Chapter 9
Are Soil Carbon Stocks in Mountain Grasslands Compromised by Land-Use Changes?

Jordi Garcia-Pausas, Joan Romanyà, Francesc Montané, Ana I. Rios, Marc Taull, Pere Rovira and Pere Casals

Abstract Mountain grasslands are generally rich in soil organic C, but the typical high spatial variability of mountain environments, together with the different management systems, makes their soil C content particularly variable. Socio-economic changes of the past decades have caused a progressive abandonment of the traditional use for grazing of some areas, while grazing pressure at easily accessible grasslands have increased. Here, we analyse the effect of these land-use changes on the factors regulating the soil C accumulation and stocks. Overgrazing generally leads to a reduction above- and below-ground litter inputs and a decrease in soil C stocks, affecting some soil physicochemical and biological properties. Additionally, the labile C inputs coming from animal faeces may accelerate the mineralisation of organic matter. Grazing abandonment causes a reduction of aboveground productivity, but the lack of consumption causes a short-term accumulation of organic matter. Its effect on belowground biomass and productivity is less clear. At longer term, grazing abandonment causes a change in the plant community composition, having the shrub encroachment the strongest effect on C storage. The low biochemical quality of shrub litter delays its decomposition and allows higher organic matter accumulation in the topsoil. But the effect of shrub proliferation at the deeper soil is less clear. The low root turnover of shrubs compared to grasses may reduce the C inputs to the soil. But, at the same time, the reduction of the root exudates may also reduce the microbial activity and the organic matter mineralisation.

J. Garcia-Pausas (✉) · F. Montané · A.I. Rios · M. Taull · P. Rovira · P. Casals
Forest Sciences Centre of Catalonia, CEMFOR-CTFC, Ctra de St. Llorenç de Morunys,
km 2, 25280 Solsona, Catalonia, Spain
e-mail: jordi.gpausas@gmail.com

J. Romanyà
Department of Biology, Health and Environment, Universitat de Barcelona,
Joan XXIII s/n, 08028 Barcelona, Catalonia, Spain

F. Montané
School of Natural Resources and the Environment,
University of Arizona, Tucson, AZ 85721, USA

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9.1 Introduction

Soil organic matter plays essential roles in terrestrial ecosystems. It maintains the soil structure, favours water infiltration and reduces the risk of soil erosion. It also increases the water holding capacity of soils and, through its decomposition by soil biota, provides nutrients to the plants.

Carbon (C) comprises about 45% of the mass of soil organic matter. Plant photosynthetic activity produces organic matter using atmospheric CO_2, which is then accumulated in soil mainly by incorporating plant residues into the soil organic matter. Although this is the primary pathway by which atmospheric CO_2–C is incorporated into the soil, some additional atmospheric CO_2–C can also be sequestered in soil in inorganic forms by rock weathering and precipitation of Ca- and Mg-carbonates. Then, the oxidation of organic matter by soil microorganisms is the main process causing a release of carbon as CO_2 to the atmosphere, leaving less decomposable organic compounds, which are accumulated in the soil. Together with this biotic process, a significant amount of soil C can also be exported from the soil by leaching. Overall soil C sequestration results from the balance between the C flux from the atmosphere into the soil and the C release back to the atmosphere through microbial decomposition. This balance determines if soil behaves as a net sink for removing CO_2 from the atmosphere or a net source that contributes to rising atmospheric CO_2.

Soils represent the main compartment of organic C in most terrestrial ecosystems, containing globally about 1550 Pg C ($1 \text{ Pg} = 10^{15}$ g), which roughly is twice the amount of C in the atmosphere (760 Pg C) and three times the amount in the biomass (550 Pg C) (Lal 2008). Given the large magnitude of these soil C stocks, potential reductions as little as 10% of the soil C content would equal to the anthropogenic CO_2 emitted over 30 years (Kirschbaum 2000), meaning significant changes in the atmospheric CO_2 concentrations and the reinforcement of the current global warming trend. So, there is a strong interest in avoiding C losses from soils and, if possible, to promote the C sequestration to mitigate the current greenhouse gases (GHG) emissions.

In this chapter, we summarise the special features of mountain alpine soils that contribute to explaining the organic C content and explore the challenges for soil C conservation due to changes in land management and use.

9.2 Mountain Soils and Their C Stocks

Mountain soils are generally steep, shallow, with relatively high erosion rates and influenced by harsh climatic conditions. Despite mountain ecosystems have much in common with those in high latitude, mountain soils are markedly different. These differences originate from both climate and soil formation processes. High-altitude mountain ranges generally receive much higher rainfall, both in quantity and intensity (high torrentiality) than lowlands. Moreover, sunshine incidence in mountain slopes is usually higher than in high latitudes and largely depends on the aspect. In south-facing slopes solar radiation is high, even in winter time, thus reducing the snow cover and the chance of frost layers. In mountain ranges of temperate areas, even on north-facing slopes, winter temperatures are warmer than in high latitude areas and because of the higher precipitation the snow cover is thicker. Consequently, mountain soils are better insulated, with high solar radiation and thus their frost layer is less thick and not permanent in most cases. The reduction or lack of permafrost of the mountain soils contributes to their general good drainage and thus wet soils (i.e. peatlands) in mountain landscapes are mainly confined to bottom areas and depressions, and they are not widespread. Conversely, in mountain slopes high rainfall and good drainage speeds up soil formation processes. However, natural disturbances also linked to the slopes such as soil erosion, rock fall, landslides, avalanches and snow ablation play an important role in rejuvenating mountain soils. As a result of these complex interactions and because of its diverse geomorphology mountain landscapes hold a large spatial variability that is depicted in both soils and vegetation.

Soils of mountain areas tend to be young and highly influenced by their bedrock and physiographic properties. The wide range of soil types occurring in mountain regions is driven by microtopography, slope and aspect which, as stated above, define the snowpack and melting patterns that influence soil temperature, nutrient leaching and soil moisture (Stöhr 2007). Young mountain soils occur in well-drained areas and are classified as Leptosols or Regosols. Leptosols are thin soils, extremely gravelly and/or stony and with strong limitations to rooting. Regosols are weakly developed mineral soils in unconsolidated materials that occur in less stony areas and are typically highly erodible. On calcareous areas Rendzic or Chromic Leptosols dominate. Rendzic leptosols have a surface layer with high accumulation of organic matter and calcium carbonate. Chromic leptosols have a red surface layer and low or no calcium carbonate content. On siliceous bedrock, Regosols and the extremely thin Lithic leptosols are commonly found. But in stable and well-drained surfaces soils are often more developed, being common Dystric Cambisols and different types of Podzols. These latter two soil types show a thick and well-developed acidic horizon, but Podzols contain a subsurface horizon with illuvial amorphous organic matter and/or Al and Fe oxides. Finally, Histosols occur in poorly drained areas. These last soils evolve from incompletely decomposed plant remains and thus their features are quite independent of the bedrock type (IUSS Working Group WRB 2015).

Mountain soils in temperate areas usually have a high organic matter content, as shown in some regional soil C maps (Baritz et al. 2010; Doblas-Miranda et al. 2013). Although plant biomass in alpine grasslands is much lower than in forests, their soil C stocks are also generally high (Table 9.1) and comparable to forested areas (Berninger et al. 2015). The large amount of soil C in alpine environments is related to the high residence time of organic matter in the soil compared to the

Table 9.1 Some examples of soil organic C stocks in grasslands of the European mountains

Mountains	C stocks (Mg ha^{-1})	n	Altitude (m a.s.l.)	Annual mean air temperature (°C)	Plant formation	References
Iberian Central System	72–324	5	1653–2051	6.5–7.0	Mesic grasslands	(1)
Pyrenees	45–365	16	1704–2092	3.2–6.1	Mesic grasslands	(1)
Pyrenees	65–300	35	1845–2900	−0.7 to 5.0	Alpine and subalpine grasslands	(2)
Austrian Alps	260 and 130	2	1700 and 1900	2.1[a]	Alpine grassland, pine bushes and shrubs	(3)
Swiss Alps	53–116	8	810–2200	0.9–8.9	Grasslands	(4)
Tatra Mountains	20–250	25	1725–2368	−2.0 to 1.6	Alpine meadows	(5)
Eastern Swiss Alps	100	6	2616–2674	−2.6	Alpine tundra with permafrost	(6)
Eastern Swiss Alps	150	6	2577–2695	−2.6	Alpine tundra without permafrost	(6)

(1) Montané et al. (2007); (2) Garcia-Pausas et al. (2007); (3) Djukic et al. (2010); (4) Leifeld et al. (2009); (5) Kopáček et al. (2006); (6) Zollinger et al. (2013)

[a] Annual mean air temperature at 2277 m a.s.l.

living biomass (Körner 2003). This fact is caused by the harsh climatic conditions of the alpine environments that slow down the degradation of organic matter. Also, while forest soils receive large amounts of organic matter coming from aboveground biomass, in grasslands the primary organic matter inputs to the soil mainly come from root turnover and deposition. Consequently, the vertical distribution of organic C along the soil profile is typically shallower in forest soils than in grasslands (Jobbágy and Jackson 2000).

Mountain soils show a great variability in their characteristics. Thus, far from being evenly distributed, soil organic C content in mountain areas is particularly variable. Not only temperature reduces and precipitation increases with the elevation, but also the significant differences in solar radiation between north- and south-facing slopes, create environments that can be highly variable over relatively short distances. This feature, together with the high variability of soil depth and the natural diversity of substrates in mountain areas, makes the alpine landscapes a mosaic of different local conditions to the development of plant growth. This variability results in a considerable heterogeneity in plant community composition and structure, which in turn shape the distribution patterns of other organisms such as arthropods, fungi and soil bacterial communities. Different land management practices (e.g. various grazing pressures in pasturelands, timber removal in subalpine forests, etc.) is another source of variation that affects the C cycling and storage. All these factors result in soils with a highly heterogeneous amount of stored C, making difficult the prediction of current stocks and its response to the expected climate and land-use changes.

9.3 Factors Controlling Soil Organic C Stocks in Mountain Grasslands

The development of soil is a complex and continuous process, driven by parent material, climate and soil biota. In the mountains, the topography also plays an important role modifying the climate and creating different landforms for soil development. All these factors determine the physical, chemical and biological properties of soils and control their capacity to accumulate organic C.

9.3.1 Bedrock Type

Mountain areas are often geologically complex, as a result of past volcanism, compression and tension faults, plate subduction and uplift. The parental material from which a soil develops determines many hydrological, ecological and pedogenic processes, having implications for the capacity of soils to store C, the C accumulation rates and its persistence in the soil. Differences in the lithology determine the differences in the mineral composition of soils and influence their texture, chemistry and weathering processes. Changes in plant composition and structure are also frequently associated with changes in the bedrock type through its effect on nutrient status and physical characteristics of the soil.

Soil texture is the most relevant characteristic that is determined by the bedrock type. For instance, soils developed on sandstones or granites usually have coarser textures than those developed on limestones or slates. Soil texture is particularly relevant for organic matter accumulation in soils, as organic matter is stabilised in soil through its interaction with the finest mineral particles. Indeed, organic matter associated with the finest particles (i.e. fine silt and clay) is usually older (Eusterhues et al. 2003) and has longer residence times (Balesdent 1996) than the organic matter in the coarser fractions. In the Pyrenees, although C and N availability were more important explaining topsoil basal respiration, soils developed on granites showed high rates of basal respiration (Garcia-Pausas et al. 2008), suggesting that they may contain a higher proportion of non-stabilised organic matter.

9.3.2 Climate

Carbon stocks are the result of the net balance between C inputs through primary production and C outputs through microbial mineralisation as well as leaching and erosion (Fig. 9.1).

In alpine areas, both primary production and microbial mineralisation are constrained by low temperatures, particularly during wintertime. Given that soils in the mountain areas have a relatively high amount of organic C, it can be suspected that microbial mineralisation might be more strongly limited by climate than primary production. However, there is some evidence that the maximum soil C stocks are found in the subalpine belt and that from that point upwards the soil organic C stocks tend to reduce with the elevation (Djukic et al. 2010), reaching close-to-zero levels at unvegetated substrates of extreme altitudes (Körner 2003). This reduction of C stocks is due to the reduced plant cover and productivity, reduced rooting depth, and also because soils are generally younger at high altitudes (Fig. 9.2). This general trend is expected to differ between the north- and south-facing slopes. Indeed, in the Pyrenees Garcia-Pausas et al. (2007) observed that the reduction in C stocks with altitude was sharper at the north-facing slopes, probably because at high altitudes the environmental conditions on the south-facing slopes are more favourable for plant growth (Fig. 9.3).

The microclimate environment also determines the characteristics of the soil organic matter and thus its turnover. There is an indirect effect mediated by climate-driven changes in the plant community composition and structure (see below), but also a direct effect of climatic conditions on organic matter quality. Soils developed on high altitudes are usually rich in labile and particulate organic C (Leifeld et al. 2009; Budge et al. 2011). As occurs with altitude, the severe conditions at the north-facing soils also cause a higher accumulation of poorly degraded organic matter than at south-facing slopes (Egli et al. 2015). These C pools appear to have long residence times, as shown by radiocarbon dating (Leifeld et al. 2009; Budge et al. 2011), which

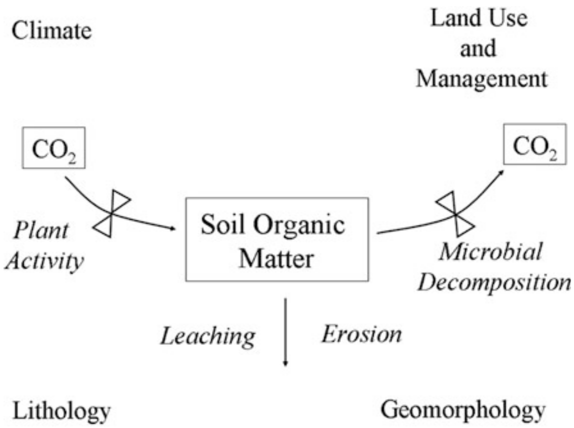


Fig. 9.1 Driving variables and processes involved in soil organic matter dynamics and stocks

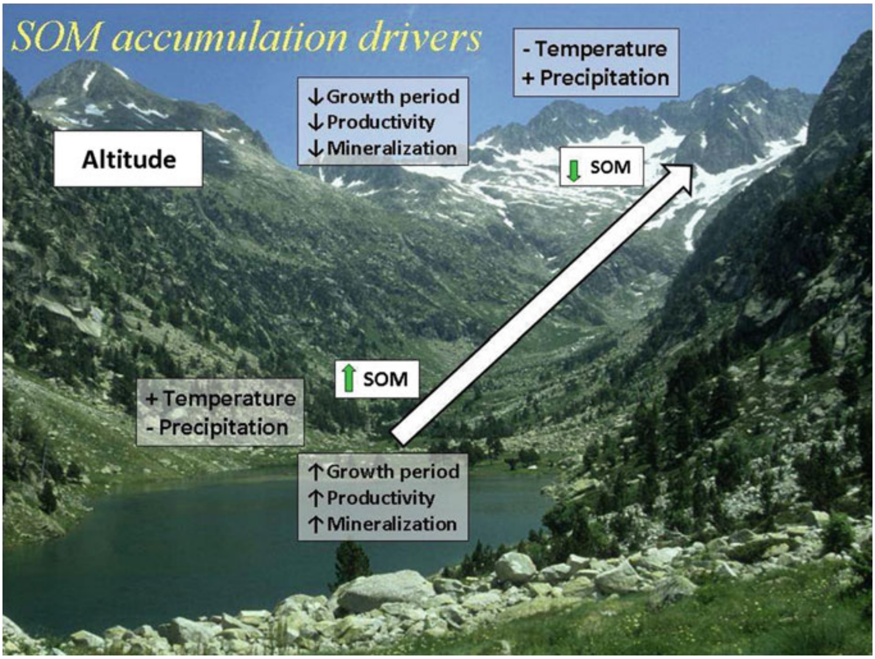
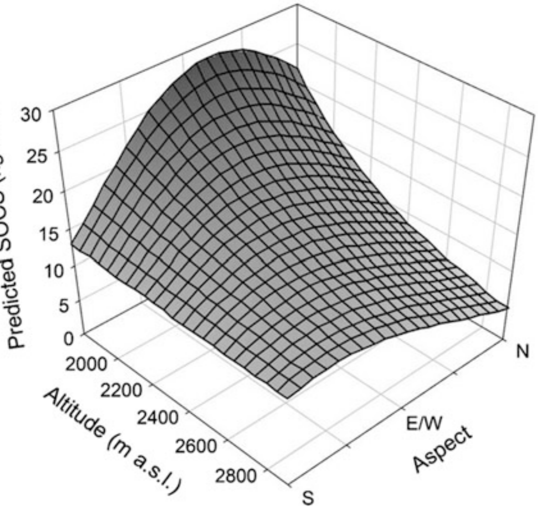


Fig. 9.2 Altitude is the primary factor of climatic heterogeneity in mountain landscapes, with high-altitude areas having generally low (−) temperatures and high (+) precipitation compared to low-altitude areas. It causes short growing seasons, low plant productivity and low soil C mineralisation rates (*downwards arrows*) in high-altitude sites compared to the bottom of the valleys. Photo: J. Garcia-Pausas

Fig. 9.3 Predicted soil organic C stocks (SOCS) as a function of altitude and aspect in the Pyrenean subalpine and alpine grasslands. From Garcia-Pausas et al. (2007) with permission of Springer



is attributed to the harsh conditions for residue decomposition, the low soil pH and nutrient limitations. However, in areas where environmental conditions are unfavourable for decomposition, the degree of physicochemical stabilisation of organic matter, as measured by incubation under standard conditions, is lower (Garcia-Pausas et al. 2008). This feature could make these C pools particularly vulnerable to future climate and land-use changes.

The temperature variations in altitude and aspect, as well as the microtopography and the predominant wind direction largely determine the distribution and duration of the snowpack cover. The duration of the snowpack cover has important implications for the soil organic C dynamics, as it determines not only the temperature and moisture of the underlying soil but also the length of the plant growing season, the plant community composition, the microbial activity and nutrient dynamics. Indeed, snow cover maintains soil temperature relatively high compared to the air temperatures during winter, allowing the maintenance of unfrozen conditions (Edwards et al. 2007). This isolation is because of the low thermal conductivity of the snow, particularly when it is fresh and non-compacted (Körner 2003). Consequently, topsoil temperature under the snow is usually stable around 0 °C, even when air temperatures are far below zero. This allows the microbial processes to continue in winter (Schmidt and Lipson 2004), causing an increase in the winter CO_2 efflux (Walker et al. 1999) and also a faster decomposition of the leaf litter (Baptist et al. 2010; Saccone et al. 2013) under the snow than in non-covered soils. However, when the snowpack melts in late winter and before the snowfall in late autumn, soils are usually exposed to temperatures well below 0 °C, undergoing frequent episodes of freezing and thawing.

Soil frost does not allow the belowground plant production, but an earlier peak in fine root production during the subsequent growing season has been observed by Tierney et al. (2001) after an experimental snow removal in forest ecosystems. They also reported significant increases in fine root mortality, resulting in an increased root turnover. In grasslands, Kreyling et al. (2008) indicated that recurrent freeze–thaw events reduced root length during the subsequent growing season, but also increased aboveground productivity.

Freeze–thaw events alter C and N dynamics, affecting root production and turnover, soil microbial activity, soil C and N availability and its mineralisation. It has been observed that repeated freeze–thaw cycles as well as prolonged frost increase C and nutrient concentration in the soil solution, which can eventually be lost by leaching (Fitzhugh et al. 2001; Freppaz et al. 2007; Wipf et al. 2015). Also, a burst of CO_2 and N_2O emissions from thawing soils has often been observed (Nielsen et al. 2001; Teepe et al. 2001; Matzner and Borken 2008), as well as higher emissions during the subsequent growing season (Blankinship and Hart 2012). This response is partially explained by the decomposition of the microbial necromass (Herrmann and Witter 2002), but a reduction of microbial biomass in thawing episodes has not been detected in alpine soils (Lipson et al. 2002; Freppaz et al. 2007). Another source of the CO_2 flush when soil thaws is the death of fine roots due to the soil frost. The decomposition of the fine root litter increases the

CO_2 efflux from these soils, but the release of soluble cell constituents from dead fine roots is the main factor that contributes to the observed short-term CO_2 and N_2O pulse after thawing (Matzner and Borken 2008), and the higher concentrations of N and P in the soil solution (Fitzhugh et al. 2001; Freppaz et al. 2007; Wipf et al. 2015) after freeze–thaw events. The third source of the CO_2 flushed upon a freeze–thaw event is the change in the soil structure. Soil freezing causes a disruption of soil aggregates because the ice crystals expand breaking the bonds between mineral particles. This breakdown of the aggregates makes the organic matter protected within the aggregates available for microorganisms. Macroaggregates are more susceptible to these disruptive forces than microaggregates, and their vulnerability is enhanced with increasing soil water content, while high clay, organic matter and Fe-oxide concentrations reduce the disruptive effects of freezing (Six et al. 2004).

9.3.3 Plant Community Composition

The effect of abiotic environment on soil C content and its stability is in part mediated by its effect on plant communities. It is well known that abiotic factors determine the composition and characteristics of the plant community, which in mountain ecosystems is also strongly related to topography (Sebastià 2004) and bedrock type. The composition of plant communities determines some functional characteristics that can be relevant for the organic matter production and allocation. For instance, although most of the root characteristics are species-specific, Pohl et al. (2011) showed that in alpine ecosystems graminoids usually have a large proportion of fine roots compared to forbs or shrubs. This feature may enhance topsoil aggregate stability under grasses (Pohl et al. 2009), which could be relevant for stabilising C in soils. Other characteristics of the vegetation such as above- and belowground productivity and allocation, rooting depth, horizontal root expansion may influence the C inputs and its persistence in the soil.

Plant community composition is in turn related to the quality of soil organic matter and, consequently to its decomposition rates. The low quality for decomposition of the organic matter produced by woody shrubs, with high lignin and polyphenol content, greatly differs from that produced by herbaceous plants, which is much more readily decomposable. But also among herbaceous plants, there can be significant differences, as occurs with the N-enriched organic matter produced by legumes. Thus plant communities differing in the biochemical characteristics of the biomass can lead to differences in the biochemical quality of soil organic matter. Indeed, Eskelinen et al. (2009) indicated that high proportion of forbs in an alpine tundra of northern Europe were related to low soil C/N ratios and high soluble N/phenolics ratios, causing in turn differences in the associated microbial communities.

9.4 Effects of Land-Use and Management Changes on Soil C Dynamics and Stocks

Although at the global scale remote areas still exist in mountain regions, in temperate European mountains the diversity of habitats resulting from the complex topography and multiple microclimates has been shaped, similarly to the lowland, by the human activities for centuries (Montserrat and Fillat 1994; Gassiot Ballbè et al. 2017 in the present book). Over the past centuries, low-intensity agriculture, farming and forestry have created and structured semi-natural habitats that constitute the contemporary landscapes in temperate mountains (Fig. 9.4). For some of these habitats, the sustainability of ecosystem services, at least at short- and mid-term, is linked to the continuity of human involvement and may be threatened by changes in the historical use of the mountain ecosystems (MacDonald et al. 2000; Regato and Salman 2008).

Due to the inherent physical constraints of the vast majority of mountain valleys that prevented the modernization of agriculture, traditional and sustainable low-input farming systems had mainly remained invariable until the last decades (Plieninger et al. 2006). In recent times, however, the long agropastoral tradition was altered by the integration of local economies into the global market and the

Fig. 9.4 Low-intensity agriculture and farming for centuries have shaped subalpine landscapes. Alinyà mountain, eastern Pre-pyrenees. Photo: Pere Casals

Table 9.2 Change (%) in the number of farms and livestock heads during 1989–2009 in five counties of the Catalan Pyrenees

	Val d'Aran	Alta Ribagorça	Pallars Sobirà	Cerdanya	Ripollès
Farms					
Bovine	−77	−56	−33	−22	−30
Ovine	−39	−44	−58	−29	−35
Livestock heads					
Bovine	−9	6	135	81	32
Ovine	21	−35	−8	−10	−43

Elaborated using data from the Ministry of Agriculture, Livestock, Fisheries and Food (Government of Catalonia)

emergence of new values and interests. As a consequence, traditional and sustainable multifunctional activities were abandoned and replaced by more purely production-oriented ones. Pastures located on steep slopes and at higher altitudes, requiring intensive labour, were abandoned while, at the same time, agriculture and livestock raising in accessible fertile lowland fields and productive mountain grasslands has intensified (Tasser and Tappeiner 2002; Bartolomé et al. 2005; Hopkins and Holz 2006). Changes in traditional farming practices have been observed across the European mountains (MacDonald et al. 2000). In the Pyrenees, traditional pastoral systems were characterised by an extensive management of the herd and the local transhumance to the communal alpine pastures in summer. Also, herds of sheep moved each year from the Ebro basin to summer mountain grasslands (Montserrat and Fillat 1994). In the last decades, in the Pyrenees, but also in most of the temperate European mountains, the redirection of the labour force to other employments, mainly related to the tertiary sector, caused changes in the farming management practices. As a consequence, some farms were abandoned while other intensified the management to accommodate socio-economic changes and labour resources. Together with a decrease in the number of farms, an increase of stocking number per farm and a shift of the stockbreeding to forms with low labour requirements (i.e. ovine to bovine) are common trends that allowed becoming more cost-efficient (Table 9.2).

9.4.1 *Grazing Intensification*

The adjustment of traditional farm households to a more intensive production and pluriactivity had entailed spatial changes in the grazing practices and land management. In the Pyrenees and Alps, the decline in shepherding has led to localised concentrations of stock around more easy-to-reach alpine grasslands, frequently resulting in overgrazing of high-quality pastures, while grazing intensity on steep slopes will likely decline (MacDonald et al. 2000).

SOC is a function of the balance between inputs from primary production and outputs through decomposition (Fig. 9.1). As a result of overgrazing, the quantity of the inputs to the soil may be reduced due to the aboveground biomass removal by animals. Also, the reduced plant biomass (i.e. less photosynthetic tissue) in heavily grazed grasslands causes a reduction of the aboveground productivity in comparison to the non-grazed grasslands (Ferraro and Oesterheld 2002). Although grazing can stimulate aboveground plant productivity under light or moderate grazing intensities through the so-called compensatory growth, it has been shown that heavy defoliation may lead to substantial reduction of the aboveground production (Chen et al. 2006; Zhao et al. 2008). In this case, plants respond to defoliation by allocating more C aboveground and thus reducing root biomass and productivity. The magnitude of this effect increases with the intensity of defoliation, the nutrient availability and water availability (Zhao et al. 2008; Klumpp et al. 2009). So there are site-specific sustainable grazing regimes that allow the conservation of C stocks, but when that grazing pressures are exceeded, inputs into the soil may be reduced (Georgaidis et al. 1989; Ferraro and Oesterheld 2002; Gao et al. 2008).

Overgrazing causes an alteration in soil physical, chemical and biological properties, resulting in changes in vegetation cover, a degradation of soil and a loss of soil C stocks. A typical feature of grazing activity is spatial heterogeneity. Animals tend to graze on areas with the most nutritious plants whereas select particular landscapes features for resting and ruminating. As a consequence, different types of vegetation develop which, in turn, influences the subsequent behaviour of the animals. Plant nutrient contents and soil nutrient availability increase from grazed to resting areas (Badia et al. 2008). In highly grazed areas, in comparison with only lightly grazed ones, the availability of P increases as a consequence of cattle grazing and defecation, which may accelerate the P cycling (Güsewell et al. 2005). An increase in fresh organic C (i.e. faeces) and nutrient availabilities as a consequence of animal frequentation may increase the microbial decomposition of native soil organic C. In addition, an excess of trampling and continuous overgrazing increases the area of bare soil and the risk of soil erosion. In the Tibetan plateau, the degradation of grasslands due to land-use change and overgrazing caused relevant losses of soil organic C in the last 30 years (Xie et al. 2007). In the Alps, erosion rates can be considerably higher (4.4–20 Mg ha^{-1} year^{-1}) on grasslands with clear signs of degradation of the vegetation cover (Meusburger and Alewell 2014).

9.4.2 Grazing Abandonment

Abandonment of pasturelands and traditional farming practices is a widespread phenomenon in the mountain areas of Europe (MacDonald et al. 2000). While the impacts on several environmental and landscape values are evident (Tasser et al. 2007), the effects on C dynamics and soil C stocks are less apparent. The net effects of land-use changes on C stocks are the result of the changes in the inputs and output drivers in the short- and long term after abandonment. Land-use changes may also affect the biochemical quality of litter inputs, which is a major factor influencing the organic C accumulation in soils (Liao and Boutton 2008). In ecosystems with high belowground allocation, such as grasslands, root dynamics represent the primary source for building up soil organic matter (Rasse et al. 2005; Piñeiro et al. 2006). This situation mostly applies to grazed grasslands, where a substantial amount of aboveground production is removed by grazing animals. When grass species are not palatable, both above- and belowground productions may be of the same order of magnitude. For example, in subalpine *Festuca eskia* grasslands in the Pyrenees, Montané et al. (2010) estimated an aboveground production of about 200 g m^{-2} $year^{-1}$ while the root production estimated by 15 cm-depth ingrowth cores was about 150 g m^{-2} $year^{-1}$.

Belowground biomass production and turnover have been related to microclimate as well as to land-use management (Guo et al. 2007; Leifeld et al. 2015). In the short term, grazing abandonment of subalpine grasslands allows higher aboveground biomass and accumulation of substantial amounts of necromass, but the effects on belowground biomass remain controversial. In general, belowground productivity increases in response to grazing removal (Ruess et al. 1998; Johnson and Matchett 2001; Smit and Kooijman 2001) but some studies did not find significant effects (McNaughton et al. 1998; Bazot et al. 2005) or even negative effects (Frank et al. 2002; Pucheta et al. 2004). Controversial findings may be partly explained by the physiological responses of plants to defoliation, but also by changes in plant species composition that may translate to differences in productivity, C allocation patterns and rooting depths at the ecosystem level. Indeed, Lanta et al. (2009) reported changes in plant species composition and richness in a 3-year field experiment with grazing and abandonment, and also showed a reduction of belowground biomass in non-grazed grasslands of the White Carpathians in the Czech Republic. In a 2-year grazing exclusion experiment in the Pyrenees, root production decreased in grazed grasslands in comparison with non-grazed ones. This response occurred right after the grazing event, and no apparent effects on yearly belowground C input were found (Garcia-Pausas et al. 2011).

9.4.3 Soil C Stocks in Grazed and Ungrazed Mountain Grasslands

The effect of grazing abandonment on soil C stocks has mostly been studied through the comparison of grazed and ungrazed areas, but the short-term effects of grazing on SOC is inconsistent to date, with both increases and decreases reported in response to increased grazing pressure. Although the effect of herbivory on plant productivity and C allocation is still under debate, abandonment of light, extensive grazing management might reduce soil stocks (Schuman et al. 1999; Pucheta et al. 2004).

Thus in a survey of grasslands in the Pyrenees, we found that abandoned grasslands had lower SOC stocks in the uppermost 20 cm of soil than grazed ones (Casals et al. 2004). However, this result may just reflect that the less productive grasslands were abandoned. In summary, changes in soil C stocks of mountain grasslands as a consequence of grazing abandonment are, at least in the short term, small and no clear trends may be stated.

9.4.4 Effects of Shrub Encroachment on Soil C Dynamics and Stocks

In the long term, grazing abandonment may involve a change in the dominant functional groups and often leads to shrub encroachment (Fig. 9.5). This shift is often observed in many mountain areas (MacDonald et al. 2000) and can lead to long-term expansion of forests (Gehrig-Fasel et al. 2007; Améztegui et al. 2010). Shrub encroachment into grasslands has been documented in the Pyrenees (Molinillo et al. 1997; Roura-Pascual et al. 2005) and the Central System ranges of the Iberian Peninsula (Sanz-Elorza et al. 2003). However, depending on the site characteristics, this can be a slow process. Indeed, Pardo et al. (2015) did not

Fig. 9.5 Shrub encroachment (*Cytisus balansae* ssp. *europaeus*) into mountain grasslands. Durro mountains (Alta Ribagorça, Central Pyrenees). Photo: Pere Casals

observe great changes in vegetation richness and composition after two decades of grazing exclusion in subalpine grasslands in the central Pyrenees. In Collada de Montalto (Central Pyrenees), shrub encroachment occurred mostly in grass patches inside the shrublands while woody proliferation into open grassland was less evident. Comparing the border between grassland and shrubland, we estimated a mean shrub expansion of the border into the mesic grassland of 2.0 ± 1.4 m (n = 263) in the period between 1997 and 2014 (unpublished data).

When woody plant invasion occurs, the shift from grass- to a shrub-dominated ecosystem entails significant changes in the production and placement of the inputs of litter (i.e. aboveground or belowground) and on factors that regulate soil organic matter mineralisation such as microclimate, biochemical quality of organic matter and the structure of the microbial community.

9.4.4.1 Litter Inputs

After shrub encroachment, the pattern of litter inputs changes from a belowground predominance in grasslands to an increase of aboveground deposition in shrublands. This shift is due to the differential allocation patterns between grasses and shrubs (Lett et al. 2004). For instance, in *Cytisus balansae* shrublands that had invaded subalpine grasslands of the Pyrenees, aboveground litter input was estimated as high as fourfold the root litter inputs in the top 15 cm of soil (Montané et al. 2010).

Surface litter is partially decomposed to CO_2, but a fraction is incorporated into the mineral horizons as a dissolved or particulate organic matter where it is mineralised or stabilised. Indeed, litter layers under shrubs may be an important source of dissolved organic C into the mineral soil, with a flux that may represent up to 35% of the annual litterfall C (Kalbitz and Kaiser 2008). Also, free particulate organic matter plays a significant role in the increase of soil organic C in the uppermost layers after woody plant encroachment in grasslands (Liao et al. 2006). Consequently, shrub encroachment into grasslands modifies the amount and placement of organic matter into the soil, but the effect on C sequestration also depends on the C loss from decomposing litter and soil organic matter.

9.4.4.2 Microclimate

Changes in the plant cover after pasture abandonment and shrub encroachment modify incoming solar radiation and precipitation to the soil. After grazing removal, the accumulation of standing necromass and litter reduces soil temperature and may increase soil water content (Rosset et al. 2001). In the Pyrenees, cumulative degree-days above 0 °C from May to November at 5 cm-depth soil were about 20% lower beneath woody canopies than under grasses (Montané et al. 2010). Lower temperatures under shrub canopies likely reduces above- and/or belowground litter decomposition which may be the predominant mechanism behind higher SOC after shrub encroachment (Smith and Johnson 2004). For instance, a reduction of soil CO_2 efflux after grazing exclusion in the Tibetan Plateau has been attributed in part to its lower soil temperature (Chen et al. 2016). In the Pyrenees, *Festuca eskia* roots incubated for 1 year in buried litterbags in a subalpine soil decomposed slightly slower under shrubs than in paired grasslands (20.1 ± 0.42% and 22.4 ± 1.44% mass loss, respectively) (Casals et al. 2010). In addition, using buried labelled wheat roots mixed with soil, Casals et al. (2010) showed that ^{13}C loss was about four percent units lower in root bags incubated for 1 year in non-grazed grassland plots and seven percent units lower under shrubs than in paired grazed grasslands. As these results derived from the incubation of standard labelled material, they mainly reflect a change to a less favourable soil environment for root decomposition due to either grazing exclusion or shrub encroachment. Therefore, a decrease in soil temperature may contribute to explain lower root decomposition rates after grassland abandonment and shrub encroachment.

9.4.4.3 Biochemical Quality and Microbial Activity

It is widely known that litter nutrient concentration and organic matter quality (e.g. lignin content) are the main factors determining litter decomposition rates (Cornwell et al. 2008). Grasslands typically have a high density of fine roots that are poorly lignified and with high turnover rates, thus providing a relatively labile C substrate for microbial activity. In contrast, the proliferation of shrubs may increase the presence of lignified roots with lower turnover rates. After shrub encroachment, low quality of litter inputs, with large amounts of secondary compounds such as lignin or polyphenolic substances, may hinder decomposition and promote C accumulation (Pérez-Harguindeguy et al. 2000; Shaw and Harte 2001; McCulley et al. 2004; Liao and Boutton 2008).

The biochemical quality of litter may differ between species. In the Pyrenees, an aboveground litter of grasses showed marked differences in the chemical composition from that of the two main invading shrubs of that area (*Cytisus balansae* and *Juniperus communis*). The litter of both shrubs had higher concentrations of recalcitrant compounds (e.g. lignin, lipids, suberin) and a low concentration of either N (conifer) or P (legume) relative to grass litter (Montané et al. 2010). Consequently, the higher organic C found in the upper mineral soil layer under shrubs compared to the grassland was mainly attributed to the slower decomposition of shrub litter and the transfer of litter-derived C into the soil. However, the presence of grass litter, with high N and P concentrations, may enhance microbial activity and prime the decomposition of recalcitrant shrub litter. As a result, at least in the short term after shrub proliferation when both shrub and grass litters coexist, the shrub litter accumulation pattern is altered (Montané et al. 2013).

Defoliation induces an increase of root exudation (Paterson et al. 2005). Therefore when grassland is abandoned a reduction of labile C inputs into the soil can be expected. Also, when shrubs proliferate, their lower fine root density may cause further reduction of C inputs by exudation. This decrease of labile C release from roots may cause a significant reduction of microbial activity (Hamilton and Frank 2001) and also a lower stimulation of soil organic matter mineralisation (i.e. priming) that usually occurs in the presence of labile C (Kuzyakov et al. 2000). Priming effect on soil organic matter mineralisation is particularly relevant in the rhizosphere and, although its magnitude is variable, it increases with the rate of rhizospheric C inputs (Paterson and Sim 2013) and may account for a substantial fraction of the SOM-derived CO_2 efflux (Cheng and Kuzyakov 2005). In addition, this reduction of priming effect may cause in turn a reduction of the nutrient availability for plants (Hamilton and Frank 2001).

The change of root exudates, as well as the fate of particulate organic matter also promotes a change in the microbial community composition (Grayston et al. 2004). Indeed, fungal growth and activity seems to be generally favoured in surface horizons after grazing or agricultural abandonment (Zornoza et al. 2009; Lopez-Sangil et al. 2011) and a higher fungal-to-bacterial activity ratio seems to promote a conservative cycling of nutrients in soil and C accumulation (Wardle et al. 2004; Gordon et al. 2008). Therefore a reduction in soil organic C decomposition in abandoned sites is expected.

9.4.4.4 Soil C Stocks in Shrub-Encroached Grasslands

In summary, shrub encroachment into mountain grasslands increases soil organic carbon in the upper soil mineral profile compared to the grassland soil (Montané et al. 2007). This net C increase may be explained by lower aboveground and belowground litter decomposition after shrub proliferation due to lower soil temperatures and lower biochemical quality of shrub organic matter. Lower litter quality may promote a shift in the composition of the microbial community to a slow-growth strategy, typical of a fungal-dominated microbial community (Bardgett et al. 2005), which may contribute to explain lower decomposition. The reduction of fine root density with the proliferation of shrubs may also reduce the rates of root exudation, which may decrease the priming effect on soil organic matter mineralisation thus contributing to the conservation of soil C stocks.

9.4.4.5 Shrubland Management and Soil C Stocks

Shrub encroachment into grasslands involves the replacement of one dominant growth form by another one, and it is likely to impact on ecosystem structure and functions (Lett and Knapp 2005). In the Pyrenees, a decrease in diversity

(Anthelme et al. 2007) and increases in soil C storage (Montané et al. 2007) have been reported after shrub proliferation into grasslands. Woody encroachment increases the risk of fire propagation by incrementing both fuel load and fuel continuity. In these encroachment-prone communities, managers may have to decide between reducing shrub proliferation to maintain biodiversity and grazing potential or allowing the shrub proliferation to increase C sequestration.

In the Pyrenees, shepherds have traditionally used fire as a management tool to improve grass productivity and transform encroached land into grassland. Today prescribed burning is usually carried out by fire brigades or foresters in winter when snowy or wet conditions limit the impact of the fire on soils and herbaceous plants (Rigolot et al. 2002). Mechanical thinning is also applied to revert encroached grasslands. How these management options affect organic matter dynamics and soil C stocks remains an issue.

9.5 Conclusions and Further Research Needs

Agricultural land-use changes in the European mountains show antagonist trends, intensification at the bottom of valleys and other productive grasslands, whereas the less productive grasslands located on steep slopes and at higher altitudes are being increasingly abandoned. A mechanistic understanding of how these changes affect relevant ecological processes, such as biodiversity or C stocks, is necessary to predict the effects of global change on ecosystem function and deliver appropriate management recommendations.

The decline of agropastoral activities is especially pervasive in high mountain grasslands. As a consequence, pasture abandonment, especially of marginal and less productive lands, and shrub encroachment into grasslands have become the most significant trends in land use, which may be observed all around European mountains, to a greater or lesser extent. Short-term changes in soil C stocks as a consequence of grazing abandonment are difficult to detect due to the large size of the organic matter pool as compared to the small changes in the C inputs, and also to the high spatial variability of soil C stocks (Conant and Paustian 2002; Smith 2004). Smith (2004), using a modelling approach, demonstrated that a change in SOC may not be detectable until about 7–10 year after the experiment, assuming an increase in soil C input of 20–25% (Smith 2004). Therefore, well monitored long-term exclusion experiments would be very useful to measure changes in the C stocks caused by management changes.

Higher soil organic matter after shrub encroachment into grasslands may be explained by the high content of recalcitrant compounds such as lignin and polyphenols in the plant-derived organic matter inputs, which slows the decomposition of soil organic matter and delays its incorporation into the protected pools in the mineral soil.

Due to high fine root density and rhizosphere exudation rates, grassland soils show higher priming effect on C mineralisation than in woodland soils (Waldrop and Firestone 2004). The effect of woody plant invasion on rhizosphere priming is still unknown and could have a significant impact on C balance.

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