Chapter 7
Ecological Consequences of Climate Change on Rangelands

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Abstract Climate change science predicts warming and greater climatic variability for the foreseeable future. These changes in climate, together with direct effects of increased atmospheric CO_2 concentration on plant growth and transpiration, will influence factors such as soil water and nitrogen availability that regulate the provisioning of plant and animal products from rangelands. Ecological consequences of the major climate change drivers—warming, precipitation modification, and CO_2 enrichment—will vary among rangelands partly because temperature and precipitation shifts will vary regionally, but also because driver effects frequently are nonadditive, contingent on current environment conditions, and interact synergistically with disturbance regimes and human interventions. Consequences of climate change that are of special relevance to rangelands are modification of forage quantity and quality, livestock metabolism, and plant community composition. Warming is anticipated to be accompanied by a decrease in precipitation in already arid to semiarid rangelands in the southwestern USA, Central America, and south and southwestern Australia. Higher

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temperatures combined with drought will significantly impair livestock production by negatively impacting animal physiological performance, increasing ectoparasite abundances, and reducing forage quality and quantity. Conversely, the warmer, wetter conditions anticipated in the northwestern USA, southern Canada, and northern Asia may increase animal productivity by moderating winter temperatures, lengthening the growing season, and increasing plant productivity. Synergist interactions between climate change drivers and other human impacts, including changes in land-use patterns, intensification of disturbances, and species introductions and movements, may further challenge ecosystem integrity and functionality. Evidence from decades of research in the animal and ecological sciences indicates that continued directional change in climate will substantially modify ecosystem services provisioned by the world's rangelands.

7.1   Introduction

Climate change science predicts warming and greater climatic variability for the foreseeable future, including more frequent and severe droughts and storms, as a consequence of increasing atmospheric concentrations of greenhouse gases (GHGs). These gases, which include carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and tropospheric ozone (O_3), reduce cooling of the Earth by partially blocking the emission of long-wave infrared radiation into space to create a "greenhouse effect" that is vital to buffering day-night temperature fluctuations on Earth. GHG concentrations are rising largely as a result of human activities (IPCC 2013) and will continue to rise for the foreseeable future even if emission rates decline because GHGs remain in the atmosphere for hundreds of years (Karl et al. 2009). Increased GHG concentrations will amplify the current greenhouse effect and further warm the Earth and modify precipitation patterns.

These changes in climate, together with the direct effects of increased CO_2 concentration on plant growth and transpiration, will influence factors such as soil water availability and nitrogen (N) cycling that regulate the provisioning of plant and animal products and other services from rangeland ecosystems (Walther 2003, 2010; Joyce et al. 2013; Polley et al. 2013). Climate change alone or in combination with impacts of other human activities, such as intensification of disturbances, may force ecosystems beyond their historical range of variability. This may result in a change in ecosystem structure and function that will be difficult to reverse on the management timescale of decades (Joyce et al. 2013).

We provide a (1) brief review of climatic trends during the twentieth century that provide evidence of a climate change signature, (2) summary of changes in climate anticipated on the world's rangelands during the twenty-first century, (3) synthesis of key "principles" from the ecological and climatological sciences that are foundational to projecting climate change impacts, and (4) assessment of three plausible climate change scenarios for rangelands.

7.2 Recent Climatic Trends: A Climate Change Signature

The Earth's climate changed throughout geological history in response to natural events, but we have entered an era in which human impacts on global fluxes of radiative energy have demonstrable effects on climate (IPCC 2013). This modern climate change signature is evident in the form of atmospheric warming, rapid glacial retreat, accelerated plant phenology, modified precipitation patterns, and increasing wild fires (Parmesan and Yohe 2003; IPCC 2013). Global mean temperature increased during recent decades, particularly in northern latitudes and over land. Each of the last three decades has been successively warmer at the Earth's surface than any preceding decade since 1850 (IPCC 2013). Six of the 10 years from 1998 through 2007 were among the hottest 10 % recorded for much of North America (NOAA National Climatic Data Center 2013).

Precipitation has also increased on average during recent decades, particularly in the Northern Hemisphere and at midlatitudes (IPCC 2013). Importantly, however, precipitation has declined by >5 % in several areas of the world with extensive grazing lands. These areas include southeastern Australia, central Africa, the Mediterranean grasslands, and woodlands in southern Europe, and rangelands of northwestern North America.

A climate change signature also is evident in the form of an increasing frequency of extreme weather events, including greater precipitation variability. The frequency of intense precipitation events has increased in North America and Europe, but there is lesser confidence that this change has occurred for other continents (IPCC 2013).

7.3 Climate Change Projections

Atmospheric temperature increased by 1 °C since industrialization (ca. 1750) largely as a result of increasing concentrations of CO_2 (Keeling et al. 2009) and other GHGs (IPCC 2007). Globally, surface air temperature is predicted to increase by 2–4 °C by the final decades of this century, relative to the 1986–2005 average (IPCC 2013). Warming is expected to be greatest at northern latitudes (Fig. 7.1) and at night.
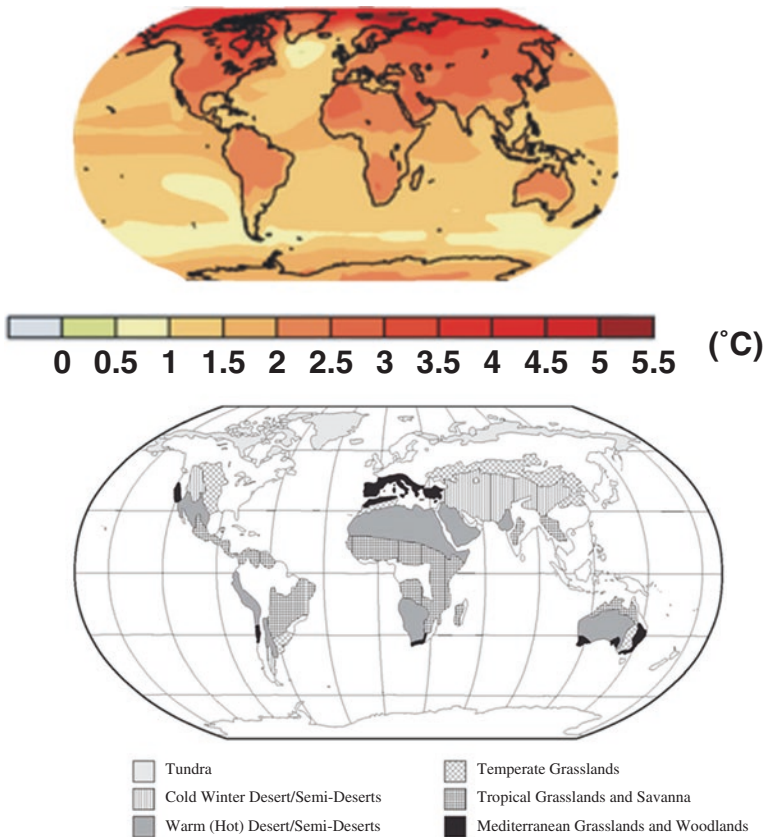
Fig. 7.1 The annual average of air temperature change at the Earth's surface as simulated by climate models for the period 2046–2065 (*upper panel*) and distribution of the world's rangelands (*lower panel*; redrawn from Allen-Diaz 1996). Temperature change is calculated relative to the average for the period 1980–1999. The *upper panel* is adapted from IPCC (2007)

Warming is anticipated to increase weather extremes, including both intra- and interannual precipitation variability and the occurrence of both drought and heat waves, by altering atmospheric circulation patterns (Easterling et al. 2000; McCabe and Clark 2006). Projections of regional and seasonal shifts in precipitation include greater uncertainty than those of CO_2 or temperature modification, but precipitation generally is expected to increase near the poles and decrease elsewhere, with significant seasonal variation (IPCC 2007). Precipitation is anticipated to increase during winter in the northwestern USA, southern Canada, and northern Asia, and during spring in central North America, but decrease by 10–20% during winter and spring in southern Africa and during spring and summer in central Asia. Average annual precipitation is expected to decrease in southwestern North America.

Reduced precipitation and more frequent droughts are forecast for much of Australia, particularly southern and southwestern regions (IPCC 2007). Climate change also may increase the size or intensity of events when they do occur (Groisman et al. 2005; Karl et al. 2009). Heat waves are anticipated to increase in both frequency and magnitude in proportion to increasing mean temperature.

The issues of global GHG accumulation and its consequences for future climate patterns are necessarily complex (Lindzen 1999), as evidenced by the unanticipated slowing of global warming for more than a decade (Smith 2013). Despite uncertainties and the apparent "pause" in the warming trend, which has been attributed partly to heat uptake by ocean waters (Guemas et al. 2013), it would be irresponsible to ignore the cumulative evidence for a climate change footprint and the well-documented and continuing GHG accumulation that, given current understanding, must eventually lead to additional warming at the Earth's surface (IPCC 2013).

The climate change drivers of warming, precipitation modification, and CO_2 enrichment each will influence rangeland structure and function with impacts on animal production. Temperature regulates rates of chemical reactions, animal metabolism, and water and energy fluxes. However, CO_2 concentration influences rates with which leaves exchange CO_2 and H_2O with the atmosphere. Precipitation regulates plant productivity and associated ecosystem processes by determining soil water availability.

7.4 Key Scientific Principles for Projecting Climate Change Impacts

In this section, we discuss key scientific findings or principles that form the basis for our assessment of climate change impacts on rangelands. We regard each principle as a critical generalization resulting from years of research in the ecological or climatological sciences. Together, these principles inform our evaluation of rangeland-climate interactions.

7.4.1 Magnified Greenhouse Effects Are Irreversible

Climatic consequences of the magnified greenhouse effect are irreversible for a minimum period of decades to centuries given current technologies. GHG concentrations and climate are changing at a rate that is and likely will continue to be exceedingly rapid compared to past changes.

Despite important uncertainties about the magnitude of atmospheric warming, dynamics in the Earth climate system make additional climate change a virtual certainty. Indeed, centuries may be required for climate to equilibrate with current levels of GHGs (Matthews and Weaver 2010). For instance, warmed oceans cause air temperature to increase even if atmospheric CO_2 concentration is stabilized. The decrease in warming that would result from slowly declining CO_2 concentrations would largely be offset by heat loss from warmed oceans (Solomon et al. 2009). Dynamics of C-cycle processes also will lead to warming by causing CO_2 concentration to continue to rise in the absence of anthropogenic emissions if, as anticipated, climate change leads to loss of organic C from terrestrial ecosystems by causing widespread forest loss or thawing of permafrost (Koven et al. 2011).

Climate is changing at an unprecedented rate. For example, rates of change were greater during the period from 1880 to 2005 than during the Little Ice Age and early Holocene (Diffenbaugh and Field 2013) and further acceleration is anticipated. These unprecedented rates of change challenge the coping capacity of social-economic-biophysical systems (Joyce et al. 2013; Chap. 15, this volume) and the ability of many organisms to track favorable climatic conditions across the landscape. Consequences include shifts in vegetation patterns and range distributions, increases in rapidly dispersed "weedy" species, and the potential occurrence of plant communities that have not previously existed (Polley et al. 2013).

7.4.2 Ecological Consequences of Climate Change Will Vary Regionally

Climate change will impact ecological processes differently in different regions because the magnitude, decadal timing, or seasonal patterns of warming and precipitation modification will be expressed differently among regions. Climate change impacts likely will be greatest for rangelands where climate shifts amplify currently positive climatic effects or exacerbate climatic limitations on plant and animal productivity or surface water supplies. For example, intensification of drought (warmer, drier conditions) may elevate the risk of extensive plant mortality and even of biome reorganization in arid ecosystems in which plants already function with limited water availability (Ponce Campos et al. 2013; see Box 7.1).

7.4.3 Climate Drivers Have Unique but Potentially Interactive Effects on Plants and Ecosystem Processes

Climate drivers have unique effects on plants and ecosystems. For example, temperature regulates water and energy fluxes between land surfaces and the atmosphere, whereas CO_2 concentration influences rates of leaf photosynthesis and transpiration, in addition to retaining thermal energy near the Earth's surface.

Text Box 7.1: Climatic drying accelerates degradation of semiarid shrubland ecosystems

A recent trend toward greater aridity intensified stresses in a semiarid shrubland in Spain on a drought-prone soil (Vicente-Serrano et al. 2012). Increased temperature increased evaporative demand causing plant cover to decline during summer and in areas in which water limitation is common. Plant cover increased between 1984 and 2009 as temperature increased on some shrublands (*top panel*), but decreased strongly in more water-limited communities on infertile gypsum soil (*lower panel*). Photographs are reproduced from Vicente-Serrano et al. (2012) with permission from the Ecological Society of America.

Text Box 7.1: (continued)

The combined effect of climate change drivers may differ from that anticipated by summing single-driver effects (Fig. 7.2; but see, Dukes et al. 2005). For instance, plant biomass responses to combined warming and CO_2 enrichment treatments often are smaller than anticipated from single-factor experiments (Morgan et al. 2011; Dieleman et al. 2012). Interactions also are evident in driver effects on plant community composition. Responses of foliar cover to experimental warming were species specific in an old field, varied through time, and were contingent on precipitation treatments (Engel et al. 2009). Warming may exacerbate effects of reduced precipitation on rangelands (Hovenden et al. 2008; Sherry et al. 2008), but the ecosystem consequences of the combination of climate change drivers generally are not as extreme as would be anticipated from single-driver effects (Wu et al. 2011; Dieleman et al. 2012).
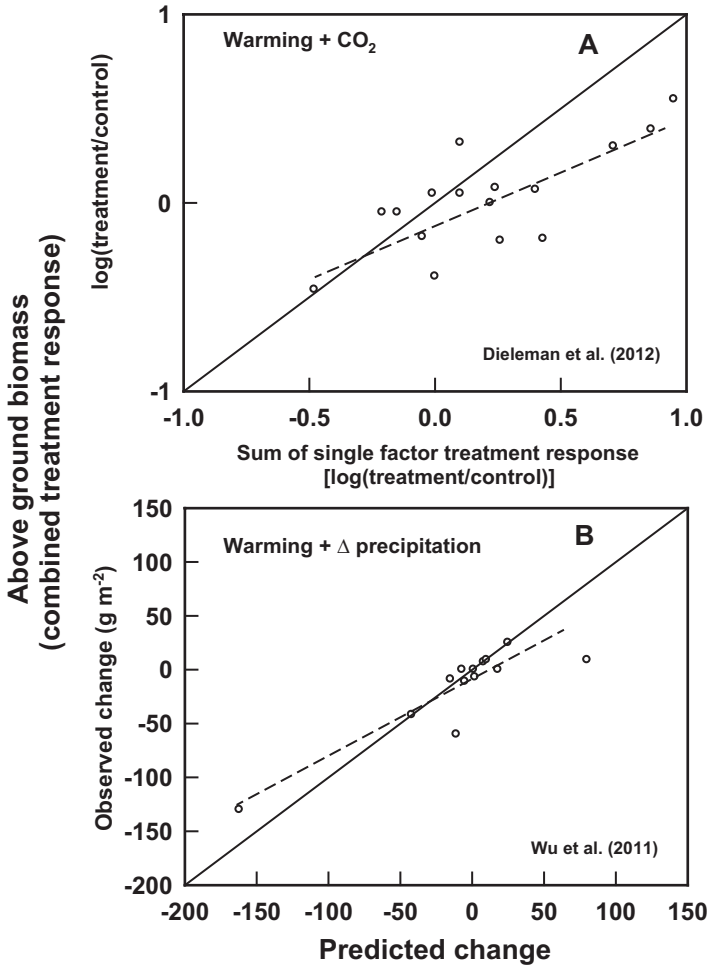
Fig. 7.2 The combined effects of warming and either CO_2 enrichment (**a**) or precipitation treatment (**b**) on aboveground biomass plotted versus biomass values predicted by summing responses from single-factor manipulations. Data are reported as either the logarithm of the ratio of treatment to control biomass (**a**) or as the difference in biomass between the treatment and control (**b**). The *solid line* is the 1:1 line representing the responses expected if warming did not modify the CO_2 or precipitation response. Most observations fall below the 1:1 line, indicating that combined treatment effects are smaller than anticipated by summing effects from single-factor manipulations

7.4.4 Rangelands Will Respond Strongly to Driver Effects on Soil Water Availability

Plant productivity and community composition are regulated by soil water availability on rangelands.

The importance of precipitation, by inference of soil water availability, to plant productivity is evident in positive relationships between plant productivity and

various measures of precipitation, both across (e.g., Rosenzweig 1968; Lieth 1973; Sala et al. 2012) and within ecosystem types (e.g., Sala et al. 1988; Huxman et al. 2004). Indeed, water is the most limiting resource on arid and semiarid rangelands (Smith and Nowak 1990). The importance of precipitation to plant community structure and composition is evident in the marked shift in grassland vegetation that occurs along a west-to-east gradient of increasing precipitation in the Great Plains of North America (Risser et al. 1981) and in the major shifts in plant composition that occurred during the 1930s' drought in the Great Plains (Weaver and Albertson 1943). The strong link between precipitation and rangeland function implies four climate change-relevant corollaries to Principle 4 (Sect. 7.4.4).

Corollary 1 Climate change drivers strongly influence precipitation patterns and rates of evapotranspiration, potentially leading to large changes in soil water availability.

Warming of the biosphere is anticipated to increase both interannual and intra-annual precipitation variability with possible shifts in precipitation seasonality (Easterling et al. 2000; McCabe and Clark 2006) and associated shifts in temporal patterns of soil water content. One of the primary ecosystem-level effects of warmer temperatures is to reduce water availability to plants by increasing evaporative demand (McKeon et al. 2009). The resulting increase in plant water stress often reduces plant productivity in the absence of compensating precipitation changes (Parton et al. 2007). One of the primary effects of CO_2 enrichment is to increase plant growth per unit of water transpired (plant water use efficiency; Ainsworth and Long 2005) and, at least temporarily, reduce canopy-level transpiration rate to slow the decline in soil water content during periods between precipitation events (Morgan et al. 2004b; Fay et al. 2012).

Corollary 2 The effect of precipitation variability on plant productivity differs among ecosystems and as a function of the current precipitation regime.

Plant productivity (NPP) of a given ecosystem varies among years in response to interannual precipitation variability, but the relationship of NPP to precipitation variability differs among rangelands as a function of the current precipitation (Fig. 7.3). The NPP-precipitation relationship differs among ecosystems partly

Fig. 7.3 The interannual coefficient of variation (CV) in aboveground net primary productivity (ANPP) for desert, grassland, old-field, and forest sites, respectively, along a gradient of increasing annual precipitation. The figure is adapted from Knapp and Smith (2001)
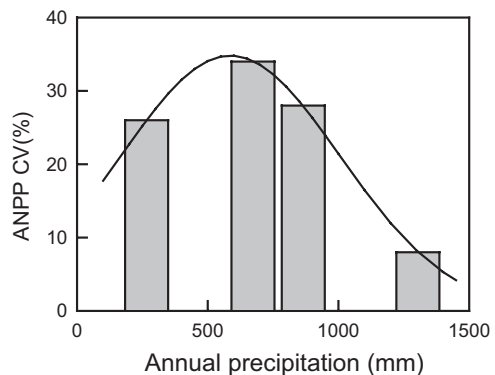
because rain-use efficiency varies among ecosystems as a result of differences in plant life history traits and biogeochemical cycling (Huxman et al. 2004). In general, NPP is more responsive to annual increases in precipitation than to precipitation declines in warm and either mesic or semiarid than in desert rangelands because the NPP response is constrained in deserts by low plant density and leaf area (Knapp and Smith 2001).

The response of rangeland NPP to intra-annual variability in precipitation also differs among ecosystems and depends on current precipitation. The anticipated shift to larger, but less frequent precipitation events (Groisman et al. 2005; Karl et al. 2009) is expected to increase the duration and severity of drought stress and hence reduce aboveground NPP (ANPP) in mesic rangelands (Knapp et al. 2002), but increase ANPP in more arid systems (Heisler-White et al. 2009). The ANPP impact of changing the size and frequency of precipitation events can be envisioned using a conceptual "soil water bucket" model (Knapp et al. 2008; Fig. 7.4). According to this model, the amount of water in the rooting zone of plants (the soil water bucket) has both upper and lower stress thresholds for plant and ecosystem processes. Plant and ecosystem processes approach maximum rates when soil water availability is neither limiting nor excessive. On mesic rangelands with annual precipitation of approximately 600–1000 mm, the soil water bucket usually is moderately full. For these ecosystems, a shift to larger, but less frequent precipitation events increases the frequency and duration of periods during which soil water content falls below the lower stress threshold by increasing water losses to runoff and percolation to groundwater. In more arid ecosystems where soil water content usually is low, precipitation that arrives in fewer, larger events is anticipated to increase the proportion of precipitation that
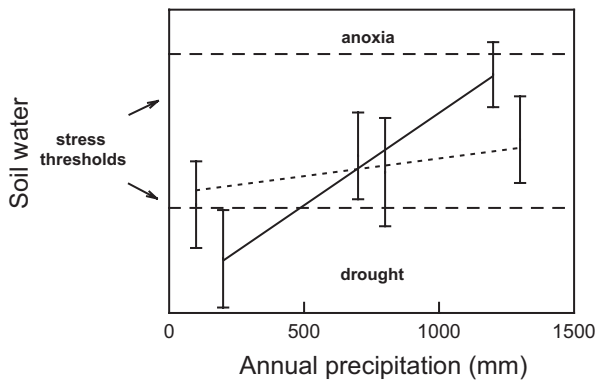

Fig. 7.4 A conceptual depiction of effects of mean annual precipitation on the response of soil water dynamics to precipitation and fewer, larger precipitation events (Knapp et al. 2008). *Vertical bars* represent temporal fluctuations in soil water content as influenced by intra-annual variation in precipitation for each of the three sites along a precipitation gradient (arid; <500 mm, mesic, wet; >1000 mm). A *solid line* connects idealized responses given the current size and frequency of precipitation events. A *dashed line* connects responses envisioned under a precipitation regime characterized by larger, but fewer events

percolates beneath upper soil layers where it is most susceptible to evaporation. Greater percolation to depth should increase ANPP by reducing the frequency or duration of periods during which soil water content remains below the lower stress threshold. Consistent with the soil water bucket model, it was found that delivering the same total of precipitation as fewer, but larger events increased ANPP by 30 % in semiarid shortgrass steppe, but decreased ANPP by 10–18 % in tallgrass prairie (Knapp et al. 2002; Heisler-White et al. 2009).

Corollary 3 Precipitation regulates the response of productivity to CO_2 but not to warming.

The ANPP response to CO_2 varies as a function of precipitation when considered across ecosystems. The ANPP-CO_2 response peaks at "moderate" levels of annual precipitation (300–400 mm) across desert and grassland ecosystems (Fig. 7.5; Nowak et al. 2004; Morgan et al. 2004b). Productivity responds relatively little to CO_2 when precipitation is very low because water stress inhibits growth and may contribute to plant senescence and mortality if it becomes sufficiently severe. The benefits of elevated CO_2 on productivity are reduced when annual precipitation is >400 mm partly because the efficient use of water use is no longer a critical variable (Nowak et al. 2004; Morgan et al. 2004b). Therefore, the average across-ecosystem response of NPP to CO_2 likely will be greatest in systems in which NPP is or will become moderately water limited (Nowak et al. 2004; Morgan et al. 2004b, 2011; Webb et al. 2012).
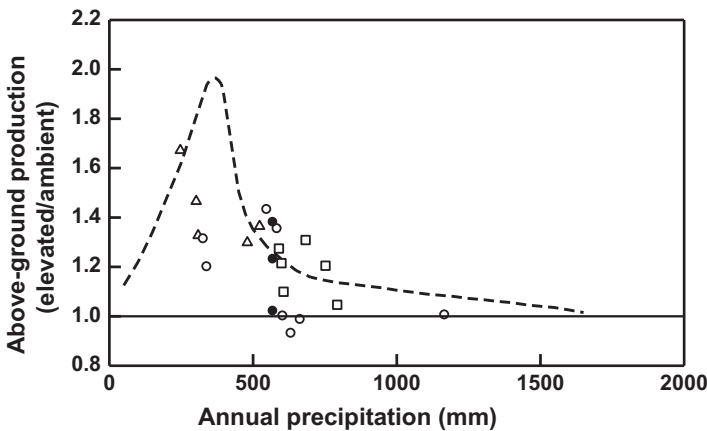

Fig. 7.5 The ratio of ANPP at elevated compared to ambient CO_2 (E/A) varies as a function of precipitation for grassland and desert ecosystems. The *dashed line* in the figure represents a conceptual model of the maximal E/A vs. precipitation relationship developed by Nowak et al. (2004). Symbols denote annual data from field experiments with open-top chambers on tallgrass prairie (*open circles*; Owensby et al. 1999), shortgrass steppe (*open triangles*; Morgan et al. 2004a), and Swiss calcareous grassland (*open squares*; Niklaus and Körner 2004), and the 5-year average of E/A for tallgrass prairie vegetation grown in elongated chambers on each of the three soil types (*closed circles*; Fay et al. 2012; Polley et al. 2012) as a function of growing season precipitation. The figure is adapted from Nowak et al. (2004) and Morgan et al. (2004b)
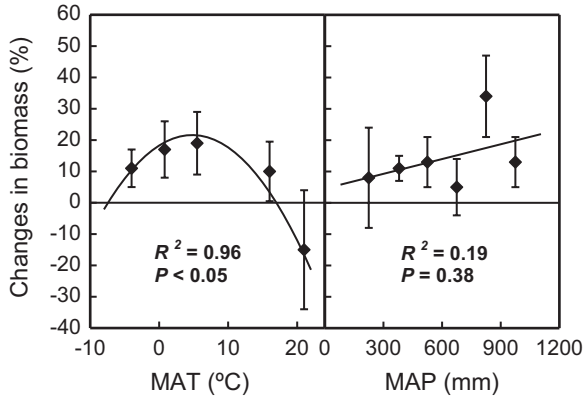
Fig. 7.6 Biomass responses of terrestrial plants to experimental warming plotted versus the mean annual temperature (MAT) and mean annual precipitation (MAP) at the site of origin. Values are means ± 95 % CI. The biomass response to warming varies as a quadratic function of MAT, but is not significantly related to MAP. Figures are adapted from Lin et al. (2010)

By contrast, there is no consistent relationship between biomass response to experimental warming and mean annual precipitation (MAP) across terrestrial plants studied (Fig. 7.6; Lin et al. 2010). Experimental warming has been shown to reduce soil water content by increasing evapotranspiration (Harte and Shaw 1995; Wan et al. 2005), with potentially negative effects on ANPP. Warming also may enhance productivity by alleviating low temperature limits on plant growth (Luo 2007; Lin et al. 2010) and increasing N mineralization (Rustad et al. 2001; Dijkstra et al. 2008). These opposing influences of warming may explain why many rangeland experiments have shown little consistent warming effect (Polley et al. 2013) and why interactive effects of warming and altered precipitation are smaller than expected from single-factor effects (Fig. 7.2b; Wu et al. 2011; Morgan et al. 2011; Xu et al. 2013).

Corollary 4 Precipitation seasonality regulates ecosystem responses to both CO_2 and warming.

Warming and CO_2 enrichment combined should lead to earlier and more rapid plant growth in ecosystems dominated by winter precipitation because warming will reduce temperature limitations on both growth and growth responses to CO_2. On the other hand, warming may reduce CO_2 benefits on arid and semiarid rangelands dominated by summer precipitation by increasing evaporative demand. The evaporative potential of air increases nonlinearly with temperature, such that a given increase in temperature will cause a disproportionately large increase in evaporative demand when temperature is high.

Plant responses to CO_2 enrichment alone also depend on the seasonal distribution of precipitation. CO_2 stimulated ANPP of Australian grassland most during years when summer rainfall exceeded rainfall during spring and autumn (Hovenden et al. 2014). High rainfall during cool spring and autumn seasons may reduce production in this grassland by intensifying N limitation to plant growth.

7.4.5 Soil Nitrogen (N) Availability both Regulates the Response of Plant Productivity (NPP) to Climate Change Drivers and Is Affected by Drivers

Plants require adequate supplies of N for growth and reproduction; consequently N availability will regulate plant responses to climate change drivers. As many of the pathways in the soil N cycle are temperature and soil water dependent, N availability is, in turn, influenced by these drivers.

Corollary 1 N regulation of NPP-climate responses differs among climate change drivers.

Most terrestrial N occurs in organic forms that are not readily available to plants; hence rangeland responses to climate change drivers depend partly on how quickly N is mineralized from organic to inorganic forms that are available to plants. Low N availability frequently limits plant productivity on rangelands (e.g. Seastedt et al. 1991) and may reduce or even eliminate any benefit of CO_2 enrichment for plant growth (Owensby et al. 1994; Reich et al. 2006; Reich and Hobbie 2012). Conversely, N availability does not appear to restrain plant response to experimental warming (Lin et al. 2010). Typically, N limits plant production in arid and semiarid ecosystems only if drought stress is alleviated (Ladwig et al. 2012), implying that N availability will have little effect on ANPP on arid and semiarid rangelands such as those in the southwestern North America and south and southwestern Australia that are predicted to become even drier.

Corollary 2 Climate change drivers may accelerate or slow N cycling with possible feedbacks on NPP.

Experimental warming increases N availability to plants by accelerating N mineralization rates, provided that soil water is available (Rustad et al. 2001; Dijkstra et al. 2008), but warming also may increase N losses (Wu et al. 2012). Water addition to dry soil greatly increases N mineralization rates, but the long-term relationship between precipitation and ecosystem N pools and N cycling is more complicated. Nitrogen pools increase along a gradient of increasing precipitation from shortgrass steppe to tallgrass prairie in the central USA, but rates of litter decomposition and of resin-captured N in soil decline (McCulley et al. 2009).

CO_2 enrichment has been hypothesized to create or reinforce N limitations on ANPP by reducing N mineralization. To the extent that CO_2 enrichment increases plant production and ecosystem C accumulation, it also increases the sequestration of N and other elements in long-lived plant material and organic matter leading over time to a decline in N availability to plants [the progressive N limitation (PNL) hypothesis; Luo et al. 2004]. Elevated CO_2 reduces soil N availability in some cases (Reich et al. 2006; Reich and Hobbie 2012), but results from most experiments indicate that the strength of this negative feedback is reduced by processes that delay the onset of N limitation or enhance N accumulation in soil-plant systems (Polley et al. 2011). For example, rates of N input in arid ecosystems are thought to be balanced by similar rates of gaseous

loss of N (Peterjohn and Schlesinger 1990), but the addition of labile C (McCalley and Sparks 2008), as may result from CO_2 enrichment (Schaeffer et al. 2003), greatly decreases N emissions. Microbial activity in arid lands is limited by available C (Schaeffer et al. 2007); consequently CO_2 enrichment may increase C inputs into soil, which then accelerate rates of soil organic N mineralization to increase the availability of inorganic N to plants (Billings et al. 2004; Jin and Evans 2007; Jin et al. 2011). CO_2 enrichment may further increase N availability by increasing the biomass and diversity of fungi (Jin and Evans 2010; Nguyen et al. 2011) that utilize recalcitrant soil substrates and by increasing the activities of enzymes involved in N and C cycling (Jin and Evans 2007; Jin et al. 2011). Increased N_2 fixation, increased N use efficiency, and increased root foraging for N at elevated atmospheric CO_2 also may delay potential decreases in soil N (Luo et al. 2006). The preponderance of evidence indicates that gradual sequestration of N in organic matter will not strongly limit the responses of rangeland plants to climate change drivers.

7.4.6 Ecosystem Responses to Climate Change Drivers Vary Because of Differences in Management Practices and Historical Land-Use Patterns

Effects of climate change drivers on ANPP and other ecosystem processes are governed by a set of variables "internal" to ecosystems. These internal controls, which include soil resource supply and characteristics, current or potential biota, and current and historical land-use patterns and accompanying disturbance regimes, all contribute to variation in ecosystem responses to climate change drivers (Lindenmayer et al. 2010; Polley et al. 2013). For example, fire indirectly affects responses to drivers by modifying soil resources and vegetation. Fires volatilize substantial quantities of N (Seastedt et al. 1991); hence frequent burning may constrain ecosystem responses to drivers by reinforcing N limitations on plant growth. Land uses such as grazing also regulate rangeland responses to climate change. Sheep grazing limited CO_2 stimulation of grassland productivity by selectively consuming the two groups of plants (legumes, forbs) with the greatest growth responses to CO_2 (Newton et al. 2014).

7.4.7 Climate Change Drivers Affect Livestock Production both Directly and Indirectly

Corollary 1 Warming causes greatest physiological impairment to livestock in environments that are currently warm.

Livestock performance is optimal when ambient temperatures are within the "thermo-neutral zone" (Ames and Ray 1983) where forage intake and energy requirements of livestock are not affected by temperature. At temperatures below

Table 7.1 Potential consequences of heat stress for cattle performance

Immediate (hours to days)	Medium term (days to weeks)	Long term (weeks to years)
Increased activity to dissipate heat (e.g., increased sweating and time in shade)	Altered metabolism (e.g., decreased feed conversion efficiency)	Increased ectoparasite loads
Increased water intake	Reduced milk production	Reduced reproduction
Reduced forage intake	Reduced growth	Possibly increased mortality

the thermo-neutral zone, animals increase energy production and forage intake to maintain homeostasis. At temperatures above the thermo-neutral zone, animals become stressed and must actively dissipate heat by reducing walking and spending more time in shade (Table 7.1). Heat stress can dramatically reduce milk production and the efficiency of feed conversion (Wayman et al. 1962; McDowell 1968) by reducing forage intake, changing nutrient portioning independent of intake, and reducing capacity to mobilize body fat and employ glucose-sparing mechanisms (Baumgard and Rhoads 2012). Heat stress also reduces reproduction rates by reducing male and female gamete production, embryonic development, and fetal growth (Hansen 2009; Kadokawa et al. 2012). Heat stress can be fatal to livestock, especially those fed large quantities of high-quality feeds, as evidenced by the mass mortality of feedlot cattle during heat waves (Hahn 1999). Values of a temperature humidity index (THI; the weighted product of air temperature and relative humidity) greater than 80 are considered heat stress days, requiring deployment of sprinklers, additional shade, or similar cooling measures to minimize deaths among feedlot cattle (Hahn 1999). The number of days that THI exceeds 80 may increase by 138 % by 2070 (Howden et al. 2008).

Detrimental effects of heat stress will be intensified if climate change results in more frequent and severe droughts, as are forecast for southwestern North America (Seager and Vecchi 2010) and south and southwestern Australia (IPCC 2007). Springs and dugouts on arid and semiarid rangelands often dry during drought, requiring that livestock travel greater distances for water. Walking increases the heat load, and animals must increase sweating and respiration rates to maintain homeostasis (Moran 1973).

Corollary 2 Climate change drivers reduce livestock production by increasing abundances of ectoparasites and reducing forage quality and quantity.

Warmer temperatures may suppress livestock productivity by increasing winter survival of ectoparasites to facilitate larger populations (Karl et al. 2009). Horn flies [*Haematobia irritans* (L.)] are the primary pest of concern for cattle in the USA (Byford et al. 1992). Horn flies can reduce cattle weight gain by 4–14 %, and adversely impact animal physiological functions by increasing cortisol production

and decreasing N retention (Byford et al. 1992; Oyarzún et al. 2008). Horn flies also promote livestock-avoidance behaviors, such as walking and tail switching (Harvey and Launchbaugh 1982). These additional activities and energy expenditures directly contribute to reduced livestock performance. Ticks (*Amblyomma americanum* Koch) reduce weight gains of British breeds, such as Hereford, by greater than 30 % (Byford et al. 1992). By contrast, ticks have less effect on Brahman crosses with British and Continental cattle, and little, if any, effect on Brahman cattle (Utech et al. 1978; George et al. 1985). Livestock gains in Australia could decrease by greater than 18 % because of increased tick infestations associated with climate change unless European and British cattle breeds are replaced by Brahmans or other tick-resistant breeds (White 2003).

Climate change drivers also are anticipated to reduce livestock performance on many rangelands by reducing forage quantity, quality, or both (Polley et al. 2013). Drought obviously reduces forage production, whereas elevated CO_2 has consistently been shown to increase plant C:N ratios and decrease tissue N concentrations (Cotrufo et al. 1998; Morgan et al. 2001), resulting in forage with reduced crude protein levels. Forage digestibility often declines at elevated CO_2 (Morgan et al. 2004a; Milchunas et al. 2005). Regional-scale analyses indicate that livestock become more nutrient limited in warmer and drier climates as both dietary crude protein and digestible organic matter content of forages decrease (Craine et al. 2010). A 4-year study in the tallgrass prairie showed that warming reduced N concentration and, correspondingly, crude protein levels of live and dormant forage from five warm-season grasses (An et al. 2005). In the absence of protein supplementation, cattle production will decline if forage quality declines too greatly because forage intake is volume limited. Forage quality may increase in cooler regions, such as the northern USA and southern Canada (Craine et al. 2010), if winters become warmer and wetter as anticipated.

7.4.8 Climate Change Indirectly Affects Vegetation Composition and Structure by Influencing Fire Regimes

Fire affects the composition of vegetation partly by favoring fire tolerant over fire-sensitive species. Fire is an important, although not exclusive, predictor of the relative abundances of comparably fire-tolerant grasses and fire-sensitive woody vegetation (Bond 2008) and of the global distribution of the savanna biome (Staver et al. 2011). By increasing fine fuel loads, exotic grasses can increase wildfire frequency to the detriment of native vegetation. Proliferation of the exotic annual grass *Bromus tectorum* (cheatgrass), for example, has significantly increased fire frequency and even the spatial areas of fires in invaded areas of the Great Basin, USA (Balch et al. 2013).

Shifts in temperature and precipitation are known to modify fire regime. Most wildfires in the western USA occur during the hottest, driest portion of the year (Westerling et al. 2003). Fires are largest in grass- and shrub-dominated ecosystems when unusually wet-growing seasons during which fine fuels accumulate are followed by dry conditions that enhance fuel flammability and ignition (Littell et al. 2009). In contrast, fires are largest in western forested ecosystems of North America when precipitation is low and temperature is high in both the fire year and the preceding year. Fire activity is projected to increase if the climate becomes both warmer and drier (Pechony and Shindell 2010).

Warmer and drier conditions are conducive to more frequent fires, but sufficient fuels will be required to sustain rangeland fires. Increased CO_2 could increase fire frequency or intensity (Sage 1996) and thereby reinforce the effects of fire on ecosystem processes by increasing plant production (fuel load) and fuel flammability or favoring fire-adapted plant species. Plant growth appears to be particularly responsive to CO_2 among several fire-adapted annual grasses, including *Bromus tectorum* and *Avena barbata* (Jackson et al. 1994; Ziska et al. 2005).

7.4.9   Climate Change May Lead to Communities That Are Unlike any Found Today, with Important Consequences for Ecosystem Function and Management

Climate change may alter the composition or relative abundances of species in plant communities. Increased weather variability is anticipated to favor short-lived plants and other organisms (e.g., animals, insects, diseases) that can response rapidly to environmental change. Vegetation shifts are expected to result largely from changes in the amount, seasonal pattern, and vertical distribution of soil water (Knapp et al. 2008; Volder et al. 2010).

Climate change will lead to combinations of seasonal temperature and precipitation that differ from current climatic conditions. Consequently, climate shifts may support plant communities that are compositionally unlike any found today (no-analog or novel communities; Williams and Jackson 2007), perhaps accompanied by changes in the number and functional types of species present. For example, species diversity is lower and the latitudinal shift in the ratio of C_3 to C_4 species is more pronounced in novel than native communities in the tallgrass prairie region of North America (Martin et al. 2014).

Past episodes of climate change drove local extinctions that led to vegetation change as geographic shifts in climatic conditions outpaced the capacity of many plant species to migrate and establish (Blois et al. 2013). Species that successfully colonize following extinctions often are ecological generalists (e.g., many "weedy" species). Increased establishment of generalist species leads, in turn, to the development of progressively more homogenous plant assemblages across

spatial scales. Climate change may exacerbate vegetation homogenization by favoring generalist and often exotic species (Everard et al. 2010; Blois et al. 2013), with potentially negative effects on ecosystem function (Isbell et al. 2011).

7.4.10 Increased Climatic Variability Increases Fluctuations in Ecological Systems, Rendering Sustainable Management More Difficult

Human learning to avoid cycles of degradation is hindered by variability in both ecological and social-economic systems (Stafford Smith et al. 2007). Increased variability in ecological systems in future climates, combined with mismatches in the temporal or spatial scales at which human impacts and ecological processes change, can lead to rangeland degradation. Stafford Smith et al. (2007), for example, described a cycle of rangeland degradation that has been repeated multiple times in Australia over the past century. Favorable climatic and economic conditions lead initially to an increase in the number of livestock maintained per unit of land area (stocking rate). Subsequent drought decreases forage production, often leading to overgrazing, especially when drought is coupled with government inducements (e.g., feed subsidies) or reduced livestock prices that lessen incentives for producers to destock (Thurow and Taylor 1999). Excessive defoliation reduces herbaceous cover potentially leading to greater soil erosion. The combined impacts of drought, current and previous stresses, including water limitation and overgrazing, and the occurrence of a warmer, drier climate might be reflected first in directional shifts in the cover or composition of the plant community or as increased variability in ANPP (Fig. 7.7). Rangeland degradation results if plant productivity and diversity decrease to levels that cannot be economically sustained or ecologically reversed (Willms et al. 1985; Milton et al. 1994) (Chaps. 8 and 15, this volume).

7.5 An Assessment of Climate Change Scenarios

Following, we provide an assessment of the implications of climate change for rangelands organized around three plausible, but regionally unique, climate change scenarios. Greater uncertainty is associated with projected changes in precipitation than CO_2 concentration or warming, particularly at regional scales. The following should be viewed as a general assessment of the collective impact of a given climate change scenario (Box 7.2).
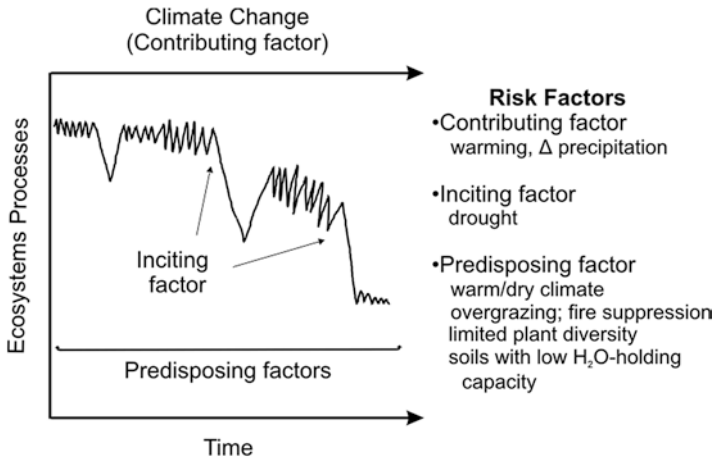
Fig. 7.7 A framework for envisioning how climate change alone or in interaction with other risks may cause a large decline in ecosystem services, including plant and livestock productivity [*upper panel*; adapted from Manion (1981)]. We consider three categories of risks—predisposing, inciting, and contributing. Predisposing factors are current and antecedent stresses that increase an ecosystem's susceptibility to short-duration stresses, such as drought (inciting factor), or to longer term change in climate (contributing factor). Predisposing factors include stresses related to current states or values of variables that are internal to ecosystems and dynamic over ecological timescales (current regional climate, soil resources, biota, and disturbance regime; *lower panel*). In the *upper panel*, we illustrate a case in which climate change (contributing factor) exacerbates negative effects of a recent stress, such as drought (inciting factor), for a rangeland on which processes already are limited by a warm/dry climate, overgrazing, or a sparse, species-poor plant canopy (predisposing factors) to increase process variability sufficiently to change average process levels

Text Box 7.2: Key risks associated with climate change for rangelands
Illustration of representative risks for livestock production on rangelands subject to each of the three general climate change scenarios. Climate-related drivers of risk are indicated by icons. Key risks are those shifts in biotic or abiotic conditions judged likely to lead to ecosystem changes that are of large magnitude or are irreversible at management timescales of decades. An overall potential risk is assessed for each scenario assuming an increase in mean temperature of either 2 or 4 °C given current management strategies and adaptation capacity. The risk associated with any given biotic or abiotic shift will vary among regions depending on current biophysical and socioeconomic factors.

Text Box 7.2: (continued)
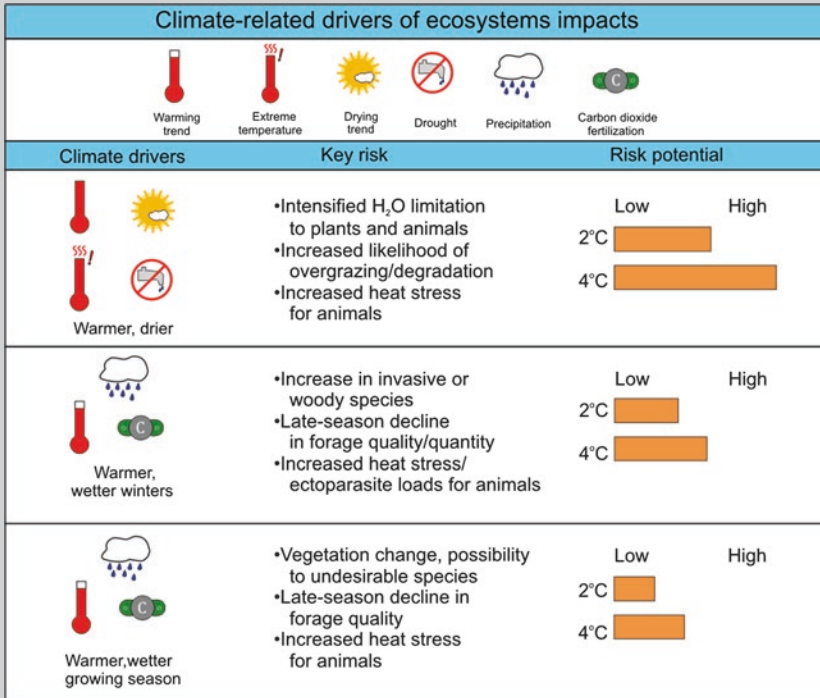
7.5.1 Warmer, Drier Climate Scenario

Regional specificity—Climate models project that warming will be accompanied by a decrease in precipitation in arid to semiarid rangelands in the southwestern North America, Central America, and south and southwestern Australia (IPCC 2007). Precipitation is projected to decrease by 10–20 % during winter and spring in southern Africa and during spring and summer in central Asia.

NPP and forage quality—Warming and drying will reduce soil water availability leading to a decrease in NPP on rangelands that already are warm and dry. NPP is more sensitive to the amount by which precipitation declines than to the amount of warming (Xu et al. 2013). Elevated CO_2 will not greatly alleviate negative effects of drying on NPP because of persistent soil water limitations. Forage quality likely will decline in response to combined effects of CO_2 enrichment, warming, and reduced precipitation.

Livestock production—Warmer and potentially drier conditions likely will reduce cattle production, resulting in fewer cattle operations. Remaining cattle operations will likely switch to the most heat tolerant of the British and European breeds (*Bos taurus*) or from *Bos taurus* breeds to the more heat-tolerant *Bos indicus* breeds, including Brahman and Brahman crosses, Romosinuano and Senepol

(Hammond et al. 1996; Kay 1997). Some ranchers may be forced to change species of livestock, such as by replacing cattle with sheep or goats which are better adapted to warm temperatures and drought (Kay 1997).

Vegetation composition—Intensification of drought (warmer, drier conditions) elevates the risk of extensive plant mortality and even of biome reorganization in arid ecosystems (Ponce Campos et al. 2013). For example, the severe drought of 2002–2003 caused greater than 90 % mortality of pinyon pine (*Pinus edulis*) in the southwestern USA whereas associated trees of *Juniperus monosperma* survived (Breshears et al. 2005, 2009). Warmer and drier conditions also may alter vegetation by favoring more frequent fires. Increasing fire frequency in the Mojave Desert and Great Basin in the past 20 years has converted communities of desert shrublands and shrub steppe to annual grasslands (CCSP 2008; Balch et al. 2013). Some shrub and woodland ecosystems of rangelands, such as those in the western USA, developed under climatic conditions more favorable than those forecast. These ecosystems may be subject to increased fire frequencies if more severe droughts lead to episodes of woody mortality that produce fuel loads sufficient to sustain fire (e.g., Breshears et al. 2005).

7.5.2   Warmer, Wetter Winters Scenario

Regional specificity—Climate models project that warming will be accompanied by an increase in precipitation in the northwestern USA, southern Canada, and northern Asia, with most of the increase occurring during winter months (IPCC 2007).

NPP and forage quality—Warming and increased precipitation, coupled with elevated CO_2 concentration, should increase NPP, especially early in the season. Experimental warming and increased precipitation generally stimulate plant growth (Wu et al. 2011). NPP likely will decline in the latter portion of the growing as warming and reduced precipitation limit soil water availability. In combination, climate change drivers may have little effect on forage quality.

Livestock production—The combination of warmer temperatures, greater precipitation, and CO_2 enrichment should increase livestock productivity, particularly in cooler regions such as the northern USA and Canada, by moderating winter temperatures (Baker et al. 1993; Eckert et al. 1995; Rötter and Geijn 1999), lengthening the growing season, and increasing NPP.

Vegetation composition—Warmer, wetter winters likely will favor plants that grow early in the season or access soil water accumulated early in the growing season. For example, ponderosa pine (*Pinus ponderosa*) established in grassland-forest ecotones in northern Colorado during years when spring and autumn precipitation were high in association with El Niño events (League and Veblen 2006). By increasing soil water content, higher CO_2 and precipitation also favor recruitment of taprooted invasive forbs like leafy spurge (*Euphorbia esula*), diffuse knapweed (*Centaurea diffusa),* and baby's breath *(Gypsophila paniculata)*, as well as some subshrubs (Owensby et al. 1999; Morgan et al. 2007; Blumenthal et al. 2008).

7.5.3 Warmer, Wetter Growing Season Scenario

Regional specificity—Climate models project an increase in winter and spring precipitation in northern portions of Great Plains region of central North America (IPCC 2007; Walthall et al. 2012).

NPP and forage quality—Warming combined with wetter conditions during the early growing season and elevated CO_2 should increase NPP, partly by extending the growing season. Grass production in tallgrass prairie in this region is highly responsive to early-season precipitation (Craine et al. 2012). The anticipated shift to larger, but less frequent precipitation events may reduce ANPP in mesic rangelands (Knapp et al. 2002), but increase ANPP in more arid systems in the region (Heisler-White et al. 2009). Forage quality may improve, especially if forage benefits of increased early-season precipitation are not negated by effects of late-season dry periods.

Livestock production—The combination of warmer temperatures, greater precipitation, and CO_2 enrichment should increase livestock productivity by moderating winter temperatures (Baker et al. 1993; Eckert et al. 1995; Rötter and Geijn 1999), lengthening the growing season, and increasing early-season NPP. Wetter growing seasons allow rangeland livestock producers to provide additional watering locations and, perhaps, shift to more heat-tolerant breeds.

Vegetation composition—Warmer temperatures and wetter winter and spring seasons likely will favor plants that grow early in the season.

7.6 Knowledge Gaps

The following are important knowledge gaps that limit our ability to predict rangeland responses to climate change.

- Uncertainty in climate projections, especially in projections of precipitation trends. Uncertainty is greater at regional than global scales.
- Limited understanding of how climate change drivers interact to affect key ecosystem variables and processes, including soil water content and dynamics, NPP, and forage quality.
- Limited capacity to discern impacts of climate change from those of management and disturbances.
- Limited capacity to breed livestock that are adapted to weather and rangeland conditions anticipated as climate changes.

Most livestock currently are selected for growth and carcass traits (Cartwright 1970). Climate change may render the capacity to survive and reproduce under harsh conditions more important than growth rate. Progress in molecular genetics and animal breeding is required to identify and select livestock with improved adaptation to warmer and drier conditions. Because the traits selected to improve

performance under harsher environments may be opposite to those traditionally selected (e.g., productivity traits; Prayaga et al. 2009), programs are required to breed animals adapted to harsh environments that also produce red meat of acceptable quality to consumers.

7.7 Summary

Climate is changing at an unprecedented rate as a consequence of increasing atmospheric concentrations of greenhouse gases including carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). Dynamics in the Earth climate system make additional climate change a virtual certainty because centuries will be required for climate to equilibrate with current levels of greenhouse gases.

Climate change science predicts warming and greater climatic variability for the foreseeable future. Warming is expected to be greatest at northern latitudes and over land. Precipitation is anticipated to increase at higher latitudes and decrease elsewhere, with significant seasonal variation and greater interannual or intra-annual variability.

The major climate change drivers—warming, precipitation modification, and direct effects of increased CO_2 concentration on plant growth and transpiration—will alter soil water availability and N cycling, processes that regulate the provisioning of plant and animal products and other services from rangelands. For example, increased precipitation variability will be manifest as shifts in precipitation seasonality and in the temporal patterns of soil water availability on some rangelands. Warmer temperatures will increase evaporative demand, thereby reducing soil water in the absence of compensating change in precipitation, whereas CO_2 enrichment could reduce transpiration rates and increase plant growth per unit of water transpired. Climate change drivers also will influence soil N availability to plants, with potential feedbacks on plant responses to drivers. Warming increases N availability by accelerating N mineralization rates when soil water is available, but CO_2 enrichment can create or reinforce N limitations on productivity by increasing the sequestration of N in long-lived plant material and organic matter. Limited N, in turn, can constrain benefits of CO_2 enrichment for plant growth.

The ecological consequences of climate change drivers will vary among rangelands partly because the magnitude, decadal timing, or seasonal patterns of warming and precipitation modification will be expressed differently among regions. Climate change impacts will be greatest for rangelands where climate shifts amplify currently positive climatic effects or exacerbate climatic limitations on plant and animal productivity.

The ecological consequences of climate change drivers also will vary among rangelands because driver effects frequently are nonadditive and contingent on current precipitation regimes. Nonadditive effects are indicated when the combined influence of shifts in climate drivers differs from that anticipated by summing single-driver effects. Plant growth responses to combined warming and CO_2

enrichment treatments often are smaller than anticipated from single-factor experiments, for example. The effects of climate drivers also vary as a function of the current precipitation regime. The responses of plant productivity to both CO_2 and precipitation variability depend on the current precipitation regime, for instance. Plant productivity generally is more responsive to interannual precipitation variability in mesic or semiarid than desert rangelands. The stimulating effect of CO_2 on productivity also depends on precipitation, peaking at moderate levels of annual precipitation (300–400 mm) when considered across desert and grassland ecosystems.

Warming, especially when combined with drought, will cause greatest physiological impairment to livestock in already warm environments by negatively impacting animal physiological performance, increasing abundances of ectoparasites, and reducing forage quality and quantity. Heat stress reduces milk production, forage intake, and reproduction rate, whereas warmer temperatures increase winter survival of ectoparasites and may reduce forage quality.

Climate change will lead to combinations of seasonal temperature and precipitation that differ from current climatic conditions. Warmer, drier conditions also are anticipated to increase fire activity. This shift in climatic conditions and fire activity could lead to plant communities that are compositionally unlike any found today. The rapid rate at which climate is changing, in combination with other drivers and disturbances, will favor ecological generalists such as short-lived plants (e.g., weeds), animals, insects, and disease organisms. Increased establishment of generalist plant species could, in turn, hasten the development of more homogeneous plant assemblages with negative effects on species diversity and animal productivity.

Rangelands increasingly are being transformed by climate change and a variety of human impacts, including change in land-use patterns, intensification of disturbances, and accelerated species introductions and movements. Singly, any of these changes will alter services provisioned by rangelands. Combined, the imprint of human activities may challenge ecosystem integrity and functionality by increasing variability in ecosystem processes and production enterprises beyond their historical range. As a result, livestock production and supply of other ecosystem services could decline to levels that cannot be economically sustained or ecologically reversed. Given this potential outcome, we suggest that an overarching goal of management and monitoring must be to improve our ability to predict the vulnerability of rangelands and rangeland production systems to continued climate change.

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