

Chapter 4

Soil Carbon Reservoirs at High-Altitude Ecosystems in the Andean Plateau

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4.1 Introduction

4.1.1 Mountain Ecosystem Coverage

Mountains and uplands represent the world's most diverse and fragile ecosystems, cover about 20% of the terrestrial surface, and are distributed across all continents and major ecoregions (Heywood et al. 1994). While about 10% of the world's population lives in these environments, mountains provide important economic resources. Mountain ecosystems are rich sources of biodiversity and provide ecosystem services for their inhabitants (Brooks et al. 2006). These regions are currently threatened by land use and land cover changes, therefore an efficient monitoring is required to capture such changes (Tovar et al. 2013). Mountain environments support human communities, ecological landscapes, and organisms which are strongly influenced by temperature and precipitation changes. For this reason, they are good indicators of the impacts of the climate change.

The Andean plateau is the main mountain range of the American continent and one of the largest in the world, measuring more than 7500 km. The high-elevation habitats of the South American Andes extend from 11°N to 56°S (Arroyo and Cavieres 2013) and involve Argentina, Chile, Bolivia, Peru, Ecuador, Colombia, and Venezuela. Global human and biodiversity responses to climate change cannot be understood without an understanding of carbon (C) dynamics and reservoirs in the Andean region (Coûteaux et al. 2002).

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© Springer International Publishing Switzerland 2015
M. Öztürk et al. (eds.), *Climate Change Impacts on High-Altitude Ecosystems*,
DOI 10.1007/978-3-319-12859-7_4

4.1.2 Soil Organic Carbon

In the past two decades, a number of studies on soil C have been conducted across different grassland types around the world (Wang and Fang 2009). These studies make it possible to analyze soil C stocks in the Andean plateau. The soil organic matter (SOM) is a cornerstone pool in the fertility management of the Andean agriculture as well as the control of erosion. Mountain soils are considered to be a large regional soil C reservoir in the global cycling. The mountain soils are headwater areas of catchments controlling densely populated valleys justified to improve our knowledge concerns to soil C reservoirs in the Andean region (Bottner et al. 2006).

The global C cycle depends mainly on the SOM dynamics (Lal 2001) and the Kyoto Protocol includes the soil C reserves in the grasslands for the reduction of green house effects (Kenneth et al. 2007). Growing interest in the potential for soils to provide a sink for atmospheric C has prompted studies of effects of management on the amount and nature of soil organic C (SOC; Ganjegunte et al. 2005). SOC reserves are the result of the balance between organic carbon (OC) inputs and the mineralization average of each SOM groups (Post and Kwon 2000).

In order to understand SOM dynamics, it is fundamental not only to quantify the OC contents but also to know the processes which provide nutrients to plants. In this sense, OC and organic nitrogen contents are essential to determine the soil C reservoirs while C/N ratio helps to determine the rate of C mineralization (Brady and Weil 2008) as well as soil respiration (Högberg and Read 2006). Moreover, it is crucial to gain knowledge about the different C pools and functional groups in order to establish the rate of SOM biodegradation (Preston et al. 1987; Stevenson 1994). Likewise, SOC is the most labile and reactive SOM fraction and it determines the C stability in the soil (Zhao et al. 2008). On the other hand, the recalcitrant C (RC) fraction provides information about the long-term C storage (Belay-Tedla et al. 2009).

4.1.3 C Reservoirs at High-Altitude Grasslands

The influence of current global climatic change on SOC reservoirs and dynamics is still not clearly understood in high-altitude grasslands (Davidson and Janssens 2006; Xu et al. 2010). Authors such as García-Pausas et al. (2008) suggested that the C stabilization mechanisms in mountain grassland soils may be affected by the climate. Zehetner and Miller (2006) assessed a slow SOM decomposition due to the lower temperatures and soil pH in the Andean agroecosystems. Many studies have focused on short-term dynamics, but there is recent evidence that the dominant slow pools of SOM are more sensitive to temperature than the fast pools. This fact implies stronger long-term responses than previously anticipated (Knorr et al. 2005).

Due to the lack of specialized surveys conducted in the Andean plateau and in order to provide essential information about this hotspot in the soil C study, further researches should be carried out in ecosystems such as the Andean high-altitude

grasslands. These singular habitats have been very poorly understood and the present altitudinal patterns are likely to be altered by future climate change in the Andean region (Zehetner and Miller 2006). The study of soil C reservoirs and the implication of the SOM in the fertility management, the erosion control, the conservation of biodiversity, and the global climate change justified to improve its knowledge on the Andean plateau (Bottner et al. 2006).

4.2 Climate Data in Andean Grasslands

In general, the Andean climate is affected by three main factors: ocean currents, winds, and orography. Rainfall tends to increase with elevation. Moisture reaches the mountains primarily from the east, but rainfall in some inter-Andean valleys and on the western flank of the cordillera is also influenced by weather originating in the Pacific (Harden 2006). The entire Andean belt is segmented into the northern, central, and southern Andes (Decou et al. 2011). There are noticeable changes in the northern Andes climate compared to that in the central and south Andes.

The northern Andes of Venezuela, Colombia, and Ecuador is called paramo and its altitude ranges between 3300 and 4800 m.a.s.l. The paramo is characterized by humid climate with 800–1300 mm of mean precipitation falling annually, mostly as rainfall during the wet season that extends from May to November (Coûteaux et al. 2002; Bottner et al. 2006). The mean annual temperature ranges from 5 to 10 °C. There is a little seasonal fluctuation in temperature (between 7 and 12 °C) and a 15–20 °C diurnal fluctuation is normally experienced (Medina and Turcotte 1999; Harden 2006; Bottner et al. 2006). Diurnal variation is more pronounced in the dry season due to reduced cloud cover (Mahaney et al. 2007). Climate in northern Peru is classified as tropical summer rain high mountain climate (Haw) according to Koppen's reformed classification (Rudloff 1981; Baigorria and Romero 2007).

In contrast, the climate of the central and the south Andes which groups southern Peru, Bolivia, Chile, and Argentina is further characterized by an expressed seasonality with a dry season of pronounced water deficit from June to September. About 85% of the annual precipitation occurs from November to March (Moreau et al. 2003). The altitude ranges from 3800 to 5100 m.a.s.l. and this ecosystem is called puna. The mean annual precipitation could range from 350 to 700 mm and the mean temperature ranges from 5 to 10 °C (Bottner et al. 2006; Muñoz and Faz 2012). A high daily thermal amplitude (from 25 to 0 °C) due to intense solar radiation and low water vapor content in the atmosphere at such high altitude (Moreau et al. 2003) with low seasonal thermal variations (differences of 8–10 °C between summer and winter) has been reported.

4.3 Geomorphology, Hydrology, Geology, and Edaphology

4.3.1 Geomorphology and Hydrology

Because the Andes are still tectonically active (Norabuena et al. 1998), the physical setting includes active volcanism, ongoing uplift, earthquakes, and high magnitude mass movements. Uplift has caused rivers to incise (Safran et al. 2005) and denudation rates to be high (Aalto et al. 2006; Harden 2006). The highest peaks reach to nearly 7000 m.a.s.l. and are snow-capped. On the Atlantic and Pacific sides, relief is dramatic and hill slopes and river gradients are steep. Most of the region is tectonically active, and sections of it are volcanically active (Harden 2006). The Andes are characterized by an abrupt topography which ranges from 5500 m.a.s.l. to drop to less than 100 m into the tropical Amazon basin (Ecuador, Peru, and Bolivia). The distance traversed in the narrowest distance is approximately 200 km in the Ecuadorian Andes, while across the Altiplano of Peru and Bolivia, the distance is 500 km.

Due to tectonic processes over millions of years, an unstable landscape has been created which is unsurpassed in variety and complexity (Bottner et al. 2006). The cordilleras of the Andes divide the Pacific from Atlantic drainages and capture and regulate the flow of water for most of the South America continent. On the Atlantic side, the Amazon River basin comprises 34% of the land area of South America. Other major drainage basins are the Orinoco (Atlantic), Magdalena (Caribbean), and Paraná (Atlantic).

The hydrological resources of the Andes are virtually unique in the world in that they can be harnessed along most parts of their rapid 4000–5000 m descent (Coûtéaux et al. 2002). Traversing both the Pacific and Amazonia slopes of the Andes are dozens of major river systems which ecologically link the highlands and the lowlands. Westward-flowing rivers from southern Ecuador to central Chile deliver water to arid lands as they flow from mountain to ocean. The Magdalena River basin of Colombia has generally received less rain in El Niño years and more in the La Niña years (Restrepo and Kjerfve 2000). Similarly, pulses of deposition from Andean headwaters, recorded in floodplain sediment cores in the Beni and Mamore river basins, two Bolivian tributaries of the Amazon, were associated with La Niña events (Aalto et al. 2003; Harden 2006).

4.3.2 Geology

According to Mahaney et al. (2007), the northern Venezuelan Andes exhibits a general near-uniform lithology/parent materials. They present terraces formed in large part due to stream incision/migration triggered by Neotectonic uplift of a Late Glacial/Early Holocene glaciolacustrine lithosequence. Bedrock in the study area is dominantly granite and gneiss (Kunding 1938; Mahaney and Kalm 1996). Terrace

surfaces are relatively flat or gently sloping toward the modern stream channel and generally well drained. Exceptionally, the current floodplain and areas designated as “wet slope” which are prone to saturation in some cases due to seepage can be found. Lithology is relatively uniform within deposits of the lower terraces. It includes nearly identical suites of both light and heavy minerals that reflect the local metamorphic bedrock (Mahaney and Kalm 1996). The highest terraces contain elevated concentrations of heavy minerals that appear as distinctive black sand concentrations.

4.3.3 Soils

Soils formed on volcanic deposits such as Andean mountain range have the reputation of being fertile and highly productive (Buytaert et al. 2006). However, the properties of these soils undergo dramatic changes in the course of pedological development. The importance of climatic conditions on the colloidal composition of volcanic ash soils has been recognized in several surveys (Parfitt et al. 1983; Nieuwenhuys et al. 2000; Zehetner and Miller 2006).

At high elevations, the soil’s clay mineralogy is dominated by active amorphous constituents (Zehetner et al. 2003; Zehetner and Miller 2006) and is a typical weathering product in volcanic ash soils. They require humid conditions for their formation (Parfitt et al. 1983; Parfitt et al. 1984). Active amorphous materials, such as allophane and aluminum–humus complexes, dominate the clay fraction where the climate is moist and soil solution silicon is removed by leaching. Halloysite is found as the dominant clay mineral in drier silicon-rich environments. Such mineralogical differences have important bearings on the biogeochemical cycling in the ecosystems of volcanic landscapes. Active amorphous materials are known for their strong sorption of phosphate and for their stabilizing effects on SOM (Parfitt et al. 1984; Shoji et al. 1993; Zehetner and Miller 2006). Moreover, the acidity induces a high content of exchangeable aluminum and free Al (Bottner et al. 2006).

Paramo soils, in Ecuador, Colombia, and Venezuela, consist of a very black, highly organic epipedon (A, Ah, and/or O horizons) discontinuously overlying an unrelated inorganic surface (Podwojewski and Poulenard 2000; Otero et al. 2011). Because mineral particles in paramo soils are eolian in origin, paramo soils near to and downwind from active volcanoes may be 1–2 m thick, while soils farther from ash sources or on glaciated surfaces may be only 20–30-cm in depth (Harden 2006). The most common soils in the páramo are Andisols, Entisols, Inceptisols, and Histosols according to the soil taxonomy (Soil Survey Staff 2010) classification, or Andosols, Regosols, Umbrisols, and Histosols in Food and Agriculture Organization’s (FAO) World Reference Base for Soil Resources (FAO-ISRIC-ISSS 2006) (Coûteaux et al. 2002; Buytaert et al. 2006; Bottner et al. 2006; Harden 2006). In the southern Andes region of Ecuador, Dercon et al. (2007) observed humic Umbrisols Andosols at 3000 m.a.s.l.

Andosols have appreciable amounts of weatherable primary minerals and pyroclastic glass (data not shown), and comparatively low clay contents, which reflect

their young age (Zehetner et al. 2003). Andosols, located at high elevation where higher rainfall and lower evapotranspiration result have greater leaching and less-pronounced seasonal drying. This has favored the formation of active amorphous materials, such as allophane, in the upper profile, which in turn has profound effects on the soil's physicochemical behavior. Active amorphous materials may also have contributed to the stabilization and accumulation of SOM in the upper horizons of the Andosols (Zehetner and Miller 2006). Andic soil properties increase with elevation and according to US soil taxonomy (Soil Survey Staff 2010). The high-elevation soils are classified as Andosols and the low-elevation soils as Inceptisols and Entisols (Zehetner et al. 2003). In more water-saturated areas or regions with less volcanic influence, organic soils such as Histosols have been found (Buytaert et al. 2006).

Northern Andean highlands of Peru were classified by Baigorria and Romero (2007) as Entisols, Inceptisols, and Mollisols according to Soil Survey Staff (2010). Entisols are usually located at lower elevation where lower rainfall and higher evapotranspiration cause less leaching and the soils experience a pronounced period of desiccation during the dry season. As a result, active amorphous materials are absent and the colloidal fraction is dominated by the less reactive clay mineral halloysite (Zehetner and Miller 2006).

Bottener et al. (2006) found Haplic Xerosol in the southern Bolivian puna. The soil was shallow, sandy, stony with very low organic matter (OM) and the exchangeable and free Al contents were negligible. On the other hand, Muñoz and Faz (2012) identified Entisols and Inceptisols Soil Survey Staff (2010) and Cambisols, Regosols, Umbrisols, and Phaeozems according to FAO's classification (FAO-ISRIC-ISSS 2006) in the northern Bolivian puna.

4.4 Soil Characteristics: C, C/N ratio, Water-Soluble OC, RC, Functional Groups, Soil Respiration, and Soil Mineralization

Two main factors determine the Andean soil type and properties: (1) the climate and (2) the existence of a homogeneous layer of volcanic ashes from quaternary volcanic eruptions (Barberi et al. 1988 and Winckell et al. 1991). The cold and wet climate and the low atmospheric pressure favor OM accumulation in the soil (Medina and Turcotte 1999; Harden 2006).

This accumulation is further enhanced by the formation of organometallic complexes strongly resisting to the microbial breakdown. Aluminum and iron in these complexes are supplied by the breakdown of volcanic ashes and bedrock (Nanzyo et al. 1993; Buytaert et al. 2006). Accordingly, the large sequestration of OM generally observed in the paramo soils can be explained by two abiotic factors: the unfavorable soil microstructure and the accumulation of free aluminum linked to the climatic and acid soil conditions, inhibiting the microbial activity physically and chemically (Bottner et al. 2006).

4.4.1 Soil OC

Zehetner and Miller (2006) studied some soil properties in Ecuadorian Andean soils and observed an OM content increase with the altitude, likely a result of slowed decomposition due to lower temperatures and lower soil pH at higher elevations. The presence of active amorphous materials may further have contributed to this accumulation by protecting OM against microbial decomposition and prevent the soil erosion. The stabilizing effects of active amorphous materials on SOM have been demonstrated by Parfitt et al. (1997) and Zehetner and Miller (2006). These authors reported decreases of OM contents upon conversion from pasture to cropland that were considerably higher in an Inceptisol than in an Andosol which contained active amorphous materials. Several authors found that around 40–60% of the SOC exist within the top 20-cm layer in high grasslands (Jobbàgy and Jackson 2000), Pyrenean mountain grasslands (García-Pausas et al. 2008), and Andean grasslands (Muñoz and Faz 2012).

Otero et al. (2011) found high concentrations of OC (6.2%) in the Andean paramo of Colombia similar to those observed by Zehetner and Miller (2006) in the Ecuadorian paramo. Coûteaux et al. (2002) observed 4.6% of OC in Entisols located in Andean Venezuelan paramo, while Bottner et al. (2006) found higher C contents (9.9%) similar to those contents found by Abadín et al. (2002) in the Venezuela highlands which ranged from 7.1 to 8.4%. Furthermore, Harden (2006) described the typical content of OM in Histosols located in the paramo to be around 30%. The paramo soils contain up to 45 kg OC m⁻² distributed over 50-cm depth.

Under the moist conditions of paramo, the soil carbon content is up to 10% and SOM seems to be the main factor determining the soil physical properties and erosion sensitivity (Poulenard et al. 2003; Bottner et al. 2006). They contain elevated amounts of OC which is typically around 100 g kg⁻¹. In wet locations (>900 mm yr⁻¹), OC contents of up to more than 40% are not uncommon (Buytaert et al. 2005). Locations with more frequent ash deposits are characterized by younger soils with a C content of about 4–10% (Zehetner et al. 2003). In dryer regions, OM accumulation could be lower, although C contents (7% of OC) were found by Podwojewski et al. (2002) in the paramo with <600 mm yr⁻¹ of rainfall.

According to Bottner et al. (2006), under the drier conditions of the puna, the C contents were less than 1%. However, high total OC (TOC) contents were observed by Muñoz and Faz (2012) with 9.1 kg C m⁻² between 0 and 5-cm depth and 13.4 kg C m⁻² between 5 and 15-cm depth in the northern Bolivian puna (500 mm year⁻¹). These OC contents are higher than those found by some authors (3.0 kg C m⁻²) in high-altitude grasslands located in the Tibet plateau at 0–10-cm depth (4100–5100 m.a.s.l; Genxu et al. 2008), while Wu et al. (2003) observed 10–12 kg C m⁻² in the Quinhay–Tibet plateau from 0 to 30-cm depth. Ganjegunte et al. (2005) studied the C reservoirs in northern High Plains grasslands in USA where the SOC contents were significantly greater in light grazing grasslands (13.8 mg ha⁻¹) than in heavy grazing or nongrazed ones with similar results to those found in the northern Bolivian puna.

The much higher SOM content in paramo, despite more favorable climatic decomposition conditions, cannot entirely be explained by the difference in plant biomass and residues production between paramo and puna (Bottner et al. 2006). The external climatic conditions acting specifically on ecosystem productivity and decomposition are often not sufficient to explain the accumulation of SOM. Schimel and Weintraub (2003) highlighted the role of the labile plant material among the classical biotic factors defining the quality of the plant residues (nutrient content and availability, C/N ratio, lignin content, N/lignin ratio, etc.). The labile plant material provides microorganisms with energy for exoenzyme activity allowing the decomposition of recalcitrant material (Bottner et al. 2006).

4.4.2 *C/N ratio*

High C/N ratio described by Abadín et al. (2002) and Coûteaux et al. (2002) in two different researches conducted in the Andean Venezuelan highlands (18.2 and 16.2, respectively) could indicate that humification would be more intense than mineralization processes. These values were similar to those assessed by Bottner et al. (2006) in Venezuelan highlands (C/N ratio 15.3) in front of the C/N ratio found in the southern Bolivian puna (7.6). However, Muñoz and Faz (2012) described the C/N ratio ranging from 11.3 to 14.3 in the northern Bolivian puna, lower than those found by Coûteaux et al. (2002) in the Venezuelan paramo and higher than the C/N ratio observed by Bottner et al. (2006) in the southern Bolivian puna.

The paramo soils could exhibit a general predominance of humification processes compared to the puna soils which could show a more equilibrated relationship between mineralization and humification processes. This difference could be explained based on the different climatological conditions, particularly, the plentiful rainfall in the paramo that triggers the higher soil moisture coupled with the formation of organometallic complexes resistant to the microbial decomposition.

4.4.3 *Water-Soluble OC*

Water soluble OC (WSOC) serves as substrate for microbial biomass turnover and it is identified as labile C with fast decomposition or fast mineralization rate (Zhao et al. 2008). Due to the lack of data from the researchers carried out in the Andean region about this parameter, we show merely data from one study conducted in the Bolivian puna that are compared with others from highlands around the world. This comparison will be presented again for other parameters such as RC, functional groups, and soil respiration.

The highest WSOC values found in the northern Bolivian puna were 671.1 mg WSOC kg⁻¹ (0–5-cm depth at surface) and 579.7 mg WSOC kg⁻¹ (5–15-cm depth at subsurface). On the contrary, the lowest WSOC contents were 249.2 and 223.8 mg WSOC kg⁻¹, at surface and subsurface, respectively (Muñoz and Faz 2012). These

WSOC contents were within the range described by Halvorson and González (2008) in grasslands (500–2000 mg WSOC kg⁻¹), while all subsurface WSOC contents were above these authors' range (200–600 mg WSOC kg⁻¹). According to Zhao et al. (2008), there is a positive relationship between WSOC fraction and mineralization processes. Based on WSOC/TOC ratio, Muñoz and Faz (2012) observed that mineralization processes would be a bit more intensive at 5–15-cm depth although the C/N ratio observed in the northern Bolivian puna did not show a clear predominance of the mineralization processes compared to the humification ones.

4.4.4 *Recalcitrant C*

Chemical fractionation of SOM into various C pools using acid hydrolysis procedure allows one to study labile pool of small molecular size characterized by rapid turnover and a large molecular weight RC fraction of slow turnover (McLauchlan and Hobbie 2004). Stable compounds of SOM include fossil or black carbon which plays many important roles in the global C storage (Kögel-Knabner et al. 2008). In terms of stability, recalcitrance can be defined as the ability to resist abiotic and/or biotic degradation (Harvey et al. 2012).

According to the survey carried out by Muñoz et al. (2013) in the northern Bolivian puna, the highest RC contents were 3.7 kg RC m⁻² at 0–5-cm depth and 1.7 kg RC m⁻² at 5–15-cm depth. The recalcitrant index (RC/TOC ratio) observed ranged between 70 and 80%. Cheng et al. (2007) found RC contents around 2.2 g RC kg⁻¹ in agroecosystems in the USA (0–15-cm depth) and a recalcitrant index around 41%. Rovira and Vallejo (2007) observed a recalcitrant index of 53% in the surface horizon of Mediterranean forest soils. The very high recalcitrant index found in the northern Bolivian puna suggests a high storage of RC. High storage of RC is advantageous to the preservation or stabilization of soil mineral particles and the long-term C sequestration (Belay-Tedla et al. 2009; Rovira and Vallejo 2007). Authors such as García-Pausas et al. (2008) suggested that the C stabilization mechanisms in mountain grassland soils may be affected by the climate, particularly by the low temperature. Knorr et al. (2005) established that higher temperature may stimulate decomposition of the recalcitrant pools. Taking into account these arguments and the high RC contents found, the northern Bolivian puna could contain very valuable stable C reservoirs likely due to the low temperature and the high plant cover (Muñoz and Faz 2009). The OM deposition from the vegetation would increase the C contents and the low temperature would decrease the RC decomposition enhancing the stable C stocks. However, the increase of the temperature due to the global change could seriously affect these essential C reservoirs.

Davidson and Janssens (2006) stated the lack of consensus on the temperature sensitivity of soil C decomposition as this effect is particularly difficult to establish due to diversity of soil organic compounds and their variable kinetic properties. However, there is recent report that the dominant slow decomposing pools of SOM are more sensitive to temperature changes than the fast pools (Zehetner and Miller 2006). Therefore, the temperature increases associated with the global climatic

change could promote more CO₂ releases from RC in some zones at the Andean plateau, similar to the findings described by Xu et al. (2010) in the cold Chinese region.

4.4.5 Functional Groups

Carbon functional groups have usually been studied by the nuclear magnetic resonance technique (NMR) ¹³C CP/MAS-NMR in order to characterize SOM quality and composition. Particularly, NMR analyses worked efficiently in the identification of the distribution of various types of C during decomposition and humification of SOM (Oades et al. 1987; Preston et al. 1994; Dignac et al. 2002). Authors such as Lorenz et al. (2006) and Mahieu et al. (1999) establish that the general composition of the SOM would be O-alkyl-C (45%), alkyl-C (25%), aromatic-C (20%), and carboxyl-C (10%). Accordingly, Muñoz and Faz (2012) observed higher alkyl-C percentages in the northern Bolivian puna ranging from 33 to 43% in comparison with those observed by other authors who established 20–25% of alkyl-C (Faz et al. 2002; Kavdir et al. 2005; Leifeld and Kögel-Knabner 2005). Moreover, the high O-alkyl subgroup signal (60–98 ppm) observed in the northern Bolivian puna indicated undecomposed plant litter based on other survey results (Kavdir et al. 2005).

According to TOC/O-alkyl-C positive correlation found in the northern Bolivian puna, it can be established that more TOC involves a high quantity of undecomposed plant litter and a highest potential for decomposition (Kavdir et al. 2005). In general, the alkyl-C/O-alkyl-C ratio (above 0.7) could indicate certain relevance of humification (Dignac et al. 2002) likely due to the singular climate conditions, although this predominance would not be very relevant based on C/N ratio which indicated equilibrium between humification and mineralization processes (Muñoz and Faz 2012).

4.4.6 Soil Respiration and Soil Mineralization

Soil respiration is the primary pathway for CO₂ fixed by plants returning to the atmosphere (Högberg and Read 2006; Wang and Fang 2009). Soil respiration in grasslands consists mainly of respiration from roots and associated mycorrhizal fungi and microbial respiration. The basal respiration rate is the parameter that most promptly responds to soil disturbance (Hungria et al. 2009). Particularly, soil biological properties seem to have a greater potential than chemical or physical properties to indicate soil fertility in this mountain heterogeneous context because they are more sensitive to land-use changes (Sarmiento and Bottner 2002). It is extremely important to know the CO₂ fluxes and its implications to the global increase of CO₂ levels in the atmosphere to add knowledge about the relevance of long-term C stocks in the Andean plateau.

Muñoz et al. (2013) determined the soil respiration rate at 15 °C (the maximum temperature in the northern Bolivian puna) and at 25 °C (the standard temperature

to determine the soil respiration rate). They observed the highest CO_2 efflux at 25°C ($2786.9 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) at 0–5-cm depth while the highest soil respiration observed at 15°C was above $1000 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ at 5–15-cm depth. The annual soil CO_2 efflux was estimated to be $400 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ for temperate grasslands in the northeast of China (Wang and Fang 2009) and around $200 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ in semiarid steppes in inner Mongolia (Zhang et al. 2003). Hence, we can establish that the northern Bolivian puna could have a higher potentially mineralizable C at 15°C than other temperate highlands in the world based on the soil respiration rate. The ratio between soil respiration at 15 and 25°C (Q_{10}) showed that the temperature increase could impose a negative impact mainly in subsurface (5–15-cm depth) where the microorganisms would be rapidly activated in the northern Bolivian puna (Muñoz et al. 2013).

The soil mineralization in the paramo was studied by Martin and Haider (1986), Carballas et al. (1978), and Miltner and Zech (1998) who observed a slower decomposition of the bulk OM and of specific compounds such as sugars, polysaccharides, or phenols in the presence of ferrihydrites and Al hydroxides. The inhibition of decomposition was ascribed to chemical stabilization processes by organo-mineral bounding, to the insolubilization of the organic compounds, and/or to the toxicity effect of Al hydroxides for microorganisms (Bottner et al. 2006).

Coûteaux et al. (2002) assessed the SOM protection based on stable organo-aluminum complexes in Andean Venezuelan highlands. In addition, Abadín et al. (2002) suggested that the high soil contents of exchangeable Al^{3+} and free Al oxides point out that Al plays an important role in SOM stabilization, lowering its mineralization in the Venezuelan northern Andes. The abundance of acidity-generating ions (H^+ and Al^{3+}) that widely dominate the soil complex of exchangeable cations also may favor the soil acidification processes because an important fraction of these ions is easily displaced from the cation-exchange capacity (CEC) to the soil solution (Abadín et al. 2002). Therefore, aluminum likely plays in these soils an important role in the OM dynamics, lowering its mineralization. Global climate models predict a warming of 1–3 $^\circ\text{C}$ in the region by 2050 (Zehetner and Miller 2006). However, regional precipitation scenarios vary greatly among different simulation models, especially for the highland areas; some models predict decreasing, others increasing, rainfall. The projected temperature increase will certainly accelerate OM decomposition, particularly where OM is not protected by active amorphous materials, as it seems to be in the central Bolivian Andes (Zehetner and Miller 2006; Bottner et al. 2006).

4.5 Biomass Production: Plant Cover, More Relevant Species Height, Weight of Biomass

Highest species richness has been found in the paramo, followed by the puna and the southern Andean steppe (Arroyo and Cavieres 2013). These geologically young habitats bear a rich vascular flora, which can be accompanied by abundant mosses,

lichens, and hepatics in the paramo. In the vast semiarid Andean highland areas of the Andean plateau where vegetation productivity is relatively low, native wetland forage grasses represent a key resource for the livestock production. The native wetland forages are mainly *totorales* (lake-shoreline rushes) and *bofedales* (heterogeneous, short and dense grasslands, crisscrossed by shallow streamlets), present in the Andean region from Venezuela to Chile (Moreau et al. 2003). In the Andean wet grasslands, the continued growth and somewhat low senescence during the Austral dry winter with small variations of plant cover has been observed (Buttolph 1998). This fact is explained by the permanent availability of water in soils (Moreau et al. 2003).

In general, Andean vegetation shows numerous adaptations to high UV radiation and the moisture stress caused by low temperatures, high rates of transpiration during sunny periods, and desiccating winds. Many plants are evergreens, have sclerophyllous leaves, or have leaves that are gray-hued to maximize UV reflectivity. “Rosette habit” and tussock-forming grasses are common, as these adaptations create a warmer and wetter microclimate around the plant (Perez 1996; Luteyn 1999). It is also common to find mosses acting as substrates for other plants, because mosses retain moisture better than some soils present (Perez 1992; Mahaney et al. 2007). Regarding the botanical identification, the dominance of perennial species could indicate better adaptation of them to the extreme climate conditions in the Andean region (English et al. 2005; Muñoz and Faz 2014).

A qualitative study of plant functional types conducted by Mahaney et al. (2007) across the terrace sequence in the Venezuelan Andes showed that older surfaces supported greater plant diversity. The paramo is characterized by high biological diversity and endemism (Schubert and Vivas 1993; Luteyn 1999). Paramo vegetation varies, but is most commonly grass (*Calamagrostis* sp., *Stipa* sp., and *Agrostis* sp.), with some shrubs in less disturbed sites (Harden 2006). Other authors such as Coûteaux et al. (2002) found that a general vegetation of giant rosettes of *Espeletia schultzii* and shrubs of *Hypericum laricoides* dominate the vegetation in the Andean Venezuelan highlands. Among the flowering plants, there is a preponderance of mainly temperate families (Apiaceae, Geraniaceae, Polygonaceae, Rosaceae). Dominant plant vascular genera are: *Acaena*, *Aciachne*, *Carex bonplandii*, *Espeletia*, *Hypericum*, *Niphogeton*, *Sisyrinchium* (Mahaney et al. 2007).

The northern Bolivian puna vegetation has been identified by altoandine and puna vegetation units according to Beck et al. (2003). Muñoz and Faz (2014) identified *Aciachne*, *Festuca*, *Deyeuxia*, *Stipa*, *Pycnophyllum*, *Tarasa*, *Azorella*, and *Lachemilla* as predominant in the northern Bolivian puna. Moreover, they identified *Plantago*, *Scirpus*, or *Luzula* in the wet zones.

Shen et al. (2011) established that the water availability is one of the critical environmental factors that regulate vegetation activities in many areas such as arid and semiarid grasslands (Ji and Peters 2003; Pennington and Collins 2007). Pangtey et al. (1990) assessed that soil water availability is essential for growth initiation of some species at the alpine grasslands in the Central Himalaya. Although a seasonality influence could be assessed for some plant species in the northern Bolivian puna, in general a predominant growing during the wet season which could depend on each species could not be established (Muñoz and Faz 2014).

Soil N is usually the other limiting factor in herbaceous biomass production in semiarid and arid grasslands as emphasized by Dregne (1998) and Xuelin et al. (2008). Animals have to cover large distances to graze in semiarid grasslands and the N excreted by animals can have a long distribution out of the root influence zone, breaking down the return rate of this element to the plant (Burke et al. 1998). Related to the grazing, disturbed vegetation was observed in the Andean northern Bolivian grasslands supporting camelid grazing influence based on the presence of genera such as *Senecio* and *Aciachne* without camelid palatability as well as the decrease of very palatable species from Cyperaceae family (Harris 2010; Klein et al. 2004; Muñoz and Faz 2014). Several genera and species of grasses such as *Carex bonplandii*, *Espeletia*, *Hypericum*, and *Rumex acetosella* have been considered as disturbance grazing indicator in the Venezuelan paramo (Mahaney et al. 2007). These authors found that the low species richness could be explained based on the disturbances caused by grazing.

4.6 Use and Management of Altitude Grasslands— Human Effects: Grazing, Land-Use Changes, and Fertilization

Mountain landscapes are also among the most fragile landscapes on earth and are sensitive to both anthropogenic and natural forces. Human activities are significantly modifying biogeochemical cycles in many ways. Changes in the land use and management are recognized as key drivers on global C dynamics (Houghton et al. 1999; Wang and Fang 2009). Forest cover, agricultural practices, grazing, urbanization, and road construction have important and spatially extensive effects on runoff, which then controls rates of erosion and sediment movement. These effects are not unique to the Andes, but are especially interesting in the Andes because of the intensity of human occupation and the special natural and cultural characteristics of Andean highland environments (Harden 2006).

As in the paramo, the scarcity of trees in the drier puna grasslands of the central Andes is thought to result from anthropogenic burning and forest removal (Gade 1999; Harden 2006). Both in the central Andes and in the wet paramo, the cultivation system is based on long fallow periods with grazing and short crop periods. The intensification of land use raises the question of dynamics of the SOM and consequences on soil stability and soil erosion. Andean ecosystems are subjected to accelerated transformations with intensified cultivation and continuous expansion of the fallow agriculture frontier (Hofstede et al. 2002; Bottner et al. 2006).

The Andean region is undergoing transition to agricultural activities such as potato farming and cattle grazing in many areas. There is a lack of data quantifying the contributions of these land uses to soil erosion and nutrient losses. According to Otero et al. (2011), potato farming had more severe impacts on soil quality compared to that of pastoral land use. They found that soil preparation for agriculture often releases part of the immobilized or captured nutrients and alters the soil

physical, chemical, and biochemical properties. The volcanic ash soils have little exchangeable Al, even at pH 5, which is likely due to strong bonding of Al with SOM and formation of Al–humus complexes. The variable charge characteristics make pH an important determinant of the soil's nutrient-retention properties. Management practices that change the pH are therefore likely to affect the fate of plant nutrients in the soil (Zehetner and Miller 2006).

Vera et al. (2007) assessed that one of the land-use change consequences is a change in the SOM cycle with a greater degree of maturation in the disturbed soils. The moder humus comes from undisturbed forest soils and it is transformed into an acidic mull in the anthropogenic disturbed soils. Consequently, paramo ecosystems with increasing agricultural settings are being deteriorated, also because these high-altitude ecosystems have low resilience and it is slowly recovered. Conversely, Sarmiento and Bottner (2002) suggested that Andean agricultural systems are commonly used for the cultivation of potatoes and cereals with long fallow periods which leads to an increase in the labile C and N pools and microbial biomass. It represents more carbon and nitrogen availability for microorganisms and plants and could trigger the soil fertility restoration. A very high stability of the OM in these mountain soils was also revealed. Its implications for the agricultural sustainability should be discussed taking into account the traditional soil management.

In many cases, ecosystems in the central and southern Andean highlands are degraded as a consequence of anthropogenic activities such as the change in soil use and unsuitable water management in addition to excessive cattle grazing (Rocha and Sáez 2003; Muñoz and Faz 2012). Many grazing practices are aimed at ensuring the sustainable use of rangelands for livestock production. However, many ecosystem components and processes like plant community structure, soil properties, and nutrient cycling are also affected by grazing management (Schuman et al. 1999; Ganjgunte et al. 2005). Lack of a clear relationship between grazing practices and SOC has been attributed to soil variations, depth of soil sampling, and insufficient evaluation of C distributions within the grazing system. However, the grazing effects in the SOC reserves could be associated with the proportion of stable humic substances in the soil (Galantini and Rosell 2006; Ganjgunte et al. 2005).

Some authors observed that a long-term grazing exclusion by cattle and sheep promoted enrichment of the labile soil carbon pool in semiarid steppes (Shrestha and Stahl 2008). The animal grazing in highlands generally causes a reduction in soil respiration rate, as described by Cao et al. (2004). They reported that soil CO₂ efflux at the lightly grazed site was almost double compared to the heavily grazed site during the growing season in an alpine meadow in the Tibet plateau. Based on C study carried out in the Bolivian Andean grasslands, Muñoz and Faz (2012) concluded that domestic camelid grazing could be affecting the C reservoirs and as a consequence the maturity and stability of these ecosystems.

Conversely, grazing lands may have a high carbon sequestration potential if the input of OM into the soil and the reduction of SOM decomposition are promoted through best management practices (Batjes 1999). In many of the grazing lands, soil receives low carbon input and tends to show an exhaustion degree as a consequence of unsuitable grassland management (Shrestha and Stahl 2008). Therefore,

preventing the decrease of the SOM stabilization degree and bringing camelid cattle overexploitation under control is essential to protect the high-altitude ecosystems in the Andean plateau.

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