Chapter 4
Soil and Belowground Processes

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Abstract Soil characteristics and functions are critical determinants of rangeland systems and the ecosystem services that they provide. Rangeland soils are extremely diverse, but an emerging understanding is that paradigms developed in more mesic forest ecosystems may not be applicable. Vascular plants, biological soil crusts, and the soil microbial community are the three major functional groups of organisms that influence rangeland soils through their control over soil structure and soil carbon, water, and nutrient availability. Rangelands occur across a broad range of precipitation regimes, but local water status can be modified by management and land use. Important processes in carbon and nutrient cycling can be unique to arid rangelands. Physical drivers such as UV radiation and soil–litter mixing can be important factors for decomposition. Precipitation, vascular species composition and spatial pattern, presence of biological soil crusts, and surface disturbance interact to determine rates of carbon and nutrient cycling. The low resource availability in rangeland soils makes them very vulnerable to drivers of global change, and also excellent indicators of small changes in resource availability. Recent large-scale experiments demonstrate that rangelands are very susceptible to changes in precipitation regimes, warming, and atmospheric carbon dioxide. Growth of molecular tools in combination with other techniques has allowed scientists to increasingly link microbial community composition and function, thereby shedding light on what was formerly

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viewed as the black box of microbial dynamics in soils. Concurrent technological advances in environmental sensors and sensor arrays allow more mechanistic understanding of soil processes while also offering new opportunities to develop questions at the landscape scale.

Keywords Atmospheric deposition • Biological soil crusts • Grazing • Soil carbon • Soil community composition and function • Soil nitrogen

4.1   Introduction

The maintenance of healthy, productive soils in rangelands is a critical management issue, determining vegetation production, cover, and composition, and the livelihood of over 2.5 billion people, most of whom live in poverty and directly rely upon the ecosystem services of rangelands for their well-being and survival (MEA 2005; Reynolds et al. 2007). Their inherently low soil carbon (C) and nutrient levels cause rangelands to be among the most responsive terrestrial land cover type to even small changes in resource availability caused by drivers of global change. This sensitivity to change, coupled with their extensive global coverage, is the primary reason that rangelands are now recognized as critical components of global biogeochemical cycles (Donohue et al. 2013; Evans et al. 2014; Poulter et al. 2014).

Their importance for a large fraction of the human population despite their low resource availability is a reason for an increased emphasis on the function and global significance of rangeland soils over the past 25 years. Prior to this scientists had developed detailed understanding of soil classification and physical characteristics, especially those properties contributing to water-holding capacity and plant water availability. However, our functional understanding of soil microbial community composition and biologically mediated processes in the carbon and nitrogen cycles had not progressed as rapidly as our knowledge of aboveground dynamics, or even soil function, in more mesic ecosystems. Recent emphases on community and ecosystem-level questions as well as development of new technologies have greatly facilitated our understanding and led to the following conceptual understandings: (1) increased awareness that paradigms developed in more mesic ecosystems may be less applicable in rangeland ecosystems, and in some cases major drivers of ecosystem function may be unique to rangelands; (2) identification of unifying principles in soil ecology is difficult because rangelands encompass many diverse ecosystems with wide variation in temperature, precipitation, and disturbance regimes; (3) rangeland ecosystems respond rapidly to perturbations in resource availability caused by anthropogenic drivers of change. The conceptual advances reaffirm that proper management and restoration are necessary to ensure ecosystem health into the future.

The broad goals are to identify the primary advances in our understanding of soil and belowground processes and function that have occurred during the past 25 years, and discuss the potential consequences of future drivers on rangeland soils.

4.2 Major Conceptual Advances

4.2.1 Community Composition and Function

4.2.1.1 Soil–Plant Interactions

Soils have a large influence on shifts in vegetation composition that are common in rangelands (Bestelmeyer et al. 2003), particularly since rangeland vegetation is extremely sensitive to soil degradation (van de Koppel et al. 2002). Vegetation composition not only responds to soils, but can also cause large changes in soil properties and functions (Diaz et al. 2002; Eviner and Chapin 2003; Bestelmeyer and Briske 2012). The magnitude and direction of soil changes, and which attributes are modified, depend on the magnitude of species composition change, as well as ecological site conditions. The most common vegetation shifts that occur in rangelands include shifts from palatable to unpalatable vegetation; shifts from herbaceous to woody dominance; changes in grass species composition; shifts from grass to forb dominance (Vetter 2005). Each of these categories are summarized below.

Shifts from palatable to unpalatable vegetation. Preferential grazing can decrease the prevalence of palatable plants and increase unpalatable plants (Bestelmeyer et al. 2003; Seymour et al. 2010). This shift tends to occur under continuous grazing regimes, particularly under lower soil nutrient availability (Wardle 2002; Harrison and Bardgett 2008), and more arid conditions (Diaz et al. 2007). Unpalatable plants represent a variety of growth forms, including other grasses, forbs, or woody species. These plants usually have lower nutrient concentrations and higher chemical defenses than palatable species, so their litter inputs decrease rates of nutrient recycling, further decreasing plant nutrient availability (Bardgett and Wardle 2003; Harrison and Bardgett 2008). Such changes in soils can lead to delayed or inhibited recovery of palatable vegetation, even after grazing has ceased (Bestelmeyer et al. 2003; Seymour et al. 2010).

Shifts from herbaceous to woody dominance. Many rangelands across the globe have experienced increasing woody encroachment over the past century (Fig. 4.1), which has been attributed to a variety of factors, including: overgrazing, decreased human disturbance, lower fire frequency, nitrogen (N) deposition, climate change, and predator suppression (Eldridge et al. 2011; Chapter 2, this volume). The encroachment of shrubs and trees into herbaceous-dominated rangeland has extremely variable impacts on multiple soil properties depending upon the plant species, local climate, and soil type (Schuman et al. 2002; Barger et al. 2011). Generally, woody plant encroachment leads to more patchy vegetation cover causing higher heterogeneity in soil conditions (Van Auken 2009; Barger et al. 2011) and lower water infiltration and increased vulnerability to erosion, particularly after fires and during droughts, in plant interspaces (Ravi et al. 2009; Barger et al. 2011). This is why in some areas, shrub encroachment has been linked with significant soil degradation and even desertification (Bestelmeyer et al. 2003; Ravi et al. 2009), but this is not true everywhere (Eldridge et al. 2011). In general, woody encroachment increases surface soil C, total N, mineralizable N, soil aggregate stability, and available
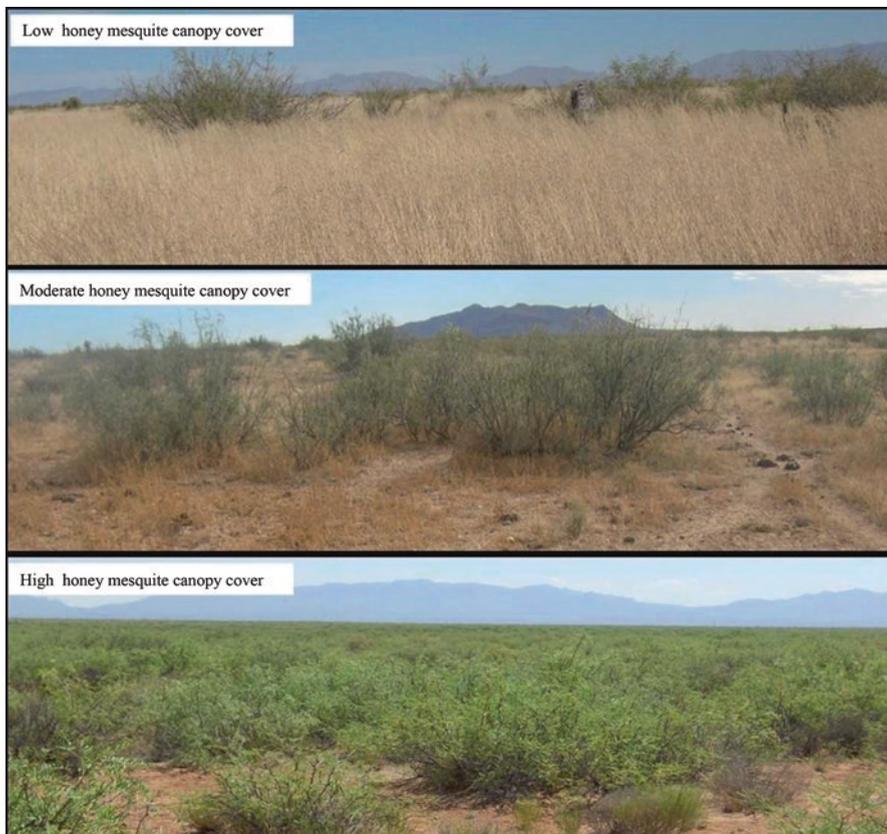
Fig. 4.1 Changes in community structure that occur during a shift in dominance from herbaceous to woody species (from Mohamed et al. 2011)

calcium (Archer et al. 2001; Schuman et al. 2002). Carbon accumulation tends to be higher in arid sites than in wetter sites (Jackson et al. 2002; Barger et al. 2011), but this strongly depends on species of shrub, soil bulk density (higher bulk density associated with more C loss), and % clay content (higher C accumulation associated with more clay) (Barger et al. 2011). In general, woody encroachment has stronger impacts on soil C pools than soil N (Van Auken 2009).

Woody encroachment into arid systems can enhance surface soil water through a combination of reduced evapotranspiration and hydraulic lift (Gill and Burke 1999). Shrub encroachment in arid ecosystems is generally patchy, leading to many areas of little to no plant cover, with low infiltration (Eviner and Chapin 2003). The effects of woody encroachment on streamflow vary with site hydrology. For example, a decrease in shrub cover can significantly enhance streamflow on sites with springs and groundwater flow, or that receive greater than 500 mm of rain per year, due to decreased transpiration rates. However, shrub removal may have no effect or even decrease streamflow in drylands or in systems where most streamflow is delivered

through overland flow (Wilcox et al. 2006; Chapter 3, this volume). Woody species may also decrease infiltration by depositing hydrophobic substances (e.g., waxes), which are very common in species such as oaks, but tend to be low in soils associated with grasses and mosses (Doerr et al. 2000; Schnabel et al. 2013).

Shifts in grass species dominance. Grazing can induce compositional shifts in some regions from perennial to annual dominated grasslands (Fernandez-Gimenez and Allen-Diaz 1999; Diaz et al. 2007). An increased prevalence of annual grasses can also be due to increased N deposition and introduction of non-native annuals (Bai et al. 2009; Ravi et al. 2009). Transition to annual plant dominance can lead to high temporal variability in plant production and cover paralleling climate variability, and little to no vegetation cover during droughts (Bai et al. 2004; Ravi et al. 2009). During these drought periods, low vegetation cover can lead to massive erosion and irreversible desertification (Ravi et al. 2009). Domination by annual plants can also homogenize spatial distribution of soil C, N, and water, eliminating the islands of fertility created by continuous litter inputs from perennial species that are important in facilitating reestablishment of other vegetation. Soil C has been shown to be higher under perennial vs. annual grasses across a range of sites in the western USA (Gill and Burke 1999). Shifts in grass composition within the annual or perennial groups can also have significant soil impacts. For example, in the shortgrass steppe, microbial biomass C and C mineralization rates were higher under perennial bunchgrasses than under rhizomatous grasses (Vinton and Burke 1995). In a tallgrass prairie, soil N mineralization rates differed tenfold across five different perennial grasses (Wedin and Tilman 1990). In California's annual grasslands, annual grass species differed in their impacts on net N mineralization and nitrification (Eviner et al. 2006).

Shifts between grass and forb dominance. Rangeland herbaceous vegetation commonly contains both grasses and broad-leafed species (forbs and legumes), with their relative dominance shifting over space and time (Fig. 4.2). Forbs tend to

Fig. 4.2 The relative dominance of grasses and broad-leaved species in many rangelands often shifts both temporally and spatially. For example, in this grassland in California the community is grass dominated (*left*) in some years, while in others forbs and legumes are dominant (*right*) (photographs by V. Eviner)

increase after disturbances that remove grass biomass (e.g., fire, grazing, gopher mounds, and herbicides) (Fernandez-Gimenez and Allen-Diaz 1999; Stahlheber and D'Antonio 2013). The effects of increasing forbs on soil processes will vary strongly by species. In general, forbs have lower C:N ratios than grasses, which could lead to higher rates of decomposition and nutrient recycling. However, many forbs contain secondary compounds that make plant litter more resistant to breakdown, and these species can slow rates of nutrient recycling (Eviner and Chapin 2003). Legumes generally increase total soil N and rates of N cycling through their fixation of atmospheric N (Eviner and Chapin 2003), and can also enhance soil organic C (Derner and Schuman 2007).

4.2.1.2   Biological Soil Crusts

Biological soil crusts are composed of cyanobacteria, lichens, mosses, fungi, and algae that intermix and form a consolidated matrix with surface soils (Fig. 4.3). The dominant organisms are autotrophic; thus they reach their greatest development in ecosystems where low water availability prevents continuous plant cover; under these conditions they can be a dominant feature of the landscape and coverage can approach 100 % in plant interspaces. The occurrence of biological soil crusts on the soil surface directly influences hydrology and soil surface stability, and autotrophs and organisms capable of biological N_2 fixation within crusts play a central role in ecosystem biogeochemistry. An extensive review of the composition and ecological roles of biological soil crusts in diverse biomes is provided by Belnap and Lange (2001).

The impacts of biological soil crusts on surface hydrology and soil stability are complex and variable (Warren et al. 2001; Rodriguez-Caballero et al. 2013). Biological soil crusts decrease erosion by protecting the soil surface from the direct impact of rain drops in a similar manner as vegetation. Greater microtopography of well-developed soil crusts can also increase pooling of water on the crust surface,

Fig. 4.3 Biological soil crusts are a consolidated matrix of organisms that stabilize soil surfaces (*left*) and can be important components of ecosystem carbon and nitrogen cycles. Coverage can be 100 % in plant interspaces. The soil crusts are the dark covering on the soil surface in the photograph on the *right*; the light shade is an artificial disturbance treatment illustrating the color of the soil underlying the soil crusts (photographs by R.D. Evans)

thus decreasing surface runoff (Rodriguez-Caballero et al. 2013). Wetting can also cause swelling of crust organisms effectively blocking infiltration into the soil (Belnap 2006; Bowker et al. 2013; Rodriguez-Caballero et al. 2013). Organisms within the crust also exude a gelatinous sheath that binds fine soil particles into larger aggregates (Belnap and Gardner 1993). This can have a negative impact on water infiltration in sandy soils because polysaccharide secretions, filaments, and accumulated fine soil particles may block pores at the soil surface reducing porosity (Warren et al. 2001). Infiltration may also be lower because the organic component of soil crusts is slightly hydrophobic. In contrast, in fine textured soils binding of soil fine particles into larger aggregates may increase effective porosity and infiltration. In general, crusts in cool and cold environments increase infiltration and reduce runoff, while crusts in very dry environments generally reduce infiltration and increase runoff, and results are mixed in intermediate locations (Belnap 2006).

Biological soil crusts have long been recognized as critical components of biogeochemical cycles in most arid rangelands. Autotrophic organisms within the crusts contribute to ecosystem C cycles (Evans et al. 2001a), and N_2 fixation by crust organisms can be the dominant source of N into many arid ecosystems (Evans and Ehleringer 1993; Evans and Belnap 1999; Evans et al. 2001a). Recent synthesis efforts estimate that biological soil crusts provide 7 % of the net primary production of terrestrial vegetation and nearly half of terrestrial biological N_2 fixation worldwide (Elbert et al. 2012). Lichens and mosses can also directly impact phosphorous availability and can promote chemical weathering of substrates (Cornelissen et al. 2007; Porada et al. 2014).

Understanding the fate of C and N assimilated by soil crusts is critical because of their central role in ecosystem C and N cycles. Rates of N_2 fixation by crust organisms are much greater than necessary for their own growth; thus it appears that a majority of the N assimilated during N_2 fixation is either emitted back to the atmosphere as nitric oxide (NO), nitrous oxide (N_2O), or ammonia (NH_3) during nitrification, denitrification, and volatilization or leached into underlying soils where they could be assimilated by microbes and vascular plants (Evans and Johansen 1999; Strauss et al. 2012). Recent studies combining molecular and microsensor approaches (Johnson et al. 2005, 2007; Strauss et al. 2012) indicate that despite significant variation in community structure across arid lands of North America, the relative magnitude of N_2 fixation, N gaseous loss, and N inputs into underlying soils was similar for all sites, with low flux rates of N to the atmosphere, indicating that biological soil crusts are net exporters of NH_4^+, NO_3^-, and organic N into underlying soils at rates commensurate with rates of N_2 fixation (Johnson et al. 2007; Strauss et al. 2012).

4.2.1.3 Soil Microbial Diversity and Function

Bacteria. Microbial diversity in rangeland soils remains poorly characterized (An et al. 2013) but this is rapidly changing with recent advancements in molecular and bioinformatics techniques. Recent studies have revealed unexpectedly large

bacterial diversities despite low microbial biomass (An et al. 2013). These diversities are described by culture-independent, DNA-based approaches, such as sequencing the 16S gene to profile bacterial communities. Generally, the composition of soil bacterial communities are site specific, but at the phylum level, the most abundant members include Proteobacteria, Bacteroidetes, and Actinobacteria (An et al. 2013; Kim et al. 2013; Steven et al. 2014); these phyla are typical of soils around the world. In a global analysis of the biogeography of soil bacteria, arid soils were observed to have the highest proportions of Actinobacteria (Fierer et al. 2009). This abundance is particularly notable as the degree of ecosystem aridity increases, the relative abundances of the Proteobacteria decrease (Neilson et al. 2012). Abundances of beta-Proteobacteria and Bacteroidetes are often correlated with carbon availability as measured by carbon mineralization (Fierer et al. 2007). Total bacterial richness has also been observed to increase with increasing C:N (An et al. 2013), suggesting that increased diversity may result from nitrogen limitations. Overall, soil texture is a good predictor of community structure (Kim et al. 2013; Pasternak et al. 2013), suggesting that the local environmental conditions that underlie habitat quality—pore structure, mineral surfaces, and water-holding capacity—influence microbial composition.

DNA-based approaches identify organisms that are present in the soil including those that are dormant when environmental conditions are not favorable for their activity. In contrast, RNA-based approaches provide a more functional approach by describing only the active members of the microbial community. This is an important distinction in rangelands where short-term stresses such as water limitations or high temperatures can cause the active microbial community to be very different from the dormant, and thus total, community. For example, in a series of sites in the Mediterranean, the community structure of the total Bacteria and Archaea revealed by DNA was driven by large-scale landscape patterns and less strongly correlated with local transient variables such as soil water (Angel et al. 2013). The RNA-based profiles were significantly more correlated to soil water, though this active subset of the microbial communities was less diverse indicating that a large portion of the community was dormant. The effect of water on these communities was stronger in Bacteria than in Archaea (Angel et al. 2013), which is consistent with other observations of the greater tolerance of Archaea to extreme conditions (Sher et al. 2013). Ammonia-oxidizing bacteria and archaea both had relatively stable community structures and were able to withstand the extreme conditions in arid systems; however the archaeal communities were more associated with the dry and hot periods, whereas the bacterial community was more responsive during the wetter periods (Sher et al. 2013).

Fungi. The fungal community is less well studied than the bacterial community in rangeland systems; yet fungi are potentially more able to withstand stressful conditions (Jin et al. 2011). Fungi are more drought tolerant than bacteria in arid soils, as fungal:bacterial ratios reported by phospholipid fatty acid profiling are negatively correlated with soil water content (Jin et al. 2011). Arbuscular mycorrhizal (AM) fungi can stimulate plant growth and drought tolerance (Querejeta et al. 2007); therefore, these plant symbionts are likely very important in arid ecosystems

characterized by patchy plant distribution. AM fungal diversity is largely controlled by local soil nutrients with lower levels of phosphorus causing more diverse AM fungal communities, and yet less diverse microbial communities, because competition for phosphorus excluded several types of microbes (Martinez-Garcia et al. 2011). Comparison of rhizosphere with bulk soil showed greater AM fungal diversity in the bulk soil, while the plant host selected for the most fit symbiont, reducing diversity in the rhizosphere (Martinez-Garcia et al. 2011). Free-living fungal communities in the bulk soils of very arid systems have relatively low diversity dominated by Basidiomycota and Ascomycota (Steven et al. 2014). Within the Ascomycota, the Dothideomycetes were highly abundant in the bulk soil (Steven et al. 2014).

4.2.2   Ecosystem Processes

4.2.2.1   Water

Water availability in rangeland systems is a critical determinant of soil community composition and function (Campbell et al. 1997). In most rangelands, precipitation inputs are low and episodic often occurring as short pulses (Austin et al. 2004). Soil physical parameters and vegetation condition are the major determinants of the fate of this water. Precipitation can evaporate from the soil or vegetation surface, run off from the surface through overland flow, or infiltrate into the soil, where the water can be stored, evapotranspired, or leached into groundwater (Wilcox 2002; Chapter 3, this volume).

Soil water-holding capacity is influenced by particle sizes, soil organic matter, and soil depth. Soil texture is critical in determining available soil water, and soil water-holding capacity can increase up to 3.7 % for every 1 % increase in soil organic matter (Bot and Benites 2005). In areas receiving less than 360 mm of precipitation per year, coarse soils decrease evaporative loss and enhance plant water availability. In areas receiving greater than 370 mm of precipitation per year, fine-textured soils increase plant water availability by enhancing water-holding capacity (Austin et al. 2004).

Soil water infiltration is critical for plant water supply and to prevent erosion through overland flow. High soil pore volume can greatly increase infiltration, and is enhanced by soil aggregation, and channels created by roots and through the activity of soil organisms. Vegetation can greatly enhance infiltration by slowing down overland flow, allowing more time for water to infiltrate into the soil. Vegetation cover is also critical in enhancing infiltration by minimizing soil compaction, decreasing the impacts of raindrops directly on the soil surface, increasing porosity through root growth, and increasing soil organic matter to promote aggregation (Li et al. 2011). For example, when 60–75 % of the ground is covered with live plants and litter, surface runoff can be as low as 2 % of rainfall. However, with 37 % plant cover, surface runoff increases to 14 % of rainfall, and when vegetation

cover is less than 10 %, up to 73 % of rainfall can run off the surface (Bailey and Copleand 1961). Biological processes can also induce soil water repellency which can decrease infiltration rates by 6–25-fold (Doerr et al. 2000) and is caused by factors that include waxy plant materials, hydrophobic compounds produced by fungi, and hot surface temperatures and fires which melt or volatilize these compounds, causing them to coat the soil surface (Doerr et al. 2000; Schnabel et al. 2013). Water repellency of soil is particularly common in semiarid and seasonally dry conditions, and in fire-prone areas, which are typical in rangeland systems. This repellency can last from seconds to weeks (Doerr et al. 2000), and is particularly high in the dry season, and in the transitions between dry and wet periods (Schnabel et al. 2013). This water repellency can lead to heterogeneity in infiltration, and soil water content, causing preferential flow paths which can accelerate leaching losses and erosion (Doerr et al. 2000, Schnabel et al. 2013).

While most rangelands are constrained by water inputs, water limitation can be caused by meteorological drought resulting from low rainfall, or agricultural drought resulting from management practices that degrade the soil's ability to infiltrate and store water, thus limiting production of crops or forage (Rockstrom 2003; Mishra and Singh 2010). Intensive grazing can decrease soil water by compacting soil, which decreases infiltration, soil water (Trimble and Mendel 1995), and soil organic matter (Hutchens 2011). In general, low-to-moderate grazing has variable effects on soil water availability. While soil water availability generally mirrors grazing effects on soil organic matter, soil water decreases when grazing leads to compaction (Derner and Schuman 2007) that can cause increased runoff and overland flow (Wilcox 2002). High stocking rates can also decrease water infiltration because livestock trampling can destroy soil aggregates critical for maintaining soil porosity, and decrease plant cover, which decreases soil organic matter and increases the erosive impact of raindrops (Briske et al. 2011). These effects seem to be more associated with stocking rate than duration/seasonality of grazing, so that a high-density, short-duration grazing regime can have larger impacts than moderate, continuous grazing. However, rotational grazing that provides rest periods greater than 1 year can improve hydrologic function. The intensity of grazing necessary to disrupt water infiltration depends on vegetation cover (Briske et al. 2011).

4.2.2.2   Decomposition

Decomposition is the physical and chemical breakdown of dead biological materials. Decomposition is responsible for the formation of soil organic matter, and transformations result in organism-available energy and nutrient sources. The chemical composition of litter is a traditional metric used in studies of decomposition because it relates directly to the stoichiometric and chemical requirements of microbial decomposers. Predictors of quality of litter, C:N and lignin:N ratios, describe energy and nutrient source as well as the relative recalcitrance of available substrates. It is for these reasons measures of climate and litter quality are correlated with rates of net N mineralization at a global level (Manzoni et al. 2008) and are

included in models of ecosystem biogeochemistry (Parton et al. 1987). However, in arid and semiarid rangelands the value of these predictors is more problematic (Throop and Archer 2009; Austin and Ballare 2010). Recent research in arid range-lands has focused on other determinants of litter to better predict rates and patterns of decomposition. The role of UV radiation has received considerable attention because litter on the soil surface is often exposed to direct solar radiation for long periods in ecosystems with low plant cover. Another key determinant is the rate of soil–litter mixing, which is relatively slow compared to more mesic ecosystems.

The role of UV radiation in aboveground decomposition has become increas-ingly apparent, especially in more xeric regions with lower plant cover. Photomineralization of litter by UV radiation can short-circuit the C cycle because it results in direct loss of C to the atmosphere (Austin and Vivanco 2006), and can alter the chemical composition of remaining litter (Austin and Ballare 2010). In contrast, in the more mesic shortgrass steppe, precipitation, litter chemistry, and UV radiation were all important factors, but precipitation was the best determinant of litter decomposition, followed by litter chemistry (Brandt et al. 2010). Intercepted radiation was the major factor observed to have a significant effect on decomposi-tion rates in the Patagonian Steppe, where filtering of UV-B and total solar radiation decrease decomposition rates by 33 % and 60 %, respectively (Austin and Vivanco 2006). Significant mass loss was associated with solar radiation in a mesocosm experiment in North America, and rates of loss were not significantly different between UV radiation alone, microbial activity alone, or UV and microbial activity in combination. The authors conclude that UV radiation can be as effective at decomposing litter as microbial activity (Gallo et al. 2006). Lignin is often very resistant to microbial attack, so decomposition rates often decrease with increasing lignin content. However, rates of photodegradation have been observed to increase with lignin concentration because it is an effective light-absorbing compound (Austin and Ballare 2010), and exposure to sunlight leads to a decrease in litter lignin concentrations. Thus, while increased lignin will decrease microbial medi-ated decomposition, it actually enhances photodegradation. An added consequence of greater photodegradation of lignin is that it allows microbial decomposers access to labile compounds protected by lignified materials.

The importance of photodegradation decreases with increasing plant cover and water, and as litter is mixed with soil (Barnes et al. 2012). The development of the soil–litter matrix is critical in our understanding of rangeland decomposition as it mediates the transition from physical breakdown from abrasion and photodegrada-tion to biologically mediated decomposition by soil microbes. In a UV–soil mixing factorial experiment in a savanna ecosystem early decomposition was enhanced by UV radiation, but the effects decreased with increasing soil–litter mixing (Barnes et al. 2012). Nearly half of the surface area of litter was covered by a film of soil particles bound with fungal hyphae after 180 days. Others have also observed a positive relationship between soil litter mixing and mass loss of litter (Hewins et al. 2013). Three mechanisms lead to the increase in decomposition with soil–litter mixing (Throop and Archer 2009). First, soil is the vector for colonization of litter by microbial decomposers. Second, mixing with soil can ameliorate temperature

and water extremes associated with the soil surface provide a more favorable micro-environment for microbial colonization. Finally, soil transport along the soil and litter interface may increase the physical abrasion of litter making it more accessible to microbial decomposers.

4.2.2.3 Rhizosphere Dynamics

The influence of plant communities and the formation of resource "islands" exert strong controls on microbial community composition in arid and semiarid soils (Angel et al. 2013; Wang et al. 2013; Steven et al. 2014), with effects being more pronounced in arid soils compared to semiarid (Ben-David et al. 2011). Plant roots create local environments that are enriched in organic C and N (Orlando et al. 2012), have improved water-holding capacity (Wang et al. 2013), and support increased microbial biomass (Marasco et al. 2012; Wang et al. 2013), including the obligate plant host for symbiotic fungi (Martinez-Garcia et al. 2011). These islands of fertility have significantly greater function as indicated by greater rates of gaseous N losses and respiration (McCalley et al. 2011, Wang et al. 2013).

Rhizosphere dynamics link multiple complex plant processes—photosynthate translocation, rhizodeposition, root demography, and mycorrhizal associations—with equally complex soil biotic factors—root herbivory, biofilm development and maintenance, and micro- and mesofaunal interactions. Further complicating our understanding of these interacting processes is the sensitivity of each of these processes to abiotic factors, including temperature, soil water, and atmospheric CO_2. Several exciting developments in rhizosphere research have shown that the microbial communities that develop around root-soil interfaces inhabit biofilms, the extracellular polymeric substance matrix typical of benthic microbial habitat everywhere, and that these biofilms mediate mineral-microbe-root chemical exchanges (Balogh-Brunstad et al. 2008) and create resilient microenvironments suitable for maintaining microbial life and sustaining terrestrial ecosystems (Schimel et al. 2007). Production by microbes within biofilms and the associated roots of higher plants can determine soil C accumulation, local pH, and rates of C and N transfer between roots and soil organisms. The development of mycorrhizospheric biofilms, by microbial and plant production of extracellular polymeric substances (EPS) and manipulation of biofilm chemistry, creates a microenvironment where microbial metabolism is buffered from extremes in soil conditions during drying and wetting.

4.2.2.4 Carbon Dynamics

The physical properties of soils exert strong controls on the soil C cycle. Soil structure created by aggregation of physical particles and organic matter increases C storage at fine scales. Greater concentrations of soil organic C are observed in soil aggregates (Wiesmeier et al. 2012; Fernandez-Ugalde et al. 2014) because

aggregation decreases the surface area per unit mass of soil increasing physical protection of soil organic matter from decomposition. This stabilization of organic C is enhanced in calcareous soils typical of many arid rangelands because the deposition of calcite crystals can decrease the overall porosity of the aggregates (Fernandez-Ugalde et al. 2014). A comparison of the C mineralization rates between soil cores with intact aggregates and those with aggregates disrupted by sieving revealed that removal of structure increased decomposition and subsequent respiration of soil C from 11- to 16-fold (Norton et al. 2012).

At broader scales, community structure in ecosystems with bunchgrasses or shrubs can create resource islands under the canopies of dominant plant species. Microbial biomass and resulting biological activity are enhanced in these areas compared to plant interspaces because of greater organic matter inputs from above- and belowground plant litter (Bolton et al. 1993; Smith et al. 1994). Resource islands can have twice the total soil C and over five times the detectable microorganisms as soils located between plant canopies (Bolton et al. 1993) resulting in much greater respiration rates (Bolton et al. 1993; Smith et al. 1994; Wang et al. 2013).

Small changes in the timing and quantity of precipitation can significantly alter the C cycle in arid systems. Additions of 2–5 mm of precipitation each week can increase soil respiration as much as 50 % (Lai et al. 2013). Changes in the seasonal timing of precipitation can also be critical. Water additions during the dry season can greatly increase microbial activity and respiration demonstrating that soil organisms are able to respond rapidly to pulses to soil water, but similar treatments during the moist season had little effect (Song et al. 2012). However, more frequent but smaller events can have detrimental effects on soil organisms. Small events can immediately increase microbial activity and respiration, but short-term increases in soil water do not persist long enough to stimulate photosynthesis in autotrophic organisms such as cyanobacteria. This leads to carbon deficits and long-term declines in their population size (Johnson et al. 2012).

Of particular interest in rangeland ecosystems is the influence of drying and wetting soils on CO_2 fluxes. Soil scientists have documented that drying soils reduces microbial activity and rewetting soils rapidly increases respiration rates (Birch 1958; Miller et al. 2005; Borken and Matzner 2009). When a dry soil was rewetted, CO_2 production could be elevated by up to 500 % over soils continuously moist (Fierer and Schimel 2002). This "Birch effect" can result in much higher respiration-related soil C loss than in soils that have not experienced soil water pulses. There is abundant discussion about the mechanism responsible for the Birch effect (Placella et al. 2012), and hypotheses include accumulation of solutes in microbial cells during drying that are rapidly mineralized during rewetting (Harris 1981), hydration, lysis, and mineralization of dead microbial cells (Schimel et al. 2007), and an increase in the availability of nonmicrobial substrates (Unger et al. 2012), exoenzyme activity (Moorhead and Sinsabaugh 2000), or physical release of CO_2 from carbonates (Billings et al. 2004). A recent study (Blazewicz et al. 2014) provides insight by combining DNA stable isotope probing and measures of soil CO_2 fluxes. CO_2 production increased significantly within 3 h of a water pulse, but this was not accompanied by significant microbial growth. Total microbial abundance did not

change significantly in the 7 days post-pulse, but substantial turnover of ~50 % was observed for both bacteria and fungi. The authors suggest that cell death that occurs during dry-down periods or during rapid changes in water potential associated with pulses generates a pool of labile C that likely contributes to the large CO_2 fluxes observed following precipitation pulses.

4.2.2.5   Nitrogen Dynamics

The relative importance of processes within the N cycle is highly variable as a function of precipitation, plant species and phenology, and disturbance regime. The soil N cycle in more xeric sites is very "open" characterized by relatively rapid fluxes into and out of the soil (Peterjohn and Schlesinger 1990). The primary eco-system input of N is N_2 fixation by biological soil crusts (Evans and Ehleringer 1993) and much of this is leached into soils in organic and inorganic forms (Johnson et al. 2005, 2007). Rates of gaseous loss from volatilization, nitrification, and deni-trification are of comparable magnitude, leading to very slow accumulation of organic N over time. Retention and internal cycling of N increase in importance with increasing precipitation. For example, nitrogen-use efficiency of plants increased along a water gradient in North America resulting in greater plant bio-mass in spite of similar rates of N mineralization (McCulley et al. 2009). Decomposition rates and release of N from litter decreased with increasing precipi-tation, resulting in larger N pools, but also greater N limitations to plants, on the mesic end of the gradient.

While average precipitation patterns can have strong impacts on nutrient dynam-ics, rangelands are also characterized by strong seasonal variations in precipitation, often with distinct wet and dry seasons, and sometimes frequent dry-wet pulses (Austin et al. 2004; Borken and Matzner 2009). During dry periods, soil microbial activity may be low, but inorganic N tends to accumulate through slow mineraliza-tion rates, and low diffusion and plant uptake (Evans and Burke 2013). Nitrogen uptake may also be facilitated during these dry periods by hydraulic lift that pro-motes mineralization even when surface soils are dry (Cardon et al. 2013). When soils rewet during a rainfall event, there tends to be a spike in N availability. The wetting up of dry soils stimulates a short-term spike in C and N mineralization through the disruption of soil aggregates (releasing physically protected soil organic matter), through lysis of microbial cells, and through microbial release of solutes to prevent them from bursting due to wet up. The size and duration of this flush of mineralization vary depending on soils and rainfall patterns, temperatures, and whether soils are hydrophobic or not (Borken and Matzner 2009; Morillas et al. 2013). Pulses tend to be higher in fine-textured soils, due to their higher C and N contents (Austin et al. 2004). Frequent wet-dry pulses often lead to lower pulses of mineralization, due to the depletion of labile soil organic matter over time. While the rates of N and C mineralization spike during these rewetting periods, cumula-tively, mineralization rates are usually higher on continuously wet soils than on dry soils during these wet-dry cycles, due to low rates during the dry periods (Borken

Fig. 4.4   Native (*left*) and invaded (*right*) grasslands on the Colorado Plateau. Cheatgrass (*Bromus tectorum*) invasion shades biological soil crusts located in plant interspaces and greatly increases aboveground litter biomass (photographs by R.D. Evans)

and Matzner 2009). These wet-dry cycles can also lead to high losses of N through leaching and trace gases, particularly since the wet-dry cycles stimulate N mineralization to a greater extent than C.

Changes in species composition as modified by local environment also impact soil N dynamics. This is exemplified by the contrasting impacts of invasion by the exotic annual cheatgrass (*Bromus tectorum* L.). In the Colorado Plateau of North America, cheatgrass invasion has established a series of positive feedbacks among biological soil crust disturbance, fire frequency, and cheatgrass abundance (Fig. 4.4), all of which result in declines in total and available soil N (Evans et al. 2001b). In this scenario cheatgrass shades autotrophic organisms within the biological soil crust decreasing N_2 fixation, which also favors cheatgrass establishment. Ecosystem N also accumulates in aboveground litter where it is not available for mineralization within the soil (Sperry et al. 2006), decreasing inorganic N availability. Subsequent range fires volatilized N within the litter, further decreasing soil fertility (Evans et al. 2001b; Sperry et al. 2006). In contrast, other studies from the Great Basin of North America (Booth et al. 2003) have observed greater total N, gross mineralization, and gross nitrification under cheatgrass than in neighboring native communities where differences in microenvironment promote greater mass loss of litter and N mineralization under cheatgrass. Nitrifier populations were also greater in invaded communities, and ultimately these differences in microenvironment and soil properties promoted greater N availability under cheatgrass compared to native communities.

Disturbance history can also influence soil N dynamics, especially in ecosystems that have evolved in the absence of large herbivores such as the Intermountain West of North America (Mack and Thompson 1982). In such cases, surface disturbance can disrupt the biological soil crust, greatly decreasing N_2 fixation. Gaseous loss continues, causing overall N loss from the ecosystem and decreases in soil fertility (Evans and Belnap 1999). For example, disturbed sites that had been allowed to recover 30 years still had total soil N content and potential N mineralization rates that were 30% and 70% lower, respectively, than adjacent undisturbed locations. This presents an interesting contrast on anthropogenic effects on the N cycle, because surface disturbance can decrease soil fertility across many rangelands,

while a majority of terrestrial ecosystems are impacted by N deposition leading to N excess (Pardo et al. 2011). Grazing can have: no effect, enhance, or decrease N recycling rates in more mesic rangelands, depending on the conditions. In general, on high-fertility soils, grazing enhances recycling rates. However, under low-fertility conditions, livestock preferentially graze high-quality plants, selecting for unpalatable plants which decrease nutrient recycling rates (Bardgett and Wardle 2003). Similarly, grazing on low-fertility soils can decrease aboveground plant production, especially during drought (Augustine and McNaughton 2006). However, the impacts of grazing can vary due to the interactions of soil fertility and precipitation. In low-rainfall conditions, grazers reduce aboveground net primary production, regardless of soil fertility. However in wetter conditions, grazing increases aboveground net primary production on high-fertility soils, but decreases it in low-fertility soils (Augustine and McNaughton 2006).

4.3   Anthropogenic Impacts and Societal Implications

4.3.1   Responses to Land-Use Change

Grazing effects on soil characteristics have been a dominant area of research in rangeland ecology. The key responses most often measured include changes in soil organic matter (McSherry and Ritchie 2013), N transformations (Anderson et al. 2006; Ingram et al. 2008), and soil texture, with its impacts on infiltration and water-holding capacity (Zhao et al. 2007, 2010). A challenge in synthesizing the impacts of grazing on soils is the extreme variability in environmental conditions and grazing practices in rangelands. As a consequence, many reviews have concluded that grazing has mixed results (Milchunas and Lauenroth 1993; Derner et al. 2006) on key soil attributes. However, with the accumulation of additional studies and novel meta-analytical tools, there is a clearer understanding of how environmental variability may interact with grazing practices to produce predictable outcomes in soil processes. For example, there is an interaction between soil texture and precipitation in determining the effect of grazing on soil C (McSherry and Ritchie 2013). On fine-textured soils, as precipitation increases the effect of grazing decreases while over the same range in precipitation, coarse-textured soils had an increase in the grazer effects on soil C. Increasing grazing intensity in rangelands dominated by plant communities utilizing C4 or mixed C4–C3 photosynthetic pathways increased soil C, while increasing grazing intensity in C3-dominant communities decreased soil C. While it is challenging to recognize context-specific grazing effects on soil processes, we are moving into a period where we can begin to predict specific effects due to grazing.

For many rangeland soils, soil loss is driven by surface disturbance of physical and biological soil crusts (Belnap et al. 2014). Dust production is best understood as the interacting processes that control the entrainment, transport, and deposition of wind-borne sediments (Chepil 1951, 1953; Ravi et al. 2011). Initially, wind erosion

research was motivated by a desire to understand the geomorphic and erosion processes associated with agriculture (Chepil 1951, 1953). In the past two decades, this research has been reinvigorated as it has become clear that airborne sediments strongly influence soil fertility, planetary energy balance (Goudie and Middleton 2001; Goudie 2008; Ravi et al. 2011), snow surface albedo, and thus melt rates on downwind mountain snowpack (Painter et al. 2010, 2012a, b). Drylands around the world are considered to naturally generate large amounts of sediment; many studies show that this is generally not true unless soil surfaces are disturbed (Belnap et al. 2014). Instead, most undisturbed soil surfaces, unless they are barren sand dunes or soils consisting of mostly fine sands, have some form of protective surface, whether physical crusts, biocrusts, rocks, or plant cover. However, almost all these protective covers are highly vulnerable to the forces associated with vehicle and animal traffic. Once disturbed, protective crusts are unable to stabilize soil surfaces. Surface disturbance due to animal traffic, off-road vehicle use, or other processes causes sediment generation to increase dramatically at most sites (Warren et al. 2001). As high winds commonly occur in rangeland regions, this destabilization often results in large dust storms originating from once stable areas. While there are some common predictors of sediment emission globally (e.g., silt content), other biophysical factors such as biocrust biomass and rock content are more important at the site scale. Soil surface disturbances are expected to increase in dryland regions, given the increasing demand for energy, minerals, recreational opportunities, and food production. With this disturbance, aeolian erosion is also expected to increase from the disturbed soils.

4.3.2 Responses to Invasive Species

Invasive, non-native plant species have become one of the most pressing rangeland management issues (Fig. 4.5). In the western USA, 51 million hectares of rangeland are now dominated by invasive plants considered to be noxious weeds (Duncan and Clark 2005), including diverse life forms such as annual and perennial grasses, annual and perennial forbs, shrubs, and trees. In over 2/3 of western rangelands, non-native annual grasses account for 50–85 % of vascular plant cover (DiTomaso 2000; Chapter 13, this volume). Invasions by exotic species are altering the structure and function of soils, including water availability and flow, C storage, nutrient availability, erosion rates, soil microbial communities, and disturbance regimes (Eviner et al. 2012; Eviner and Hawkes 2012).

   While invasive plants have the potential to strongly impact soil, the specific impacts of any invasion strongly depend on environmental conditions and the unique functional traits of the invasive compared to native species. For example, the invasion of medusa head wildrye (*Taeniatherum caput-medusae* (L.) Neviski) into western US rangelands is associated with loss of soil C (Eviner and Hawkes 2012). In contrast, in New Zealand, the exotic mouse-eared hawkweed (*Hieracium pilosella* L.) increases soil organic matter and productivity in overgrazed pastures, but

Fig. 4.5 Senesced (background) grasses are naturalized annual species in California's rangelands. Medusa head and goatgrass are present in the foreground, and both are invasive noxious weeds (photograph by V. Eviner)

this effect depends on grazing intensity and aspect (Scott et al. 2001). Invasive species may enhance N availability through increases in decomposition and N mineralization rates (Ehrenfeld 2003; Corbin and D'Antonio 2004; Liao et al. 2008), although some invasive species decrease N availability, such as goatgrass (*Aegilops triuncialis*) into grasslands of California, USA (Drenovsky and Batten 2007), and crested wheatgrass (*Agropyron cristatum* L.) into the northern Great Plains of the USA (Christian and Wilson 1999). The effects of cheatgrass and spotted knapweed (*Centaurea maculosa*) on soil N vary with local soil and climate conditions, with different studies showing an increase, decrease, or no change (Eviner and Hawkes 2012). Even when invaders don't alter the total amount of soil resources, they can change the timing, location, and type of resource availability, restricting which plant species have access to these resources. For example, replacement of native perennial species by the annual cheatgrass alters the timing of soil N availability, with high N availability occurring after its senescence because perennials are not present to assimilate inorganic N released during decomposition of cheatgrass litter (Adair and Burke 2010). Subsequent leaching in the absence of active plant cover redistributes soil nitrate deep in the soil profile. Cheatgrass is a winter annual, while native grasses resume activity in spring; so root growth by cheatgrass during winter and early spring allows it to assimilate this leached nitrogen pool before native grasses are active later in spring. This enhances cheatgrass growth at the expense of the native grasses (Sperry et al. 2006). Invasive plants also can alter the form of N available. For example, in California grasslands, USA, invasive grasses increase the soil bacterial nitrifier populations responsible for nitrification (Hawkes et al. 2005). Conversely, the invasion of gamba grass (*Andropogon gayanus*) into Australian grasslands inhibits nitrification (Rossiter-Rachor et al. 2009). Changes in the form

of available N can alter competition between species (Marschner 1986; Crabtree and Bazzaz 1993). The largest impacts of invasive plants on soils can be mediated through changes in disturbance regimes. For example, invasion of cheatgrass and medusa head can greatly increase fire frequency, which greatly increases potential loss of soil C and N. Soil nutrient availability may briefly spike after disturbances, stimulating reestablishment of invaders (Eviner et al. 2012; Eviner and Hawkes 2012). Increased fire frequency in response to annual grass invasion can also lead to higher erosion rates after fire, leading to potential desertification of rangelands (Ravi et al. 2009).

Many invasive species alter soil in ways that shift competitive balance from native to non-native species resulting in "invasional meltdown" (Simberloff and Von Holle 1999). For example, changes in the soil environment caused by the invasion of cheatgrass favor medusa head, and further modification of soils favors exotic forbs (Eviner et al. 2012). Similarly, changes in the soil microbial community caused by smooth brome (*Bromus inermis*) can favor the establishment of the invader leafy spurge (*Euphorbia esula*) (Jordan et al. 2008). Controlling the positive soil feedbacks of invaders requires a specific understanding of the mechanism of feedback, which can vary greatly by species, and even within a species across sites (Eviner and Hawkes 2012). Early eradication is critical, as the strength of soil feedbacks tends to increase with time since invasion. For example, extensive erosion as a result of invasion of spotted knapweed (*Centaurea maculosa*) (Lacey et al. 1989) can take decades to centuries to reverse via soil formation processes and the gradual buildup of organic matter by the restored plant community.

4.3.3   Responses to Global Climate Change

4.3.3.1   Precipitation Change

Climate is a major controlling factor over ecosystem structure and function and changes in the frequency and intensity of drought caused by anthropogenic activity are the most likely to negatively impact rangeland ecosystem processes. Drought restricts biological activity, primary production, timing of plant growth, patterns of mortality, organic matter dynamics, and nutrient availability (Borken and Matzner 2009; Evans and Burke 2013; DeMalach et al. 2014). For example, extended drought produced region-wide tree mortality in the southwestern USA (Breshears et al. 2005). There have been a number of studies that evaluate two critical elements of precipitation change: (1) the timing of precipitation, independent of total amount, and (2) changes in the amount of precipitation.

While soil water is a principal driver of soil processes in rangelands, it is very likely that precipitation change will interact strongly with rising temperatures—particularly extreme heat waves. One of the most promising advances in understanding rangeland soil responses to climate change is the addition of factorial experiments that look at the individual and combined effects of various climate change factors. Relatively modest

changes in soil water content can produce much larger changes in ecosystem processes, including soil CO_2 efflux (Fay et al. 2011). A 15 % decrease in soil water that accompanied precipitation variability treatments caused measured responses to decrease by up to 40 %. In addition to modifying precipitation timing, year-round warming can cause a change in plant phenology and shift the seasonality of microbial activity with higher winter soil CO_2 flux and lower summer soil CO_2 flux. While the effects of changing precipitation variability and warming were modest compared to large between year variability, they are likely ecologically significant. While this experiment altered mean patterns, additional studies have begun looking at extreme events including the interactions between extreme drought and heat waves and found that even extreme warming had only modest effects on plant production and community composition and that the majority of observed changes were driven by soil water effects. In addition, drought and precipitation variability could impact ecosystem function. Drought has a greater impact when it occurs in the wettest portion of the year when organisms are most active, in contrast to typical seasonally dry periods. In addition, heat waves and droughts late in the growing season had no significant effects on ecosystem dynamics.

4.3.3.2   Elevated CO_2

Arid and semiarid soils are critical components of the Earth's C budget (Evans et al. 2014; Poulter et al. 2014). Recent increases in atmospheric [CO_2] are unprecedented as emissions have accelerated from 1 % year^{-1} from 1990 to 1999 to 2.5 % year^{-1} from 2000 to 2009 (Friedlingstein et al. 2010). The increase in atmospheric [CO_2] has the potential to dramatically alter the biogeochemistry of rangeland soils. The direct effects of increasing [CO_2] on soils are negligible because soil [CO_2] greatly exceeds that of the atmosphere (Drigo et al. 2008); however, increases in atmospheric [CO_2] can indirectly impact soil elemental cycles by altering the amount and chemical composition of organic matter inputs in the form of above- and belowground plant litter, rhizodeposition, and mycorrhizal associations. Carbon dioxide is also the dominant greenhouse gas influencing climate, so increases in atmospheric [CO_2] impact ecosystem function through changes in ambient temperatures.

Early studies demonstrated that elevated [CO_2] could increase rates of C assimilation and decrease stomatal conductance, causing increased water-use efficiency (Nowak et al. 2004; Chapter 7, this volume). This led to predictions that water-limited ecosystems, including many rangelands, would be most responsive to future atmospheric conditions. A conceptual model was proposed (Strain and Bazzaz 1983) that predicted that the magnitude of ecosystem responses to elevated [CO_2] was controlled by water and N availability. Ecosystems with sufficient water, or where N was limiting, would see limited response to elevated [CO_2]. In contrast, water-limited ecosystems with sufficient N would exhibit the greatest responses. It has since been recognized that N limitations to net ecosystem productivity can increase over time with increased exposure to elevated [CO_2] as organic matter is sequestered into recalcitrant materials such as woody biomass and soil pools with slow turnover (Gill et al. 2002), a process termed progressive nitrogen limitation (Luo et al. 2004).

Fig. 4.6 The Prairie Heating and CO_2 Enrichment (PHACE) study located manipulated temperature and CO_2 concentration in C3–C4 shortgrass steppe. Warming was controlled by infrared heaters at the top of each plot, while CO_2 was controlled by emitting gas from the ring at the bottom of the plot (photograph by Sam Cox, (former) USDA-ARS Biological Science Technician, (now) Natural Resource Specialist with Wyoming BLM)

Results from long-term elevated [CO_2] experiments in rangelands demonstrate complex responses to elevated [CO_2] especially in those studies that consider multiple environmental drivers. Three experiments in North American rangelands occur along a precipitation gradient from 134 mm year^{-1} for the Nevada Desert FACE Facility (NDFF) and 384 mm year^{-1} for the Prairie Heating and CO_2 Enrichment (PHACE) in the C3–C4 shortgrass steppe (Fig. 4.6) to 914 year^{-1} mm at the site of two experiments in the C3–C4 tallgrass prairie (Fig. 4.7). Biogeochemical cycling at the xeric end of the precipitation gradient is characterized by C limitations to microbial activity and very open C and N cycles, so significant increases in ecosystem C and N were observed over the life of the experiment (Evans et al. 2014). Greater soil C under elevated CO_2 resulted from death of enhanced plant growth that occurred during periods of adequate soil water that could not be supported during intervening drought, and significantly greater rhizodeposition (Jin and Evans 2010). Progressive N limitation has yet to be observed as increased C has accelerated rates of N transformations increasing gross N mineralization and organism N availability (Billings et al. 2004; Jin et al. 2011). Nutrient availability was further enhanced by increases in microbial diversity and abundance (Jin and Evans 2010), especially for fungi that are able to utilize the recalcitrant C and N that dominate these soils (Billings et al. 2004). Elevated [CO_2] also increased retention of N within the soil by promoting microbial immobilization of N and decreasing rates of gaseous N loss (Schaeffer et al. 2003; McCalley and Sparks 2008, 2009).

Fig. 4.7 The CO_2 concentration-gradient study in the tall-grass steppe. Air with an elevated CO_2 concentration simulating future conditions is introduced at one end and the concentration decreases through photosynthesis as it moves through the tunnel. This allows scientists to examine plant and soil responses ranging from preindustrial to expected levels in 2050 in the same experiment. The experimental infrastructure also allows manipulation of other variables such as soil type (photograph by F.A. Fay)

Similar results were observed in open top chamber (OTC) experiments in the shortgrass steppe. Elevated $[CO_2]$ stimulated above- and belowground production and increased rhizodeposition almost 100 % (Pendall et al. 2004). Results also suggest that available soil N remained high during the 5-year experiment presumably due to increased soil water promoting more rapid N mineralization (Dijkstra et al. 2008). No differences were observed in gaseous N loss (Mosier et al. 2002). Research on elevated $[CO_2]$ in the shortgrass steppe was subsequently expanded to include effects of warming through the PHACE experiment, and $[CO_2]$ and warming produced contrasting effects on soil processes. In contrast to earlier studies, elevated $[CO_2]$ resulted in a more closed N cycle by promoting microbial immobilization of N, decreasing soil inorganic N availability (Dijkstra et al. 2010; Carrillo et al. 2012). In contrast, warming enhanced inorganic N presumably because of greater rates of decomposition. Similar results have been observed for grasslands in Australia, where elevated $[CO_2]$ decreased available soil N, but warming of 2 °C plus elevated $[CO_2]$ prevented this effect (Hovenden et al. 2008). Results from PHACE also suggest that the interacting effects of warming and elevated CO_2 may decrease ecosystem C storage (Pendall et al. 2013). Microbes from the combined warming–elevated $[CO_2]$ treatments exhibited greater decomposition activity than other treatments suggesting greater rates of decomposition and C loss, a conclusion supported by direct measurements of soil C efflux (Pendall et al. 2013).

Two experiments at the most mesic end of the precipitation gradient strongly support progressive N limitation under elevated CO_2. In the first, intact C3–C4 grasslands were exposed to a gradient in $[CO_2]$ from 200 to 560 μmol CO_2 mol^{-1} (Gill et al. 2002; Gill et al. 2006). A threefold decrease in N availability was observed with increasing $[CO_2]$ (Gill et al. 2002) and N transferred from soil organic matter to plant pools (Gill et al. 2006). Similarly, transfer of soil C from recalcitrant to labile pools was observed resulting in greater C loss through respiration with increasing $[CO_2]$. Greater respiration was offset by enhanced NPP at higher $[CO_2]$ resulting in no change in the overall C balance, but future C sequestration may be limited by progressive N limitations. This experiment was followed by the establishment of the lysimeter CO_2 gradient study using the same gradient in $[CO_2]$ but incorporating three soil treatments. Results from this study strongly emphasize the importance of soil type in controlling responses to drivers of global change. For example, elevated $[CO_2]$ favored forbs over grasses on only one of the three soil types (Fay et al. 2012; Polley et al. 2012). Similar responses were observed for soils where elevated $[CO_2]$ enhanced soil water availability on only two of the three soil types (Fay et al. 2012). In contrast to earlier research, no changes were observed in soil N availability with increasing $[CO_2]$ across all soil types.

4.3.3.3 Atmospheric Deposition

Ecosystems affected by atmospheric deposition are often located downwind of large urban centers, near point emission sources, or in regions with a mix of urban and agricultural emission sources (Fenn et al. 2003a, b). Background rates of atmospheric deposition are generally less than 3 kg N ha^{-1} year^{-1}, but can approach and may even exceed 30 kg N ha^{-1} year^{-1} in the most heavily impacted areas (Fenn et al. 2003b). Research addressing the effects of atmospheric deposition on rangeland soils is rare compared to forest and aquatic ecosystems (Pardo et al. 2011). Assessing the regional importance is difficult because accurate sampling networks for wet and dry deposition are either widely separated or absent in most rangelands around the globe, and when studies do occur they often focus on plant or aquatic species rather than soils.

Attempting to extrapolate the effects of atmospheric deposition from many fertilization studies can be misleading. The major effects of elevated atmospheric deposition result from long-term, chronic addition of low amounts of N. Most fertilization studies apply N in one or a few applications that may overwhelm the assimilation capacity of plants and microbial populations, leading to artificially high rates of leaching and gaseous loss from the soil. Application rates can also greatly exceed rates of deposition observed even in the most impacted areas. Atmospheric deposition in most rangelands is still less than 10 kg N ha^{-1} year^{-1}, and rates exceeding 20 kg N ha^{-1} year^{-1} are found only in ecosystems adjacent to heavily industrialized areas. Critical loads for most ecosystem components are less than 10 kg N ha^{-1} year^{-1} (Pardo et al. 2011); thus application rates in excess of 30–40 kg N ha^{-1} year^{-1} have minimal value when attempting to understand or predict

ecosystem responses to atmospheric deposition. Finally, experiments must not only apply realistic amounts spread throughout the year, but must also match the form of deposition most common in that region because oxidized and reduced forms can have very different effects on soil processes.

It is for these reasons that the best studies of the effects of atmospheric deposition are most often those that occur in currently impacted areas. Even here the responses are complex due to interactions between the form and amount of N deposition and their interaction with local soils making generalizations difficult (Greaver et al. 2012). A common observation is that increased atmospheric deposition relieves N limitations to growth and activity by plants and soil organisms (Aber et al. 1989). Initial increases in net primary production are often observed in N-limited soils. Further deposition can exceed rates of plant assimilation leading to increases in nitrification, denitrification, and emissions of greenhouse gases such as NO and N_2O (Fenn et al. 1996, 2003b; Templer et al. 2012). Chronic, high rates of atmospheric deposition may ultimately lead to significant leaching of nitrate from soils into surrounding aquatic ecosystems and groundwater, decreases in base saturation, acidification of soils, and cation limitations to plant and microbial activity (Aber et al. 1989). N deposition can greatly alter plant species composition, particularly promoting invasive species.

4.3.4 Restoration

Rangelands are extremely variable and multiple stable states may exist depending on precipitation patterns, grazing, fire, and land use (Campbell et al. 1997; Reynolds et al. 2007) (Chapter 6, this volume), but functioning soils are the key to resilience under these varying conditions (Briske et al. 2006). Soil functions that are critical for rangeland resilience include infiltration, water storage, erosion control, soil fertility, and net primary production (MEA 2005; Briske et al. 2006), and their degradation can limit restoration of productive communities and the ecosystem services they provide (Bestelmeyer et al. 2003; MEA 2005; Seymour et al. 2010; Li et al. 2013). The key factor to maintaining soil resilience is vegetation cover. This can be disrupted through overgrazing, fire suppression, and drought that may contribute to state shifts from grassland to shrublands, which often increases bare ground and erosion.

Degradation due to soil erosion can be difficult, if not impossible, to reverse (Li et al. 2013), so the best management options are those that prevent it from occurring. Grazing practices to maintain plant cover are the key to preventing erosion (Pulido-Fernandez et al. 2013), with low-to-moderate grazing intensities, and seasonal grazing tending to have minor impacts on soils, while continuous intensive grazing can deplete C and N and degrade soil structure (Kotze et al. 2013; Xu et al. 2014). Grassland productivity can often be maintained by leaving critical levels of plant biomass as residual dry matter. The amounts of residual biomass vary depending on slope and precipitation (Bartolome et al. 2007; Xu et al. 2014), but managing

for this target can be difficult due to fluctuations in precipitation, and thus livestock-carrying capacity (Kiage 2013). Restoration of degraded soils often requires cessation of grazing during the recovery period.

4.4   Future Perspectives

The development and application of molecular tools are revolutionizing disciplines within the life sciences. This is especially apparent in soils, where microorganisms are responsible for a majority of the biological activity, but available technologies caused them to be treated as a black box termed "microbial biomass." Recent advances now allow for descriptions of microbial diversity and community structure, and continued development of high-throughput sequencing and metagenomics approaches permits discovery of new organisms and large-scale comparisons across diverse ecosystems (Zak et al. 2006; Weber et al. 2011; Dunbar et al. 2012). Stable isotope probing, where substrates with distinct isotope composition are assimilated by organisms that are later identified using DNA (Zak et al. 2006) or cell wall profiles (Jin and Evans 2010), now has the potential to directly link functional groups of organisms with their biogeochemical function. Quantifying functional genes that encode specific enzymes also allows grouping of organisms into functional groups focused on specific processes (Zak et al. 2006).

Efforts are also under way to describe the functional state of rangeland soil microbial communities using proteomics, the study of protein structure and function (Bastida et al. 2014). Proteomic profiling is potentially very powerful for soil ecology, as the proteome encompasses the overall metabolism of the system, and the cellular machinery that is poised to respond to new conditions. Key functions identified in this study included dehydrogenases, catalases, and superoxide dismutases. The presence of a large number of carboxysome proteins and other C fixation proteins (phycocyanins) in highly degraded, low-C soils suggests that there is large capacity for C fixation that is not favored for environmental reasons such as substrate availability or microbial vigor (Bastida et al. 2014). As proteomic analyses of soils continue to develop, new knowledge of how local conditions regulate soil metabolism is likely to emerge.

Technological advances are not confined to soil microbiology; development of new microelectronics, digital computation, and networking has created a data deluge in rangeland ecology. These new sensors are facilitating our understanding of water fluxes (Reeves and Smith 1992; Paige and Keefer 2008; Flerchinger and Seyfried 2014), soil electrical connectivity, plant and soil microenvironments, incoming radiation amount and quality, and soil CO_2 fluxes (Kao et al. 2012; Taylor and Loescher 2013; Loescher et al. 2014). Rangeland ecologists are now able to monitor microclimate with high spatial and temporal resolution with better precision at costs well below standard prices in past decades. Capacitance and time domain reflectometry measurements of soil water have become commonplace in many rangeland studies, allowing for direct connections between soil water

availability and ecological processes. One of the key attributes of the new National Ecological Observatory Network in the USA is the high level of sensor integration into a continental-scale research network (Kao et al. 2012; Taylor and Loescher 2013; Loescher et al. 2014) that offers the potential to ask complex, landscape-scale ecological questions using wireless sensor networks (Simoni et al. 2011; Kerkez et al. 2012; Rosenbaum et al. 2012; Chaiwatpongsakorn et al. 2014). With the promise of a future of inexpensive, spatially and temporally expansive data comes the challenges of managing, integrating, analyzing, and interpreting these data.

Fortunately for soil biologists, many of the challenges that come in a data-rich science have been addressed by bioinformaticians trained to apply computational techniques to analyze information tied to biomolecules, including genomics, gene expression, structural biology, and other molecular applications. Environmental research is quickly requiring the same informatics tools to deal with sensor data (Michener and Jones 2012; Porter et al. 2012) leading to the new field of ecological informatics (Suri et al. 2006; Michener et al. 2007; Michener and Jones 2012).

4.5   Summary

The past 25 years have seen increased emphasis on understanding soil function and sustainability in rangelands, and their significance in global biogeochemical cycles. Research demonstrates that rangelands are extremely diverse and future studies should strive to further develop common unifying principles. It is also apparent that paradigms developed in more mesic ecosystems may not be applicable in rangelands because of their extreme environments and inherently low and often stochastic resource availability. Plant community composition is a major driver of soil function. Grazing can cause shifts to species with lower nutrient content, higher concentrations of defense compounds, or more woody vegetation, lowering nutrient availability and impacting soil water dynamics. Increased emphasis is also being placed on nonvascular components of the rangeland ecosystems. Biological soil crusts are common on surface soils of ecosystems with less than 100 % plant coverage. Soils crusts enhance soil stability and can be the dominant source of N through nitrogen fixation. Recent results demonstrate that N assimilated by crusts is subsequently leached into soils making it available for uptake by plants and soil microbes. Growth of molecular tools with high throughput has greatly expanded our understanding of the diversity and community composition of the archaea, fungi, and bacteria responsible for most transformations within soils. Combining molecular approaches with other techniques has allowed scientists to increasingly link composition and function in soils, thereby shedding light on what was formerly viewed as the black box of microbial dynamics in soils.

Decomposition is a major driver of nutrient availability in all ecosystems. Unlike more mesic ecosystems, photodegradation caused by UV radiation can be a major determinant of rates of decomposition, especially in more arid rangelands. The rate of mixing of litter into soils is also important as this enhances inoculation by micro-

bial decomposers. Carbon and nutrients can also enter soils directly through rhizodeposition through plant roots and mycorrhizae. At small scales, the greatest soil C is associated with soil aggregates and significant amounts of soil C can be protected by soil structure. The unique patchiness of vegetation in many rangelands controls C dynamics at larger scales, and larger microbial populations, greater plant and microbial activity, and greater C fluxes are associated with the canopies of higher plants, rather than in plant interspaces. Soil nutrient cycles are controlled by precipitation, plant species, and disturbance regimes. Nutrient cycles in more xeric ecosystems are characterized as being very "open" with rates of input balanced by relatively equal rates of loss. In contrast, nutrient contents are greater with increasing precipitation, and cycling rates are more "closed" and characterized by internal cycling. Seasonal patterns of precipitation are also important and can lead to pulses of nutrient availability following rain events. Restoration efforts in rangelands must adapt to local conditions, but keys to maintaining soil condition and function are infiltration, water storage, erosion control, and maintaining soil C and nutrients.

Rangeland responses to land-use change are diverse matching their highly variable composition and associated grazing practices. Surface disturbance can increase soil loss in more xeric rangelands by disrupting the biological soil crusts. The impact of invasive plant species on rangeland soils can also be highly variable. For example, cheatgrass can increase, decrease, or not alter available nitrogen. Invasive species can also alter the timing, location, and type of resources available. One of the most profound responses of rangeland soils to changing atmospheric conditions is likely to be responses to the increase in the frequency and intensity of drought. Water is a primary driver of soil processes in rangelands and decreases in water availability can negatively impact microbial activity, nutrient availability, and subsequent plant growth. Of special concern is the interaction between drought and predicted increases in extreme temperatures, which will greatly exacerbate responses observed under drought alone. Precipitation regime will also determine ecosystem responses to increases in atmospheric CO_2. Experiments in more xeric ecosystems found that soil C and N cycling was energy limited and increasing [CO_2] enhanced nutrient availability and C storage. In contrast, additional C in more mesic ecosystems led to microbial sequestration of N and progressive N limitation over time. Although soils have received less recognition than vegetation or climate the knowledge summarized in this chapter demonstrates that they are essential to the resilience of rangeland ecosystems.

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