Rangeland Ecol Manage 66:493–511 | September 2013 | DOI: 10.2111/REM-D-12-00068.1

Invited Synthesis

Climate Change and North American Rangelands: Trends, Projections, and Implications

H. Wayne Polley,[1] David D. Briske,[2] Jack A. Morgan,[3] Klaus Wolter,[4] Derek W. Bailey,[5] and Joel R. Brown[6]

Authors are [1]Research Ecologist, USDA-ARS Grassland, Soil and Water Research Laboratory, Temple, TX 76502, USA; [2]Professor, Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843, USA; [3]Plant Physiologist, USDA-ARS Crops Research Laboratory, Fort Collins, CO 80526, USA; [4]Research Associate, National Oceanic and Atmospheric Administration, Earth Systems Research Laboratory, Boulder, CO 80305, USA; [5]Professor, Animal and Range Sciences Department, New Mexico State University, Las Cruces, NM 88003, USA; and [6]Rangeland Management Specialist, USDA-NRCS Jornada Experimental Range, New Mexico State University, Las Cruces, NM 88003, USA.

Abstract

The amplified "greenhouse effect" associated with increasing concentrations of greenhouse gases has increased atmospheric temperature by 1°C since industrialization (around 1750), and it is anticipated to cause an additional 2°C increase by mid-century. Increased biospheric warming is also projected to modify the amount and distribution of annual precipitation and increase the occurrence of both drought and heat waves. The ecological consequences of climate change will vary substantially among ecoregions because of regional differences in antecedent environmental conditions; the rate and magnitude of change in the primary climate change drivers, including elevated carbon dioxide (CO_2), warming and precipitation modification; and nonadditive effects among climate drivers. Elevated atmospheric CO_2 will directly stimulate plant growth and reduce negative effects of drying in a warmer climate by increasing plant water use efficiency; however, the CO_2 effect is mediated by environmental conditions, especially soil water availability. Warming and drying are anticipated to reduce soil water availability, net primary productivity, and other ecosystem processes in the southern Great Plains, the Southwest, and northern Mexico, but warmer and generally wetter conditions will likely enhance these processes in the northern Plains and southern Canada. The Northwest will warm considerably, but annual precipitation is projected to change little despite a large decrease in summer precipitation. Reduced winter snowpack and earlier snowmelt will affect hydrology and riparian systems in the Northwest. Specific consequences of climate change will be numerous and varied and include modifications to forage quantity and quality and livestock production systems, soil C content, fire regimes, livestock metabolism, and plant community composition and species distributions, including range contraction and expansion of invasive species. Recent trends and model projections indicate continued directional change and increasing variability in climate that will substantially affect the provision of ecosystem services on North American rangelands.

Key Words: atmospheric CO_2, atmospheric warming, climate variability, greenhouse gases, livestock production, precipitation patterns

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). A climate change footprint has become evident in the form of atmospheric warming, rapid glacial retreat, accelerated plant phenology, modified precipitation patterns, and increasing wildfires (Parmesan and Yohe 2003; IPCC 2007). These changes to the Earth system are consistent with those of a warmer and more variable climate and have important consequences for the provisioning of ecosystem services to an increasing and more affluent human population (Walther 2003, 2010). Greater warming and climatic variability, expressed against the backdrop of large-scale and accelerating shifts in land use, pose a major challenge to society and more directly to natural resource managers, producers, and policymakers (Parmesan and Yohe 2003; Rockstrom et al. 2009).

The science of climate change inevitably contains uncertainties partly because climatic and ecological systems are complex and the consequences of this unprecedented phenomenon will be expressed over long time frames. Despite these uncertainties, it would be irresponsible to ignore the cumulative evidence for climate change—both the current footprint and model projections—on the basis that the rates and magnitude of change are not fully known. Unfounded optimism regarding climatic consistency currently constrains our ability to anticipate and develop effective contingency plans for nominal weather variation, and this perspective will pose a challenge to the development of strategies for confronting climate change (Joyce et al. 2013 [this issue]).

This synthesis was developed to provide an objective, concise assessment of climate trends and projections and potential

---

This article was commissioned by the board of directors of the Society for Range Management in support of the society's position on climate change.

The alternate editor-in-chief, M. K. Owens, was responsible for the editorial handling of this manuscript.

Correspondence: Wayne Polley, USDA-ARS Grassland, Soil, and Water Research Laboratory, 808 E. Blackland Rd, Temple, TX 76502, USA. Email: wayne.polley@ars.usda.gov

Manuscript received 22 May 2012; manuscript accepted 24 June 2013.

ecological implications of climate change that are of direct relevance to North American rangelands. This synthesis is organized to summarize individual and integrated impacts of the three major climate change drivers—elevated atmospheric carbon dioxide (CO_2), biospheric warming, and modified precipitation regimes—on ecological processes relevant to the provision of rangeland ecosystem services. Specific objectives are to 1) present climatic trends documented during the 20th century 2) identify predictions for climate change in the 21st century, and 3) present evidence for ecological implications of current and future climate change, including synoptic scenarios of four ecoregions. We draw on data and case studies specific to North American rangelands, but we anticipate that this synthesis will have broader implications by informing management and policy recommendations and guiding future research programs. Adaptation and mitigation strategies designed to contend with climate change are presented in a companion paper (Joyce et al. 2013 [this issue]).

CLIMATE TRENDS AND PROJECTIONS

Recent Climatic Trends

Climate change refers to a significant and lasting change in the statistical distribution of meteorological conditions and variations. The Earth's climate has changed throughout geological history in response to natural events, including orbital variation of the planet's axis and volcanic eruptions that altered the amount of solar energy reaching Earth. However, the Earth has now entered an era in which human impacts on the fluxes of radiative energy through the Earth system have demonstrable effects on climate (Intergovernmental Panel on Climate Change [IPCC] 2007; Fig. 1). The rapid increase in atmospheric concentration of trace gases known collectively as GHGs represents the dominant mechanism contributing to climate change. 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. The "greenhouse effect" is vital to life on Earth, as it buffers day-night temperature fluctuations to maintain a relatively constant mean planetary temperature of 15°C by balancing incoming solar radiation with the emission of infrared radiation into space. A doubling of atmospheric CO_2 would disrupt this energy balance by about 2% (Lindzen 1999) to produce what is called "climate forcing" or "radiative forcing." GHG concentrations will continue to rise for the foreseeable future even if emissions rates decline because GHGs may remain in the atmosphere for hundreds of years (Karl et al. 2009). Increased GHG concentrations will amplify the current greenhouse effect to further warm the Earth and thereby modify numerous interrelated processes within the Earth system.

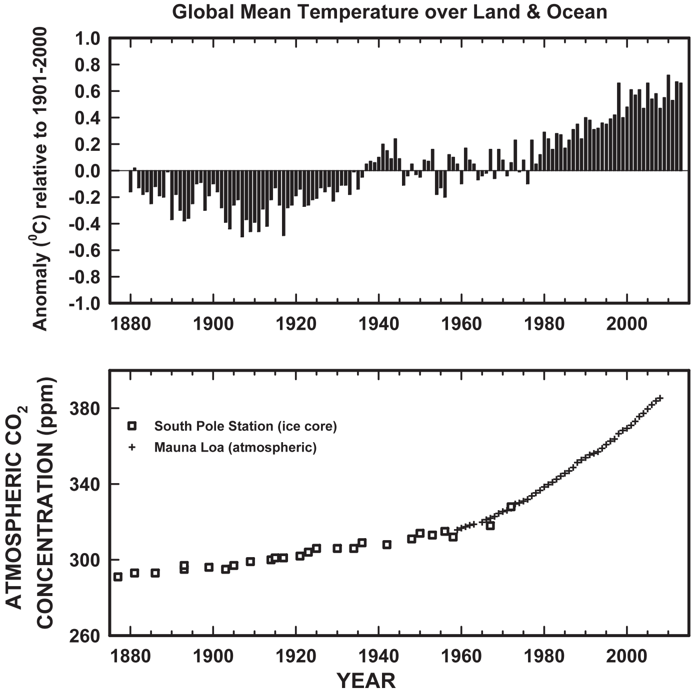

Figure 1. Departure of the global mean temperature from the average global temperature for the period 1901–2000 (temperature anomaly; upper panel) and atmospheric CO_2 concentration (lower panel). A positive temperature anomaly during a given year indicates that the observed temperature was warmer than the long-term average. The CO_2 concentration is from air extracted from dated layers of ice cores from the South Pole, Antarctica, and direct measurements of atmospheric CO_2 at Mauna Loa, Hawaii (lower panel). The temperature figure is from http://www.ncdc.noaa.gov/cmb-faq/anomalies.php. The CO_2 figure was redrawn from Friedli et al. (1986) and updated with data from Keeling et al. (2009).

Global mean temperature has risen during recent decades, particularly in northern latitudes and over land (IPCC 2007). Six of the 10 years from 1998, the hottest year on record, to 2007 were among the hottest 10% recorded in the United States, and 2012 was the hottest year ever recorded for the contiguous United States (NOAA National Climatic Data Center 2013). The mean frost-free period for the United States has increased by 2 weeks since 1900 in response to this warming trend. Warming over the last century has been even greater than projected by climate models in the western United States (Fig. 2; e.g., Menne and Williams 2009; Menne et al. 2009) possibly because of poorly understood feedback mechanisms or "natural" climate variability associated with the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and the North Atlantic Oscillation (NAO; Hurrell et al. 2003). On the other hand, temperature has changed little in other portions of the United States and has even decreased in the Southeast over the last century.

Precipitation increased by 7% in the United States during the last century, but precipitation trends varied among regions (US Climate Change Science Program [CCSP] 2008; Fig. 3). Precipitation increased over much of the central Great Plains, especially during summer months, but changed little during the last century in the western United States with the exception of a large decrease in southwestern Arizona (e.g., Menne and Williams 2009; Menne et al. 2009). Over shorter time periods (years to decades), precipitation patterns are influenced by decadal changes in PDO–El Niño Southern Oscillation or NAO and may appear to be inconsistent with longer-term climate trends.

A climate change signature also is evident in the form of an increasing frequency of "extreme weather events," including greater precipitation variability. Heat waves are increasing in

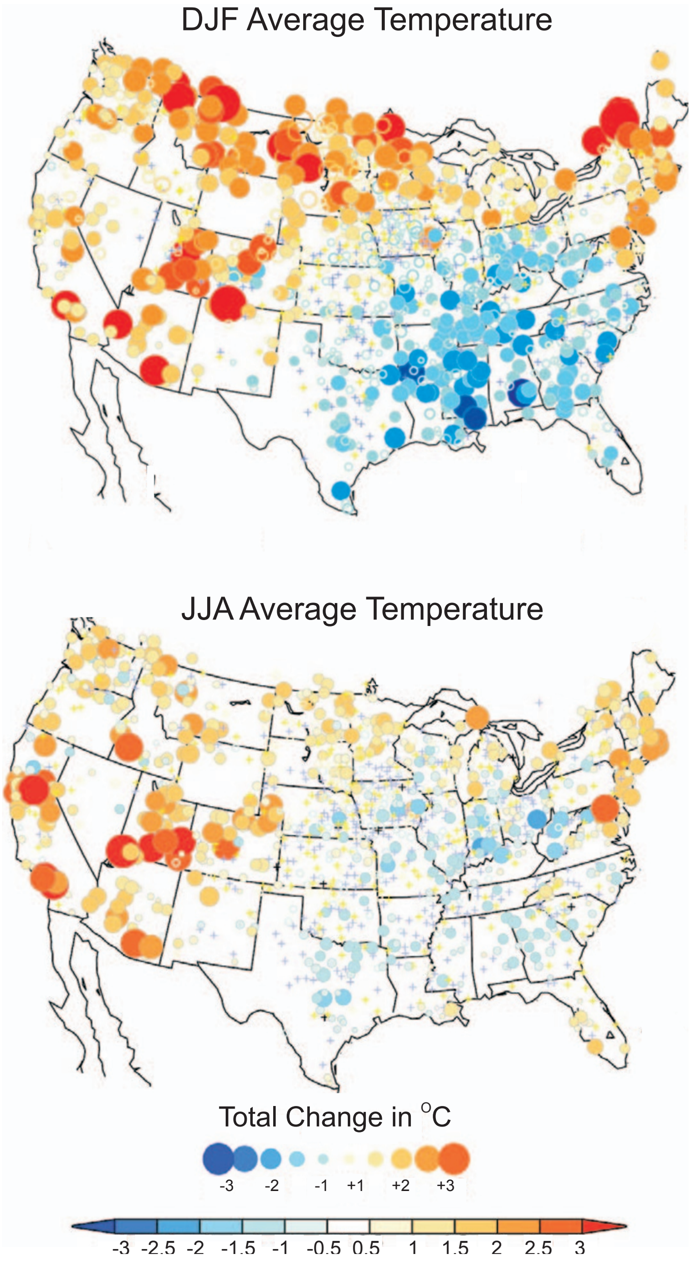

Figure 2. US temperature trends (°C) over the last century (1911–2010) as derived using data from the Global Historical Climate Network, data version 2.9. Upper panel: December/January/February (DJF); lower panel: June/July/August (JJA). Filled symbols indicate statistically significant trends.

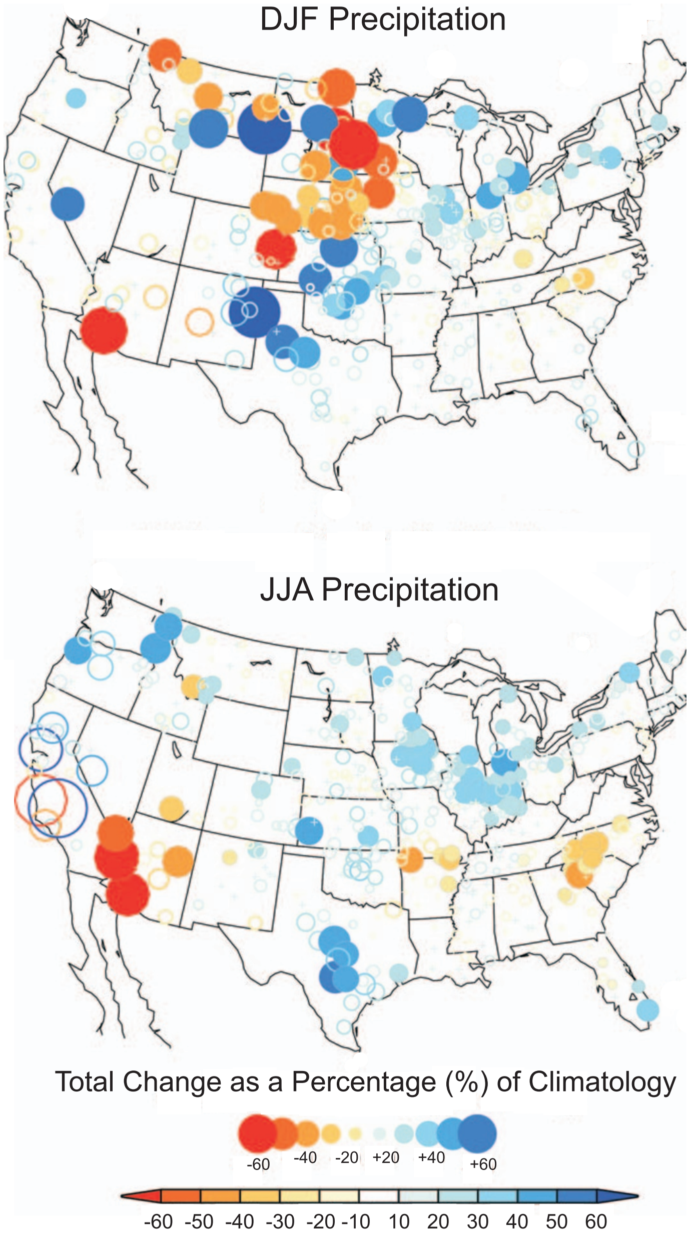

Figure 3. US precipitation trends over the last century (1911–2010), expressed as change over this period divided by its long-term average for each station. Upper panel: December/January/February (DJF); lower panel: June/July/August (JJA). Filled symbols indicate statistically significant trends.

frequency (e.g., Meehl et al. 2009), and daily precipitation events are increasing in size over most of the United States but currently are significant only east of the Mississippi River (Kunkel et al. 2003; Groisman et al. 2004). The amount of annual precipitation that has fallen as the most intense 1% events has increased by 20% over the last century, even though total precipitation has increased by only 7% (Groisman et al. 2004; CCSP 2008). The mean proportion of the United States affected by drought was 14% in the 20th century, but it has been 35–40% in recent years compared to 65% in 1934 (CCSP 2008). By contrast, flooding events are fewer in the southwestern United States and show no significant trend with long-term changes in GHG concentrations in other regions of the country (Hirsch and Ryberg 2012).

Climate Change Projections

An ensemble of coupled climate models was used to simulate temperature and precipitation projections for the year 2050 (Meehl et al. 2007) based on a scenario of "moderate" rates of GHG emissions during coming decades (IPCC 2007). Climate change models project that average annual temperature will increase by about 2–4°C in the western United States (Fig. 4), with minimum temperatures increasing more rapidly than maximum temperatures (i.e., warming will be greatest at

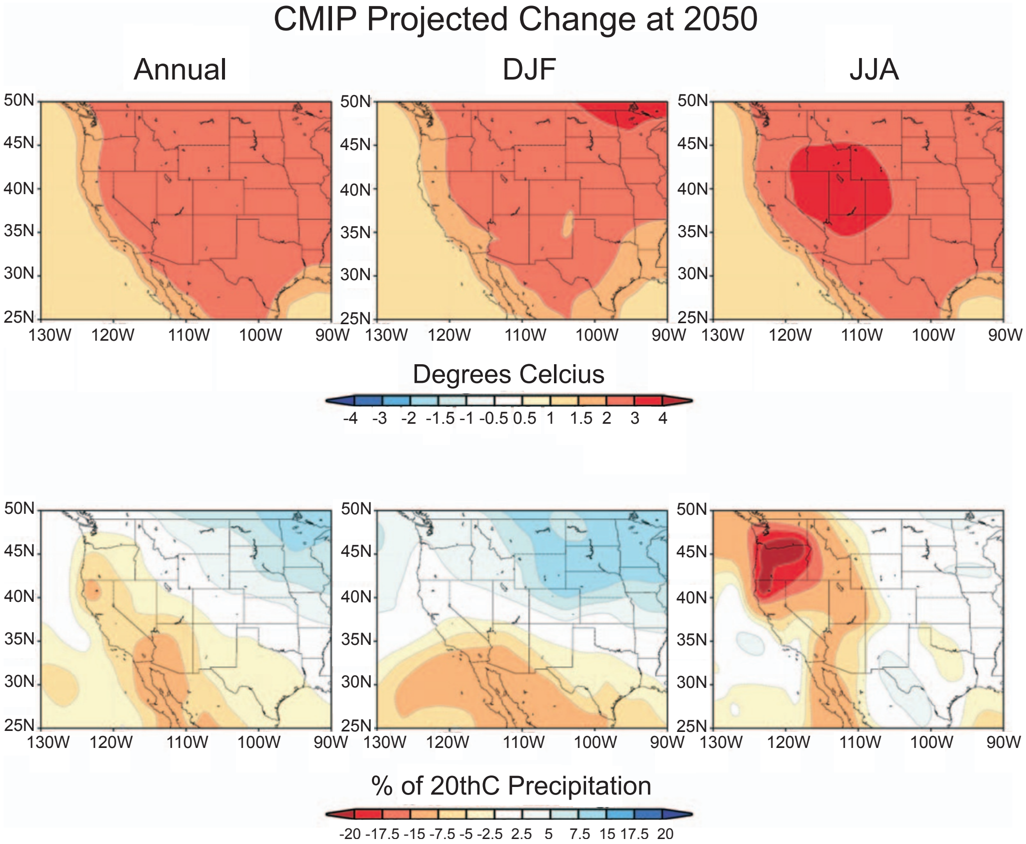

Figure 4. Climate model (Coupled Model Intercomparison Project) projections of temperature (top) and precipitation (bottom) for 2050 relative to the 20th century. Values are presented for the entire year (left), winter (center), and summer (right).

night). Warming is expected to be greatest in the North and during the winter throughout North America, except in the West, where it will be greatest in the summer (IPCC 2007). Greater uncertainty is associated with projected changes in precipitation than CO_2 concentration or warming, but the current consensus is for drier summers in much of western United States and wetter winters in northern United States and southern Canada (Seager and Vecchi 2010). The increase in winter precipitation could exceed the decline in summer precipitation in the North, but annual precipitation is expected to decline by $> 2.5\%$ in the Southwest. It is not known whether climate change will favor El Niño over La Niña events in the future (IPCC 2007). La Niña typically heralds drier-than-average conditions in the Southwest.

Warming is anticipated to increase weather extremes and both intra- and interannual precipitation variability by altering atmospheric hydrological processes and circulation patterns (Easterling et al. 2000; Hoerling and Kumar 2003; McCabe and Clark 2006). Warming is anticipated to reduce the frequency of rainfall events but increase the size or intensity of events when they do occur (Groisman et al. 2005; Wentz et al. 2007; Karl et al. 2009). Heat waves are anticipated to continue to increase in both frequency and magnitude in proportion to increasing mean global temperature, while extreme freezing events are expected to moderate more rapidly (Kharin et al. 2007). For example, hot days that would have occurred once every 20 yr last century are anticipated to occur every 3 yr by 2050 (CCSP 2008). The resulting increase in frost-free periods is anticipated to be a major driver of community composition and range distributions (Weiss and Overpeck 2005). Precipitation extremes are expected to vary more greatly than annual or seasonal means (CCSP 2008). These extreme events by definition fall outside the normal range of variation, so they are likely to have adverse effects on ecosystems and may induce cascading effects over long periods by modifying the amount and seasonality of soil water (Kharin et al. 2007; CCSP 2008; Reyer et al. 2013). The timing of extreme events may be as important as their intensity and frequency because major ecological consequences may be restricted to narrow temporal windows (Craine et al. 2012).

Snowpack reductions likely will continue and be greatest in the milder climates of the Oregon Cascades and at mid-elevations and smallest at high elevations in the Rockies and southern Sierras (Mote et al. 2005; Christensen and Lettenmaier 2006; Ray et al. 2008). Reduced snowpack will have pronounced ecological effects on stream flow and the structure and function of riparian systems (Marshall et al. 2008). Earlier and more rapid snowmelt, in conjunction with higher temperatures and an increased fraction of precipitation as rainfall, may result in both an earlier initiation and cessation of ecological processes that may amplify the intensity of summer drought.

Uncertainties necessarily attend issues as complex as the calculation of global GHG accumulation and its consequences to current and future climate patterns. Several uncertainties recently have been resolved (see Supplemental Material; available online at http://dx.doi.org/10.2111/REM-D-12-

00068.s1), but uncertainty remains as to the sensitivity of future climate to higher GHG concentrations. Alone, a doubling of CO_2 will increase temperature by a mean of about 1°C, similar to that experienced during the last 150 yr (Lindzen 1999). Current climate models project a much greater increase in temperature partly because they incorporate feedbacks from water vapor and clouds and from temperature on infrared emissions that act to amplify temperature sensitivity to CO_2 and other GHGs. Warming will accompany GHG accumulation even in the absence of positive feedbacks from water vapor albeit at a lower rate than currently projected.

ECOLOGICAL IMPLICATIONS OF CLIMATE CHANGE

The drivers of climate change, coupled with greater frequency and intensity of extreme weather events, will collectively affect soil water availability to influence many aspects of ecosystem structure and function, even though these drivers have unique and potentially counteracting effects (Luo 2007; Knapp et al. 2008; Morgan et al. 2011). Climate change impacts will vary regionally because the magnitude, decadal timing, or seasonal patterns of warming and precipitation modification will be expressed differently among regions and interactive effects among climate drivers are nonadditive. Ecosystem responses to these climate change drivers will vary among locations within a given region because of local differences in soil characteristics, including water-holding capacity, the extant plant species pool, management practices (e.g., grazing intensity, fire regimes), and historical land use patterns (Fig. 5). The potential consequences of these climate change drivers, individually and in combination, on primary productivity, vegetation composition, plant phenology, ecosystem C dynamics, and livestock production are discussed in the following sections.

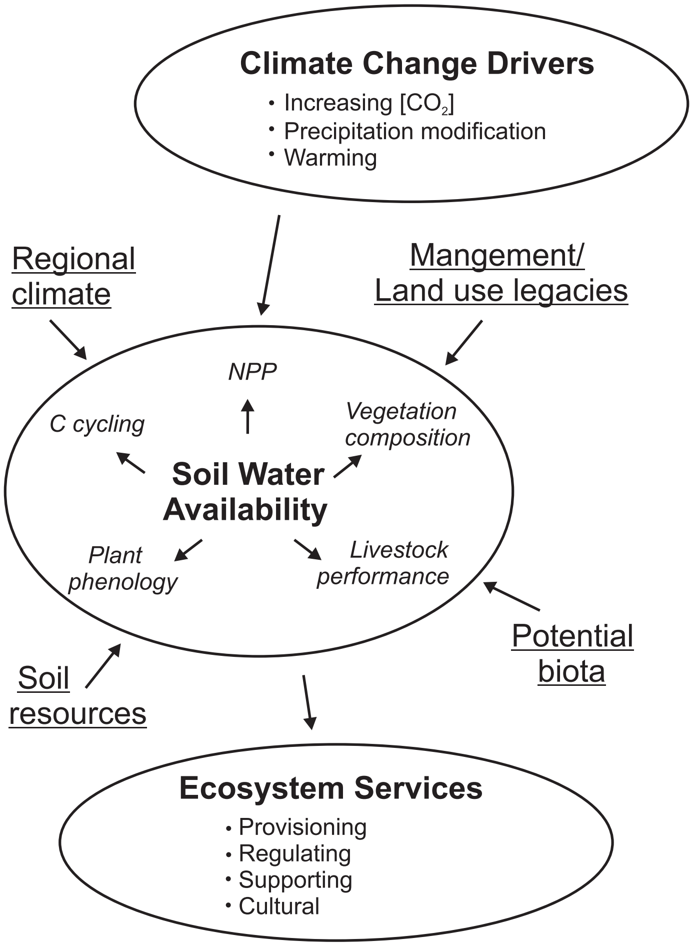

Figure 5. A conceptual model illustrating the response of rangeland systems to climate change. Climate change drivers will affect ecological processes/properties (italicized) largely by modifying spatial and temporal dynamics of soil water availability and secondarily by altering plant photosynthesis and water use efficiency. Climate change effects on ecological processes will differ among regions and even locations within regions in response to differences in mediating variables (underlined). Both positive and negative consequences of climate change are anticipated and will affect the services that humans derive from rangeland ecosystems.

Primary Productivity

Rangeland plant (primary) productivity (NPP) and carbon cycling depend primarily on the amount and seasonal distribution of precipitation and only secondarily on other climatic variables. This is demonstrated by the strongly linear relationship between aboveground net primary productivity (ANPP) and mean annual precipitation for most rangelands (Sala et al. 1988).

Precipitation Variability. Rangeland ANPP varies among years in response to interannual precipitation variability, but

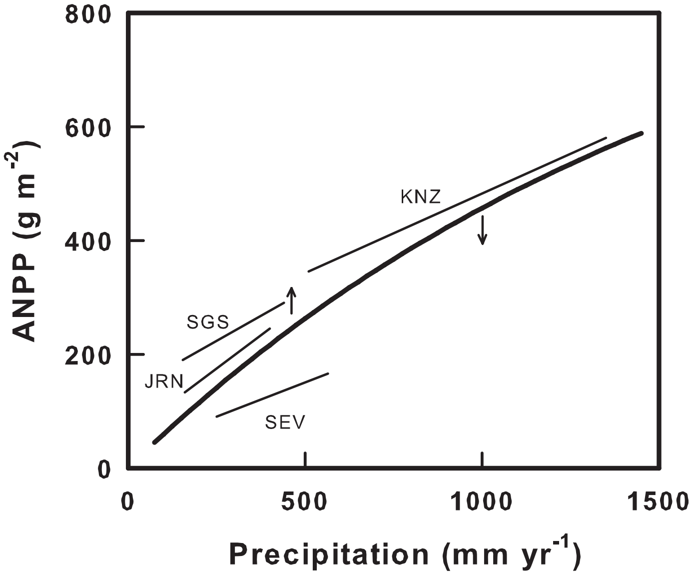

Figure 6. The relationship between rangeland ANPP and precipitation. ANPP increases, on average, as mean precipitation increases (bold line) but varies more in response to interannual precipitation variability in mesic and semiarid than arid rangelands, as indicated by lines illustrating ANPP-precipitation responses for mesic (Konza Prairie, Kansas [KNZ]), semiarid (Shortgrass Steppe, Colorado [SGS]), and desert (arid) grasslands (Jornada, New Mexico [JRN] and Sevilleta, New Mexico [SEV]). Delivering a given amount of annual precipitation as fewer but larger events reduces ANPP in mesic systems but increases ANPP in arid and semiarid systems, as illustrated with arrows. The figure is modified from Huxman et al. (2004b). ANPP indicates aboveground net primary productivity.

Table 1. Responses of plant attributes to CO_2 enrichment in six ecosystems. Key citations are listed for each experiment. CO_2 treatments are presented in the second row. Responses to CO_2 were positive (+), negative (–), or not significant (0). The predominant response is listed first. Water relations refers to measurements of plant or soil water status, with "+" and "–" indicating more and less available water, respectively.

Rangeland CO_2 experiments	Shortgrass steppe, Colorado[1–3]	Mixed-grass prairie, Wyoming[4,5]	Temperate grassland, Tasmania[6–9]	Annual grassland, California[10–12]	Tallgrass prairie, Texas[13,14]	Tallgrass prairie, Kansas[15,16]
Carbon dioxide (ppmv)	Ambient to 720	Ambient to 600	Ambient to 550	Ambient to 680	250–500	Ambient to 720
Plant biomass	+	+,0	+,0	0	+,0	0,+
	41% increase in ANPP; 100% increase during a dry year	25% increase in ANPP; no response during a wet year	60% increase in ANPP		0–117% increase in ANPP among soils and years	No response of ANPP in wet years
Phenology		0	0	Forbs, slightly advanced; Grasses delayed		
Water relations	+	+	0,+,–	+	+	+
Functional group responses for biomass	+ C_3 grasses + C_3 shrub 0 C_4	+ C_3 grasses +,0 C_4 grasses	+ C_4 grass 0 C_3 grasses	– forbs 0 grasses	+ C_4 tall grass – C_4 mid-grass	0 C_4 grasses – C_3 grasses + forbs

[1] Morgan et al. (2004a). [2] Milchunas et al. (2005). [3] Morgan et al. (2007). [4] Reyes-Fox (2008). [5] Morgan et al. (2011). [6] Williams et al. (2007). [7] Hovenden et al. (2008a). [8] Hovenden et al. (2008b). [9] Pendall et al. (2011). [10] Zavaleta et al. (2003a). [11] Dukes et al. (2005). [12] Cleland et al. (2006). [13] Fay et al. (2012). [14] Polley et al. (2012b). [15] Owensby et al. (1993). [16] Owensby et al. (1999).

variability in ANPP does not increase proportionately with precipitation variability (Fig. 6). ANPP is more responsive to interannual variability in precipitation in mesic and semiarid than desert rangelands because most ANPP ($>70\%$) in mesic systems is associated with rainfall pluses that coincide with periods of high light and soil N availability (Knapp and Smith 2001). ANPP does not respond as dramatically to precipitation pulses in arid (particularly desert) systems because plant growth is limited by inherently low leaf area and plant density. Greater sensitivity of ANPP to interannual precipitation variability in mesic than arid rangelands implies that the response of ANPP to multiyear drought will be greatest in the most productive rangelands.

Impacts of fewer but larger precipitation events on NPP will be contingent on mean annual precipitation currently received (Knapp et al. 2008). Larger but less frequent precipitation events in mesic systems are likely to increase the frequency and duration of dry periods as well as water losses to runoff and percolation to groundwater. As a result, soil water content will fall below plant stress thresholds more often than under the current precipitation regime. In contrast, precipitation that arrives in fewer, larger events is anticipated to reduce seasonal water stress and promote plant growth in arid ecosystems by increasing the proportion of water that percolates into deeper soil layers, where it is less susceptible to evaporative loss and potentially available for absorption by plants. These contrasting responses are illustrated in field experiments where the same total annual precipitation delivered 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). A 10% reduction in tallgrass ANPP following precipitation delivery as fewer, larger events (Knapp et al. 2002) was comparable to a decrease in ANPP caused by a 30% reduction in total rainfall with ambient frequency and intensity of events (Knapp et al. 2002; Fay et al. 2003; Swemmer et al. 2007). The response of soil water content to modified precipitation delivery will also depend on how soil texture influences runoff, infiltration, deep drainage, and evaporation rates (Noy-Meir 1973; Huxman et al. 2004a; Knapp et al. 2008).

CO_2. Net effects of CO_2 enrichment on NPP (Table 1) also depend largely on the amount and seasonal distribution of precipitation. Individual plants respond to elevated CO_2 with an increase in photosynthesis rates (Pearcy and Ehleringer 1984) and decrease in stomatal conductance that reduces transpiration and increases water use efficiency (WUE; photosynthesis/transpiration; Wand et al. 1999). Elevated CO_2 stimulates plant growth to the greatest extent in systems in which NPP is or will become moderately water limited (Morgan et al. 2004b, 2011; Nowak et al. 2004; Webb et al. 2012) and soil nitrogen (N) is readily available (Luo et al. 2004; Reich et al. 2004).

Warming. Temperature regulates the rates of chemical reactions in both soils and plants and drives water and energy fluxes between land surfaces and the atmosphere. These two direct influences of warming often have contrasting effects on NPP. Warming may enhance productivity by alleviating low temperature limits on plant growth (Luo 2007; Lin et al. 2010), extending the growing season, and increasing N mineralization rates provided that sufficient water is available (Rustad et al. 2001; Parton et al. 2007; Dijkstra et al. 2008). Alternatively, warming may reduce ANPP (Pepper et al. 2005; Hovenden et al. 2008a) by increasing the vapor pressure deficit of air, leading to greater evapotranspiration and reduced soil water availability (Harte et al. 1995; Wan et al. 2002; Hovenden et al. 2008a; Sherry et al. 2008) and a decrease in plant water or transpiration use efficiency (McKeon et al. 2009). These opposing influences of warming may explain why many grassland experiments have shown little to no effect of warming on plant growth or NPP (Table 2; Dukes et al. 2005; Klein et al. 2007; Pendall et al. 2011; but see Lin 2010). However, warming in the presence of elevated CO_2 may increase NPP in semiarid systems because of the water-conserving effect of CO_2 enrichment (Morgan et al. 2011).

Vegetation Composition

Climate change may modify plant community composition, shift the geographical distribution of communities, and contribute to expansion and contraction of the distributional ranges of exotic, invasive plant species. Range expansions are anticipated when the functional traits of species are better suited to the altered climatic conditions. Climate change will affect plant species composition largely by shifting the amount, seasonal pattern, and vertical placement of soil water to influence the outcome of plant competition (Dukes and Mooney 1999; Knapp et al. 2008; Volder et al. 2013). Land cover change resulting from overgrazing, woody encroachment, and exotic plant invasion currently impact rangeland hydrology and will influence water and vegetation responses to climate change (Wilcox et al. 2011).

CO_2. Plant species and functional groups differ considerably in their responses to elevated CO_2 (Table 1), contributing to variable responses of species relative abundance and community composition. CO_2 enrichment preferentially stimulates photosynthesis in species with the C_3 compared to C_4 metabolic pathway (often considered "cool-season" and "warm-season" species, respectively) and thus may favor forbs, small shrubs, and even trees over warm-season grasses (Ehleringer and Monson 1993; Owensby et al. 1999; Polley et al. 2003; Morgan et al. 2007; Buitenwerf et al. 2012). Elevated CO_2 may also contribute to shifts in species composition by reducing transpiration to prolong soil water availability within a growing season (Morgan et al. 2004b; Polley et al. 2012a), provided that low light or N availability does not limit the growth or establishment of potentially responsive species (Owensby et al. 1999). Results from a simulation model imply that CO_2 enrichment will lead to a strong directional increase in woody vegetation in African deserts, grasslands, and savannas (Higgins and Scheiter 2012). Woody abundance is anticipated to increase both because CO_2 enrichment enhances photosynthesis and growth among trees and shrubs and because increased woody growth initiates a positive feedback involving light competition that favors trees over grasses. The transition from grasses to trees depends critically on grazing history, fire regime, and soil type; consequently, a clear climate change signal on woody encroachment has remained elusive (Archer et al. 1995).

Warming. Plant responses to warming are species specific because individual species possess unique temperature optima and encounter different limitations to growth (Table 2; Loik and Harte 1997; Luo 2007). Woody plants generally show a more consistent response to warming than do herbaceous species (Lin et al. 2010). Models based on the current correlation between climate and C_3 and C_4 abundances predict that warming will favor warm-season over cool-season grass species in rangelands of North and South America (Epstein et al. 2002). However, CO_2 enrichment is anticipated to reduce adverse effects of warming on photosynthetic efficiency of C_3 plants and limit changes in the geographic ranges of C_3 and C_4 species (Sage and Kubien 2003).

Intra-Annual Variability in Precipitation. Plant species have evolved unique traits and life history strategies in response to environments with varied amounts, depths, and seasonal patterns of soil water availability (Noy-Meir 1973). Consequently, sustained alteration of precipitation delivery may alter species abundances or community composition (Ignace et al. 2007; Resco et al. 2008). Experimental variation of precipitation seasonality modified species richness and density of a sotol grassland community in the Chihuahuan Desert (Robertson et al. 2010). Grasses were more responsive to summer rainfall, whereas forbs were most sensitive to winter rainfall. Herbaceous plants and shallowly rooted woody plants are often more responsive to small rainfall events than are deeper rooting woody species (BassiriRad et al. 1999; Huxman et al. 2004a).

A shift to larger, less frequent precipitation events may also influence vegetation change by creating pulses of high soil N availability. N pulses occur during periods of water stress when mineralization exceeds plant N absorption (Austin et al. 2004; Augustine and McNaughton 2006; Yahdjian and Sala 2006). These N pulses will be preferentially accessed by species that quickly resume growth following a period of drought (Gebauer and Ehleringer 2000), and this species-specific variation may alter both competitive interactions among established plants and plant recruitment and invasion (Lloret et al. 2004; Peñuelas et al. 2004; Volder et al. 2010).

Interannual Variability in Precipitation. It is well established in both the historical (Weaver and Albertson 1943; Breshears et al. 2005, 2009) and the paleoecological records that severe multiyear drought can substantially modify species composition (Woodhouse et al. 2010). For example, the 1930s drought induced major shifts in community composition in the Great Plains (Weaver and Albertson 1943). Cover of blue grama (*Bouteloua gracilis*) declined precipitously in eastern Colorado, where it had been the dominant perennial grass, whereas western wheatgrass (*Pascopyrum smithii*), a subordinant cool-season grass, became a dominant species throughout much of the central Great Plains, apparently by taking advantage of limited water available early in the growing season. Most forbs succumbed to the drought, especially in the shortgrass steppe and mixed grass prairie, with the complete loss of shallowly rooting forbs early in the drought, later followed by deeper-rooted forbs. Collectively, evidence from the 1930s drought illustrates that plant species with deep roots, high water use efficiency, or growth patterns that match the seasonality of precipitation likely will fare best during protracted droughts.

Severe drought may also shift the balance between trees and grasses by reducing competition from grass to favor woody recruitment and reducing mortality of woody plants relative to grasses (Scholes and Archer 1997; Van Auken 2000; Bond 2008; Volder et al. 2010). On the other hand, severe drought has caused extensive mortality of trees worldwide recently (Breshears et al. 2005; van Mantgem and Stephenson 2007; Allen et al. 2010) and could at least temporarily slow woody encroachment or consolidation.

Fire Regimes. Climate change can indirectly affect rangeland vegetation by altering fire regimes. Increasing fire frequency leads to a replacement of fire-sensitive with fire-tolerant plant species (Nelson and Hu 2008). Patterns of prairie expansion during the Holocene appear to have been driven by both climate and fire, for example (Nelson and Hu 2008). Globally, fires over the past two millennia have been strongly influenced by climatic conditions (Marlon et al. 2008). Most wildfires in

Table 2. Responses of plant attributes to an experimentally imposed increase in air or soil temperature in eight ecosystems. Key citations are listed for each experiment. Temperature treatments are presented in the second row. See Table 1 for an explanation of the symbols used to indicate responses.

Rangeland warming experiments	Semiarid grassland, New Mexico[1]	Mixed-grass Prairie, Wyoming[2,3]	Temperate grassland, Tasmania[4–6]	High-elevation meadow, Tibet[7]	High-elevation shrubland, Tibet[7]	Annual grassland, California[8–11]	High-elevation meadow, Colorado[12–14]	Tallgrass prairie, Oklahoma[15,16]
Temperature treatments	Nighttime (average 2.5°C air warming)	1.5/3°C day/night canopy warming	2°C canopy warming	1–2°C air warming	1–2°C air warming	1°C canopy/air warming	1.7°C soil warming	1.1°C air warming; 2.0–2.6°C soil warming
Plant biomass	25% increase in plant cover (1 yr only)	0	0	13% decrease in ANPP	0	0	0,+	9–21% increase in ANPP
Phenology		Flowering advanced (3 of 5 species)	Flowering advanced			Greening, flowering advanced		Flowering advanced in early species; delayed in late species
Water relations	−	−	−,+	0	0	+	−	−,0
Functional group responses for biomass	+ southern C_4 grass 0 northern C_4 grass	+ C_4 grass 0 C_3 grass	Variable	− grass	− grass + shrub	− forbs 0 grasses	+ shrub 0 grasses 0,-,+ forbs	+ C_4 grass 0 C_3 grass

[1] Collins et al. (2010). [2] Reyes-Fox (2008). [3] Morgan et al. (2011). [4] Hovenden et al. (2008a). [5] Hovenden et al. (2008b). [6] Pendall et al. (2011). [7] Klein et al. (2007). [8] Zavaleta et al. (2003a). [9] Zavaleta et al. (2003b). [10] Dukes et al. (2005). [11] Cleland et al. (2006). [12] Harte and Shaw (1995). [13] Loik and Harte (1997). [14] de Valpine and Harte (2001). [15] Wan et al. (2002). [16] Sherry et al. (2007).

the western United States occur during the hottest, driest portion of the year (Westerling et al. 2003), and the size of the area burned during any single year is correlated with the current drought condition (i.e., Palmer drought severity index) and with wetter-than-normal conditions in May and August of the previous year. Fires are largest in grass- and shrub-dominated ecosystems when unusually wet summers during which fine fuels accumulate are followed by dry conditions that enhance fuel flammability and ignition (Littell et al. 2009). Conversely, fires are largest in western forested ecosystems when precipitation is low and temperature is high in both the fire year and the preceding year. Fire activity is projected to increase considerably in the western United States as the climate becomes both warmer and drier (Pechony and Shindell 2010).

Exotic Plant Invaders. Climate change need not favor exotic or invasive over native plant species, but successful exotics often share traits that could contribute to a capacity to increase relative abundances and rapidly shift or extend ranges and exploit habitat openings (Dukes and Mooney 1999). These traits include short generation times, high fecundity and strong dispersal ability to expand into new habitats, broad environmental tolerances for attributes critical in the establishment of new individuals, rapid growth and high fecundity for colonization including the efficient use of resources like CO_2 and N, and independence from mutualistic organisms (Bradley et al. 2010). Despite these common traits, the particular mechanisms by which rising CO_2 or climate change will influence invasive species depends on plant community composition and competition for critical soil resources (Dukes and Mooney 1999), both of which can vary considerably among ecosystems. Consequently, invasive species will be addressed more fully in a section on regional scenarios.

Resource pulses and more frequent droughts are anticipated to favor exotic species, especially when dominant natives are suppressed by disturbances (Dukes and Mooney 1999; Smith et al. 2000; Buckland et al. 2001; Dukes et al. 2011), and to increase opportunities for invasive plant establishment by reducing competition from native species (White et al. 2001). For example, drought is thought to have contributed to the invasion of California grasslands by exotic annual grasses by reducing the density of native species (Jackson 1985; Everard et al. 2010).

Climate change will lead to combinations of seasonal temperature and precipitation that differ from current climatic conditions. This shift in climatic conditions, together with species differences in dispersal and the introduction or spread of exotic species, may produce plant communities that are compositionally unlike any found today (no-analog communities; Williams and Jackson 2007). No-analog communities (also termed "novel" or "emerging" communities or ecosystems) represent species combinations and relative abundances that have not occurred previously in a given biome (Hobbs et al. 2006). Novel communities of species having different biogeographical origins exist in grasslands in the central Plains as the result of human transformation (Wilsey et al. 2011). Climate change is anticipated to contribute to novel communities first in areas that warm the faster, possibly including the western United States (Williams and Jackson 2007).

Plant Phenology

Observational data indicate that warming is leading to earlier spring bud burst and flowering and a longer growing season in mid- and high-latitude regions (Badeck et al. 2004; Menzel et al. 2006). Meta-analyses of global data document an advancement of spring events by 2.3 d per decade and shifts in species ranges (Parmesan and Yohe 2003). Results from manipulative experiments generally confirm this trend, as experimental warming tends to advance the onset of growth and reproduction of plants (Zavaleta et al. 2003b; Cleland et al. 2006; Sherry et al. 2007; Hovenden et al. 2008b; Reyes-Fox 2008), although responses vary considerably among species and years (Table 2). Indeed, warming can retard phenological development of some species (Sherry et al. 2007) but promote earlier growth in other species and expose plants to more frequent damage from late frosts (Inouye 2008). Warming thus may lengthen the growing season for plant communities (Stelzer and Post 2009), and is projected to continue to do so especially on high-latitude and high-altitude rangelands unless plant responses are constrained by water limitation (Cleland et al. 2006).

Soil Organic Carbon and Sequestration

Carbon fluxes between soil and atmospheric pools are the net effect of well-understood ecological processes (Follett et al. 2001; Piñeiro et al. 2010) that are controlled by precipitation patterns and land use management. However, background variation associated with soils, geomorphology, vegetation, and disturbance regime add considerable complexity to these dynamics. Plant compounds are decomposed by soil microbes to form a relatively dynamic soil fraction known as particulate organic matter (POM). Most of the C in POM is rapidly released into the atmosphere as CO_2 via microbial respiration, but a small portion may be stabilized within aggregates associated with clay or silt particles and turn over on decadal time scales. These aggregates, assemblages of mineral and organic materials, are the repository for active soil C, the soil C pool that responds most readily to management, but may be lost locally to soil erosion (Post and Kwon 2000). Recalcitrant organic C (charcoal) and inorganic C (calcium carbonate) may also form significant pools of soil C, but they generally are not responsive in management time frames.

Precipitation. The amount and seasonality of precipitation directly control C input into soil through their strong effect on NPP. Most rangeland ecosystems are characterized by short periods of high C uptake (2–3 mo) and long periods of C balance or small respiratory C loss (Svejcar et al. 2008). Ungrazed sagebrush steppe and Great Plains grasslands were C sinks during most years of investigation, whereas desert sites in the southwestern United States were consistent C sources (Svejcar et al. 2008). NPP increases to a greater extent than respiration during wet years, resulting in a net increase in (positive) ecosystem exchange (NEE; C assimilation-emission), but NEE declines and often becomes negative during drought years to represent a C source (Zhang et al. 2010). Intra-annual variation in NEE also is highly correlated with precipitation patterns and other water-related environmental variables (Polley et al. 2010).

CO_2. CO_2 enrichment may either increase soil organic C by stimulating NPP (Hungate et al. 1997; Williams et al. 2000) or exert little effect if the rate of soil organic matter (SOM) decomposition increases to match that of NPP (Table 3; Gill et al. 2002; Pendall et al. 2004, 2011; Polley et al. 2006; Carrillo et al. 2011) Increased C inputs to soil often are accompanied by enhanced losses of pre-existing and mineral-associated SOM at elevated CO_2, apparently because microbes preferentially decompose older SOM to acquire sufficient N (Gill et al. 2002; Pendall et al. 2003, 2011). For example, SOM pools in mesic grassland did not change over 4 yr in response to experimentally elevated CO_2 (Gill et al. 2002), whereas modest amounts of SOC accumulated in annual grassland at elevated CO_2 when productivity increased slightly (Hungate et al. 1997).

Warming. Soil microbial and plant respiration, like photosynthesis, are sensitive to temperature, implying that warming may reduce NEE and soil C by preferentially increasing respiration and C flux to the atmosphere. However, a meta-analysis of warming (0.3–6.0°C) effects on tundra, grassland, and forest systems indicated that C inputs (NPP) increased by about the same percentage as soil respiration (19–20%; Rustad et al. 2001). Warming (1–2°C) increased soil respiration in tallgrass prairie in eastern Oklahoma during the spring and fall but reduced soil respiration during the summer (Wan et al. 2005; Zhou et al. 2006). The proportional response of soil respiration to warming was similar to that of NPP, implying that warming had little effect on NEE.

Livestock Production

Climatic change may affect livestock production both directly via physiological impacts on animal performance and indirectly via modifications to forage quality and quantity (the latter discussed previously) and the abundance of ectoparasites (Table 3). Warming likely will adversely affect livestock production in warm regions, such as the southwestern United States, but increase it in cooler regions by moderating winter temperatures (Baker et al. 1993; Eckert et al. 1995; Rotter and Van De Geijn 1999). Ames and Ray (1983) described a thermo-neutral zone in which food intake and energy requirements of livestock are not affected by temperature. However, at temperatures below the thermo-neutral zone, termed "lower critical temperature," animals increase energy production and food intake to maintain homeostasis. At temperatures above the thermo-neutral zone, termed "upper critical temperature," animals become heat stressed and must dissipate heat by reducing walking and spending more time in shade. Extreme heat and cold may alter voluntary animal intake by –50% and +30%, respectively (CCSP 2008).

Table 3. Summary of anticipated responses of key rangeland variables to climate change. See Table 1 for an explanation of the symbols used to indicate responses.

Response variable	↑[CO_2]	Warming	↑ Precipitation variability	Drought
C sequestration	0,+	0,−	0	−
C_3/C_4 species ratio	0,+	−		+
Livestock production	−,+	− southern and warm areas + cool areas	− mesic + arid	−

Thermal Livestock Stress. Heat stress decreases forage intake and milk production (Wyman et al. 1962) and the efficiency of feed conversion (McDowell 1968). One of the most critical outcomes of heat stress is reduced reproductive rates. Male and female gamete production, embryonic development, and fetal growth can be adversely affected by heat stress (Hansen 2009). Heat stress can be fatal to livestock, especially those fed large quantities of high-quality feeds (Haun 1997). This accounts for the occurrence of mass animal mortality in feedlots during heat waves. Temperature humidity index (THI; the weighted product of air temperature and relative humidity) values greater than 85 are considered an emergency for feedlot cattle (Haun 1997). Increases in temperatures of 1–5°C could cause high mortality among feedlot cattle unless sprinklers, additional shade, or similar measures to cool animals are employed (Howden et al. 2008). When nighttime temperatures remain above 23°C, feedlot cattle also may not be able to recover from high daytime temperatures, and the probability of animal mortality increases. Howden and Turnpenny (1997) reported that the number of "heat stress" days for cattle ($THI > 80$) increased by 60% during the last 40 yr in some areas of Australia.

Warmer temperatures may further suppress livestock performance by increasing winter survival and abundance of ectoparasites and their adverse impacts on animals (Karl et al. 2009). Of the 50 or more species of ectoparasites that affect cattle, horn flies (*Huematobia irrituns* [L.]) are the biggest concern in the United States (Byford et al. 1992). Horn flies can reduce cattle weight gain by 4–14%, and both increase water intake and reduce nitrogen retention (Byford et al. 1992). Horn flies also affect livestock behavior by increasing time spent walking and engaging in other avoidance behaviors, such as tail switching (Harvey and Launchbaugh 1982). These additional activities and energy expenditures directly contribute to reduced livestock performance. Of all ectoparasites, ticks (*Amblyomma americanurn* Koch) have the most adverse impact on cattle performance and can reduce weight gains of British breeds, such as Hereford, by $> 30\%$ (Byford et al. 1992). By contrast, ticks have little if any effect on Brahman cattle. In a modeling exercise, White et al. (2003) reported that livestock gains in Australia could decrease by $> 18\%$ because of increased tick infestations associated with climate change unless European and British cattle breeds are replaced by Brahmans or other tick resistant breeds.

Forage Quality. The effects of rising CO_2 and temperature on plants are complex and are likely to have mixed and site-dependent effects on forage quality. Rising CO_2 can increase shoot total nonstructural carbohydrates, thereby increasing forage quality (Read et al. 1997; Lilley et al. 2001), but also reduce forage quality, especially in dry, N-limited rangelands, by increasing the C:N ratio, lowering crude protein content, and increasing fiber content (Cotrufo et al. 1998; Morgan et al. 2001), all of which decrease digestibility (Morgan et al. 2004a; Milchunas et al. 2005; Owensby et al. 1996; but see Allard et al. 2003). Forage quality is suppressed to a greater extent in C_3 than C_4 grasses by elevated CO_2, but crude protein content and digestibility are inherently higher in C_3 grasses (Wand et al.

1999; Barbehenn et al. 2004). For example, CO_2 enrichment to 600 ppmv reduced the crude protein content of C_3 grasses in all years, whereas the sole C_4 species blue grama (*B. gracilis*) showed greatest reductions only in dry years (Milchunas et al. 2005). Increases in temperature can increase lignin and cell wall contents in plants (Ford et al. 1979; Cherney and Hall 2007; Sanz-Sáez et al. 2012; Thorvaldsson 2007), which lowers digestibility.

Ecosystem-level responses to warming may amplify or dampen warming effects on forage quality of individual plants or species. For example, warming may accelerate organic matter mineralization to enhance soil N availability (Rustad et al. 2001; Pendall et al. 2004; Dieleman et al. 2012) and shoot N concentration in grasslands (Dijkstra et al. 2010). However, warming also may reduce (Link et al. 2003; An et al. 2005) or have no effect on shoot N concentration, depending on prevailing temperatures, plant species, soils, the degree of warming, water availability, and time (Turunen et al. 2009). The few experiments in which effects of both higher CO_2 and warmer temperatures were investigated show declining forage quality as a result of reduced crude protein and higher fiber contents (Dieleman et al. 2012; Sanz-Sáez et al. 2012), but little of this work has been done on rangelands.

Variation in precipitation adds even more complexity to forage quality. Moderately dry conditions can increase forage quality by concentrating N in plant tissues (Murphy et al. 2002) and delaying maturity (Craine et al. 2009), but severe drought that results in plant senescence has a decidedly negative effect. Forage N concentration, cell soluble contents, and digestibility decrease rapidly during senescence, and values for recent dead forage can be less than one-half of those of live forage (Kamstra 1973).

An extensive analysis of cattle fecal material collected throughout the continental United States (21 000 samples collected over 14 yr) provided evidence that livestock become more nutrient limited in warmer and drier climates as both the dietary crude protein and the digestible organic matter content of forages decrease (Craine et al. 2010). Warmer temperature had a stronger negative effect on forage quality than did decreasing precipitation. At the spatial scale of this analysis, trends in forage quality reflected both direct and indirect effects of climate, the latter including effects on management strategies and ecosystem properties, such as plant species composition. Consequently, these trends may not reflect those observed in a specific ecosystem in response to climate change. For example, forage protein content increases across the continental United States as precipitation increases (Craine et al. 2010), whereas plant N concentration often is lower and plant C:N ratios are higher in grasses in mesic than arid ecosystems (Wedin 1995; Murphy et al. 2002).

The differential effects of climate change drivers on plant species (Izaurralde et al. 2011; Polley et al. 2012b) will contribute to species shifts on rangelands that may either increase (Polley et al. 2011) or decrease (Morgan et al. 2007) forage quality, depending on which species are favored. For example, elevated CO_2 reduced forage digestibility on shortgrass steppe partly by increasing production of the grass with the lowest digestibility, *Stipa comata* (Morgan et al. 2004a). Unfortunately, our ability to predict plant community species shifts and the consequences for forage quality are generally poor. Regions like the Southwest that are expected to experience more extreme drought (Seager and Vecchi 2010) will be vulnerable to declines in forage quality that result because drought hastens plant senescence. However, forage quality may change little or even be enhanced in ecoregions in which combined changes in climate change drivers have little effect on species composition and have a less adverse effect on or even promote plant growth. The length of growing season will provide the primary constraint on forage quality and quantity by establishing the duration and periodicity when live forage is present. Reduced forage quality is associated with greater methane production per unit of gross energy consumed (Benchaar et al. 2001). Therefore, livestock may become a greater source of methane in the future if the reduction in forage quality is not offset by a decrease in forage intake.

REGIONAL SCENARIOS

The ecological consequences of climate change will vary substantially among geographic regions in response to antecedent environmental conditions and nonadditive interactions among major climate change drivers (Fig. 5). Climate change models project unique climatic scenarios for the southwestern United States and northern Mexico, the southern Plains, the northern Plains and south-central Canada, and the northwestern United States and southwestern Canada (IPCC 2007). Therefore, the ecological consequences of these unique projections are assessed independently for greater geographic specificity and to emphasize this regional variation. Two important qualifiers are associated with the interpretation of regional scenarios: climate change models simulate average regional values, meaning that results cannot be reliably downscaled to local areas or short time periods (years to decades; Kerr 2011), and greater uncertainty is associated with projected changes in precipitation than CO_2 concentration and warming.

Southwestern United States and Northern Mexico

Climate Projections. Climate change is well under way in this region with clear trends of both warming and drying (US Global Change Research Program 2009; Seager and Vecchi 2010). This is partially a consequence of a northward shift in the track of winter and spring storms. Temperatures are expected to increase by 2.0–3.0°C by 2050 (Fig. 4) and 2.2–5.5°C by 2100, and spring precipitation is anticipated to decrease by 20–40% by the end of the century, but the contribution of summer monsoon remains uncertain (US Global Change Research Program 2009). Monsoons have been delayed by approximately 10 d in northern Mexico over the last half century. Multiyear droughts are projected to increase by mid-century, with some persisting for a decade or more (Cayan et al. 2010). In spite of this drying trend, flooding events are anticipated to increase in response to greater storm intensities falling on a larger proportion of bare soil.

NPP and Forage Quality. Warming and drying will synergistically reduce soil water availability to decrease NPP. Greater plant WUE resulting from elevated CO_2 and an increase in the proportion of available soil water resulting from fewer but larger precipitation events will likely be insufficient to offset regional warming and drying. Forage quality is very likely to decrease in response to synergistic interactions among warming, elevated CO_2, and drought stress.

Livestock Production. Livestock production will be reduced by lower forage quantity and quality and a decrease in voluntary animal intake associated with lower-quality forage, higher temperatures, and more frequent heat stress (CCSP 2008). Heat stress can be fatal for cattle in feedlots in this region if temperature increases by 1–5°C, especially for those fed large quantities of high-quality feeds (Haun 1997; Howden et al. 2008).

Extremely high temperatures combined with water deprivation can result in livestock losses on rangelands (Kay 1997). Surface water availability will decrease as springs and dugouts dry during drought, requiring that livestock travel greater distances for water. Walking increases the heat load on animals such that livestock must increase sweating and respiration rates to maintain homeostatis (Moran 1973). Consequently, livestock modify their behavior on rangelands by spending more time near water and shade and in riparian areas (Kay 1997; Parsons et al. 2003), reducing the total area grazed with negative effects on plant communities and forage production. Management responses likely will include a switch in cattle breeds. *Bos indicus* (“Indian” or oriental breeds, such as Brahman) are better adapted to high temperature and water limitations than are *Bos taurus* (“European” breeds, such as Angus) cattle. The skin of Brahmans has greater capacity for nonevaporative heat transfer (Finch 1986; Carvalho et al. 1995), hair color and structure is more resistant to solar radiation (Peters et al. 1982), and water turnover rates are one-half those of European cattle breeds (MacFarlane et al. 1971).

Vegetation Composition. More frequent and severe droughts may contribute to species specific replacement and to episodic die-offs to modify vegetation composition. For example, the severe drought of 2002–2003 caused greater than 90% mortality of pinyon pine (*Pinus edulis*) in the Southwest, whereas associated trees of *Juniperus monosperma* survived (Breshears et al. 2005, 2009). Rainfall amount was similar during the recent and 1950s droughts, but die-off was greater during the 2000s drought because current temperatures are warmer than previously, leading to greater drying and plant water stress. The Sonoran Desert may exhibit major species and community range shifts, including those of such iconic species as Saguaro cactus (*Carnegiea gigantean*) and Joshua trees (*Yucca brevifolia*), in response to an increasing frequency of serve drought and wildfires (Weiss and Overpreck 2005; CCSP 2008). Increasing fire frequency in the Mojave Desert and Great Basin in the past 20 yr has converted communities of desert shrublands and shrub steppe to annual grasslands (CCSP 2008; Balch et al. 2013).

Climate change is anticipated to both positively and negatively affect exotic or invasive species by facilitating local extinctions, migration, and new invasions. Yellow starthistle (*Centaurea solstitialis*) is projected to maintain its current area and expand into more of California and Nevada (Bradley et al. 2009). Rising CO_2 may contribute to the invasive nature of cheatgrass and its close relative red brome (*Bromus madritensis* subsp. *rubens*; Smith et al. 2000; Ziska et al. 2005), although climate change is also expected to reduce the risk for cheatgrass invasion from current portions of its southern range in southern Nevada and Utah (Bradley and Wilcove 2009; Bradley et al. 2009). Red brome may replace cheatgrass in some of its southern range (Salo 2005). Shifts from snow to rain may favor cheatgrass invasion at higher elevations because rainfall frequency is more critical to its success than rainfall amount (Concilio et al. 2013). Increased aridity will have a less negative impact on recruitment of exotics like *Tamarix* compared to more drought-sensitive natives such as willows (*Salix* spp.) and cottonwoods (*Populus* spp.) in riparian corridors (Perry et al. 2013), which could enhance invasion by these exotics. However, expansion of *Taramix* and likely other such riparian species beyond these corridors may be limited (Bradley et al. 2009).

Community boundaries were documented to synchronously migrate upslope along a 2 000-m elevation gradient in the Santa Rosa Mountains of California during the past 30 yr (Kelly and Goulden 2008). These elevational increases in community boundaries closely correspond to mean temperature increases observed over this time period and imply a direct effect of warming on the migration of entire plant communities rather than only specific species.

Southern Plains

Climate Projections. Warming and drying are projected for this region as for the Southwest. Warming will be greatest in the North and drying greatest in the South (Fig. 4). Temperature is projected to increase by as much as 3.3°C in 2050 and 5.5°C in 2100, and precipitation may decrease by 5–10% by midcentury (US Global Change Research Program 2009).

NPP and Forage Quality. Warming and drying are anticipated to reduce both NPP and forage quality as described for the Southwest. Warming (2°C) alone increased plant production by as much as 21% in tallgrass prairie in Oklahoma, but the growth responses were negative during the dry summer (An et al. 2005; Wan et al. 2005). A decrease in forage quality may necessitate that producers provide additional supplementation to meet the nutritional requirements of livestock, which of course would increase operating costs. Supplements and other feeds currently account for more than one-half of the direct operating expenses of cow–calf operations (Short 2001).

Livestock Production. Responses are likely to be similar to those in the Southwest but may be less severe.

Vegetation Composition. More frequent and severe droughts are anticipated to lead to species-specific replacement and episodic die-offs that will modify vegetation composition. For example, eastern red cedar (*Juniperus virginiana*) was the only southern savanna dominant in which neither survival nor aboveground mass was adversely affected by experimentally imposed warming and intensified summer drought (Volder et al. 2010, 2013). Growth of both eastern red cedar and post oak (*Quercus stellata*) were reduced by intensified summer drought, but growth of eastern red cedar increased in response to warming, while that of post oak did not. Similarly, establishment and growth of *Quercus emoryi* were especially sensitive to intensified summer drought in the Southwest (Weltzin and McPherson 2000). These results suggest that juniper encroachment is very likely to accelerate in response to climate change based on greater drought tolerance and positive response to warming (Volder et al. 2010, 2013).

Northern Plains and South Central Canada

Climate Projections. A temperature increase of 4.3°C (2.8–7.1°C) and a precipitation increase of 15% (8–31%), especially in the winter, are projected for the region (Fig. 4; IPCC 2007). The amount of precipitation falling as snow is anticipated to continue to decline.

NPP and Forage Quality. Warming and increased precipitation, coupled with elevated atmospheric CO_2 concentrations, are anticipated to increase NPP by alleviating environmental growth limitations to both initiate growth earlier and extend the growing season (CCSP 2008). Warming has been shown to increase NPP in semiarid grasslands if combined with elevated CO_2 because of the water-conserving effect of CO_2 enrichment (Morgan et al. 2011). Forage quality is likely to remain constant or even increase, unless the benefits of increased precipitation for forage quality are offset by negative effects of CO_2 enrichment and, possibly, warming.

Livestock Production. Increased NPP and length of growing season, along with reduced feeding costs during the winter, will likely increase total production and the efficiency of production (CCSP 2008). However, subtle shifts in the periodicity of annual rainfall can significantly modify livestock production. For example, mid- and late-summer precipitation had offsetting effects on bison weight gain in tallgrass prairie (Craine et al. 2009). Late-season precipitation increased animal gain, but midsummer precipitation decreased gain by stimulating culm development in these grasses that reduced forage quality and animal performance.

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 may favor recruitment and subsequent growth 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). On the other hand, climatic suitability for spotted knapweed (*Centaurea biebersteinii*) is expected to shift to higher elevations, leading to both contractions and expansion in Montana, Wyoming, Utah, and Colorado. Leafy spurge (*E. esula*) is likely to retreat from Nebraska, and parts of Oregon and Idaho, reducing invasion risk in the northern Plains but increasing invasion risk in southern Canada (Bradley et al. 2009).

Northwest

Climate Projections. Temperature is projected to increase by 3.4°C (2.0–5.7°C), and precipitation is expected to show a modest increase (5%) in winter but a decrease in summer by the end of this century (IPCC 2007; US Global Change Research Program 2009; Diffenbaugh et al. 2005). Snow cover and depth have declined in the western United States since the mid-20th century with reductions approximating 25% and 10% in the Oregon Cascades and high elevations of the Rockies and southern Sierras, respectively (Mote et al. 2005; Christensen and Lettenmaier 2006; Ray et al. 2008). Snowpack reductions likely will continue by as much as 40% by mid-century in the Cascades. Spring snowmelt and stream flow is occurring 20–40 d earlier than in 1900 (Mote et al. 2005). An increased amount and intensity of winter rain is anticipated to produce greater flooding and increase wildfire frequency in conjunction with drier summers.

NPP and Forage Quality. Warming is likely to decrease soil water availability, especially in the latter portion of the growing season, and reduce NPP. Earlier snowmelt (10–15 d in 50 yr) and reduced stream flow is anticipated to reduce production in riparian systems (CCSP 2008). Elevated CO_2, coupled with warming and drying, has the potential to suppress forage quality, but net effects of climate change are uncertain.

Livestock Production. Benefits of milder, wet winters may offset negative effects of longer and drier summers on livestock production, with negligible net effect of climate change. Animals may require supplemental feed during the extended dry summers.

Vegetation Composition. The current range of yellow starthistle (*C. solstitialis*) in northern California, Oregon, and Washington is expected to remain relatively constant, although greater proliferation within the region is expected (Bradley et al. 2009). Shrublands and grasslands in the intermountain West are currently invaded or under threat of invasion by cheatgrass (*Bromus tectorum*), medusahead (*Taenetherum capetmedusa*), and red brome. Increasing atmospheric CO_2 and greater frequencies of fire and other disturbances are expected to exacerbate these threats, especially at higher elevations and in northern parts of these species' current ranges (Smith et al. 2000; Ziska et al. 2005; Chambers and Pellant 2008; Bradley et al. 2009).

SYNOPSIS OF ECOLOGICAL IMPLICATIONS

- The three major drivers of climate change—rising atmospheric CO_2 concentration, atmospheric warming, and modified amounts and temporal patterns of precipitation—collectively affect soil water availability to influence many aspects of rangeland systems.
- The ecological consequences of climate change will vary substantially among biogeographic regions in response to antecedent environmental conditions and the differing expression of warming and precipitation modification among regions. Ecosystem processes such as NPP will decrease in the South in response to warming and a decrease in precipitation, increase in the North as a result of warming

and greater precipitation, and decrease in the Northwest as a result of drier summers.

- Climate change may modify the composition of rangeland vegetation and induce a shift in geographic distributions of plant species, including exotic (invasive) species. In some instances, vegetation reorganization may produce communities that are compositionally unlike any found today (i.e., no-analog communities).
- An increasing occurrence of climatic extremes, specifically successive wet vs. dry seasons or years, will likely increase the frequency and extent of wildfires in grasslands and necessitate greater attention to fuel management and safeguards to human life and property.
- Climate change will have modest and regionally variable effects on soil organic C content that will minimize the magnitude of shifts in C content, making them difficult to detect with current technology. This has important implications for the development and monitoring of successful mitigation strategies emphasizing C sequestration (Joyce et al. 2013 [this issue]).
- Livestock production systems will be increasingly constrained by the combined effects of reduced forage quality and quantity, greater thermal stresses on animals, and increasingly adverse effects of ectoparasites. Varied and often multiple adaptation strategies will be required to sustain economically viable livestock enterprises (Joyce et al. 2013 [this issue]).
- Directional change in climatic means and increasing climatic variability and extreme events indicate that a “business as usual” approach to rangeland management is no longer viable. Previous climatic and weather patterns may no longer serve as a reliable guide to future conditions.

KNOWLEDGE GAPS

- Precise projections of mean climatic trends, especially at regional levels, and of the intensity, frequency, and ecological consequences of extreme climatic events (Diffenbaugh et al. 2005; Reyer et al. 2013).
- Sufficient insight into interactive effects among climate change drivers on soil water and NPP in major rangeland ecoregions (Fay et al. 2008; Knapp et al. 2008; Heisler-White et al. 2009).
- Extent of species and community shifts that may occur in response to climate change, including range shifts in invasive species and the expansion of native woody plants, and plant and animal pathogens (Weiss and Overpeck 2005; Bradley et al. 2009).
- Response of riparian systems to warming, decreasing snowpack, earlier and smaller stream flows, and prolonged summer dry periods (Mote et al. 2005; Christensen and Lettenmaier 2006).
- The capacity of existing concepts, models and tools within the profession to accommodate the dynamics and uncertainty associated with climate change.
- A national database for archiving and managing information to document the various impacts of climate change on rangeland systems, including the outcomes of climate change drivers on major management strategies (IPCC 2007; US Global Change Research Program 2009).

MANAGEMENT IMPLICATIONS

A compelling footprint of climate change has been emerging since the mid-20th century that lends tremendous credibility to model projections of increased deviation from mean climatic trends and greater climatic variability. Uncertainties regarding climate projections and the specific consequences of these changes are to be expected given the unprecedented rate and scale of this phenomenon. However, it would be irresponsible to ignore the cumulative evidence for climate change and its current and future implications. The long-recognized significance of climate variability in rangeland ecosystem function and enterprise viability clearly justifies the need for an objective and comprehensive assessment of the implications of climate change for management recommendations, policy decisions, and research agendas. Increased preparedness for climate change does not require a precise projection of future conditions, only a recognition that sufficient directional change and greater extremes may exist to modify the services provisioned by current ecosystems to adversely affect human well-being.

Consensus projections of numerous climate change models indicate that the Southwest and southern Plains will become both warmer and drier, the Northwest will become warmer and drier during summer with reduced snowpack in winter, and the northern United States and southern Canada will become warmer and wetter, especially during the winter. Substantial variation among ecoregions demonstrates that climate change will not be expressed as a uniform series of events at a continental scale but rather will be characterized by substantial spatial and temporal variability. Increasing variability and uncertainty may be of greater consequence to rangeland systems than the long-term deviation in climatic trends.

We contend that an unrealistic perception of climatic consistency has hindered the development and implementation of sufficient contingency planning to manage for current weather variability and that it poses a major impediment to recognition of the emerging consequences of climate change as well as development of effective strategies to contend with these consequences. It is essential for the rangeland profession to recognize that 1) shifts in mean climatic trends have already been documented, 2) accelerated rates of climate change will have dramatic effects on the provisioning of rangeland services and human well-being, and 3) many of the adverse consequences of climate change may be effectively confronted with the proactive development and implementation of appropriate adaptation and transformation strategies (Joyce et al. 2013 [this issue]).

ACKNOWLEDGMENTS

Matt Reeves and Rebecca Sherry provided helpful reviews of the manuscript prior to submission. The associate editor, Jeanne Chambers, and an anonymous reviewer provided valuable guidance for manuscript organization and presentation. Jon Eischeid prepared the temperature and precipitation graphics.

LITERATURE CITED

Allard, V., P. C. D. Newton, M. Lieffering, H. Clark, C. Matthew, and Y. Gray. 2003. Nutrient cycling in grazed pastures at elevated CO_2: N returns by animals. *Global Change Biology* 9:1731–1742.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J-H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.

Ames, D. R., and D. E. Ray. 1983. Environmental manipulation to improve livestock productivity. *Journal of Animal Science* 57:209–220.

An, Y., S. Wan, X. Zhou, A. A. Subedar, L. L. Wallace, and Y. Luo. 2005. Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. *Global Change Biology* 11:1733–1744.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? *Climatic Change* 29:91–99.

Augustine, D. J., and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall in a semi-arid savanna. *Ecosystems* 9:1242–1256.

Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.

Badeck, F. W., A. Bondeau, K. Bottcher, D. Doktor, W. Lucht, J. Schaber, and S. Sitch. 2004. Responses of spring phenology to climate change. *New Phytologist* 162:295–309.

Baker, B. B., J. H. Hanson, R. M. Bourdon, and J. B. Eckert. 1993. The potential effects of climate change on ecosystem processes and cattle production on US rangelands. *Climatic Change* 25:97–117.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology* 19:173–183.

Barbehenn, R. V., Z. Chen, D. N. Karowe, and A. Spickards. 2004. C_3 grasses have higher nutritional quality than C_4 grasses under ambient and elevated CO_2. *Global Change Biology* 10:1565–1575.

BassiriRad, H., D. C. Tremmel, R. A. Virginia, J. F. Reynolds, A. G. de Soyza, and M. H. Brunell. 1999. Short term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecology* 145:27–36.

Benchaar, C., C. Pomar, and J. Chiquette. 2001. Evaluation of dietary strategies to reduce methane production in ruminants: a modeling approach. *Canadian Journal of Animal Science* 81:563–574.

Blumenthal, D., R. A. Chimner, J. M. Welker, and J. A. Morgan. 2008. Increased snow facilitates plant invasion in mixed grass prairie. *New Phytologist* 179:440–448.

Bond, W. J. 2008. What limits trees in C_4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39:641–659.

Bradley, B. A., D. M. Blumenthal, D. S. Wilcove, and L. H. Ziska. 2010. Predicting plant invasions in an era of global change. *Trends in Ecology and Evolution* 25:310–318.

Bradley, B. A., M. Oppenheimer, and D. S. Wilcove. 2009. Climate change and plant invasions: restoration opportunities ahead? *Global Change Biology* 15:1511–1521.

Bradley, B. A., and D. S. Wilcove. 2009. When invasive plants disappear: transformative restoration possibilities in the western United States resulting from climate change. *Restoration Ecology* 17:715–721.

Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers, and C. W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* 102:15144–15148.

Breshears, D. D., O. B. Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, C. D. Allen, N. G. McDowell, and W. T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7:185–189.

Buckland, S. M., K. Thompson, J. G. Hodgson, and J. P. Grime. 2001. Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology* 38:301–309.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: > 50 years of data suggests CO_2 as a driver. *Global Change Biology* 18:675–684.

Byford. R. L., M. E. Craig, and B. L. Crosby. 1992. A review of ectoparasites and their effect on cattle production. *Journal of Animal Science* 70:596–602.

Carrillo, Y., E. Pendall, F. A. Dijkstra, J. A. Morgan, and J. M. Newcomb. 2011. Responses of soil organic matter pools to elevated CO_2 and warming in a semi-arid grassland. *Plant and Soil* 347:339–350.

Carvalho, F. A., M. A. Lammoglia, M. J. Simoes, and R. D. Randel. 1995. Breed affects thermoregulation and epithelial morphology in imported and native cattle subjected to heat stress. *Journal of Animal Science* 73:3570–3573.

Cayan, D. R., T. Das, D. W. Pierce, T. P. Barnett, M. Tyree, and A. Gershunov. 2010. Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences of the United States of America* 107:21271–21276.

[CCSP] US Climate Change Science Program. 2008. Synthesis and assessment product 4.3 (SAP 4.3): the effects of climate change on agriculture, land resources, water resources, and biodiversity in the United States. Washington, DC, USA: US Climate Change Science Program.

Chambers, J. S., and M. Pellant. 2008. Climate change impacts on northwestern and intermountain United States rangelands. *Rangelands* 30(3):29–33.

Cherney, J. H., and M. V. Hall. 2007. Forage quality in perspective: agronomy facts 30. University Park, PA, USA: Pennsylvania State University. Available at http://www.forages.psu.edu/agfacts/agfact30.pdf. Accessed 5 August 2013.

Christensen, N., and D. P. Lettenmaier. 2006. A multimodel ensemble approach to assessment of climate change impacts on the hydrology and water resources of the Colorado River basin. *Hydrology and Earth System Sciences Discussion* 3:1–44.

Cleland, E. E., N. R. Chiariello, S. R. Loarie, H. A. Mooney, and C. B. Field. 2006. Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* 103:13740–13744.

Concilio, A. L., M. E. Loik, and J. Belnap. 2013. Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. *Global Change Biology* 19:161–172.

Cotrufo, M. F., P. Ineson, and A. Scott. 1998. Elevated CO_2 reduces the nitrogen concentration of plant tissues. *Global Change Biology* 4:43–54.

Craine, J. M., A. J. Elmore, K. C. Olson, and D. Tolleson. 2010. Climate change and cattle nutritional stress. *Global Change Biology* 16:2901–2911.

Craine, J. M., J. B. Nippert, A. J. Elmore, A. M. Skibbe, S. L. Hutchinson, and N. A. Brunsell. 2012. Timing of climate variability and grassland productivity. *Proceedings of the National Academy of Sciences of the United States of America* 109:3401–3405.

Craine, J. M., E. G. Town, A. Joern, and R. G. Hamilton. 2009. Consequences of climate variability for the performance of bison in tallgrass prairie. *Global Change Biology* 15:772–779.

De Valpine, P., and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82:637–648.

Dieleman, W. I. J., S. Vicca, F. A. Dijkstra, F. Hagedorn, M. J. Hovenden, K. S. Larsen, J. A. Morgan, A. Volder, C. Beier, J. S. Dukes, J. King, S. Leuzinger, S. Linder, Y. Luo, R. Oren, P. de Angelis, D. Tingey, M. R. Hoosbeek, and I. A. Janssens. 2012. Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature. *Global Change Biology* 18:2681–2693.

Diffenbaugh, N. S., J. S. Pal, R. T. Trapp, and F. Giorgi. 2005. Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Sciences of the United States of America* 102:15774–15778.

Dijkstra, F. A., D. Blumenthal, J. A. Morgan, E. Pendall, Y. Carrillo, and R. F. Follett. 2010. Contrasting effect of elevated CO_2 and warming on nitrogen cycling in a semiarid grassland. *New Phytologist* 187:426–437.

Dijkstra, F. A., E. Pendall, A. R. Mosier, J. Y. King, D. G. Milchunas, and J. A. Morgan. 2008. Long-term enhancement of N availability and plant growth under elevated CO_2 in a semi-arid grassland. *Functional Ecology* 22:975–982.

Dukes, J. S., N. R. Chiariello, E. E. Cleland, L. A. Moore, M. R. Shaw, S. Thayer, T. Tobeck, H. A. Mooney, and C. B. Field. 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS Biology* 3(10):e319. doi:10.1371/journal.pbio.0030319

Dukes, J. S., N. R. Chiariello, S. R. Loarie, and C.B. Field. 2011. Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. *Ecological Applications* 21:1887–1894.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135–139.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.

Eckert, J. B., B. B. Backer, and J. D. Hanson. 1995. The impact of global warming on the local incomes of range livestock systems. *Agricultural Systems* 48:87–100.

Ehleringer, J. R., and R. Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24:411–439.

Epstein, H. E., R. A. Gill, J. M. Paruelo, W. K. Lauenroth, G. J. Jia, and I. C. Burke. 2002. The relative abundance of three plant functional types in temperature grasslands and shrublands of North and South America: effects of projected climate change. *Journal of Biogeography* 29:875–888.

Everard, K., E. W. Seabloom, W. S. Harpole, and C. de Mazancourt. 2010. Plant water use affects competition for nitrogen: why drought favors invasive species in California. *American Naturalist* 175:85–97.

Fay, P. A., J. D. Carlisle, A. K. Knapp, J. M. Blair, and S. L. Collins. 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. *Oecologia* 137:245–251.

Fay, P. A., V. L. Jin, D. A. Way, K. N. Potter, R. A. Gill, R. B. Jackson, and H. W. Polley. 2012. Soil-mediated effects of subambient to increased carbon dioxide on grassland productivity. *Nature Climate Change* 2:742–746.

Fay, P. A., D. M. Kaufman, J. B. Nippert, J. D. Carlisle, and C. W. Harper. 2008. Changes in grassland ecosystem function due to extreme precipitation events: implications for responses to climate change. *Global Change Biology* 14:1600–1608.

Finch, V. A. 1986. Body temperature of beef cattle: its control and relevance to production in the tropics. *Journal of Animal Science* 62:531–542.

Follett, R. F., J. M. Kimble, and R. Lal. 2001. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, FL, USA: Lew Publishers. 442 p.

Ford, C. W., I. M. Morrison, and J. R. Wilson. 1979. Temperature effects on lignin, hemicellulose and cellulose in tropical and temperate grasses. *Australian Journal of Agricultural Research* 30:621–634.

Friedli, H., H. Lötscher, H. Oeschger, U. Siegenthaler, and B. Stauffer. 1986. Ice core record of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries. *Nature* 324:237–238.

Gebauer, R. L. E., and J. R. Ehleringer. 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. *Ecology* 81:1415–1424.

Gill, R. A., H. W. Polley, H. B. Johnson, L. J. Anderson, H. Maherali, and R. B. Jackson. 2002. Non-linear grassland responses to past and future atmospheric CO_2. *Nature* 417:279–282.

Groisman, P. Y., R. W. Knight, D. R. Easterling, T. R. Karl, G. C. Hegerl, and V. A. N. Razuvaev. 2005. Trends in intense precipitation in the climate record. *Journal of Climate* 18:1326–1350.

Groisman, P. Y., R. W. Knight, T. R. Karl, D. R. Easterling, B. Sun, and J. H. Lawrimore. 2004. Contemporary changes of the hydrological cycle over the contiguous United States: trends derived from in situ observations. *Journal of Hydrometeorology* 5:64–85. doi:10.1175/1525–7541

Hansen, P. J. 2009. Effects of heat stress on mammalian reproduction. *Philosophical Transactions of the Royal Society of Biological Sciences* 364:3341–3350.

Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* 267:876–880.

Harte, J., M. Torn, F.-R. Chang, B. Feifarek, A. P. Kinzig, R. Shaw, and K. Shen. 1995. Global warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications* 5:132–150.

Harvey, T. L., and J. L. Launchbaugh. 1982. Effect of horn flies on behavior of cattle. *Journal of Economic Entomology* 75:25–27.

Haun, G. L. 1997. Dynamic responses of cattle to thermal heat loads. *Journal of Animal Science* 77:10–20.

Heisler-White, J. L., J. M. Blair, E. F. Kelly, K. Harmoney, and A. K. Knapp. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Global Change Biology* 15:2894–2904.

Higgins, S. I., and S. Scheiter. 2012. Atmospheric CO_2 forces abrupt vegetation shifts locally, but not globally. *Nature* 488:209–212.

Hirsch, R. M., and K. R. Ryberg, 2012. Has the magnitude of floods across the USA changed with global CO_2 levels? *Hydrological Sciences Journal* 57:1–9.

Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P. R. Epstein, J. J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, D. M. Richardson, E. W. Sanderson, F. Valladares, M. Vilà, R. Zamora, and M. Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15:1–7.

Hoerling, M., and A. Kumar. 2003. The perfect ocean for drought. *Science* 299:691–694.

Hovenden, M. J., P. C. D. Newton, K. E. Willis, J. K. Janes, A. L. Williams, J. K. Vander Schoor, and M. J. Nolan. 2008a. Influence of warming on soil water potential controls seedling mortality in perennial but not annual species in a temperate grassland. *New Phytologist* 180:143–152.

Hovenden, M. J., A. L. Williams, J. K. Pedersen, J. K. Vander Schoor, and K. E. Wills. 2008b. Elevated CO_2 and warming impacts on flowering phenology in a southern Australian grassland are related to flowering time but not growth form, origin or longevity. *Australian Journal of Botany* 56:630–643.

Howden, S. M., S. J. Crimp, and C. J. Stokes. 2008. Climate change and Australian livestock systems: impacts, research and policy issues. *Australian Journal of Experimental Agriculture* 48:780–788.

Howden S. M., and J. Turnpenny. 1997. Modelling heat stress and water loss of beef cattle in subtropical Queensland under current climates and climate change. *In:* D. A. McDonald and M. McAleer [eds.]. Proceedings of the International Congress on Modelling and Simulation. Canberra, Australia: Modelling and Simulation Society of Australia. p. 1103–1108.

Hungate, B. A., E. A. Holland, R. B. Jackson, F. S. Chapin III, H. A. Mooney, and C. B. Field. 1997. The fate of carbon in grassland under carbon dioxide enrichment. *Nature* 388:576–579.

Hurrell, J. W., Y. Kushnir, M. Visbeck, and G. Ottersen. 2003. An overview of the North Atlantic Oscillation. *In:* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.]. The North Atlantic Oscillation: climate significance and environmental impact. Washington, DC, USA: American Geophysical Union. Geophysical Monograph Series 134. p. 1–35.

Huxman, T. E., K. A. Knyder, D. Tissue, A. J. Leffler, K. Ogle, W. T. Pockman, D. R. Sandquist, D. L. Potts, and S. Schwinning. 2004a. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–268.

Huxman, T. E., M. D. Smith, P. A. Fay, A. K. Knapp, M. R. Shaw, M. E. Loik, S. D. Smith, D. T. Tissue, J. C. Zak, J. F. Weltzin, W. T. Pockman, O. E. Sala, B. M. Haddad, J. Harte, G. W. Koch, S. Schwinning, E. E. Small, and D. G. Williams. 2004b. Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654.

Ignace, D. D., T. E. Huxman, J. F. Weltzin, and D. G. Williams. 2007. Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia* 152:401–413.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.

[IPCC] Intergovernmental Panel on Climate Change. 2007. Climate change 2007: the physical science basis, contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *In:* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller [eds.]. Cambridge, UK: Cambridge University Press. 996 p.

Izaurralde, R. C., A. M. Thompson, J. A. Morgan, P. A. Fay, H. W. Polley, and J. L. Hatfield. 2011. Climate impacts on agriculture: implications for forage and rangeland production. *Agronomy Journal* 103:371–381.

Jackson, L. E. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* 12:349–361.

Joyce, L. A., D. D. Briske, J. R. Brown, H. W. Polley, B. A. McCarl, and D. W. Bailey. 2013. Climate change and North American rangelands: assessment of mitigation and adaptation strategies. *Rangeland Ecology & Management* 66:512–528.

Kamstra, L. D. 1973. Seasonal changes in forage quality of some important range grasses. *Journal of Range Management* 26:286–291.

Karl, T. R., J. M. Melillo, and T. C. Peterson [eds.]. 2009. Global climate change impacts in the United States. Cambridge, UK: Cambridge University Press. 196 p.

Kay, R. M. B. 1997. Responses of African livestock and wild herbivores to drought. *Journal of Arid Environments* 37:683–694.

Keeling, R. F., S. C. Piper, A. F. Bollenbacher, and J. S. Walker. 2009. Atmospheric CO_2 records from sites in the SIO air sampling network. *In:* Trends: a compendium of data on global change. Oak Ridge, TN, USA: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy. doi: 10.3334/CDIAC/atg.035.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105:11823–11826.

Kerr, R. A. 2011. Vital details of global warming are eluding forecasters. *Science* 334:173–174.

Kharin, V. V., F. W. Zwiers, X. Zhang, and G. C. Hegerl. 2007. Changes in temperature and precipitation extremes in the IPCC ensemble of global coupled model simulations. *Journal of Climate* 20:1419–1444.

Klein, J. A., J. Harte, and X.-Q. Zhao. 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan plateau. *Ecological Applications* 17:541–557.

Knapp, A. K., C. Beier, D. D. Briske, A. T. Classen, Y. Luo, M. Reichstein, M. D. Smith, S. D. Smith, J. E. Bell, P. A. Fay, J. L. Heisler, S. W. Leavitt, R. Sherry, B. Smith, and E. Weng. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience* 58:811–821.

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484.

Kunkel, K. E., D. R. Easterling, K. Redmond, and K. Hubbard. 2003. Temporal variations of extreme precipitation events in the United States: 1895–2000. *Geophysical Research Letters* 30:1900. doi:10.1029/2003GL018052

League, K., and T. Veblen. 2006. Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. *Forest Ecology and Management* 228:98–107.

Lilley, J. M., T. P. Bolger, M. B. Peoples, and R. M. Gifford. 2001. Nutritive value and the nitrogen dynamics of *Trifolium subterraneum* and *Phalaris aquatic* under warmer, high CO_2 conditions. *New Phytologist* 150:385–395.

Lin, D., J. Xia, and S. Wan. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist* 188:187–198.

Lindzen, R. S. 1999. The greenhouse effect and its problems. *In:* T. R. Gerholm [ed.]. Climate policy after Kyoto. Brentwood, UK: Multi-Science Publishing Company. 170 p.

Link, S. O., J. L. Smith, J. J. Halvorson, and H. Bolton. 2003. A reciprocal transplant experiment within a climatic gradient in a semiarid shrub-steppe ecosystem: effects on bunchgrass growth and reproduction, soil carbon, and soil nitrogen. *Global Change Biology* 9:1097–1105.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. *Ecological Applications* 19:1003–1021.

Lloret, F., J. Peñuelas, and R. Ogaya. 2004. Establishment of co-existing Mediterranean tree species under a varying soil moisture regime. *Journal of Vegetation Science* 15:237–244.

Loik, M. E., and J. Harte. 1997. Changes in water relations for leaves exposed to a climate-warming manipulation in the Rocky Mountains of Colorado. *Environmental and Experimental Botany* 37:115–123.

Luo, Y. 2007. Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology, Evolution, & Systematics* 38:683–712.

Luo, Y., B. Su, W. S. Currie, J. S. Dukes, A. Finzi, U. Hartwig, B. Hungate, R. E. McMurtrie, R. Oren, W. J. Parton, D. E. Pataki, M. R. Shaw, D. R. Zak, and C. B. Field. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54:731–739.

MacFarlane, W. V., B. Howard, H. Haines, P. J. Kennedy, and C. M. Sharpe. 1971. Hierarchy of water and energy turnover in desert mammals. *Nature* 234:483–484.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1079.

Marlon, J. R., P. J. Bartlein, C. Carcaillet, D. G. Gavin, S. P. Harrison, P. E. Higuera, F. Joos, M. J. Power, and I. C. Prentice. 2008. Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience* 1:697–702.

Marshall, J. D., J. M. Blair, D. P. C. Peters, G. Okin, A. Rango, and M. Williams. 2008. Predicting and understanding ecosystem responses to climate change at continental scales. *Frontiers in Ecology and the Environment* 6:273–280.

McCabe, G. J., and M. P. Clark. 2006. Shifting covariability of North American summer monsoon precipitation with antecedent winter precipitation. *International Journal of Climatology* 26:991–999.

McDowell, R. E. 1968. Climate versus man and his animals. *Nature* 218:641–645.

McKeon, G. M., G. S. Stone, J. I. Syktus, J. O. Carter, N. R. Flood, D. G. Ahrens, D. N. Bruget, C. R. Chilcott, D. H. Cobon, R. A. Cowley, S. J. Crimp, G. W. Fraser, S. M. Howden, P. W. Johnston, J. G. Ryan, C. J. Stokes, and K. A. Day. 2009. Climate change impacts on northern Australian rangeland livestock carrying capacity: a review of issues. *The Rangeland Journal* 31:1–29.

Meehl, G. A., C. Covey, T. Delworth, M. Latif, B. McAvaney, J. F. B. Mitchell, R. J. Stouffer, and K. E. Taylor. 2007. The WCRP CMIP3 multi-model dataset: a new era in climate change research. *Bulletin of the American Meteorological Society* 88:1383–1394.

Meehl, G., C. Tibaldi, G. Walton, D. Easterling, and L. McDaniel. 2009. Relative increase of record high maximum temperature compared to record low minimum temperature in the US. *Geophysical Research Letters* 36:L23701. doi:10.1029/2009GL040736

Menne, M. J., and C. N. Williams, Jr. 2009. Homogenization of temperature series via pairwise comparisons. *Journal of Climate* 12:1700–1717. doi:10.1175/2008JCLI2263.1

Menne, M. J., C. N. Williams, Jr., and R. S. Vose. 2009. The U.S. historical climatology network monthly temperature data, version 2. *Bulletin of the American Meteorological Society* 91:993–1007.

Menzel, A. T., H. Sparks, E. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alum-Kübler, P. Bissolli, O. Braslavská, A. Briede, R. M. Chmielewski, Z. Crepinsek, Y. Curnel, A. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatczak, F. Mage, A. Mestre, O. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F-E Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.

Milchunas, D. G., A. R. Mosier, J. A. Morgan, D. R. LeCain, J. Y. King, and J. A. Nelson. 2005. Elevated CO_2 and defoliation effects on a shortgrass steppe: forage quality versus quantity for ruminants. *Agriculture, Ecosystems and Environment* 111:166–184.

Moran, M. B. 1973. Heat tolerance of Brahman cross, buffalo, banteng, and shorthorn steers during exposure to the sun and as a result of exercise. *Australian Journal of Agricultural Research* 24:775–782.

Morgan, J. A., D. R. Lecain, A. R. Moiser, and D. G. Milchunas. 2001. Elevated CO_2 enhances water relations and productivity and affects gas exchange in C_3 and C_4 grasses of the Colorado shortgrass steppe. *Global Change Biology* 7:451–466.

Morgan, J. A., D. R. LeCain, E. Pendall, D. M. Blumenthal, B. A. Kimball, Y. Carrillo, D. G. Williams, J. Heisler-White, F. A. Dijkstra, and M. West. 2011. C_4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476:202–206.

Morgan, J. A., D. G. Milchunas, D. R. LeCain, M. West, and A. R. Mosier. 2007. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. *Proceedings of the National Academy of Sciences of the United States of America* 104:14724–14729.

Morgan, J. A., A. R. Moiser, D. G. Milchunas, D. R. Lecain. J. A. Nelson, and W. J. Parton. 2004a. CO_2 enhances productivity, alters species composition, and reduces digestibility of shortgrass steppe vegetation. *Ecological Applications* 14:208–219

Morgan, J. A., D. E. Pataki, C. Körner, H. Clark, S. J. Del Grosso, J. M. Grünzweig, A. K. Knapp, A. R. Mosier, P. C. D. Newton, P. A. Niklaus, J. B. Nippert, R. S. Nowak, W. J. Parton, H. W. Polley, and M. R. Shaw. 2004b. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia* 140:11–25.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society* 86:39–49.

Murphy, K. L., I. C. Burke, M. A. Vinton, W. K. Lauenroth, M. R. Aguiar, D. A. Wedin, R. A. Virginia, and P. N. Lowe. 2002. Regional analysis of litter quality in the central grassland region of North America. *Journal of Vegetation Science* 13:395–402.

Nelson, D. W., and F. S. Hu. 2008. Patterns and drivers of Holocene vegetational change near the prairie-forest ecotone in Minnesota: revisiting McAndrews' transect. *New Phytologist* 179:449–459.

NOAA National Climatic Data Center. 2013. State of the climate: national overview for annual 2012. Available at: http://www.ncdc.noaa.gov/sotc/national/2012/13. Accessed 30 January 2013.

Nowak, R. S., D. S. Ellsworth, and S. D. Smith. 2004. Functional responses of plants to elevated atmospheric CO$_2$—do photosynthetic and productivity data from FACE experiments support early prediction? *New Phytologist* 162:253–280.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:23–51.

Owensby, C. E., R. C. Cochran, and L. M. Auen. 1996. Effects of elevated carbon dioxide on forage quality for ruminants. *In:* C. Körner and F. Bazzaz [eds.]. Carbon dioxide, populations and communities. Physiological Ecology Series. London, UK: Academic Press. p. 363–371.

Owensby, C. E., P. I. Coyne, J. M. Ham, L. M. Auen, and A. K. Knapp. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated levels of CO$_2$. *Ecological Applications* 3:644–653.

Owensby, C. E., J. M. Ham, A. K. Knapp, and L. M. Auen. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO$_2$. *Global Change Biology* 5:497–506.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

Parsons, C. T., P. A. Momont, T. DelCurto, M. McInnis, and M. L. Porath. 2003. Cattle distribution patterns and vegetation use in mountain riparian areas. *Journal of Range Management* 56:334–341.

Parton, W. J., J. A. Morgan, G. Wang, and S. Del Grosso. 2007. Projected ecosystem impact of the prairie heating and CO$_2$ enrichment experiment. *New Phytologist* 174:823–834.

Pearcy, R. W., and J. Ehleringer. 1984. Comparative ecophysiology of C$_3$ and C$_4$ plants. *Plant, Cell and Environment* 7:1–13.

Pechony, O., and D. T. Shindell. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences of the United States of America* 107:19167–19170.

Pendall, E., S. Del Grosso, J. Y. King, D. R. LeCain, D. G. Milchunas, J. A. Morgan, A. R. Moiser, D. S. Ojima, W. A. Parton, P. P. Tans, and J. W. C. White. 2003. Elevated atmospheric CO$_2$ effects and soil water feedbacks on soil respiration components in a Colorado grassland. *Global Biogeochemical Cycles* 17:1046. doi:10.1029/2001GB001821

Pendall, E., A. R. Mosier, and J. A. Morgan. 2004. Rhizodeposition stimulated by elevated CO$_2$ in a semiarid grassland. *New Phytologist* 162:447–458.

Pendall, E., Y. Osanai, A. L. Williams, and M. J. Hovenden. 2011. Soil carbon storage under simulated climate change is mediated by plant functional type. *Global Change Biology* 17:505–514.

Peñuelas, J., I. Filella, X. Y. Zhang, L. Llorens, R. Ogaya, F. Lloret, P. Comas, M. Estiarte, and J. Terradas. 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* 161:837–846.

Pepper, D. A., S. J. Del Grosso, R. E. McMurtire, and W. J. Parton. 2005. Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO$_2$], temperature and nitrogen input. *Global Biogeochemical Cycles* 19:1004. doi:10.1029/2004GB002226

Perry, L. G., P. B. Shaforth, D. M. Blumenthal, J. A. Morgan, and D. R. LeCain. 2013. Elevated CO$_2$ does not offset greater water stress predicted under climate change for native and exotic riparian plants. *New Phytologist* 197:532–543.

Peters, K. J., P. Horst, and H. H. Kleinheisterkamp. 1982. The importance of coat colour and type as indicators of productive adaptability of beef cattle in a subtropical environment. *Tropical Animal Production* 7:296–304.

Piñeiro, G., J. M. Paruelo, M. Oesterheld, and E. G. Jobbágy. 2010. Pathways of grazing effects on soil organic carbon and nitrogen. *Rangeland Ecology & Management* 63:109–119.

Polley, H. W., W. Emmerich, J. A. Bradford, P. L. Sims, D. A. Johnson, N. Z. Salendra, T. Svejcar, R. Angell, A. B. Frank, R. L. Phillips, K. A. Snyder, and J. A. Morgan. 2010. Physiological and environmental regulation of interannual variability in CO$_2$ exchange on rangelands in the western United States. *Global Change Biology* 16:990–1002.

Polley, H. W., P. A. Fay, V. L. Jin, and G. F. Combs Jr. 2011. CO$_2$ enrichment increases element concentrations in grass mixtures by changing species abundances. *Plant Ecology* 212:945–957.

Polley, H. W., V. L. Jin, and P. A. Fay. 2012a. CO$_2$-caused change in plant species composition rivals the shift in vegetation between mid-grass and tallgrass prairies. *Global Change Biology* 18:700–710.

Polley, H. W., V. L. Jin, and P. A. Fay. 2012b. Feedback from plant species change amplifies CO$_2$ enhancement of grassland productivity. *Global Change Biology* 18:2813–2823.

Polley, H. W., H. B. Johnson, and J. D. Derner. 2003. Increasing CO$_2$ from subambient to superambient concentrations alters species composition and increases above-ground biomass in a C$_3$/C$_4$ grassland. *New Phytologist* 160:319–327.

Polley, H. W., P. C. Mielnick, W. A. Dugas, H. B. Johnson, and J. Sanabria. 2006. Increasing CO$_2$ from subambient to elevated concentrations increases grassland respiration per unit of net carbon fixation. *Global Change Biology* 12:1390–1399.

Post, W. M., and K. C. Kwon. 2000. Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology* 6:317–327.

Ray, A. J., J. J. Barsugli, K. B. Averyt, K. Wolter, M. Hoerling, N. Doesken, B. Udall, and R. S. Webb. 2008. Climate change in Colorado—a synthesis to support water resources management and adaptation. Report by the Western Water Assessment for the Colorado Water Conservation Board, Boulder. 58 p. Available at: http://cwcb.state.co.us/public-information/publications/documents/reportsstudies/climatechangereportfull.pdf. Accessed 5 August 2013.

Read, J. J., J. A. Morgan, N. J. Chatterton, and P. A. Harrison. 1997. Gas exchange and carbohydrate and nitrogen concentrations in leaves of *Pascopyrum smithii* (C$_3$) and *Bouteloua gracilis* (C$_4$) at different carbon dioxide concentrations and temperatures. *Annals of Botany* 79:197–206.

Reich, P. B., D. Tilman, S. Naeem, D. S. Ellsworth, J. Knops, J. Craine, D. Wedin, and J. Trost. 2004. Species and functional group diversity independently influence biomass accumulation and its response to CO$_2$ and N. *Proceedings of the National Academy of Sciences of the United States of America* 101:10101–10106.

Resco, V., D. D. Ignace, W. Sun, T. E. Huxman, J. F. Weltzin, and D. G. Williams. 2008. Chlorophyll fluorescence, predawn water potential and photosynthesis in precipitation pulse-driven ecosystems—implications for ecological studies. *Functional Ecology* 22:479–483.

Reyer, C. P. O., S. Leuzinger, A. Rammig, A. Wolf, R. P. Bartholomeus, A. Bonfante, F. de Lorenzi, M. Dury, P. Gloning, R. Abou Jaoudé, T. Klein, T. M. Kuster, M. Martins, G. Niedrist, M. Riccardi, G. Wohlfahrt, P. de Angelis, G. de Dato, L. Francois, A. Menzel, and M. Pereira. 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. *Global Change Biology* 19:75–89.

Reyes-Fox, M. 2008. Interactive effects of elevated CO$_2$, warming and water additions on the timing and rates of plant development in a northern mixed-prairie ecosystem: enhancing the GPFarm model [thesis]. Fort Collins, CO, USA: Colorado State University. 188 p.

Robertson, T. R., J. C. Zak, and D. T. Tissue. 2010. Precipitation magnitude and timing differentially affect species richness and plant density in the sotol grassland of the Chihuahuan Desert. *Oecologia* 162:185–197.

Rockström, J., W. S. Steffen, K. Noone, A. Persson, F. S. Chapin III, E. F. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, and J. A. Foley. 2009. A safe operating space for humanity. *Nature* 461:472–475.

Rotter, R., and S. C. Van De Geijn. 1999. Climate change effects on plant growth, crop yield and livestock. *Climate Change* 43:651–681.

Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, and J. Gurevitch. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.

Sage, R. F., and D. S. Kubien. 2003. Quo vadis C$_4$? An ecophysiological perspective on global change and the future of C$_4$ plants. *Photosynthesis Research* 77:209–225.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.

Salo, L. F. 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. *Biological Invasions* 7:165–180.

Sanz-Sáez, Á., G. Erice, J. Aguirreolea, F. Muñoz, M. Sánchez-Díaz, and J. J. Irigoyen. 2012. Alfalfa forage digestibility, quality and yield under future climate change scenarios vary with *Sinorhizobium meliloti* strain. *Journal of Plant Physiology* 169:782–788.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.

Seager, R., and G. A. Vecchi. 2010. Greenhouse warming and the 21st century climate of southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America* 107:21277–21282.

Sherry, R. A., E. Weng, J. A. Arnone, D. W. Johnson, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2008. Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology* 14:2923–2936.

Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone III, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America* 104:198–202.

Short, S. D. 2001. Characteristics and production costs of U.S. cow-calf operations. USDA Statistical Bulletin 974-3. Available at: http://www.ers.usda.gov/publications/sb974-3/sb974-3.pdf. Accessed 6 August 2010.

Smith, S. D., T. E. Huxman, S. F. Zitzer, T. N. Charlet, D. C. Housman, J. S. Coleman, L. K. Fenstermaker, J. R. Seemann, and R. S. Nowak. 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79–82.

Stelzer, H., and E. Post. 2009. Seasons and life cycles. *Science* 324:886–887.

Svejcar, T., R. Angell, J. A. Bradford, W. Dugas, W. Emmerich, A. B. Frank, T. Gilmanov, M. Haferkamp, D. A. Johnson, H. Mayeux, P. Mielnick, J. Morgan, N. Z. Saliendra, G. E. Schuman, P. L. Sims, and K. Snyder. 2008. Carbon fluxes on North American rangelands. *Rangeland Ecology & Management* 61:465–474.

Swemmer, A. M., A. K. Knapp, and H. A. Snyman. 2007. Intra-seasonal precipitation patterns and above ground productivity in three perennial grasslands. *Journal of Ecology* 95:780–788.

Thorvaldsson, G., G. F. Tremblay, and H. T. Kunelius. 2007. The effects of growth temperature on digestibility and fibre concentration of seven temperate grass species. *Acta Agriculturae Scandinavica B Soil and Plant Science* 57:322–328.

Turunen, M., P. Soppela, H. Kinnunen, M.-L. Sutinen, and F. Martz. 2009. Does climate change influence the availability and quality of reindeer forage plants? *Polar Biology* 32:813–832.

US Global Change Research Program. 2009. Global climate change impacts in the United States. T. R. Karl, J. M. Melillo, and T. C. Peterson [eds.]. Cambridge, UK: Cambridge University Press. Available at: http://www.globalchange.gov/usimpacts. Accessed 5 August 2013.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology & Systematics* 31:197–205.

Van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperature forest. *Ecology Letters* 10:909–916.

Volder, A., D. D. Briske, and M. G. Tjoelker. 2013. Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. *Global Change Biology* 19:843–857.

Volder, A., M. G. Tjoelker, and D. D. Briske. 2010. Contrasting physiological responsiveness of establishing trees and a C_4 grass to rainfall events, intensified summer drought, and warming in oak savanna. *Global Change Biology* 16:3349–3362.

Walther, G. R. 2003. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6:169–185.

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B* 365:2019–2024.

Wan, S., D. Hui, L. L. Wallace, and Y. Luo. 2005. Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles* 19:2014. doi:10.1029/2004GB002315

Wan, S., Y. Luo, and L. L. Wallace. 2002. Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology* 8:754–768.

Wand, S. J. E., G. F. Midgley, M. H. Jones, and P. S. Curtis. 1999. Responses of wild C_4 and C_3 grass (Poaceae) species to elevated atmospheric CO_2 concentrations: a meta-analytic test of current theories and perceptions. *Global Change Biology* 5:723–741.

Weaver, J. E., and F. W. Albertson. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. *Ecological Monographs* 13:63–117.

Webb, N. P., C. J. Stokes, and J. C. Scanlan. 2012. Interacting effects of vegetation, soils and management on the sensitivity of Australian savanna rangelands to climate change. *Climatic Change* 112:925–943.

Wedin, D. A. 1995. Species, nitrogen, and grassland dynamics: the constraints of stuff. *In:* C. G. Jones and J. H. Lawton [eds.]. Linking species and ecosystems. New York, NY, USA: Chapman & Hall. p. 253–263.

Weiss, J. L., and J. T. Overpeck. 2005. Is the Sonoran desert losing its cool? *Global Change Biology* 11:2065–2077.

Weltzin, J. F., and G. R. McPherson. 2000. Implications of precipitation redistribution for shifts in temperate savanna ecotones. *Ecology* 81:1902–1913.

Wentz, F. J., L. Ricciardulli, K. Hilburn, and C. Mears. 2007. How much rain will global warming bring? *Science* 317:233–235.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2003. Warming and earlier spring increases Western U.S. forest wildfire activity. *Science* 313:940–943.

White, N., R. W. Sutherst, N. Hall, and P. Whish-Wilson. 2003. The vulnerability of the Australian beef industry to the cattle tick (*Boophilus microplus*) under climate change. *Climate Change* 61:157–190.

White, T. A., B. D. Camp, P. D. Kemp, and C. L. Hunt. 2001. Impacts of extreme climatic events on competition during grasslands invasions. *Global Change Biology* 7:1–13.

Wilcox, B. P., M. G. Stone, and M. H. Young. 2011. Dryland ecohydrology in the Anthropocene: taking stock of human-ecological interactions. *Geography Compass* 5:112–127.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and Evolution* 5:475–482.

Williams, M. A., C. W. Rice, and C. E. Owensby. 2000. Carbon dynamics and microbial activity in tallgrass prairie exposed to elevated CO_2 for 8 years. *Plant and Soil* 227:127–137.

Wilsey, B. J., P. P. Danesghar, and H. W. Polley. 2011. Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands. *Perspectives in Plant Ecology, Evolution and Systematics* 13:265–276.

Woodhouse, C. A., D. M. Meko, G. M. MacDonald, D. W. Stahle, and E. R. Cook. 2010. A 1,200-year perspective of 21st century drought in southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America* 107:21283–21288.

Wyman, O., H. D. Johnson, C. P. Merilan, and I. L. Berry. 1962. Effect of ad libitum and force feeding of two rations on lactating dairy cows subject to temperature stress. *Journal of Dairy Science* 45:1472–1478.

Yahdjian, L., and O. E. Sala. 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology* 87:952–962.

Zavaleta, E. S., M. R. Shaw, N. R. Chiariello, B. D. Thomas, E. E. Cleland, C. B. Field, and H. A. Mooney. 2003a. Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. *Ecological Monographs* 73:584–604.

Zavaleta, E. S., B. D. Thomas, N. R. Chiariello, G. P. Asner, M. R. Shaw, and C. B. Field. 2003b. Plants reverse warming effect on ecosystem water balance. *Proceedings of the National Academy of Sciences of the United States of America* 100:9892–9893.

Zhang, L., B. K. Wylie, L. Ji, T. G. Gilmanov, and L. L. Tieszen. 2010. Climate-driven interannual variability in net ecosystem exchange in the northern Great Plains grasslands. *Rangeland Ecology & Management* 63:40–50.

Zhou, X., R. A. Sherry, Y. An, L. L. Wallace, and Y. Luo. 2006. Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem. *Global Biogeochemical Cycles* 20:GB1003. doi:10.1029/2005GB002526

Ziska, L. H., J. B. Reeves, and B. Blank. 2005. The impact of recent increases in atmospheric CO_2 on biomass production and vegetative retention of cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology* 11:1325–1332.