CLIMATE ACTIONS

LOCAL APPLICATIONS

AND PRACTICAL SOLUTIONS

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4 Climate Change in Grassland Ecosystems
Current Impacts and Potential Actions for a Sustainable Future

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4.1   BACKGROUND

4.1.1   Why Should We Care about Grasslands and the Impacts of Climate Change on Grassland Ecosystems?

For millions of years, humans have relied on grassland ecosystems for our survival – grasslands are globally ubiquitous and support agricultural livelihoods and the global food economy, provide forage for domesticated grazers, are cultivated for biofuels and fiber and are key regulators of global hydrological and biogeochemical cycling. Despite the vital services grasslands provide, they are often overlooked in favor of other, more charismatic ecosystems. Grasslands are often presumed to lack the beauty and visual grandeur of mountainous regions, or the rich history of old-growth forests. Compared with tropical forests, grasslands might appear to have lower bio-diversity or productivity. Grasslands are also typically presumed to lack the unique and fantastic physiological adaptations allowing organisms to survive in climatically extreme locations, as in the Arctic tundra or hot deserts in the subtropics. However, there are few ecosystems that provide as many critical services for human demands, or that have been as heavily impacted as grasslands.

As the climate changes, many of the key services provided by grassland ecosystems are threatened (Section 4.3). The importance of grasslands to human civilization might lead one to assume that assessing, forecasting and mitigating the consequences of climate change in grassland ecosystems would be of paramount interest. And yet, grasslands are typically among the last terrestrial ecosystems to rally conservation concern. Due to extensive global modification of grasslands, undisturbed or "natural" ecosystem states are uncommon. For this reason, it is impractical to assess how climate change impacts "undisturbed grasslands" because there are almost none of those areas remaining today. Thus, we must instead consider how climate change impacts grasslands in the context of disturbance – both natural disturbances, such as fire and periods of severe drought, and human-caused disturbances, such as habitat fragmentation and changes in land management.

Despite being highly modified for human use, grasslands are often resilient and responsive to management intervention. Grasslands can "bounce back" from small-scale or minor perturbations and return to pre-disturbance conditions (a response defined as high resilience). However, when modifications are severe in scope or continue for extended periods of time, grassland resilience is reduced and the likelihood

of persistence in permanent, degraded conditions is high. The threats to grasslands posed by climate change are extensive, interactive and harbor the potential to negatively and irreparably (in the context of human lifespans) alter the species present and services provided by these ecosystems. For these reasons, an assessment of climate change impacts and potential solutions to mitigate grassland ecosystem degradation are imperative.

4.1.2   THE SCOPE AND STRUCTURE OF GRASSLAND ECOSYSTEMS

Grasslands are typically defined as "open ecosystems" characterized by high cover of grasses and other grass-like plant species, including sedges and rushes (Bond, W. J., 2019). This is in direct contrast with "closed ecosystems," in which tree canopies have sufficient density to restrict light from reaching the ground surface, preventing the development of an herbaceous understory layer. While many grassland ecotypes receive sufficient annual rainfall to support tree growth and the development of a closed ecosystem, frequent disturbance in the form of climate variability (drought, flooding and extreme temperatures), fire and grazing by large mammalian herbivores maintains a stable, open ecosystem. This unique attribute of grasslands results in the restriction of the classical ecological concept of succession toward a "climax community" (Bond, W. J. 2019). Given that grasslands are old ecosystems that predate hominin evolution (Strömberg, C. A. 2011), the view that grasslands are part of an ecological continuum toward a forest ecosystem has been thoroughly debunked (Veldman et al. 2015). Instead, grasslands exist as a stable ecosystem state, unique from woodlands or forests so long as key ecosystem drivers are present (Staver et al. 2011).

Data were derived from the ESRI World Terrestrial Ecosystems package *https:// landscape12.arcgis.com/arcgis/rest/services/World_Terrestrial_Ecosystems/ ImageServer*

Current estimates classify 31–40% of terrestrial surface as grassland (36.7 million km^2; Gibson, D.J. & Newman J. A. 2019) (Figure 4.1). Grassland ecosystems occur on every continent except Antarctica– it is the largest biome (in terms of precolonial acreage) in Africa and North America (~3 million km^2 each) and comprises large regions of South America and northern Australia (Dixon et al. 2014). The species composition and physiognomic structure of grassland ecosystems varies biogeographically, often according to global gradients in aridity and temperature as well as the intensity of top-down drivers, including fire and herbivory (Bond 2019). Grasslands are associated with the vegetative dominance by grass species, and can often include high grass biomass production. Characteristic grassland ecosystems include the Patagonian and Mongolian steppes, Eurasian meadows and grasslands of the Great Plains region of North America. Grasslands can also commonly contain mosaics of other plant types, including forbs (herbaceous, non-grass species) and succulents, as well as trees and shrubs in varying distributions. Grassland ecotypes with a substantial woody layer include the open-savanna Cerrado of South America, the dry steppes of Eurasia and the tropical and semitropical savannas of Africa and Australia. Thus, despite an initial apparent simplicity ("it's just grass"), the types of plant species and their distributions can vary markedly across grassland types.
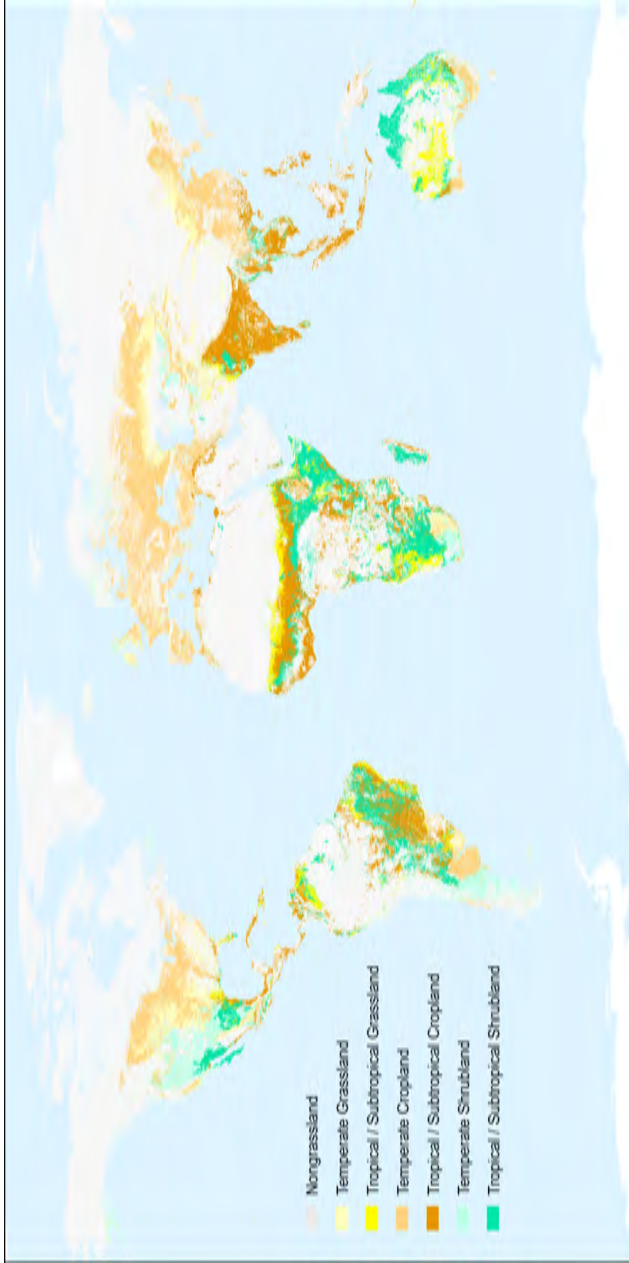
FIGURE 4.1   Global distribution of temperate and tropical grasslands, shrublands and croplands.

These dynamics can also be highly variable within a grassland ecotype. High plant species richness and diversity is a common characteristic of grasslands around the world (Knapp et al. 1998; Blair et al. 2014). Dominant grass species coexist with a wide range of forbs, sedges, wetland plants and woody species. In addition to this large variety of plant functional types, grasslands also contain a variety of plant life-forms – depending on the grassland ecosystem, climate and evolutionary history, some grasslands are characterized predominantly by annual species (Mediterranean grasslands and grasslands in California), while others are predominantly perennial (African savannas and North American prairies). In short, all grasslands have a mosaic of species with varying life history and morphological and physiological attributes (Knapp et al. 1998; Blair et al. 2014). However, this high species richness reported is somewhat paradoxically accompanied by high species dominance by a few grass species. This pattern of high dominance accompanied by high overall diversity likely reflects the local interplay of multiple interacting drivers – fire, grazing and climate. These dynamics create increased niche space and locations where competition for resources is very high (where a few species will rise to dominance) as well as locations where only species with specialized adaptations to low resource availability or frequent disturbance can persist. The legacies of grazing systems and fire also impact plant species richness and dominance. For example, while frequent fire alone promotes the production of a few dominant grass species, grazing by large mammals reduces dominant grass cover and promotes forb establishment, increasing grassland plant diversity (Hartnett et al. 1996).

The high rates of growth and production by grasses in grassland ecosystems may be attributable to their unique morphology and physiology. As noted earlier in this chapter, many grasslands experience frequent disturbance as well as wide swings in short-term weather and longer term climate conditions. One key adaptation that benefits grass species is the location of their basal meristems, which is the site of new growth. Grasses position their meristems just below the soil surface, protecting these vital tissues from disturbance. This is one of the primary reasons that frequent fires actually promote grass growth rather than suppress it. After fire removes the litter and aboveground biomass, the bare soil surface quickly warms and the high-light environment facilitates rapid growth of new grass tissue from the protected meristems. In turn, grass production during the growing season provides biomass that acts as fuel for subsequent fire. In this way, frequent disturbance effectively maintains these open, diverse, grass-dominated ecosystems (Blair et al. 2014).

4.1.3 Ecosystem Services Provided by Grasslands

Grasslands provide many key ecosystem services, defined as the direct or indirect benefits of healthy environments to humans and societies. The most obvious direct ecosystem service provided by grassland ecosystems is their key role in global food security. Conversion of grassland to cropland underlies modern agriculture, and the direct, positive benefits to humans by this conversion is obvious. However, roughly 70% of global grassland area and 50% of global savanna area have been converted to agricultural land (Ramankutty et al. 2008), and these conversions often result in a loss of most indirect grassland ecosystem services (see Section 4.3 for a more

detailed discussion of this topic). In addition to conversions to cropland, sustainable management of rangelands and grasslands provides pasture for domesticated live-stock and supports a grazing economy of US$63 billion/year in the United States alone (Allred et al. 2014). This ecosystem service benefits ranchers and pastoralists from diverse walks of life in both first and third world countries and takes place in nearly all grassland ecosystems worldwide.

Some of the primary indirect ecosystem services provided by grasslands include (1) sequestration of carbon (C) belowground; (2) regulation of the water cycle; and (3) provisioning of habitat for invertebrates (including pollinators), wildlife and humans. Grassland plant species typically allocate more biomass belowground than aboveground (Gibson 2009), and these dense root systems contribute to the development of soil organic C pools over time, effectively removing C from the atmosphere. Grassroot systems are also adept at maintaining soil structure and minimizing erosion during high-intensity rain events. Grassland plant species regulate the water cycling by minimizing runoff, facilitating water infiltration within the soil profile and ultimately recycling this moisture back to the atmosphere via transpiration. The varying physiognomy of grasslands, along with high plant species diversity, provides mosaics of habitat and benefits for a wide range of animal species. A key trait of many grassland ecosystems is the functional redundancy provided by similar species (e.g., different grass species providing similar ecological roles), which allows for a robust maintenance of these ecosystem services as populations of specific species increase and decrease in response to disturbance through time.

Climate change impacts these direct and indirect ecosystem services by threatening the unique characteristics of grassland ecosystems. One might presume that effective adaptation to disturbance – a key grassland trait – posits that grasslands should be highly buffered against alterations caused by climate change. Indeed, grasslands are well adapted to disturbance, but the changes associated with a warming climate are often interactive and are occurring faster than historical changes in climate (USGCRP 2018). When these changes result in alterations to grassland vegetative structure, they can result in degraded lands, shifts to alternative ecosystem states (woodland or forest) or loss of habitat to invasive species. In Section 4.2, we will explain the direct consequences of climate change on grassland ecosystems, including how increasing atmospheric CO_2 concentrations, increasing global temperatures and altered rainfall patterns impact the growth dynamics and competitive relationships among grassland species. In Section 4.3, we will discuss several indirect consequences of climate change, primarily due to interactions with changes in land-use or land-cover mediated by humans. Finally, in Section 4.4, we highlight many of the potential climate solutions that we can participate in now, which could provide both smaller and greater remedies to offset the negative consequences of climate change on one of Earth's greatest ecosystems.

4.2   DIRECT CLIMATE CHANGE IMPACTS

Natural changes in the Earth's climate have occurred on the scale of hundreds to millions of years throughout geologic time. This natural variability is influenced by

large-scale events, including predictable changes in the Earth's tilt and orbit around the sun (Milankovitch cycles), fluctuations in the intensity of solar radiation reaching the Earth, movement of tectonic plates and volcanic eruptions. Human activity, particularly the burning of fossil fuels since the onset of the Industrial Revolution, has resulted in sharp deviations from those natural, long-term climate dynamics. The buildup of greenhouse gases – CO_2, methane and nitrous oxide, among others – in the atmosphere creates a "greenhouse effect" by absorbing long-wave radiation (heat) emitted from the Earth's surface that would otherwise pass through the atmosphere. This trapped energy heats the atmosphere and has resulted in increasing global mean temperatures through time. Current atmospheric CO_2 concentrations are nearly 420 parts per million (ppm), whereas concentrations in the mid-1700s were roughly 280 ppm – this is nearly a 70% increase in only a few hundred years. As a result, mean global surface temperatures have increased by ~1.14°C since 1880 and are projected to increase another 1–6° by the end of the century. Because warm air is able to hold more moisture than cooler air, this increase in air temperature also impacts global rainfall patterns and is expected to facilitate more variable and extreme precipitation regimes. Changes at this scale have both direct and indirect impacts on ecosystems around the world, affecting water availability, growing season lengths, plant productivity and phenology and global nutrient cycling. However, climate change will not impact all plant species or ecosystems in the same way. For example, some species may respond positively to increased CO_2 concentrations, but simultaneously respond negatively to increased temperature and rainfall variability. Forecasting the consequences of climate change on grassland ecosystems requires an understanding of how key plant species respond to changes in CO_2 concentration, temperature and rainfall variability, and how shifts in their abundance impacts soil communities, C-cycling and nutrient fluxes.

4.2.1 Atmospheric CO_2 Concentrations

CO_2 is the inorganic C substrate required for photosynthesis and the starting point for the vast majority of the complex organic molecules synthesized on Earth. CO_2 is generally well-mixed in the atmosphere and present in similar concentrations around the world on an interannual timescale. There are local and temporal variations that reflect differences in seasonality between the two hemispheres, the impact of increased emissions associated with urban environments and the ecological differences reflecting varying C-assimilation and respiration rates among different ecosystem types. Increased CO_2 concentrations typically correspond with increased rates of photosynthesis so long as other resources (e.g., soil moisture, light and nutrients) are available and environmental conditions promote growth. Therefore, it follows that rising atmospheric CO_2 concentrations would lead to increased rates of plant growth and global primary productivity. This response is often referred to as the "fertilization effect" and is typically viewed as a potentially positive outcome of rising greenhouse gas emissions. As noted previously, this fertilization effect hinges on the availability of other plant-limiting resources – especially water (Körner 2006).

To investigate the impacts of rising CO_2 on plant growth, experiments began in the 1980s, both in laboratory and in greenhouse settings, or in natural environments and outdoor experiments, for a large number of terrestrial ecosystems – forests, grasslands, tundra and semiarid desert, in both temperate and tropical regions. Many syntheses and reviews that detail the outcomes of these experiments have been previously published. While most of the field-based, or "natural," CO_2 fertilization experiments did exhibit increased rates of photosynthesis and growth in the short term, the longer-term consequences often varied from original predictions and illustrated how ecological interactions mediate the fertilization effect and vary among plant species, ecosystem type and geographic region (Körner 2006).

One major characteristic that modifies a plant species response to changes in atmospheric CO_2 concentrations is the specific photosynthetic pathway utilized. Over 85% of the plant species on Earth use the C_3 photosynthetic pathway. For these plant species, CO_2 assimilation reflects the concentration of CO_2 in the atmosphere (supply) and the concentration of CO_2 inside of the leaf (demand). Leaf internal CO_2 concentrations are largely regulated by the small pores that exist within the leaf surface that open and close to allow diffusion of air into the leaf and, simultaneously, water out of the leaf. Thus, as the supply of CO_2 in the atmosphere increases, the rate of C-assimilation in C_3 plant species increases (Pearcy and Ehleringer 1984). Within our tropical and temperate grasslands, many grass species use an alternative photosynthetic pathway, referred to as C_4 photosynthesis. C_4 plant species have a unique morphological adaptation within leaves that keeps CO_2 concentrations very low in the leaf internal spaces, which increases CO_2 demand, while simultaneously concentrating CO_2 in specialized bundle sheath cells containing the enzyme responsible for C-fixation. The outcome of this spatial separation of photosynthesis is the high rates of photosynthesis common to C_4 grass species (Pearcy and Ehleringer 1984). Given that photosynthesis in C_4 grasses is already occurring in a high-CO_2 environment (bundle sheath cells) near maximum enzymatic capacity, these species were not expected to show a growth response to increased atmospheric CO_2 concentrations compared to coexisting C_3 plant species. While this prediction typically holds when growing conditions are optimal (as in greenhouses or growth chambers), experiments in natural grasslands often show conflicting or non-intuitive results (Reich et al. 2018). These results illustrate how multiple resource limitations– including non-optimal soil moisture, light or nutrient availability – modify resource interactions to complicate ecological predictions based on increasing atmospheric CO_2 concentrations.

How did many C_4 grass species defy initial physiological predictions of being insensitive to increased atmospheric CO_2, and in some cases even perform better than coexisting C_3 plant species? The answer requires an understanding of how ecological interactions vary according to multiple resource limitations. As previously mentioned, grasslands are characterized by periods of low water availability resulting in dormancy or periods of low growth rates. When water availability is low, plants must reduce their photosynthetic rates in order to reduce water loss via transpiration – if leaf pores remain open to allow for photosynthesis to continue during drought conditions, the plant risks desiccation. Although this physiological

process is driven by soil water conditions, it reduces rates of photosynthesis because CO_2 uptake and water loss occur through the same pores on the leaf surface. Even if atmospheric concentrations are high, photosynthesis remains low if the leaf pores are partially or fully closed due to low soil water conditions. C_4 grass species benefit more than C_3 species under conditions of low water availability and high CO_2 concentrations based on the previously described supply–demand dynamics of CO_2. C_4 grasses have a lower internal leaf CO_2 concentration compared to C_3 grasses due to their ability to concentrate CO_2 in the bundle sheath cells. Therefore, the driving gradient for CO_2 diffusion from the atmosphere into the leaf internal spaces is larger in C_4 species, even under low soil water conditions when resistance to diffusion through leaf pores is high (Dijkstra et al., 2010). Thus, these experiments have shown that the theoretical impacts of elevated CO_2 can deviate from real-world conditions, and also illustrated that global warming conditions that result in increased intensity or frequency of drought have the capacity to counteract any positive consequences of increased CO_2 on plant photosynthesis and grassland primary productivity.

4.2.2 TEMPERATURE

Surface air temperatures have increased in grasslands worldwide as a consequence of global warming, and this trend is expected to continue throughout the century, with increases dependent upon varying global warming projections. There are two unique features of many grasslands and savannas worldwide that could, in theory, mute the negative consequences of future warmer air temperatures on grassland species and ecosystem processes. First, many grasslands currently occur in regions that have historically experienced periods of high air temperature. These periods may occur predictably during the summer growing season or can be associated with interannual climate anomalies such as El Niño or La Niña conditions. This history of periodic drought has resulted in grasslands and savannas being well adapted to periods of low water availability. Second, for many grassland ecosystems, the dominant grass species utilize the C_4 photosynthetic pathway. The optimal temperature conditions for C-assimilation in C_4 species are higher (33–37°C) than species utilizing the C_3 photosynthetic pathway (28–32°C) (Sage and Kubien 2007). For this reason, higher air temperatures could be expected to have fewer negative impacts on physiological functioning in C_4 species. However, as has been reported multiple times in this chapter, the drivers of climate change do not occur in isolation, and the dynamics of ecological communities have complex responses to interactive environmental factors. For these reasons, increased air temperatures as a consequence of global warming are expected to have several negative consequences for grassland ecosystems.

The most proximal direct effect of warmer air temperatures is increased leaf energy budgets and increased cellular and soil respiration rates. Increased air temperatures alter the energy budgets of leaves by changing energy dissipation pathways (both sensible and latent heat exchange) and energy transfer. Reduced energy exchange with the atmosphere increases leaf temperature and leads to greater potential of physiological stress. Cellular-level stress increases because C-assimilation is enzymatically driven, and enzymatic processes operate within certain temperature

conditions (Sage and Kubien 2007). Exceeding optimum temperatures for extended periods of time increases leaf stress and typically results in reduced photosynthetic rates and growth. Increased air temperature also impacts C-assimilation through tighter regulation of leaf gas exchange. As temperatures increase, the vapor pressure deficit that exists between a leaf and the atmosphere increases, resulting in higher rates of leaf water loss for a given stomatal (leaf pore) aperture. Thus, grassland species have to reduce rates of gas exchange, and therefore reduce CO_2 uptake, in order to minimize the risk of desiccation. Finally, increased air temperature directly increases cellular and soil respiration rates. For every 10°C increase in temperature, cellular respiration rates double – a phenomenon referred to as a Q10 response (Tjoelker et al. 2001). Consequently, increased air temperatures in grasslands speed up the rate of C-cycling for both vegetation and soil communities, ultimately leading to a reduction in the amount of C stored by the ecosystem (Figure 4.2).

In addition to the potential for increased physiological stress associated with higher air temperatures, there are many indirect community-level consequences. Increased annual air temperatures are resulting in changes in the length of vegetation growing seasons, especially for temperate grassland regions where the dormant season is associated with cold temperatures. As temperatures warm, the growing season shifts earlier in the year and typically lasts longer. These shifts in season can result in phenological mismatches between plants and their pollinators or herbivores, or between periods when fires occur naturally and when plant species are physiologically less sensitive to fire (dormant vs. actively growing vegetation). Additionally, an earlier initiation of spring growth, coupled with a longer overall growing season and
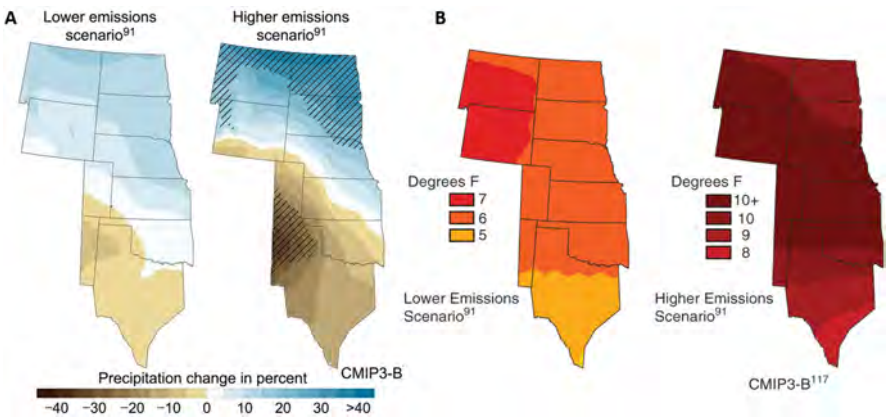
FIGURE 4.2 Forecast changes in (A) precipitation and (B) air temperature for the Great Plains region of the United States by the end of the century. Compared to baseline data in the region from 1960 to 1979, precipitation change is projected to increase in the northern Great Plains, corresponding with a decrease in the southern Great Plains for both emission scenarios. Air temperature is expected to increase across the entire region, with the largest increases in northern states. *Image credit*: *U.S. Global Climate Change Impacts in the United States: A State of Knowledge Report from the U.S. Global Change Research Program*, editors: Karl, T. R., J. M. Melillo, and T. C. Peterson. 2009.

later fall senescence, will likely result in larger reductions in available soil moisture and more pronounced growing season drought effects. Even with no reduction in annual precipitation amount, longer growing seasons result in larger annual evapo-transpirative fluxes, greater depletion of stored soil moisture and increased physiological stress on plants. If these stresses accumulate early in the growing season, late-season flowering plant species may experience more frequent disruptions in their life cycles. So far, this discussion of elevated air temperature modifying local ecohydrology has assumed no overall changes in magnitude of annual precipitation amount, timing or intensity, but the next section will detail the expected changes to grassland precipitation patterns as the climate warms.

4.2.3 PRECIPITATION VARIABILITY

In addition to increasing global mean air temperatures, climate change is expected to have substantial impacts on the global hydrologic cycle (Giorgi et al. 2019). Most model projections agree that precipitation variability will increase as the climate continues to warm (Pendergrass et al. 2017), likely resulting in longer periods of drought punctuated by more extreme precipitation events. Globally, water is the main limiting resource for plants, and precipitation and soil water availability are some of the major determinants of biome distributions. Both the magnitude of total annual precipitation and the timing and size of precipitation events are often critical in maintaining ecosystem dynamics and function, and grasslands are no exception to this trend.

Changes in precipitation patterns associated with climate warming will not be uniform in all grassland ecosystems. Grasslands located in midlatitude or subtropical dry regions are expected to experience a net decline in annual precipitation, while grasslands at higher latitudes have mixed predictions regarding changes in total annual amount (Gibson and Newman 2019). While the magnitude of change in precipitation will vary regionally, general circulation models (GCMs) consistently predict that intra-annual variability in precipitation will increase as the climate warms (IPCC 2007). Productivity in grassland ecosystems is largely impacted by inter- and intra-annual precipitation patterns (Knapp et al. 2016). Low annual precipitation is associated with lower aboveground net primary productivity (ANPP) (Nippert et al. 2006), owing in part to lower soil moisture availability and increased plant water stress resulting in lower photosynthetic rates. However, increasing duration of drought events, even when total annual precipitation does not change, can decrease grassland productivity to a similar degree as low annual rainfall (Knapp et al. 2002). Less frequent, more intense precipitation events can also reduce infiltration of water into the soil and increase runoff, erosion, flooding and leaching of nutrients from the soil.

The impact of increased rainfall variability on grassland productivity is also expected to vary based on local climate conditions (Heisler-White et al. 2009). Experimentally altering precipitation frequency while maintaining overall amount of growing season precipitation (i.e., fewer, but larger, rainfall events) has been shown to increase productivity in semiarid grasslands (Heisler-White et al. 2008), while decreasing productivity in more mesic grassland ecosystems (Fay et al. 2003).

4.2.4   Special Grassland Example: Impacts of Increasing Precipitation Variability in Tallgrass Prairie

The North American tallgrass prairie exists within the mesic temperate biome of the central Great Plains (Hayden 1998). This grassland region is characterized by high grass productivity, driven in part by a climate regime that includes both warm growing-season temperatures and rainfall inputs that typically exceed losses from evapotranspiration (Briggs & Knapp 1995; Nippert et al. 2006). Historically, ~75% of rainfall events occur between March and September each year. Periods of low rainfall resulting in drought are characteristic of this region. These droughts can result from years with below-average total precipitation, or extended periods without rainfall within the growing season without a change in the total annual amount (Knapp et al 2002).

Many long-term experimental precipitation manipulations have been conducted in tallgrass prairie, starting in the mid-1990s. These experiments were designed to test grassland responses to multiple predictions of precipitation change forecast for tallgrass prairie, and mesic grasslands more broadly. To date, these experiments have included three main rainfall manipulations: (1) passive, but chronic, reduction in total annual rainfall amount with no change across years; (2) change in precipitation variability whereby no change in total annual rainfall amount, but rain events are larger and less frequent, resulting in longer intervals of dry days between larger rain events; (3) reductions in total rainfall amount for multiple consecutive years, followed by multiple consecutive years without rainfall reductions to investigating drought legacies (Figure 4.3); and (4) factorial designs. On occasion, these rainfall manipulations have included passive infrared air temperature increase of a few degrees or the simulation of heat waves, which can accompany drought in this region.

Several key results can be inferred from these precipitation experiments. As expected, reductions in total amount of annual rainfall reduces surface soil moisture availability and annual grassland biomass. The entire herbaceous community experiences reduced plant growth, with aboveground plant biomass typically having larger biomass reductions compared to belowground (Smith, 2011; Wilcox et al. 2017).

FIGURE 4.3   The climate extremes experiment at the Konza Prairie Biological Station. Experimental manipulations of precipitation using large rain-out shelters allow ecologists to test the predictions of climate change on intact grassland communities. *Image credit*: Melinda D. Smith.

Changes in precipitation variability, without changes in the total amount of rain delivered per year, have resulted in chronic droughts, reduced biomass, altered soil respiration fluxes and changes in species composition (Knapp et al. 2002, Fay et al. 2011). Precipitation manipulations that sequentially expose grasslands to years of reduced rainfall followed by recovery illustrate a high resilience (e.g., reduced biomass and canopy cover during drought, but recovery to pre-drought conditions in subsequent years) of the C_4 grass species to these changes, but reduced resilience by the coexisting forb communities (Hoover et al. 2014). In total, these experiments illustrate that this mesic grassland is highly responsive to changes in both precipitation amount and timing. Future changes in rainfall are highly likely to impact both ecosystem function with regard to C uptake and cycling, as well as the abundance and cover of the plant species in this grassland community (Felton et al. 2019; Knapp et al. 2020).

As discussed earlier in this chapter, changes in atmospheric CO_2 concentration, increased air temperatures and changes in precipitation pattern and amount are likely to have singular and interactive effects on grassland processes. The ability of grasslands to maintain their structural (number and proportion of species present) and functional (ecosystem services) processes depends on the maintenance of ecosystem resilience. Resilience describes the ability of an ecosystem to maintain stability and critical services despite perturbations (i.e., direct or indirect climate change impacts). In Figure 4.4, we summarized the likely impacts of the direct climate change discussed on grassland and rangeland. While local impacts will vary from place to place, cumulatively we can expect these climate change drivers to negatively impact grassland structure and function. Perhaps most alarming, the direct climate change impacts on grasslands are likely to exacerbate the indirect threats to grasslands – namely, woody encroachment and the spread of invasive plant and insect species. In Section 4.3, we detail these indirect impacts, explain why these impacts threaten grassland ecosystems and describe the potential acceleration of conversion from grassland to degraded land under future climate scenarios.

4.3   SECONDARY (INDIRECT) IMPACTS

4.3.1   LAND-USE/LAND-COVER CHANGE

In addition to the direct impacts of climate change on grassland ecosystem dynamics, these changes also indirectly impact grasslands via interactions with human-driven modifications in land-use and land-cover. Here, land-use and land-cover changes refer to anthropogenic modifications of the landscape resulting in an alteration of goods and services compared to a natural grassland ecosystem. In many parts of the world, the first lands cultivated for agriculture were those with relatively flat topography in productive grassland ecosystems. With increased population growth and subsequent demand for food, less productive grasslands and remnant fragments have been converted to agriculture, resulting in widespread reductions in the spatial extent of native grasslands. Humans also continue to drive reductions in the quality of remaining grasslands through modified fire regimes (too frequent or infrequent),

	↑ CO_2	↑ Temperature	↑ Precip. Variability	Interactions/ Net Effects
Native Grassland Stability	Cancels out	More drought/ metabolic stress	More drought stress, changes in infiltration dynamics	Interactions between climate drivers will decrease grassland resilience
Agriculture/Rangeland Productivity	Fertilization effect	Photorespiration, More drought stress	More drought stress, Incr. need for irrigation	Potentially faster growth, but likely offset by increased stress and declining crop/forage productivity
Woody Encroachment	Fertilization effect	Photorespiration	Increased infiltration	Woody species benefit more than grass species with higher CO2 and greater water infiltration to depth
Spread of Invasive Species	Fertilization effect	Favors C_4 invasives	Decrease native species growth	Direct effects that reduce stability of native grasslands will make it easier for invasive species to spread

FIGURE 4.4 Predicted impacts of direct climate change on grassland processes (stability, productivity – discussed in Section 4.2) and indirect climate change impacts (woody encroachment and invasive species – discussed in Section 4.3).

overgrazing, introduction of exotic and/or invasive species and fragmentation of habitat.

4.3.1.1 Agriculture, Urbanization and Habitat Fragmentation

Approximately one-third of Earth's terrestrial surface is used for agriculture (4.8 billion ha; Food and Agriculture Organization of the United Nations (FAO) report), and native grasslands historically comprised a large majority of this area. The original conversion of grasslands rather than forests to annual agriculture occurred primarily because (1) it is generally easier to replace a diverse grassy community with crop species, many of which are also grasses, and (2) land clearing of forests is laborious, intensive and still results in soils that retain large woody roots and stumps that make cultivation difficult. Indeed, conversion to agricultural land is the primary threat of grassland ecosystems globally (Gibson 2009). Initially, the first grasslands converted to agriculture were locations with the most fertile soils. With increased human population growth, demand for agricultural commodities increased, requiring increased production. Without more highly fertile lands to be converted to agriculture, the only options available were increased yields on existing lands through genetic breeding of key cultivars, and by the conversion of marginal grasslands (e.g., locations with less productive soils, or lower yield potentials) to agricultural land. Both of these scenarios are outcomes of increased industrialization of agriculture to support human demand, and both scenarios have resulted in increased losses of grasslands globally. Importantly, when marginally productive (less fertile) grasslands are converted to agriculture, more land is required to produce agricultural yields that feed the same number of people.

A secondary impact of grassland conversion to agriculture is landscape fragmentation. As the landscape is cultivated, small portions of the original landscape remain in isolated, small-acreage patches. This fragmentation reduces habitat availability for animal populations, results in the loss of natural grassland corridors that facilitate movement on the landscape and is particularly impactful on highly mobile populations of birds or migratory animals. Fragmentation also reduces genetic diversity of plant populations by reducing plant species richness and abundance within fragments and lowering the total number of species present within a given area (Krauss et al. 2010). With continued human population growth and increased migration of humans from rural to urban environments, the urban/suburban expansion is typically at the expense of agricultural and grassland regions that surround cities. These former grasslands are developed into urban environments or become degraded lands supporting low-income human populations in regions with large wealth disparities.

Expected future changes in climate, detailed in Section 4.2, increase the uncertainty of agricultural production and are a distinct threat to food security. Many key commodity species grown in grassland regions, like wheat, soybeans and barley, utilize the C_3 photosynthetic pathway and exhibit decreased production under warmer air temperatures (Ainsworth and Ort 2010), irrespective of irrigation and soil water status. The combination of warmer temperatures and increased precipitation variability is expected to further increase the likelihood of crop failure and lower yields for many agricultural species. The impacts of climate change on human livelihoods are not globally uniform, however. Climate change will disproportionately affect

people living in grassland regions that already face malnourishment due to chronic poverty and income-based obstacles to sustainable agricultural intensification (e.g., sub-Saharan Africa and South-East Asia). Compounding the severity of this issue, these areas are also predicted to have the highest rates of population growth over the remainder of this century, resulting in rapidly increasing demand for a reduced supply of food. Beyond crop production, domesticated livestock depend on grasslands for forage. Future changes in climate are expected to reduce grass productivity, resulting in less forage available for livestock. Reduced available forage increases the potential for animal stress and the likelihood of livestock mortality, particularly if temperature increases and drought become more frequent (IPCC 2019).

For these reasons, climate change is likely to threaten global food security. However, modern agriculture could potentially be further facilitating changes in climate (Tilman et al. 2011), particularly through increased methane emissions and disruption of natural nitrogen cycling. In addition, high-yielding lands for sustainable agriculture are no longer available, and yet the future demand for larger amounts of food in the context of an uncertain climate is increasing. Future efforts must focus on novel methods of sustainable agriculture that can produce higher yields from existing agricultural land, reduce chemical inputs leading to reductions in soil quality or environmental contamination and reduce food waste and the disparity in food security that exists across nations and regions.

4.3.1.2 Woody Encroachment

The conversion of grasslands to agricultural land has led to a rapid and substantial decrease in grassland area worldwide. The fragmentation of remaining grasslands – due to continued conversion to agriculture, urbanization and changes in land-use – has facilitated an increase in woody plants in historically grass-dominated areas. This phenomenon is referred to as woody encroachment, and it is occurring in grasslands and savannas around the world. In many cases, the proliferating woody species are native to the region, but were historically restricted to riparian zones or have a patchy distribution throughout the landscape, as in savannas. Increased woody cover has led to a direct loss of grasslands and their ecosystem services – namely, quality forage for livestock grazing – by reducing herbaceous productivity and species richness (Archer et al., 2017). In addition, woody encroachment directly alters C and water cycling by shifting C-storage from primarily belowground (in soils and grass roots) to aboveground (in woody tissues) and increasing rates of evapotranspiration (O'Keefe et al. 2020) (Figure 4.5).

The primary drivers of woody encroachment are complex, and vary by grassland type (e.g., semiarid vs. mesic, or temperate vs. tropical). The amount of rainfall received each year establishes the maximum potential for tree or shrub cover in a grassland or savanna ecosystem, whereby potential woody cover increases with mean annual precipitation (Sankaran et al. 2008). The amount of annual rainfall largely determines the drivers that suppress woody cover. For example, in arid and semiarid grasslands, woody cover is primarily limited by precipitation – when precipitation is too low to support woody vegetation, woody cover will remain low. In more mesic grasslands that receive enough precipitation to support a higher abundance of woody
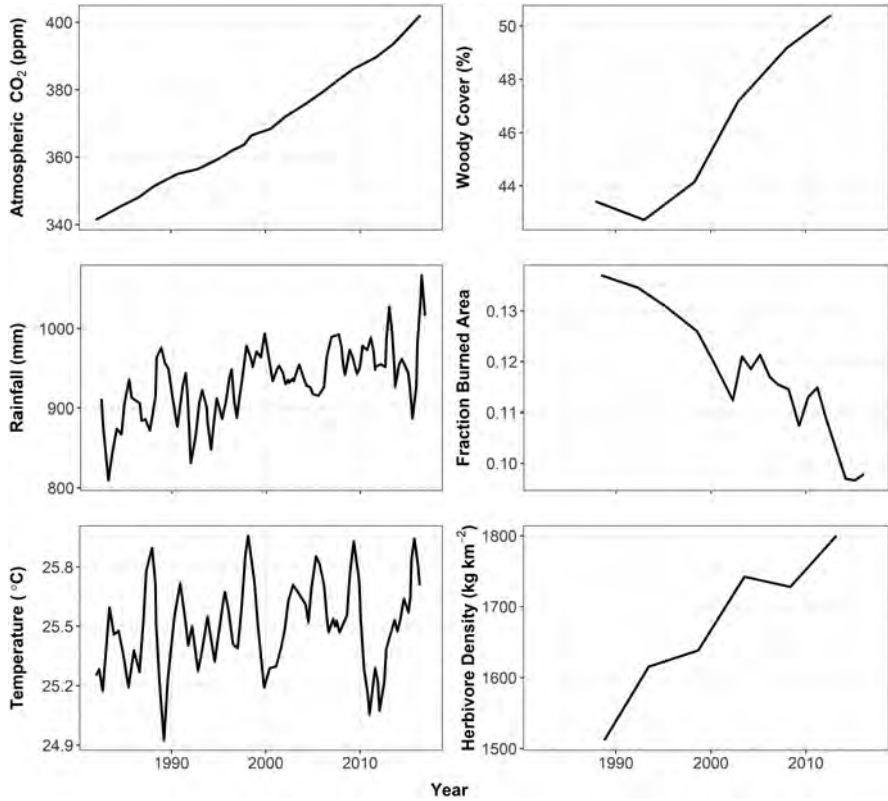
FIGURE 4.5 Changes in atmospheric CO_2, rainfall, air temperature, woody cover, fraction burned cover and herbivore density for sub-Saharan Africa over 1985–2015. Woody cover has increased over the past three decades, corresponding with increases in many environmental variables (CO_2, rainfall, air temperature and herbivore density), along with an overall decrease in the fraction burned area. *Source*: Figure modified from Venter et al. 2018.

plants, woody cover is limited by frequent disturbance – namely, fire and herbivory (Archer et al. 2017). Browsing and frequent fire suppress the spread of woody species by killing or injuring tree saplings and small shrubs, preventing them from establishing and maturing. When fire is frequent, it is sufficient to keep woody species in this vulnerable zone, but when fire frequency declines, woody plants have more time between fire events to establish and grow. If young trees are able to grow tall enough to escape the impacts of fire, or if shrubs grow large enough to shade out grasses, reduce fine fuels and fire intensity and prevent fire from damaging stems in the shrub interior, these woody plants can escape the "fire trap" (Ratajczak et al. 2014; Archer et al. 2017). Often, decreased fire frequency, decreased browsing and/ or overgrazing at the local level are considered the predominant drivers of woody encroachment. However, interactions with changing climate conditions are likely to exacerbate this process.

Increased atmospheric CO_2 concentration is expected to speed up woody plant establishment and growth – more CO_2 in the atmosphere often leads to increased carbon fixation via photosynthesis and can subsequently reduce water loss because stomatal conductance typically decreases with increasing $[CO_2]$. This "fertilization effect" is likely to be most beneficial to juvenile woody plants, which are the most vulnerable to disturbances such as fire and browsing. Increased growth rates facilitated by increasing CO_2 concentrations would accelerate the transition from juvenile to adult size classes in woody species, increasing their survival after disturbance. Additionally, greater carbon gain increases carbon storage in woody tissues that is used to produce new tissues following fire and browsing.

In addition to elevated atmospheric CO_2 concentrations, shifts in regional precipitation patterns are expected to differentially affect woody and herbaceous plants and further facilitate woody encroachment in grassland ecosystems. As discussed previously in this chapter, many grasslands are expected to experience more extreme and prolonged droughts punctuated by periods of unusually heavy rainfall as precipitation variability increases. These predicted changes in precipitation patterns are expected to benefit deep-rooted woody plants over shallow-rooted grasses (Kulmatiski and Beard, 2013). Deep roots give access to deep water sources that provide a consistent water source during dry periods and reduces woody plant competition with grasses for shallow soil water. Predicted increases in the intensity of rain events and magnitude of winter precipitation may increase soil water infiltration, recharging water in the deep soil layers and disproportionality benefitting deep-rooted woody plants over grasses.

Woody encroachment is a major risk to grassland ecosystems because the consequences are long-lasting and difficult to manage. Infrequent or lack of burning leads to a gradual grassland-to-woodland transition (Briggs et al. 2005; Bond 2019). Several lines of evidence suggest that the spread of woody vegetation in grassland ecosystems can reach a point of hysteresis, where it is impossible (or exceedingly difficult) to reverse this grassland-to-woodland transition (Bestelmeyer et al. 2011). Once woody vegetation has become established in the absence of fire, reimplementation of frequent fire is typically not sufficient to reverse the transition and restore grass cover (Staver et al. 2011; Miller et al. 2017). Spread of woody vegetation typically decreases fire frequency as surface fuel loads (grasses) are reduced and grass cover becomes patchier (Drewa and Havstad, 2001). This decrease in fire frequency further promotes the spread of woody vegetation, resulting in a positive feedback loop. Although woody encroachment in grasslands leads to lower frequency of surface fires, it can also result in higher fire intensity when wildfires do occur. This represents a shift in fire regime from the frequent surface fires that maintain open grasslands to less frequent, but more intense crown fires when woody vegetation does ignite, typically during periods of drought (Brooks et al. 2004).

4.3.1.3 Specific Grassland Example – Woody Encroachment in African Lowveld Savannas

The distribution of savannas is determined by a seasonal climate, occurring in locations with hot, wet summers and cooler, dry winters. The cycle of the wet and dry seasons has shaped the savanna ecosystem by driving the distribution and migration

of large mammals and promoting hot fires after the dry season. These climate and land-use drivers have complex interactions maintaining an open canopy with low tree: grass ratios. African savannas are unique in that they span a large precipitation gradient (150–1,200 mm mean annual precipitation) and host a large diversity of mammals that feed on grasses (grazers) and woody plants (browsers). While precipitation determines the amount of woody plants the system can support, herbivory and fire suppress woody plant growth and kill woody saplings. It is hypothesized that semiarid savannas are stable systems where low water availability (<650 mm yr[1]) maintains low tree:grass ratios (Sankaran et al. 2008). In contrast, mesic savannas are reliant on frequent fires to maintain low tree abundance. Mesic savannas are considered particularly vulnerable to woody encroachment because of increased water availability and are reliant on frequent and intense fires to maintain low tree abundance. However, woody encroachment is occurring across the precipitation gradient in lowveld savannas, including mesic savannas that experience historical fire frequencies, suggesting global drivers likely interact with local changes to fire frequency and herbivore abundance (Stevens et al. 2016; Case and Staver 2017).

Africa hosts the world's last remaining intact megaherbivore guilds and many of the remaining large predators. The degradation of savannas and loss of biodiversity due to woody encroachment directly conflict with conservation goals to protect and conserve remaining ecologically intact savannas. Conservation areas, including National Parks and private reserves, rely on ecotourism to fund these protected areas. Increased tree and shrub cover is likely to negatively affect ecotourism as animals become harder to see with high woody cover (Gray and Bond 2013). Additionally, loss of habitat and forage may have cascading effects on the grazers and other mammals that rely on open, grassy systems. These effects may include a restructuring and redistribution of mammal communities as obligate grazers are lost and browsers become more frequent in encroached areas (Smit and Prins 2015). Management at the local level is likely required to combat encroachment, including frequent prescribed fire and bush clearing. Although these techniques can be expensive and time- and labor-intensive, they are likely required to combat woody encroachment in the face of global drivers (Figure 4.6).

Impacts of woody encroachment on grassland hydrology vary, depending on the local climate and geomorphology, the types of species present and the local land-use history. Due in part to their access to deeper, more consistent water sources, woody species typically have much higher rates of transpiration than grasses (O'Keefe et al. 2020), leading to greater overall water flux and potentially depletion of deeper soil water over time (Acharya et al. 2017). Transpiration in woody encroached areas has the potential to exceed precipitation inputs during a given growing season if deep soil water is available, which could result in watershed-scale water deficits. Woody encroachment also contributes to increased canopy interception of precipitation. Woody canopies typically intercept more rainfall than grass canopies, particularly when the woody community consists largely of coniferous species (mainly *Pinus* or *Juniperus* species in the United States) (Archer et al. 2017). Increased interception of rainfall further increases evapotranspiration in woody encroached areas compared to open grassy areas. Although impacts of woody encroachment on water yield vary

FIGURE 4.6 *Upper panel:* Lowveld savanna of Pilanesberg National Park, South Africa. The aboveground portions of the smaller trees (*Acacia* spp.) were completely killed by a recent fire and had begun to resprout. Note that tall trees have outgrown the "fire trap" and appear unaffected by the fire. *Lower panel:* A closer look at the resprouting *Acacia* spp. Note the dead branches with no leaves that were killed by the fire. The base of the tree was filled with resprouting shoots to recover from fire. The ability to resprout increases the persistence of woody species in highly disturbed environments such as grasslands and savannas. *Image credit*: Emily R. Wedel.

based on local climate and geomorphology (Huxman et al. 2005), woody encroachment generally results in an overall increase in evapotranspiration and decrease in groundwater recharge (Acharya et al. 2018). These impacts of vegetation change are typically most pronounced in mesic grasslands, where precipitation is high enough to recharge deeper soil water layers (Huxman et al. 2005).

In addition to increases in evapotranspiration, the proliferation of deeper, coarser root systems of woody species can impact water flow paths through the vadose zone (Zou et al. 2014; Acharya et al. 2018). Root systems have substantial impacts on the flow and retention of water in the soil profile (Cresswell et al. 1992; Scholl et al. 2014) as well as connectivity between water sources on a landscape. Coarse woody roots form large soil macropores more readily than finer grass roots, and these soil pores can alter flow paths and cause shifts in hydrologic partitioning in grassland systems by creating preferential flow paths deeper into the soil profile (Sullivan et al. 2019). These shifts have the potential to alter stream discharge and drainage through

the vadose zone into groundwater, particularly during large rainfall events (Vero et al. 2018).

4.3.1.4   Specific Grassland Example – Juniper Encroachment in the Southern Great Plains, United States

Encroachment of Ashe juniper (*Juniperus ashei*) and eastern redcedar (*Juniperus virginiana*) in the southern Great Plains, United States, has resulted in substantial conversion of open grasslands and rangelands to juniper woodlands over the past 50–60 years (van Auken 2009). This transition is known to result in the loss of grassland small mammals and birds (including the now endangered lesser prairie chicken), reduced livestock production as the amount of quality forage declines and potentially alterations to local hydrologic cycles. Both juniper species have deeper rooting systems than the grass species they replace and can substantially alter surface soil conditions as hydrophobic litter layers are deposited (Wine et al. 2012). In addition to the loss of herbaceous forage for livestock, a major concern of land managers in the southern Great Plains has been the impact of juniper encroachment on streamflow and groundwater recharge (i.e., local water yield). However, the hydrologic impacts of juniper encroachment are not straightforward – they are heavily impacted by local climate conditions (especially annual precipitation) and geomorphology. Here, we will consider two contrasting consequences of juniper encroachment in different regions of the southern Great Plains.

In studies on southern Oklahoma, United States, in a region with relatively deep soil (1–2 m) underlain by shale and limestone bedrock, juniper encroachment has been linked to declines in runoff and streamflow. Surface runoff in grassland and rangeland systems in this region are typically dominated by infiltration excess overland flow – that is, when rainfall events result in saturated soil conditions, excess water that can no longer infiltrate contributes to surface runoff (Qiao et al. 2017). Juniper encroachment facilitates greater infiltration of water into deeper soil layers, resulting in less frequent soil-saturating rain events and lower rates of surface and subsurface runoff (Qiao et al. 2017). Rather than contributing to surface runoff and ultimately streamflow, infiltrating water instead contributes to recharge of deep soil water stores, which likely benefit deep-rooted junipers over more shallow-rooted grasses. Access to consistent deep soil water aids these juniper species in photosynthesizing year-round and in tolerating summer drought conditions.

In contrast, some studies on the Edwards Plateau in Texas have reported increased streamflow following encroachment by Ashe juniper (a species that is functionally equivalent to eastern red cedar (Qiao et al. 2017)). This region is characterized by a semiarid climate, shallow soils and highly permeable karst geology (Maclay 1995) where baseflow is the dominant contributor to streamflow (Wilcox and Huang 2010). In contrast to the above example, streamflow has actually increased through time as encroachment by Ashe juniper has progressed, and this change is not associated with a concurrent increase in precipitation (Wilcox and Huang 2010). The Edwards Plateau region experienced massive overgrazing by cattle from the late 1800s until roughly 1960, leading to overall degradation of existing rangelands (Wilcox and Huang 2010). Woody plants, particularly Ashe juniper, expanded after grazing

pressures declined and increasing streamflow has been associated with improved infiltration of water to deeper portions of the soil. In this example, encroachment of Ashe juniper following the widespread land degradation in a karst geologic system led to an increase in streamflow rather than a decline. A separate study on juniper encroachment on the Edwards Plateau reported that removal of junipers did not result in an increase in groundwater recharge (Bazan et al. 2013). This example highlights the importance of land-use history – in combination with local climate, geomorphology and geology – in modulating the effects of woody encroachment on local water cycling.

As juniper encroachment becomes increasingly widespread in the southern Great Plains, understanding how this transition will impact runoff, streamflow and deep soil water recharge will be vital for land managers interested in maintaining rangeland forage quality and water resources in the future.

4.3.1.5   Specific Grassland Example – Subsection Invasive Species

In the United States alone, the negative impacts caused by invasive species accounts for nearly US$120 billion per year (Pimentel et al. 2005). Increased temperatures and precipitation variability associated with climate change puts native grassland communities at increased risk of invasion (Thomas et al. 2004). Exotic, invasive species are non-native and are typically accidentally introduced to a new grassland ecosystem by way of human activity. Invasive grassland species are able to survive and spread in the new ecosystem after being freed from the "restriction" of their native habitat. Native species are often replaced by invasive species as they become established and subsequently outcompete existing vegetation. For invasive grassland species that were intentionally introduced, the goal is commonly to increase forage quality for grazers or to reduce erosion. Unfortunately, these introductions typically result in altered species composition and declines in ecosystem productivity and biodiversity. Decreased diversity is often associated with loss of ecosystem resilience, or the ability of the ecosystem to tolerate disturbance such as fire or extreme climate events. In addition, replacement of diverse, native communities with monocultures of invasive species often leads to a decrease in productivity, in part due to alterations of fire dynamics and soil biogeochemistry.

Native plant species have evolved alongside the ecosystem they exist in – evolutionary pressures and competition with other native flora and fauna result in species that are well-adapted to their habitat. Changes to those conditions associated with human activity (e.g., nutrient additions, habitat fragmentation, increasing climate variability) are often much more rapid than the ability of species to change and adapt, resulting in opportunities for non-native species to establish and outcompete native species. Plant species that successfully invade grassland ecosystems typically contain innate characteristics that allow them to survive in a wide range of environmental and climatic conditions, allowing them to take advantage of novel and/or severe disturbances.

Particularly when coupled with changes in climate, human disturbance plays a key role in grassland invasion by exotic species. Grasslands with minimal human impacts historically have low rates of invasion. However, very few grasslands are free

from anthropogenic impacts. Grasslands in Australia and North and South America are typically highly managed and have experienced high levels of fragmentation due to the increasing spread of agriculture and urbanization. These disturbances have led to increased invasibility, which can drastically alter species composition, productivity and ecosystem function, all of which have long-term ecological consequences (Gibson and Newman 2019).

4.3.1.6 Specific Grassland Example – Exotics in California Grasslands

California grasslands may be one of the best representations of an invaded ecosystem, as they have been converted from a diverse plant community with a large proportion dedicated to native bunchgrasses to an invaded landscape dominated by non-native Mediterranean annual grasses, which include, but are not limited to, grasses in the genera *Avena*, *Hordeum*, *Bromus* and *Schismus*. Such species have become dominant, as the climate in California is similar to the home ranges of these annual invasives. Interestingly, many of these California exotics do not dominate within their original range but serve as an early successional species (Jackson 1985). This is likely due to non-native species being better competitors for limiting resources and more tolerant to disturbances resulting from poor management strategies (high-intensity grazing) (HilleRisLambers et al. 2010).

The increase of human disturbances and rise of exotic annual species have resulted in the subsequent decline of native species. Not only is there a direct effect on other plant species, but there are also negative consequences such as increases in insects like aphids. Aphids are detrimental to plant health, as they feed on the carbohydrate-rich sap within phloem tissues, but they also serve as vectors for many plant viruses. Non-native annual grasslands have also been observed to alter soil nitrogen content and cycling that can result in long-term effects, mainly the deterrence of native perennial grasses reestablishment from the legacy of nitrogen-rich soils (Parker & Schimel 2010). While nitrogen serves as one of the most important macronutrients, it also serves to benefit fast-growing annual species. In this situation, the invasive annuals are able to outcompete slower growing native perennials. Not only are nitrogen cycles being altered by invasive species, but carbon dynamics have also been seen to increase in frequency and intensity. In contrast to the native perennial bunch grasses found in California, the invasive annuals have greater fuel loads and decreased fuel gaps which increase the probability and frequency of fires (Davies & Nafus 2013). The more frequent and intense fires moving across this region inhibit the growth of native species while simultaneously spurring the growth of invasives. All of the previously mentioned alterations to California grasslands were enabled and exacerbated by climate change, mainly human disturbances. Unfortunately for these grasslands, ecological dynamics now exist that reinforce the success of invasive species over native species and will require tremendous restoration and specific management practices to overcome.

4.3.1.7 Subsection Nutrient Deposition

Nitrogen availability varies among grassland ecosystems worldwide, tending to be lowest in semiarid temperate grasslands and in tropical grasslands with old soils

(McCulley et al. 2009, Risch et al. 2019). N availability is a key regulator of productivity across grasslands ecosystems worldwide (Stevens et al. 2015) and also impacts species richness and community characteristics (Midolo et al. 2019). Given that this critical resource is often limiting in many grassland ecosystems and grassland plant communities exhibit species-specific adaptations to this limitation, increased N availability has the potential to speed up local N cycling and alter ecosystem processes in addition to reordering species abundance to favor high N demanding species over those that adapted to low-N conditions.

One consequence of the green revolution is that synthetic fertilizer production now rivals (~100 Tg N yr[1]) amounts of naturally occurring N fixation at a global scale (Galloway et al. 2004). These synthetic fertilizers have been applied to improve agricultural yields to support our growing human population. While agronomic improvements of key crop species have reduced N requirements, and advances in application timing and amount have reduced N losses, a substantial portion of N is lost to runoff and leaching or is converted to gaseous forms and transported in the atmosphere to locations other than where originally applied. Rates of atmospheric N deposition are not uniform across regions. Regions with high acreages of commercial agriculture have higher rates of atmospheric transport and N deposition. Because many native grasslands were converted to row-crop agriculture, the remaining grassland ecosystems tend to be proximally associated with agricultural regions. As N accumulates in grasslands, it has the potential to eutrophy the local ecosystem, alter microbial dynamics and N cycling and reorder plant species populations (Johnson et al. 2008). These changes in N availability and a shift from a more N-limited system to N eutrophication represent a fundamental shift in grassland ecosystem dynamics and can stimulate negative outcomes via interactions with other global change drivers (e.g., rising air temperatures and more frequent drought).

4.4   CLIMATE ACTION SOLUTIONS

In this chapter, we have outlined the threats to grasslands posed by multiple climate change drivers, including elevated atmospheric [CO_2], increased daytime and nighttime air temperatures, changes in precipitation patterns and intensity and altered nutrient deposition. The impacts of these drivers have taken over 150 years to develop and establish the trajectory of catastrophic global changes we are now experiencing. Our collective understanding of these threats and their impacts have developed over the past 30 years, as long-term data collection and observational ecological studies allowed for a documentation of change, and experimental studies facilitated the development of a mechanistic understanding of grassland responses to climate change. This research is composed of site-based and cross-site studies that have grown in complexity through time. Continuation of this research is necessary as effective and sustainable maintenance of grasslands requires better forecasting (both climatological and ecological) of grassland responses to climate change to develop effective climate solutions.

Developing a climate action plan is complex and difficult because the scope of climate change is large, the trajectory for recovery is long and the potential impacts

of an individual or groups of individuals feel small. In the case of grasslands, solutions are especially overwhelming and pressing given the magnitude of the loss of grasslands due to agriculture, urbanization and degradation. Despite these difficulties in conserving grasslands, there is still a need for protecting and sustainably managing remaining grasslands to preserve their ecosystem services and biodiversity. The solution requires collective effort at the individual, community, national and ultimately global levels to influence policy, reduce the rate of climate change and conserve and restore grasslands (Figure 4.7). In this section, we explore options for climate actions, which if successful will result in meaningful long-term conservation and restoration of grassland ecosystems in the face of climate change.

4.4.1   Individual-Based Climate Actions That Promote Grassland Conservation in the Era of Global Change

At an individual level or within our local communities, it feels like an insurmountable challenge to make meaningful contributions to reducing global CO_2 emissions when governments have the greatest influence through net-zero energy policies that limit the choices of industries and individuals to reduce carbon emissions. While mitigating the trajectory of climate change requires fundamental policy changes at the national and global scale, there are several individual- and community choice-based steps that are impactful with collective action: (1) Exercise your consumer choices that prioritize supporting businesses that invest in renewable/net-zero C emission energy policies. While small individually, collective consumerism can enact progressive change. (2) Develop a deeper understanding of how increased CO_2 emissions impact our climate system, and why changes in temperature and precipitation negatively impact grassland ecosystems. The details of climate science can be confusing and has led to inaction for many individuals and nations. Spending time to learn how this change has happened, and why the threats are so dire will allow you to factually inform family and friends about this process. Thorough, simple and fact-based education is the key to dispelling misinformation and raising awareness that leads to action. (3) Support international conservation programs whose mission is to protect natural landscapes and recover degraded areas back into natural habitats. Organizations like The Nature Conservancy (among others) have a mission

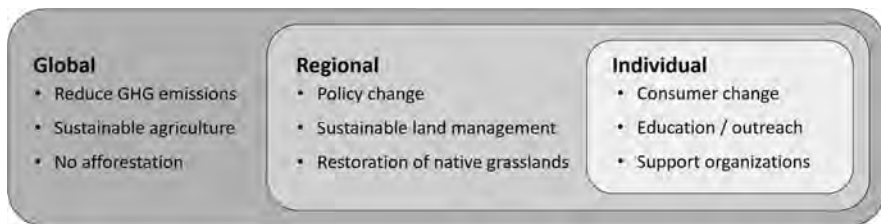| Global	Regional	Individual
• Reduce GHG emissions	• Policy change	• Consumer change
• Sustainable agriculture	• Sustainable land management	• Education / outreach
• No afforestation	• Restoration of native grasslands	• Support organizations

FIGURE 4.7   Climate actions for impactful long-term grassland conservation and restoration are possible at multiple levels. Section 4.4 outlines achievable actions possible at individual, regional and global levels.

to protect grassland ecosystems worldwide, and have the organization structure required to impact local, regional and national policies. Given that these organizations are nonprofit, they rely upon the support of the public to maintain their mission and continue to enact impactful climate actions.

4.4.2 Conserving and Restoring Local Grasslands

Protecting the grassland habitat that remains is the most impactful activity that we can all engage in. As noted throughout this chapter, grassland ecosystems throughout the world have been greatly impacted and transformed into agriculture, urban environments and degraded environments. The grassland habitat that remains – whether in natural environments or as fragments within urban environments or agricultural corridors – have intrinsic value. Mosaics of remnant grasslands provide key refugia for plant and animal species, resulting in increases in plant and animal diversity, as well as beneficial local ecosystem services like reduced runoff/erosion, increased C-storage belowground (in grassy plant roots), pollination services, reduced disease threats and habitat for migratory bird species. Given that functional grassland ecosystems take decades to centuries to establish (Baer et al. 2020), protection of existing grasslands should always be prioritized as our most important conservation action.

In the United States and likely in many locations throughout the world, local grassland societies have been organized. These societies typically have dual missions to protect specific locations, or regional grasslands, to provide educational outreach and to provide recreational opportunities for the public to engage with grassland ecosystems. Local grassland societies are powerful advocates for protecting remnant grasslands and maintaining functional grassland mosaics across the landscape. Supporting these local grassland societies with financial contributions or with your personal service and advocacy is one of the most meaningful climate actions available. At a larger scale, national and international conservation organizations commonly engage with landowners to establish Land Trusts. Land Trusts are established as part of estate planning and specify extended periods of time whereby natural lands remain undeveloped for agriculture or for urbanization. These activities ensure that grasslands will continue to provide functional ecosystem services across generations.

Conservation of intact ("natural") grasslands is definitively the most important climate action available for grassland ecosystems. As noted previously in this chapter, woody plant encroachment in grassland ecosystems is driven by a combination of global climate drivers and changes in local land-use drivers. This conversion of grassland ecosystems from grassy-dominated to woody-dominated results in a fundamental shift in ecosystem properties and services, and typically results in biodiversity losses (Ratajczak et al. 2012). Because the transition from grassland to shrubland/woodland-dominated represents an alternative stable state (Ratajczak et al. 2017), hysteresis in the system often slows recovery of the original grassland ecosystem (Collins et al. 2021) or requires intensive management options (Nippert et al. 2021). Specifically, because the transition from a shrub-dominated back to a grassy-dominated ecosystem is so challenging, the best course of action involves management plans that restrict woody plant expansion in the first place. Typically, this includes sound management policies that prioritize regular burning on the

landscape (Twidwell et al. 2013). For grassland locations where prevention of woody encroachment is no longer possible, prescriptive policies to physically remove woody plants (i.e., brush-cutting and tree removal) are often the only option. These campaigns are often laborious and expensive. However, many states agencies have funding available for woody removal as part of broader conservation goals. Limiting the spread of woody encroachment or implementing tree removal are a key first step for ecological restoration of grassland ecosystems.

Given the highly impacted nature of grassland ecosystems, ecological restoration is widely utilized to recover diversity and ecological functioning in previously degraded grasslands. As already mentioned, restoration can occur following woody encroachment, in locations previously converted to agriculture, or following removal of invasive species. Engagement with grassland restoration provides many opportunities to promote meaningful climate actions. Perhaps most importantly, the process of reintroducing native plant species (and native genotypes) into the environment has carryover positive impacts that initiate the process of restoring soil fertility, growing healthy root systems that store carbon in the soil, hydrological benefits that include reduced erosion and leaching as well as increased infiltration pathways (leading to vadose-zone soil moisture recharge). Grassland restoration also provides habitat for vertebrates and invertebrates species. For example, using diverse assemblages of local plant species provides increased niche space for specialized invertebrates, increased pollination services and an ecological platform that facilitates greater abundance and diversity of vertebrate species. The process of grassland restoration doesn't only apply to large acreage locations. There can be large benefits from establishing small grassland communities in urban environments. The simple act of replacing turf with mixes of native species reduces eutrophication and runoff (from lawn fertilizers), helps conserve water since native species are often more water-use efficient than turfgrass cultivars and provides ecosystem services like pollination and habitat for birds, small mammals and insects.

4.4.3 ENGAGEMENT IN COMMUNITY EDUCATION

Developing a long-term culture of appreciation for the natural world often begins with effective K–12 educational programs that seek to teach children about nature. Teaching and developing an appreciation for grassland ecology and grassland ecosystems at a young age is key to developing an informed population that values these lands for their inherent services beyond a commodity-based value system only. Starting with the youngest age groups, science educators are able to instill wonderment about grassland ecosystems, the species they harbor and the ecosystem services they provide. With older children, these basic concepts can be supplemented with science-based inquiry that explains the threat of climate change to grasslands and the corresponding impacts on local plant, animal and human communities. Building scientific concepts through time facilitates educational scaffolding providing both breadth and depth of scientific understanding in children and develops a population that both values *and* understands the natural world. If you are a local educator, reach out to local grassland societies or conservation groups for suggestions on incorporating educational materials, including field trips, within your curriculum.

Don't forget that many online curriculums and programs exist! If you are a parent, encourage your children's teachers and administrators to engage in grassland ecology education and science-based discussions of climate change drivers, impacts and consequences. If you are engaged citizen, encourage your local city councils and commissioners to support science-based and nature-based educational programs within your communities. Often, increased science-learning and science-based educational opportunities can happen with a few field trips per year, online engagement with outreach coordinators from grassland ecosystems and typically do not require large increases in financial expenditure. Perhaps more than any other climate action suggested, developing an appreciation and understanding of climate change impacts and climate action for grassland ecosystems among K–12 students has the most significant potential for long-term substantial climate actions.

4.4.4 Global Actions

There is no viable scientific explanation for these climate changes that doesn't include increased anthropogenic fossil fuel emissions as the primary driver of change. For this reason, there is no viable solution to the problem that doesn't include a large-scale reduction in fossil fuel emissions and the resultant CO_2 emissions of this energy-conversion process. Any "solution" that doesn't include drastic reductions in CO_2 is untenable. For this simple reason, impactful climate action for the long-term conservation of natural ecosystems like grasslands must include a detailed transition away from C-based energy sources toward zero net-emission energy sources.

Long-term observational and experimental research has increased our understanding of the impacts of climate change on grasslands and has led to an appreciation of the mechanisms that maintain grassland stability in response to disturbance. The biodiversity and stability of natural grasslands have become a model for sustainable agriculture, which aims to maintain economic viability while improving social equity and protecting environmental health and natural resources. These efforts, inspired by natural systems, include increasing biodiversity to help mitigate pest outbreaks and agrosystem resilience and patch-burn grazing that increases ecosystem biodiversity and improves habitat for wildlife. Transformative agricultural organizations like The Land Institute (Salina, KS, USA) use native grass species to develop deep-rooted perennial crops that protect soil health and increase C sequestration. The goal of perennial agriculture is to create productive, profitable agricultural systems that mimic the benefits of carbon and water cycling in grasslands. Thus, long-term grassland and climate research is directly related to the development of sustainable agriculture, which is becoming increasingly pressing in the face of climate change and a growing human population.

4.4.4.1 Case against Global Tree-Planting Campaigns in Grasslands

"Let Us Plant the Right Trees, in the Right Place, for the Right Reasons"

– William Bond.

It's tempting to look for actionable items that have been effective for climate change mitigation in other ecosystems, and then apply them to grasslands. One climate action that is relatively easy to implement, has widespread public enthusiasm and can be performed over large regions has been the sponsorship of tree-planting campaigns in deforested regions. Increased tree planting has the potential to sequester increased amounts of atmospheric CO_2 in woody biomass and alter radiative forcing and energy exchange through the development of complex tree canopies. Unfortunately, these "good ideas" to plant trees are often applied to afforested regions (Bond 2019), which typically include grasslands. A common misconception by the public is that the "good" of planting trees as a feasible climate action outweighs any inherent ecosystem services and innate climate buffering provided by native grassland communities. This is not the case, as grassland ecosystems are not a midpoint along a continuum from a degraded state to a forested state (Veldman et al. 2015). Planting trees in locations where trees have not previously existed in high abundance risks major biodiversity losses, changes in biogeochemical cycling, altered fire risks and increased water fluxes.

Perhaps a more appropriate climate action to offset the impacts of global changes is widespread perennial grass-planting campaigns. As we've already discussed, native grassland species provide a wide array of ecosystem services. Grassland ecosystems are often quite comparable in carbon sequestration to forests, especially when species with dense and deep root systems establish. Global climate change has increased the frequency and intensity of droughts for many locations worldwide. Grassy species are more resilient to drought, and their recovery from drought is often more robust compared to woody plant species (Choat et al. 2018). Widespread tree-planting campaigns intended for locations that experience natural and/or climate-change-driven drought may actually accelerate carbon losses. When forests are hit with drought and die, these locations are then more susceptible to fire, and fire-based C emissions (Dass et al. 2018). For these reasons, when the risks of fire and climate uncertainty (i.e., drought) are considered, the benefits of planting trees in grassland regions as a climate action seem clearly misguided.

4.4.5 CONCLUSION

Grasslands provide tremendous ecological and societal value worldwide. These ecosystems are key regulators of global processes like carbon, nutrient and water cycling as well as serving as key reservoirs of biological species diversity. As we've specified in this chapter, the threats of climate change are acutely present in grasslands. These impacts may vary across continents and grassland types, but there is a similar negative consequence of loss of function and a reduction in diversity that is felt worldwide. For these reasons, climate actions must be undertaken immediately. As outlined in this section, climate action plans can be prescribed at multiple scales (Figure 4.7). We are each able to begin making an impact within our local communities. These climate actions include our choices as consumers as well as supporting local grassroots organizations to protect and restore grasslands. The actions we take as individuals impact regional policies and education and outreach to promote

sustainable grassland management with regulations to minimize further degradation and reward public and private entities involved in grassland restoration. These regional changes will ultimately translate to large-scale (global) climate actions that reduce greenhouse gas emissions, prioritize grasslands and avoid false solutions like afforestation of grasslands. Working together at both local and national scales, we can help implement actions and policies that slow the negative impacts of climate change, and through time recover these ecosystems. Doing so, we will be protecting an ecosystem that provides beauty, key human services and an inherent sense of place to billions of people worldwide.

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