM stocks through plant roots and their activity (Klumpp *et al.*, 2009). Changes in C dynamics after grazing cessation may be slow (Klumpp *et al.*, 2009) and not lead to C sequestration in soils, where the mineral particles are already saturated with OM (Steffens *et al.*, 2009). In contrast, light or moderate grazing does not necessarily decrease SOM contents (Cui *et al.*, 2005). Grassland management by mowing may reduce C turnover as compared to grazing (Herald *et al.*, 2014). It was found, that long-term grazing with cattle was more favourable for macroaggregation and aggregate stability and thus carbon storage than harvest by mowing (Franzluebbers *et al.*, 2000). This corresponds to the increase of net C storage measured by CO₂ fluxes in temperate grazing systems compared to mowed grasslands (Senapati *et al.*, 2014). The higher C storage was attributed to greater export by harvest under cutting regime, whereas under grazing a substantial amount of C is returned in form of dung and urine (Senapati *et al.*, 2014). However, grazing and mowing may also stimulate differently plant physiology and rhizospheric C input, thereby probably altering SOM storage in soil. In terms of macronutrients, grasslands were found to favour the accumulation of organic P forms, which may be relatively available as compared to insoluble inorganic P forms, which accumulate during cultivation (Sharpley and Smith, 1985, Crew and Brooks, 2014).

Grazing as well as cutting seems to remove P from grassland soils (Lilienfein *et al.*, 2000; Pätzold *et al.*, 2013). Although there are few studies on P forms under different grazing regimes, a return of higher amounts of inorganic P compared to the ingested vegetation was found, suggesting transformation of organic forms in inorganic ones during the transit in the digestive tube (McDowell and Stewart, 2005). While P present in dung was found to parallel P concentrations in feed (McDowell *et al.*, 2008), grazing animals lead to substantial uncoupling of C from N and P (Soussana and Lemaire, 2014). The majority of P and N are returned to the soil by urine or dung deposition, whereas about 70% of the ingested C is emitted as CO₂ by respiration (Parson *et al.*, 2013). Intensive dairy farming may however also increase P loss in dissolved organic form (Javie *et al.*, 2010). N export from the site is usually complete in mowing systems and higher in dairy pastures compared to dry livestock ones (Parson *et al.*, 2013). The return of N and P with animal excrements by manure occurs generally in labile form, which is much more mobile compared to initial feed (see above), and increases the N and P leaching losses if applied without prior treatment (Jouquet *et al.*, 2011).

Apart from presence and absence of grazing animals, management of grassland may include the application of fertilisers (Figure 1; Table 1). Fertilisation is usually applied to counteract nutrient export and to maintain or intensify forage production. Many soils have been over fertilised in the past and therefore are high in organic matter leading to oversupply and subsequent nutrient loss from soil after grazing cessation (McGovern *et al.*, 2014). Recently it has been shown that loss of reactive P from high P soils may be reduced by manipulation of N fertilizer regime in order to stimulate P uptake through increased plant growth (Dodd *et al.*, 2014).

Due to its effect on plant production, fertilisation may impact SOM storage. However, this effect is not entirely clear. While Ammann *et al.* (2007) concluded that conversion of arable land to grassland leads to a positive carbon balance only if the system receives extra nitrogen inputs, no relationship between the intensity of management and SOC stocks was found for Alpine grasslands (Zeller *et al.*, 1997; Bitterlich *et al.*, 1999). A review of global data sets revealed fertilised grasslands had, on average, higher SOC stocks than natural or less intensively managed systems (Conant *et al.*, 2001). While the use of N fertilisers in most managed grassland systems seems absolutely necessary to maintain grassland productivity, soil P stocks of most temperate agricultural soils seem to be sufficient. Accordingly, Nyborg *et al.* (1997) found with increasing level of N fertilisation larger SOC contents associated with higher productivity for Canadian grasslands, while no change of SOM stocks was noted with increasing P fertiliser rates despite higher aboveground production for pastures in New Zealand (Schipper *et al.*, 2012). In some cases, N and P fertilisation may even lead to decrease of SOM stocks by increasing microbial activity and altering C substrate utilisation pattern of soil microbial communities through changes of plant biomass composition (Li *et al.*, 2014). These examples may illustrate that management effects on SOM are diverse and strongly dependent on pedoclimatic parameters (Mcsherry and Richie, 2013). (Table 1).

The mechanisms and in particular soil type effects, which lead to these contrasting results yet need to be elucidated. Moreover, the effects of different grassland management practices were assessed up to now mostly for topsoil horizons, although perennial species may affect a much larger volume of soil and greater soil depth than annual species (Beniston *et al.*, 2014).

Table 1. Contrasting effect of different management practices on element cycles and SOM storage

Management practice	Effect on soil and nutrient forms	Reference
Mowing	C and nutrient export with harvest	Parson <i>et al.</i> , (2013)
	Reduced turnover of mineral associated OC	Herold <i>et al.</i> (2014)
Grazing	Decoupling of N, P, C cycles with reduction of C longevity	Parson <i>et al.</i> (2013) Soussana <i>et al.</i> , (2014)
	Decrease of SOM storage	Steffens <i>et al.</i> (2008, 2009)
	Stimulation of belowground activity	Hamilton <i>et al.</i> (2008)
	Increase of C flux below ground	Holland <i>et al.</i> (1996)
Fertilisation	Increase of SOM storage	Conant <i>et al.</i> (2001)
	No change in SOM storage	Schippers <i>et al.</i> (2012)
	Decrease of SOM storage	Li <i>et al.</i> (2014)
Species diversity	Increasing aggregate stability	Peres <i>et al.</i> (2013)
	Changes of nutrient acquisition efficiency	Oelmann <i>et al.</i> (2011)
Legume introduction	Decrease of aggregate stability	Peres <i>et al.</i> (2013)
	Increase of aggregate stability	Angers <i>et al.</i> (1999)
	Higher contribution of organic P	Crème <i>et al.</i> submitted
	Higher soil N and C	Fustec <i>et al.</i> (2010), Paustrian <i>et al.</i> (1990) Agbenin and Adeniyi (2005)
	No change in soil C and N	Bell <i>et al.</i> (2012) Crème <i>et al.</i> submitted
	Increased resistance to water stress	Sanoullah <i>et al.</i> (2012)

5. Plant species and their impact on SOM and forms of macronutrients

The formation of SOM and the forms of macronutrients in soil may be influenced by species composition of grasslands. In natural grasslands, species diversity is large compared to sown ones, which are rarely composed of more than three species. Introduction of animals tends to reduce this diversity due to selective grazing and varying stress resistance of different grassland species (Bargett *et al.*, 1998). Diverse species rich grasslands are known to be characterised often by higher amounts of aboveground biomass than those consisting of few species (Hooper *et al.*, 2005). They also penetrate larger volumes of soil due to diverse and complementary root traits (Körner and Spehn, 2002). Due to increased root activity and in turn higher soil organic carbon and soil microbial biomass concentrations, aggregate stability was found to be increased in soil under grasslands with high species diversity. (Peres *et al.*, 2013). However, plant species diversity was also shown to decrease soil concentrations of plant available N due to complementary uptake (Niklaus *et al.*, 2001). This is in contrast to plant available P, which was found to be unchanged in soil solution under more diverse grasslands (Oelmann *et al.*, 2011). Diverse grasslands, seem to develop highly efficient P exploitation strategies, thereby being better prepared to respond to P limitations (Oelmann *et al.*, 2011). The introduction of forage legumes, able to fix atmospheric nitrogen through symbiosis with *Rhizobium* into grasslands generally has a favourable impact on soil due to their deep rooting system and easy decomposable organic residues rich in nitrogen, which promote the development of micro-fauna and soil microflora. The direct availability of the fixed N to the roots minimizes nitrogen losses (Crews and Peoples 2005) and reduces the risk of NO₃ leaching,

acidification of soil, ammonia volatilization (Crews and Peoples 2004) and N₂O emissions by denitrification (IPCC 2013). The introduction of legumes in pasture systems can increase the soil N content and cycling efficiency through legume residue deposition and root exudation (Fustec *et al.*, 2010; Rasmussen *et al.*, 2012; Schipanski and Drinkwater 2012). Symbiotic nitrogen fixation is the key process in N and C dynamics in agricultural systems containing legume species. It couples soil nitrogen and carbon cycles. In roots nodules of legume species, N₂ fixing bacteria benefit from carbon inputs provided by the plant and make nitrogen available to the plant in mineral form. They reduce the atmospheric N₂ in NH₃, then NH₄, using energy from the oxidation of carbohydrates (Butterbach-Bahl *et al.*, 2011). The nodule metabolism depends on carbohydrate products fixed by photosynthesis in shoots and transported to the roots. The principal compound is sucrose. Each day, the nodule metabolism uses 40-50% of all photosynthetic products and 50% of this is returned to the atmosphere as CO₂ by respiration (Gordon 1992). Legumes require more P than grasses. The high-energy cost of N₂ fixation requires adenosine tri-phosphate (ATP) and therefore P to build and maintain functioning nodules. As a consequence, legume plants show higher concentration of P compared to other plants (Tsvetkova and Georgiev, 2007) and in soil under legume, organic forms of P tend to be present in higher concentrations compared to soil under grass species (Daroub *et al.*, 2001 ; Crème *et al.*, submitted).

The transfer of N and P from the legumes to the soil occurs by returning shoot and root litter after plant death as well as root exudates during the plant life. In the case of mowed grassland, only rhizodeposition will lead to enrichment of soil organic matter due to removal of the aboveground biomass. However, even in mowed grassland part of the biomass is lost during harvesting and readily decomposable (Sanaullah

et al., 2010). In Lucerne grasslands, 3% to 4.5% of the fixed N is released as soluble compounds. However, roots and senescent nodules appear to be the main source of nitrogen in legume grasslands, especially as rhizodeposition increases with the age of the plants (Fustec *et al.*, 2010).

When combining grasses with legume species in grassland systems, N fixation is more efficient with 9% to 18% more N fixed than in legume monocultures (Nyfeler *et al.*, 2011; Schipanski and Drinkwater 2012) leading to higher the forage yields (Rasmussen *et al.*, 2012; Schipanski and Drinkwater 2012). Higher soil N and C storage and cycling efficiency under legume-grass mixture was observed compared to legume monoculture (Paustian *et al.*, 1990; Fustec *et al.*, 2010; Rasmussen *et al.*, 2012; Schipanski and Drinkwater 2012; Bell *et al.*, 2012). This was explained by competition for soil N and also facilitation concerning soil N uptake between different species for example due to different root systems (Carlsson and Huss-Danell 2003; Schipanski and Drinkwater 2012) and N transfer between legumes and grasses (Louarn *et al.*, 2014). However, the effect of legume species on soil parameters under grassland associations may depend on the associated grass species (Crème *et al.*, submitted). This may explain the contrasting observations made for physical soil properties such as aggregate stability, i.e. increase under legume species (Angers *et al.* 1999) and decrease compared to grasses (Peres *et al.*, 2013). This contrasting impact of different legume – grass associations (Table 1) may be explained by species related differences in N uptake and N transfer mechanisms (Louarn *et al.* 2014) as well as differential root activity leading to contrasting microbial activity in the rhizosphere (Sanaullah *et al.*, 2011). In general, introduction of legume species into grasslands may be positive due to their effect on soil fertility, plant growth and stress resistance. However, legume

species are more competitive than grass species for example regarding drought resistance (Sanaullah *et al.*, 2012), making the maintenance of equilibrated mixtures a management challenge.

6. Conclusion

Although grasslands are in general favourable systems in terms of SOM storage and nutrient cycling, intensification of grassland management may decouple elemental cycles and favour losses of reactive N and P. Grazing regime and fertilisation influence biogeochemical cycling of carbon and major plant nutrients mainly through their effect on plant activity, which greatly influences rhizosphere processes and nutrient uptake or release. Elemental coupling and decoupling processes controlling SOM storage may occur via plants or microorganisms and controlled by specific fertiliser additions. Further progress is necessary in order to optimise grassland management strategies through species choice, fertilisation, and grazing intensity in order to ensure maximal ecosystem services and productivity of intensively used grassland systems. The vulnerability of the system needs to be reduced especially regarding the expected climate change scenarios. At the current stage of knowledge, we lack information about the impact of physiological plant responses to grassland management on biogeochemical C, N and P cycling in soil. In particular their effects on processes affecting SOM properties and its storage at greater depths are poorly understood. We also crucially need information about the processes controlling the stability of organic N and P forms. Management effects on SOM accumulation and availability of plant nutrients are case dependent and may be strongly related to the pedoclimatic context. More research is needed to disentangle belowground complexity, which may be controllable via management effects on plant activity.

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