Rangeland Drought: Effects, Restoration, and Adaptation

Deborah M. Finch

Rosemary L. Pendleton

Matt C. Reeves

Jeffrey E. Ott

Francis F. Kilkenny

Jack L. Butler

Jacqueline P. Ott

Jeremy R. Pinto

Paulette L. Ford

Justin B. Runyon

Mark A. Rumble

Stanley G. Kitchen

D.M. Finch is a Biologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Albuquerque, NM 87102.

R.L. Pendleton is a Research Plant Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Albuquerque, NM 87102.

M.C. Reeves is a Research Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Missoula, MT 59807.

J.E. Ott is a Research Geneticist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

F.F. Kilkenny is a Research Biologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

J.L. Butler is a Research Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Rapid City, SD 57702.

J.P. Ott is a Post-Doctoral Research Botanist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Rapid City, SD 57702.

J.R. Pinto is a Research Plant Physiologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Moscow, ID 83843.

P.L. Ford is a Research Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Albuquerque, NM 87102.

J.B. Runyon is a Research Entomologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Bozeman, MT 59717.

M.A. Rumble is a Research Wildlife Biologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Rapid City, SD 57702.

S.G. Kitchen is a Research Botanist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Provo, UT 84606.

Introduction

Drought can have severe impacts on rangeland ecosystems in North America. For the purposes of this chapter, rangelands include natural grasslands, savannas, shrublands, many deserts, tundras, alpine communities, marshes, meadows, and woodlands. Drought impacts vary depending on the severity, frequency, duration, and aerial extent of the drought(s); how the land is managed; and whether plans are in place and implemented to respond to drought. Drought can be simply defined as "a lack of water" characteristic of time, not of place; or it can be defined in a climatic context, as "precipitation levels that are much lower than the annual average" (chapter 2). Chapter 2 identifies four drought classifications: (1) meteorological drought which focuses on water in the atmosphere, (2) hydrologic drought which focuses on available surface water, (3) agricultural or soil moisture drought which emphasizes crop response to declining moisture in soils, and (4) socioeconomic drought which emphasizes the social and economic impacts of drought. These classifications emphasize the harmful impacts of drought, particularly on managed systems and people.

One of the most harmful droughts impacting American rangelands and farmlands was the drought of the 1930s known as the Dust Bowl. Direct effects of the drought were both agricultural and socioeconomic; the drought caused damage to crops, livestock, and ultimately humans. The 1930s drought was several distinct events occurring in such rapid succession that affected regions were unable to recover adequately before another drought began. These severe, sequential droughts and the vast aerial extent the droughts covered, in combination with poor agricultural practices, overexpansion, and poverty associated with the Great Depression, made the 1930s drought period the most widely accepted "drought of record" for the United States (Hurt 1981, Warrick 1980). Reduced plant cover and increased bare ground led to dust storms (during high winds) and loss of topsoil. The resulting agricultural depression contributed to the Great Depression's bank closures, business losses, increased unemployment, and other physical and emotional hardships.

Many lessons in resiliency and adaptation were learned in response to the calamitous effects of the Dust Bowl. Proactive measures following the 1930s drought included increased conservation practices and irrigation, improved farming and ranching practices, and diversified regional economy. Other actions included new or enlarged reservoirs, improved domestic water systems, new insurance and aid programs, and removal of some of the most sensitive agricultural lands from production (Riebsame and others 1991). These learned strategies helped to reduce the region's vulnerability to the negative impacts associated with drought.

With these adaptations, the likelihood of having a rangeland drought as catastrophic as the Dust Bowl has lessened substantially. Nevertheless, given the recent history, paleo-record, and recurring nature of drought and its relationship to climate change, it remains critical to understand the full range of its effects on natural and managed lands; to know techniques to reduce species and ecosystem vulnerability to drought; and to have information available that will assist in recovering natural and managed systems from the impacts of drought. High temperatures and lack of precipitation associated with the Dust Bowl would not only have affected crops, livestock, and people, they would also have affected native plants and animals, and they would have created water shortages—yet these ecological effects were not well-understood or reported at the time. Thus, while agricultural and socioeconomic classifications of drought have sharp bearing on rangelands and farmlands, they do not adequately encompass the ecological impacts of drought on native rangeland species, plant communities, and wildlife habitat. The direct and indirect consequences of severe and extended drought are complex, interactive, and numerous. There are a number of early ecological indicators that signal the impending possibility of serious agricultural and socioeconomic drought on rangelands, and they are important to understand and monitor. Listed sequentially, these early ecological indicators include:

- Water shortages stress plants and animals

- Vegetation production is reduced

- Plant mortality increases

- Plant cover is reduced

- Amount of bare ground increases

- Soil erosion become more prevalent

- Habitat and food resources for wildlife are reduced

- Wildlife mortality increases

● Rangeland fires may increase

● Some insect pests and invasive weeds may increase

● Forage value and livestock carrying capacity decreases

● Economic depression in the agricultural sector sets in

To convey the full importance of drought impacts on rangelands in both natural and managed settings, our goals in this chapter are to describe: (1) the ecological history of rangeland drought, (2) the ecological consequences of drought to native rangeland species and ecosystems, (3) the effects of drought on natural disturbances, (4) the effects of drought on land management practices, and (5) the adaptive responses of ecosystems to drought.

Types and Patterns of Rangeland Drought

Droughts are of grave concern to policymakers, livestock producers, and the agricultural sector because droughts are among the most costly of disasters (Andreadis and others 2005), and they significantly impact numerous goods and services. Large-scale, persistent droughts have periodically occurred across North American rangelands and are not unusual (Andreadis and others 2005, Cook and others 2007, Weakley 1965). Dai and others (1998) suggest that trends in drought intensity over the past two to three decades derive from global warming. While severe, these conditions have not yet clearly exceeded drought severity in the 20th century (e.g., the Dust Bowl era) (Cook and others 2010). Similarly, a review of drought trends by Cook and others (2010) suggests that the Western United States has recently entered a period of protracted aridity; a perspective accentuated by the particularly troublesome, ongoing situations in Texas and California. The year 2011 was the single worst year on record for Texas with drought continuing into a third year. That year, wildfires in Texas burned 2.7 million acres along with 2,725 residential homes (National Interagency Fire Center; http://www.predictiveservices.nifc.gov/intelligence/2011_statssumm/fires_acres.pdf, date accessed: October 15, 2015). Cattle sector losses were reported at $3.23 billion just for a single year (Amico and others 2011).

The 2011 drought conditions in Texas are an example of "flash drought" when soils dry very rapidly. These events coincide with high temperatures, low cloud cover, low rainfall, and high winds. Because they generally occur during the growing season, flash droughts can be particularly devastating for agriculture and livestock grazing (Otkin and others 2013).

Drought Trends and Regional Effects

To understand long-term trends and impacts of drought over rangelands of the coterminous United States, we present trends from three sources including Parameter-elevation Relationships on Independent Slopes Model (PRISM) project data (1982–2012), weekly drought maps from the U.S. Drought Monitor (2000–2013), and Normalized Difference Vegetation Index (NDVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) at 250-m^2 spatial resolution (2000–2013). We wanted to illustrate the number of seasonal periods indicative of a drying landscape where seasonal or annual temperatures have been increasing while precipitation has been decreasing. Such an index is a practical way to assimilate large amounts of data for understanding impacts of changing climates on vegetation and other resources (Zargar and others 2011).

In figure 8.1, warmer tones indicate increasingly restrictive growth conditions. Since 1982, the southern part of the United States has been exhibiting unfavorable trends in growing conditions resulting from warmer temperatures and decreasing precipitation. Relative to other western regions, much of Arizona, Texas, New Mexico, and the Oklahoma Panhandle exhibit the most notable decreasing trends in growing conditions. The reddish regions in north central New Mexico correspond with the massive dieoff (90 percent) of pinyon pine (*Pinus edulis*) and illustrate the scale of vegetation change these conditions can induce (Breshears and others 2005). A loss of this magnitude of a long-lived, arid-adapted tree is attributed to persistent drought accompanied by warmer temperatures, resulting in greatly reduced soil moisture and water stress (Breshears and others 2005). Conversely, much of the upper Midwest and northern Great Plains have become wetter and slightly warmer, indicating improved growing conditions. It is worth noting that this type of climatic trend assessment will not usually capture the episodic or ephemeral droughts; those events are more appropriately captured in shorter timeframes, such as the weekly spatially explicit data from the U.S. Drought Monitor.

Since 2000, there have been several significant events in which intense drought has enveloped western
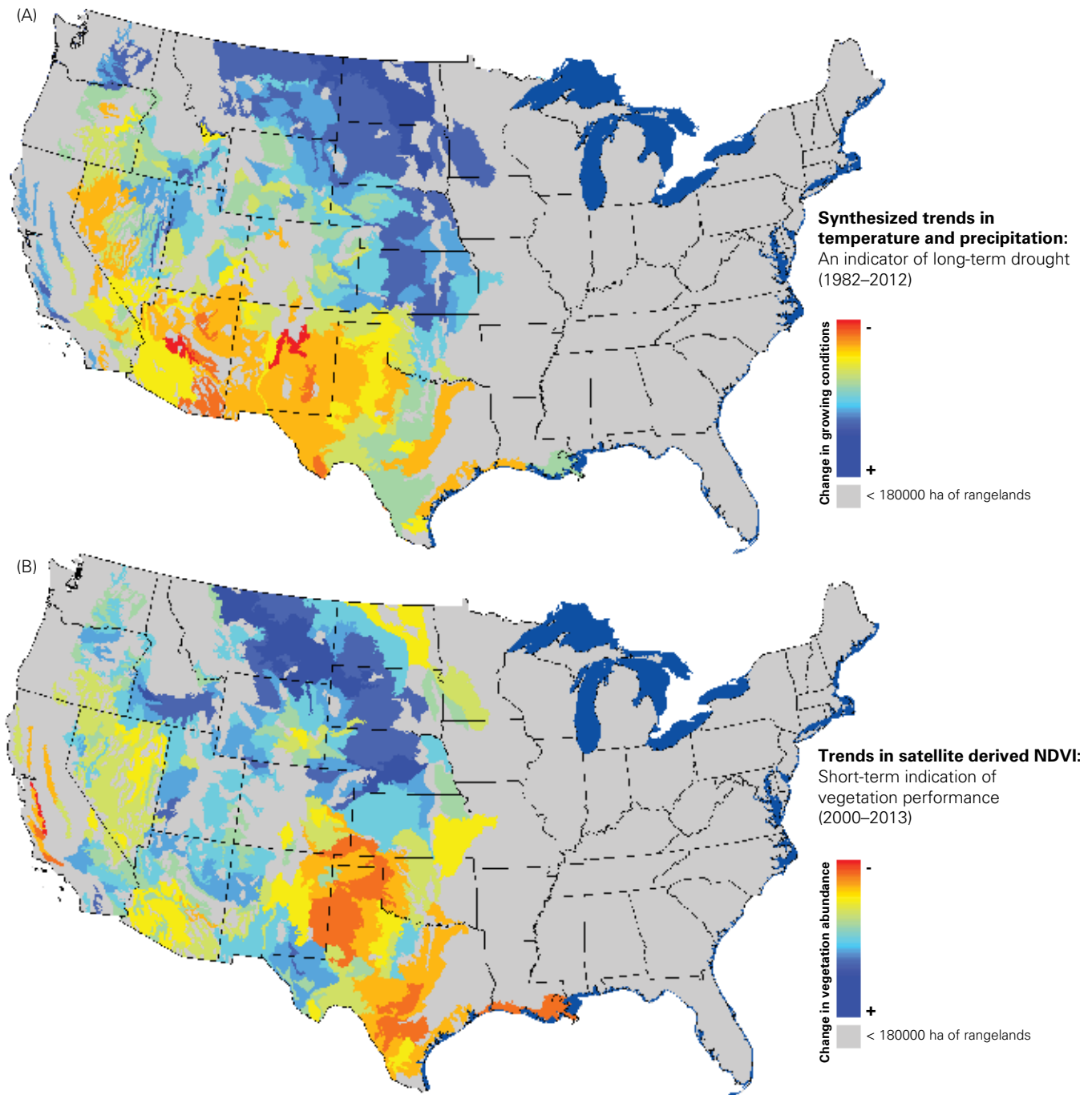
(A)

Synthesized trends in temperature and precipitation:
An indicator of long-term drought (1982–2012)

Change in growing conditions

-

+

< 180000 ha of rangelands

(B)

Trends in satellite derived NDVI:
Short-term indication of vegetation performance (2000–2013)

Change in vegetation abundance

-

+

< 180000 ha of rangelands

Figure 8.1—Drought intensity and effects on vegetation. Top panel (A) represents trends in gridded surface climatology from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) project, 1982–2012. Warmer tones indicate areas where temperature has been increasing while precipitation has been decreasing; cooler tones represent improved growing conditions. Bottom panel (B) represents the trend of Normalized Difference Vegetation Index (NDVI) from Moderate Resolution Imaging Spectroradiometer (MODIS) at 250-m² spatial resolution averaged over ecological subsections (Bailey and Hogg 1986), 2000–2013. Warmer tones indicate where vegetation abundance has been decreasing through time (i.e., a "browning" of the landscape), while cooler tones represent greater vegetation (i.e., a "greening") of the landscape. (Maps created by Matt Reeves).

rangelands (fig. 8. 2). Since 2011, the average area occupied by the most significant drought category (D4 in fig. 8.2) has more than doubled compared with 2000–2010 records. The information in figure 8.3 was developed from weekly estimates of drought categories very similar to that represented in figure 8.2. Figure 8.2 depicts the ongoing drought conditions over much of Texas and California. These drought episodes combined with longer term deterioration of growing conditions seen in other regions (fig. 8.1) have negatively affected the growth and abundance of rangeland vegetation. Because rangeland vegetation responds relatively quickly to changing meteorological conditions, it can be efficiently monitored using satellite remote sensing.

Reeves and Baggett (2014) developed an algorithm for quantifying trends in MODIS 250-m^2 NDVI for the United States. For this report, we evaluated vegetation types or U.S. Ecological Systems (Comer and others 2003) associated with negative vegetation trends since 2000. Table 8.1 indicates that many vegetation types have experienced declining trends

on over 30 percent of the total area they occupy in the coterminous United States. Over 41 million ha of vegetation (~15 percent of all rangeland vegetation in the coterminous United States) (Reeves and Mitchell 2011) has exhibited declining trends in abundance since 2000. From a regional perspective, vegetation has responded in a similar pattern as indicated by the PRISM climatology. Note the decline of rangeland vegetation abundance on the southern Great Plains area in addition to the marked declines in the central California region (fig. 8.1). Although drought events in California in the 20th century were less frequent than previous patterns, there have been a number of recent drought episodes of significance to natural systems and socioeconomic well-being (Hughes and Brown 1992). At least three drought years (2000, 2002, 2008) occurred in the Southwestern United States during the 2000s, making the early 21st century the driest period in several centuries (Cayan and others 2010). Even more recently, California has been in drought since 2012, with record dry years reported and the majority of the State in extreme or exceptional drought as of the spring of 2014 (see fig. 8.2) (U.S. Drought Monitor report http://www1.ncdc.noaa.gov/pub/data/cmb/sotc/drought/2014/04/20140429_usdm.jpg. Date accessed: April 29, 2014). The climatological index derived here using PRISM data does not reflect the recent drought episodes in California, due to the relatively longer time period of the climate data compared with the recentness of the drought period. This illustrates the need to include a variety of data sources over multiple time periods to more completely understand drought effects on vegetation and other resources.

Variability in North American Drought Over Time: The Paleo-Record

Recurrent drought is to be expected with frequencies in sync with the phenomena that drive fluctuations in climate across broad spatial and temporal scales (Herweijer and others 2007). Droughts vary across time (frequency and duration), space, and severity in rangelands and other ecosystems. An understanding of the full range of natural variability in each dimension is needed to provide context for assessing the "normality" of historic drought in rangelands relative to past events and for projecting the novelty of future climatic conditions.

Consistent characterization of a drought or series of droughts is dependent upon selection of appropriate metrics that remain consistent across time and space. Instrumental meteorological data are sufficiently
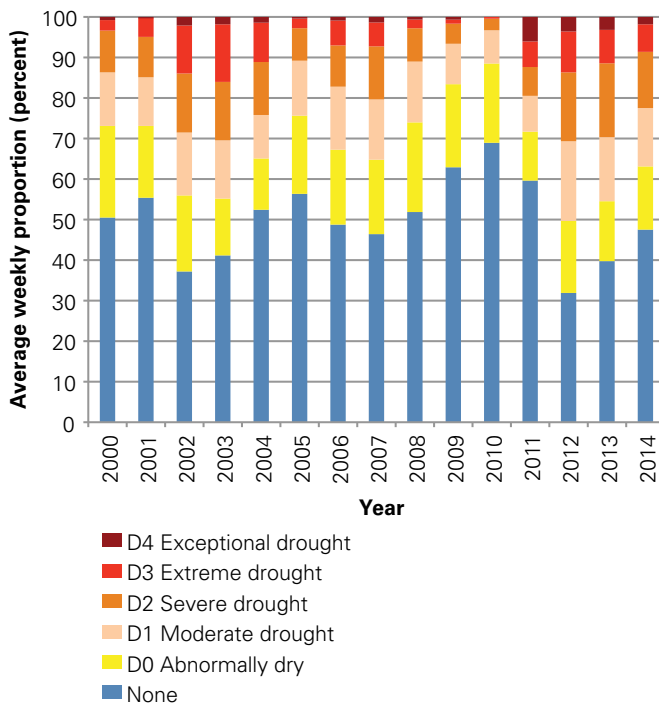

Figure 8.2—Drought categories derived from annualized U.S. Drought Monitor maps (weekly), 2000–2014 in the coterminous United States. Data courtesy of the U.S. Department of Agriculture (USDA) and the National Oceanic and Atmospheric Administration (NOAA). The y-axis represents the annual average of weekly proportion of land in each drought category. So, for the year 2000, averaged over 52 data points (weeks), about 50 percent of lands experienced "none", i.e., no drought.
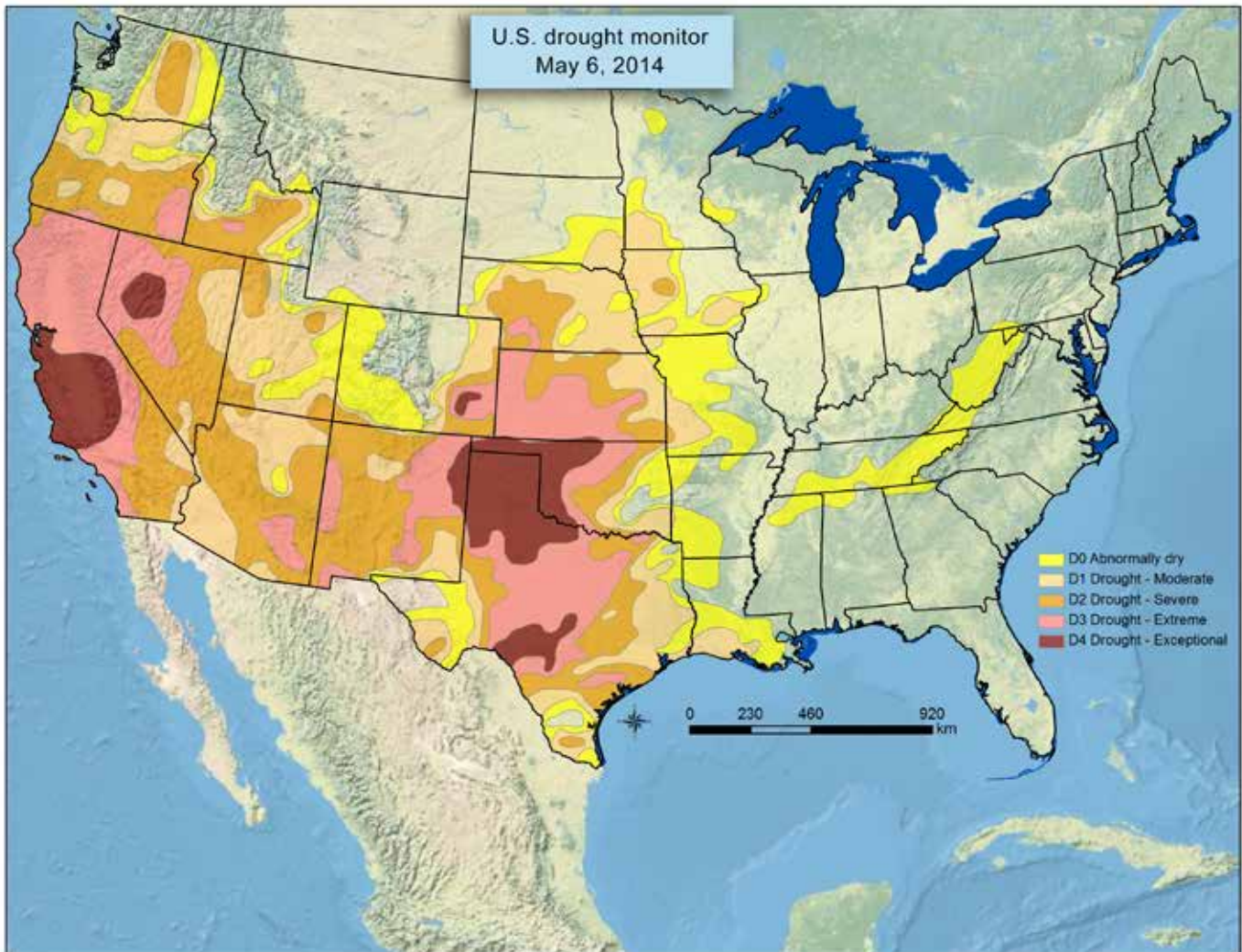
Figure 8.3—These data represent drought categories for the week of May 6, 2014. Notice the exceptional drought category in central California and northern Texas. Data courtesy of the U.S. Department of Agriculture (USDA) and the National Oceanic and Atmospheric Administration (NOAA).

Table 8.1—Breakdown of the top 20 U.S. Ecological Systems exhibiting negative trends in vegetation performance since 2000

Ecological System	Negative NDVI area (ha)	Area in declining trend (percent)
Tamaulipan Mixed Deciduous Thornscrub	225,588	56
California Annual Grassland	1,942,520	43
Tamaulipan Calcareous Thornscrub	604,070	41
South Texas Sand Sheet Grassland	434,402	40
Tamaulipan Mesquite Upland Scrub	3,460,482	37
Western Great Plains Mesquite Woodland and Shrubland	7,058,207	35
Edwards Plateau Limestone Shrubland	4,141,955	35
Southern California Coastal Scrub	938,878	33
Tamaulipan Savanna Grassland	634,618	33
Central Mixedgrass Prairie	8,473,944	32
Central and Southern California Mixed Evergreen Woodland	646,718	32
Sonora-Mojave Semi-Desert Chaparral	425,250	32
Western Great Plains Sandhill Steppe	3,782,085	30
Southern California Oak Woodland and Savanna	253,198	29
Chihuahuan-Sonoran Desert Bottomland and Swale Grassland	174,880	29
Western Great Plains Shortgrass Prairie	16,499,262	28
California Mesic Chaparral	1,220,700	27
Western Great Plains Foothill and Piedmont Grassland	256,282	26
Southern California Dry-Mesic Chaparral	837,099	25
Sonora-Mojave Mixed Salt Desert Scrub	352,823	24

NDVI = Normalized Difference Vegetation Index.

consistent but lack temporal depth for long-term analysis. Historic documents extend the record for North American drought by a few centuries, but have major spatial and temporal gaps. In addition, these records are largely subjective and difficult to quantify, rendering them of limited value by themselves for analyzing large-scale patterns of variability. During the Holocene (last 10,000+ years), western North America experienced multi-century episodes when conditions were consistently drier than the present. Examples include the mid-Holocene warm period lasting from 7,500–6,000 years before present (YBP) (Benson and others 2002, Grayson 2011) and a late-Holocene period of persistent drought that occurred in the central Great Basin (but not further north) from about 2800 to 1850 YBP (Mensing and others 2013). The later dry period was characterized by drops in lake levels, shifts to more xeric-adapted vegetation, an upward shift in upper tree line, and increased alluvial fan aggradation; collectively, those changes have been attributed to conditions that were warmer and drier than present.

Numerous studies have used tree-ring-based reconstructions of the Palmer Drought Severity Index (PDSI) (Cook and others 1999, 2004; Herweijer and others 2007) and other supportive data to compare the severity, duration, and spatial patterns of historical drought to those that occurred during the last 2,000 years. Long-term reconstructed streamflow for the Potomac (Maxwell and others 2011) and the Colorado Rivers (Meko and others 2007) reveal more severe and longer lasting droughts prehistorically than those known from 20th century instrumented records. Analyses of paleo-drought from the Central United States using multiple proxies (Woodhouse and Overpeck 1998) and continental-scale studies (Herweijer and others 2007) using tree-ring reconstructions of PDSI suggest that megadroughts during the Medieval Climate Anomaly (MCA), also known as Medieval Warm Period, were of similar severity but longer duration (20–40 years) and possibly greater spatial extent than those of the 20th century. Temporal analyses identified climate cycles at interannual to centennial scales (Herweijer and others 2007, Meko and others 2007, Stambaugh and others 2011). Herweijer and others (2007) determined that the central and western regions of the continent had the highest climate variability, and the Central and Southwestern United States were drought centers with highest drought activity over time. Drought spatial patterns supported a strong linkage of drought to the El Niño Southern Oscillation (ENSO) of Pacific sea surface temperature (SST), and this and other studies (Cole and Overpeck 2002, Cook and others 2004, Stahle and others 2000) suggest a persistent La Niña-like phase, unlike any observed in recent centuries, may have been responsible for prolonged drought events in the past.

Collectively, these studies indicate that 20th century measures of climate, including drought, represent only a subset of the full range of conditions experienced in the past as a result of natural variation. Although drivers and feedback mechanisms are not fully understood, there is sufficient indication from past climate records and future projections to prioritize development of effective strategies for coping with the consequences of more frequent, more severe, and longer drought, especially in central and western regions of North America where water resources are already scarce.

The Future of Drought on Rangelands

Although it is difficult to model a detailed picture predicting the occurrence and extent of future drought, it is clear that higher temperatures will increase severity of drought episodes when they occur. Drought in North America appears to be strongly related to Pacific Ocean SSTs and is sensitive to even small temperature changes (Cayan and others 2010). Change in SSTs induced the recent severe drought in California, 2013–2014, and the associated circulation patterns were intensified— perhaps even created—by global warming (Wang and others 2014). Higher temperatures will reduce soil moisture critical to plant productivity, species composition, and erosion potential (Polley and others 2013). Models of net primary productivity predict overall better growing conditions for the northern Great Plains, while the opposite is true of the southern Great Plains (Polley and others 2013, Reeves and others 2014). Trends indicated by PRISM and NDVI data may continue with persistent and increasing aridity for the southern Great Plains and central California (figs. 8.1 and 8.2). Cayan and others (2010) predict droughts in this century will extend for periods of time of ≥12 years in the Southwest, which will severely tax already limited water supplies (Foti and others 2012). More frequent drought episodes interspersed with fewer episodes of higher-than-average rainfall indicate vegetation in the Southwest may not recover to what is currently considered a typical or average state (Seager and others 2007).

Although the future of SST patterns is uncertain, warmer temperatures will exacerbate any deficit in soil moisture, and several studies point towards more frequent and severe drought along with large-scale

ecological change for the future (Breshears and others 2005, Cayan and others 2010, Cook and others 2007). Drying may be particularly pervasive in the Southwestern United States, northern Mexico, and the interior West (Andreadis and Letternmaier 2006, Seager and others 2007). California can expect continued intensification of drought episodes (Wang and others 2014).

Drought severity has not increased recently in other regions of the United States, including the northern Great Plains; this indicates that although these regions will still be subject to periodic drought, they may be better able to recover after drought episodes under current management practices (Andreadis and Letternmaier 2006, Clark and others 2002). Of particular interest to the sustainability of ecosystem services are megadroughts—spanning decades rather than years, they are unprecedented for our recorded history, and thus not integrated into disaster preparedness or resource contingency plans (Cook and others 2010). It is unclear if global change will induce megadroughts or not, but predicted warmer temperatures and unchanged or declining precipitation across rangelands could induce negative, persistent impacts.

Effects of Drought on Rangelands

This section reviews how drought influences water availability, soil moisture, and plant physiology, as well as plant growth, abundance, and productivity, vegetation changes, and wildlife habitat.

Water Availability, Soil Moisture, and Plant Productivity

Soil moisture is affected by a number of factors in addition to the amount of annual precipitation. Soil recharge is heavily influenced by the season, timing, and amount of precipitation events. Event size, number of events, and length of time between events influence vegetation in different ways (Lauenroth and Sala 1992). In hot summer months, moisture is quickly lost through evaporation from the soil surface and vegetative transpiration. In winter, evaporation and transpiration are reduced, allowing moisture to accumulate and infiltrate to deeper soil levels (Weltzin and others 2003). Cooler summer temperatures may explain the observation of decreased interannual variability in grass production in northern regions as compared with hotter southern regions (Sala and others 1988). Infiltration from gentle rains of long duration is most effective at recharging

soil profiles. Infrequent, small precipitation events may wet only the soil surface, where moisture is quickly lost through evaporation. Lauenroth and Sala (1992) reported that a precipitation event of at least 15–30 mm was necessary in order to wet those soil layers that have largest effect on production. High-intensity summer storms may result in sheet runoff, with most infiltration occurring in lower lying areas. Dry, bare ground can take nearly three times longer to rewet than vegetated areas (Weaver and Albertson 1943).

Vegetative growth and reproduction is ultimately and directly linked to soil moisture. Multiple studies have reported a direct correlation between aboveground net primary production (ANPP) and mean annual precipitation (Briggs and Knapp 1995, Haddad and others 2002). Variability in annual rainfall may affect productivity more in grasslands than in all other biomes of North America (Knapp and Smith 2001). An analysis of 9,500 sites across the Central United States confirmed the tremendous importance of water availability to plant productivity (Sala and others 1988). Regional patterns in ANPP were correlated with an east-to-west gradient in annual precipitation. Production levels during years of drought were observed to shift eastward, with high production levels restricted to the more mesic eastern plains. Vicente-Serrano and colleagues (2013), using satellite imagery for the continental United States, also found a direct correction between precipitation and ANPP.

Plant Physiological Responses to Drought

The consequences of drought on plant physiological functioning can vary depending on the duration and severity of the drought. When droughts occur, critical edaphic variables such as soil moisture, temperature, and vapor pressure deficit (VPD) are affected and have impacts on plant physiological functioning. Of largest consequence for grassland plants is the reduction in soil water content, which leads to plant moisture stress and possibly mortality (Poirier and others 2012). This is because the critical link between desiccation and carbon gain (or starvation) is regulated through plant stomata, where fluxes of carbon dioxide (CO_2) and water vapor share the same pathway. The longer plants can withstand desiccation, the better their prospects for drought survival and recovery (Larcher 2003).

Drought, to varying degrees, will impact plant available moisture in the soil profile (James and others 2003). For periods of short drought duration, large deficits in plant available water may occur at the soil surface;

conversely, deeper in the soil profile, plant available water may be higher. As droughts lengthen in duration and become more severe, deeper soil moisture reserves will also decrease. These spatial and temporal differences are critical for short- versus long-rooted species as well as their strategies for avoiding or tolerating drought effects (Kozlowski and Pallardy 1997, Larcher 2003).

As drought severity increases and water availability decreases for perennial grassland species, a number of ecophysiological strategies can be employed to prevent mortality (fig. 8.4) (Volaire and others 2014). Growth maintenance, dehydration delay, dehydration tolerance, and dormancy strategies work on a continuum from no drought to severe drought, respectively. From a whole plant perspective, low-to-moderate drought stress may

still allow some leaf and root growth, albeit reduced. These low soil moisture conditions are often linked to reduced stomatal conductance and photosynthesis (Milbau and others 2005). From this, corresponding shifts in carbon allocation patterns emerge: leaf growth is reduced, followed later by reduced root growth, while carbon reserves may increase. As drought conditions increase, leaf senescence is employed to reduce transpirational surface area. Eventually, extreme drought stress will cause irreversible damage to the protoplasm, leading to leaf and tiller mortality.

Shrub species in grasslands employ similar strategies to endure drought conditions. Dehydration delay and the control of transpiration during drought are critical for maintaining water balance in woody species. Kozlowski and Pallardy (1997) list five adaptations to reduce
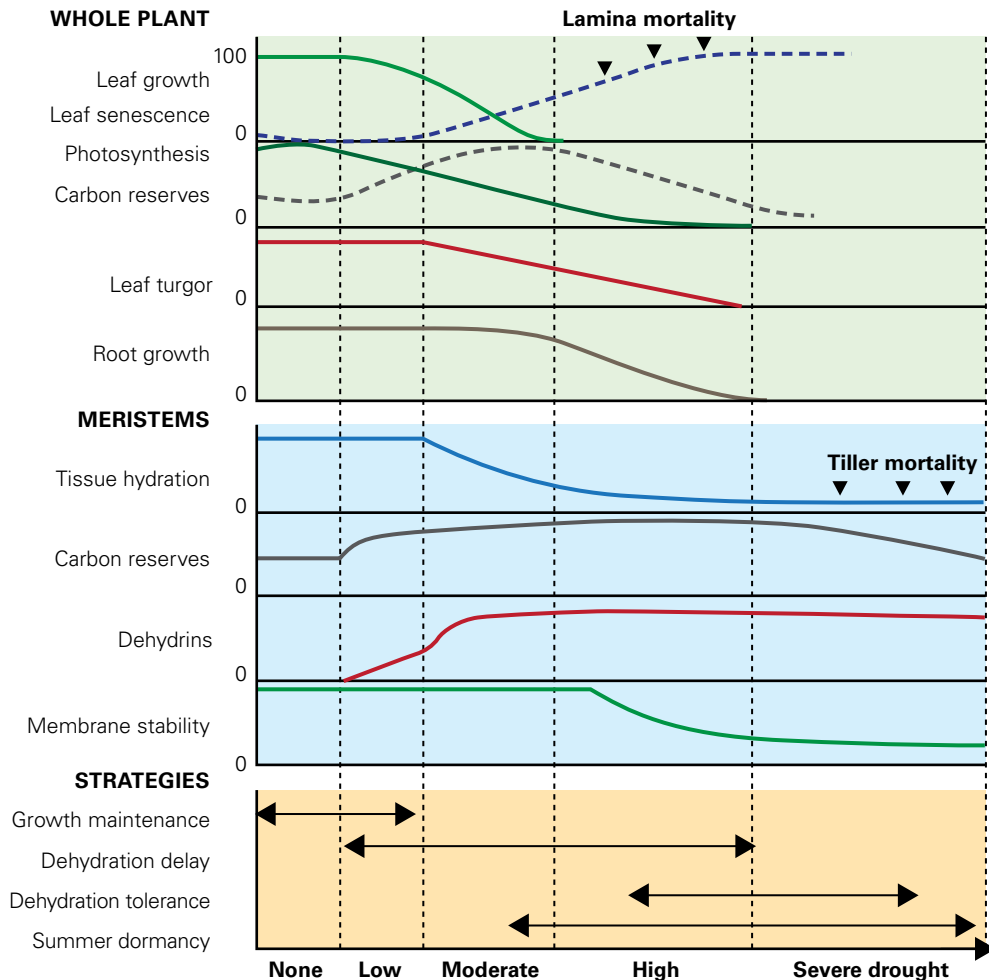

Figure 8.4—Perennial grass whole plant and meristem responses and ecophysiological strategies to increasing drought. Volaire and others (2014).

transpiration: (1) reduced capacity for growth, (2) reduced leaf size and altered morphology, (3) leaf abscission, (4) cuticular effectiveness, and (5) stomatal control. Kolb and Sperry (1999) found that these adaptations are similarly employed by different subspecies of big sagebrush (*Artemesia tridentata*) across elevation and precipitation gradients of the Great Basin of North America. However, their ability to withstand dry conditions and preserve hydraulic functioning varied. The subspecies from an arid locale showed greater resistance to xylem cavitation (50-percent loss) than subspecies from mesic conditions.

In some cases, plants are known to acclimate to drought conditions through repeated exposure (Bruce and others 2007). In Mediterranean shrubs, two species showed differences in photosynthesis and water-use efficiency from repeated drought and re-watering cycles, with one species showing much better photosynthesis recovery and improved water-use efficiency (Galle and others 2011). Grass has also shown acclimation to drought repetition with improved photoprotection, yet plants still experience an overall reduction in photosynthesis (Walter and others 2011). The mechanisms by which "stress imprints" occur are still largely under investigation. Drought-stress recovery will no doubt vary by species and degree, but the critical question is whether grassland species have the capacity and resiliency for the potentially repeated and worsened events caused by climate change (Scheffer and others 2001).

Effects of Drought on Vegetation

Climate instability and recurrence of extreme events can have a more profound effect on vegetation than do changes in average conditions (Weltzin and others 2003). Climate of the 20th century and early 21st century has been highly variable, exhibiting fairly rapid shifts between wet and dry periods that vary geographically (Grissino-Mayer and others 2002). This period has been marked by several large-scale droughts as well as several more local short-term droughts. The Great Plains experienced the unprecedented Dust Bowl drought of the 1930s. New Mexico experienced its worst multiyear drought between 1945 and 1963 (Betancourt and others 1993, Swetnam and Betancourt 1998), known as the 1950s drought. This drought extended from southern Arizona north to the Colorado River Basin, and east to western Texas and some parts of the Southeast. In 1985, there was a large-scale drought throughout much of the West, whereas the central and eastern portions of the United States experienced large-scale drought in 1988 (Kogan 1995). The effects of drought are cumulative. The longer a

drought persists without water recharge, the greater the severity. Using a standardized precipitation index, McKee and others (1993) reported that the single worst drought of the 20th century was that of the 1950s, whereas four consecutive droughts of shorter duration combined to produce the exceptional water deficits of the 1930s.

Vegetation response to historic drought—The great drought of the 1930s resulted from the combined effects of widespread cultivation of the soil and overgrazing brought on by the post-war demand for meat, and it was exacerbated by 6 preceding years of below average precipitation and high temperatures (Albertson and Weaver 1942). Average precipitation was 33–39 percent below normal, with most of the deficit occurring during the growing season. High winds whipped the dry, friable soil particles, creating enormous dust storms and smothering vegetation with thin blankets or deep drifts of silt.

Albertson and Weaver (1942, 1944) documented vegetation response and recovery from the drought over an 11-year period from 1933 to 1943 at locations near Hays, KS. Grasses and forbs died as deeper soil layers were depleted (Weaver and Albertson 1943). Basal area of little bluestem (*Andropogon scoparius*) declined 78 percent between 1932 and 1939, disappearing entirely from many areas, with little recovery exhibited by 1944 (Albertson and Weaver 1944). Hillsides dominated by little bluestem converted to more drought-tolerant sideoats grama (*Bouteloua curtipendula*) and shortgrass species. Uplands dominated by buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) declined in cover, but recovered with only slight shifts in dominance. Big bluestem (*A. gerardii*), decreased 79 percent in cover between 1932 and 1939, but did survive and later reestablished. Bare areas gradually recovered to shortgrass prairie dominated by buffalograss and blue grama. Species that reproduce vegetatively or those having deeper root systems were more resilient to drought. The overall result was a long-lasting shift in species composition: loss of little bluestem and an increase in grama grasses, buffalograss, and wheatgrass (*Agropyron smithii*).

The 1930s drought extended far beyond the southern plains. Sagebrush steppe of the upper Snake River Plain experienced several periods of severe drought. The summer of 1934 was the driest on record, accompanied by high temperatures and strong winds. The preceding years had also been drier than normal (Pechanec and others 1937). Shrub density, mostly of

sagebrush (*Artemisia* spp.), decreased to 46.8 percent of that present in 1932; the decrease was caused by dieback or death of whole plants. Basal area of perennial grasses declined 60 percent. The disintegration and death of grass clumps continued well into 1935 despite favorable conditions. Anderson and Inouye (2001) monitored vegetation at a similar location in the Snake River Plain between 1950 and 1975. Perennial grass cover increased from 0.5 percent in 1950 to 6.2 percent in 1975. Shrub cover, dominated by big sagebrush (*Artemisia tridentata*), increased from 17 percent in 1950 to 25 percent in 1975, although a subsequent drought during the late 1970s resulted in substantial mortality of big sagebrush. The authors postulated that high rainfall years can set up species for death when followed by sudden drought. They further noted that a lag time can occur between the resumption of normal rainfall and the response of vegetation. The presence of a lag time before vegetative recovery has also been noted by others (Ji and Peters 2003).

Ellison and Woolfolk (1937) documented the effects of a sustained drought near Miles City, MT, that peaked in 1934; this drought was aggravated by above-average temperatures and preceding years of below-normal precipitation. They documented substantial death of pine, juniper, and cottonwood, but also noted declines in sagebrush and other species. All shrubs experienced considerable dieback. Grass cover was reduced by up to 79 percent depending on the species. Effects of the drought were multiyear despite a favorable season in 1935. Needle-and-thread grass (*Stipa comata*) and Sandburg bluegrass (*Poa secunda*) were able to recover relatively quickly, despite mortality, through the establishment of new seedlings. Stands of big sagebrush experienced considerable mortality and did not regenerate, whereas silver sagebrush (*A. cana*) was able to resprout from the base.

Reports from other droughts also document large reductions in perennial grass cover, as well as shifts in plant community composition. Lauenroth and Sala (1992) found that 39–45 percent of the interannual variation in forage production over a 52-year period in north-central Colorado was explained by precipitation. Tilman and El Haddi (1992) reported an initial 47-percent decrease in plant biomass due to the 1980s drought. While biomass did recover within 2 years, species richness did not. Hobbs and others (2007) observed considerable changes in individual species' abundance over a 20-year study

in response to variation in rainfall amounts. Species richness also varied with precipitation. Morecroft and others (2004) recorded an approximate 50-percent reduction in vegetative cover in response to a drought occurring from 1995 to 1997. The relative proportion of vegetation also changed from one dominated by perennial grasses to one dominated by ruderal forbs. In a drought manipulation experiment, Evans and others (2011) found that 11 years of drought resulted in large reductions in total cover and cover of the dominant species, but significant differences did not emerge until the fourth and seventh year of drought.

Mechanisms of vegetation change—Ecosystems differ in their response to drought (Knapp and Smith 2001). On a biome scale, vulnerability to drought is thought to be greater in more humid regions, such as tallgrass prairie, where drought has historically occurred less frequently. Vegetation of arid and semiarid regions is more resilient to drought, as many species are adapted to water shortage. The response of the dominant vegetation may depend on the average time-scale at which drought typically occurs (Vicente-Serrano and others 2013). Seasonality of precipitation also affects ecosystems differently. In the southern Great Plains, precipitation during the summer growing season had the greatest effect on productivity (Albertson and Weaver 1942, 1944; Pechanec and others 1937). In the Great Basin and regions northward, accumulation of winter snow recharges soil moisture, resulting in a flush of spring growth.

Individual plant species also differ in their ability to tolerate and recover from drought. Deep-rooted species, such as big bluestem, can persist through longer periods of drought provided the deeper soil layers were moist to begin with (Albertson and Weaver 1942, Fay and others 2003, Morecroft and others 2004). An ability to reproduce vegetatively through resprouting, tillering, or the production of rhizomes or stolons, may also increase a plant's ability to recover from drought (Albertson and Weaver 1942, Pechanec and others 1937). Dominant species in wet areas may not tolerate drought well (Swemmer and others 2007). Plants of more arid regions have many adaptations for coping with moisture deficits. Small leaves, thick cuticles, sunken stomates, trichomes, or photosynthetic stems limit the amount of water vapor lost through evapotranspiration. Avoidance adaptations, such as drought-deciduous leaves or an annual habit, limit periods of photosynthesis to the most favorable times of year (Rundel and Gibson 1996).

Plants differ in their depth of rooting as well as in root morphology, both of which affect their ability to take up water from different soil layers (Ehleringer and others 1991, Schwinning and Ehleringer 2001, Walter 1971 as cited in Schwinning and others 2005). Grasses with shallow fibrous roots can extract water rapidly after a pulse event, but they are also the first to run out of water as soils dry (Schwinning and others 2005). Species with taproots can take up water from deeper levels and, consequently, are able to take up water during longer periods of drought. Many dominant shrubs, including juniper, have an extensive shallow root system in addition to roots that can penetrate to several meters in depth (Krämer and others 1996, Lin and others 1996). This allows them to exploit moisture from multiple soil depths, giving them an advantage over herbaceous root systems during drought. Reynolds and others (2000) postulated that such water resource partitioning can only occur when annual precipitation exceeded a certain threshold. Otherwise, soil recharge was not sufficiently deep to allow extraction from deeper soil layers.

Variability in species responses to drought can help to buffer productivity. Although species richness often declines during periods of drought (Cleland and others 2013, Hobbs and others 2007, Tilman and El Haddi 1992), plots with greater diversity have been reported to be more stable over time (Hobbs and others 2007). Cleland and others (2013) suggest that a large regional species pool can buffer site-level diversity from variation in climate. Known as the insurance hypothesis, this hypothesis states that differential species' responses to environmental change allow for functional compensation, as individual species come and go. Overall plant cover can then be maintained despite variations in species makeup (Yachi and Loreau 1999). Rates of species turnover are higher in dry areas, largely as a function of rare or annual species (Cleland and others 2013, Morecroft and others 2004, Tilman and El Haddi 1992).

A lag in plant recovery response after drought, even when precipitation is good, has been noted by a number of researchers (Ellison and Woolfolk 1937, Ji and Peters 2003, Lauenroth and Sala 1992, Pechanec and others 1937) and may result from a number of reasons. Plants may need to build up reserves before expending energy on renewed growth. A 2-year lag may result as seed is matured during the first good year followed by a year of recruitment. Many arid land species have inherently low growth rates, requiring substantial amounts of time before cover is restored to pre-drought levels.

Plant productivity and nutrient cycling—Another potential reason for reduced productivity in years following drought is due to changes in nutrient cycling. Haddad and others (2002), working in tallgrass prairie, followed plant production and diversity over an extended period that included a 2-year drought. Production was stable for 5 years preceding the drought, then oscillated on a 2-year cycle for 9 years after the drought. They concluded that the drought-induced oscillation was related to nutrient resources. In mesic systems, carbon and nitrogen cycling are coupled through production and decomposition of organic matter because water is available for plant and decomposer metabolism. In more arid systems and under drought conditions, these cycles become decoupled and nutrients accumulate until moisture is sufficient to reactivate biogeochemical processes (Asner and others 1997, Austin and others 2004, Evans and Burke 2013).

The loss of herbaceous cover due to drought can result in a substantial increase in soil erosion by both water and wind, with an accompanying loss of soil nutrients (Li and others 2007, Okin and others 2001, Schlesinger and others 2000). Grasses, in particular, help to bind together soil particles of the upper horizon (Worster 1982). The more sparsely distributed woody species are generally ineffective in reducing wind erosion compared with grasses (Li and others 2007). Erosion by wind differentially removes finer soil particles that contain more of the soil nutrients, resulting in a coarser, less fertile soil (Hennessy and others 1986, Leys and McTainsh 1994). Blowing dust redistributes soil, denuding some areas while killing plants by burial or abrasion (Okin and others 2001).

Biological soil crusts—Where vegetation is sparse, interspaces in rangelands are often colonized by biological soil crusts (BSCs), a group of organisms consisting of algal filaments, lichens, and mosses that bind surface soil particles together, reducing wind erosion (Belnap and Gillette 1997, Williams and others 1995). BSCs occur from the Columbia River Basin, south through the Great Basin and Colorado Plateau to the southern Mojave, Sonoran, and Chihuahuan Deserts, and from California chaparral east to the Great Plains. Smooth crusts composed of cyanobacteria and green algae dominate in hot desert sites, with lichen and moss cover increasing northward to the less arid conditions of the Great Basin and Columbia River Basin (Rosentreter and Belnap 2003). Crusts of those areas with colder winters are pinnacled or gently rolling in topography. In the Great Plains, BSCs

are most abundant in short-grass steppe and consist mostly of green algae and cyanobacteria, along with vagrant lichens that roll about, unattached to the soil. The highly pinnacled crusts of the Colorado Plateau are composed of cyanobacteria, with up to 40-percent cover of lichens and mosses. Many crust species are ubiquitous and can be found throughout the Western United States. Others are adapted to a specific range of temperatures or to certain substrates, such as calcium carbonate or gypsum (Rosentreter and Belnap 2003).

Biological soil crusts fix both carbon and nitrogen, adding to fertility of the soils. They also increase soil surface roughness, thereby increasing the capture of nutrient-rich soil fines (dust) and water-holding capacity of the soil (Belnap 2003). The organisms comprising soil crusts are only metabolically active when wet and are highly responsive to temperature (Belnap 2003, Stradling and others 2002). Most are adapted to withstand extended periods of high heat with little or no water by suspending all metabolic processes. However, prolonged periods of drought can effectively starve soil crust organisms, increasing the incidence of mortality. Lichens and mosses are particularly vulnerable, and the resulting crust composition is simplified, mimicking an earlier successional state (Belnap 2003). The timing of precipitation events also has an impact on crust function. Small, frequent events during periods of high temperature means that crusts dry quickly, resulting in less carbon available to produce or repair protective pigments and a loss of lichen cover and richness (Housman and others 2006). Conversion of soil crusts back to early successional stages results in large reductions of carbon and nitrogen inputs into the ecosystem (Housman and others 2006), which can affect plant growth and competitive interactions. Recovery rates from early to later successional stages is thought to be on the order of decades or centuries, depending on the amount of effective precipitation (Belnap 2003). Recovery, if it occurs, would be significantly slowed under extensive drought conditions. Loss of soil crusts would result in increased rates of wind erosion, blowing dust, and soil deposition similar to that described earlier.

Effects of Drought on Wildlife and Wildlife Habitat

Wildlife habitat occupancy is typically associated with structural characteristics of rangeland vegetation communities (Rotenberry and Wiens 1980, Wiens and Rotenberry 1985). Precipitation is the primary

cause of variability in grasslands (Wiens 1974), and structure and production of herbaceous vegetation is reduced during drought and can lag behind recovery of the precipitation (Laurenroth and Sala 1992). Height and density of herbaceous vegetation (structure) is strongly related to biomass (Benkobi and others 2000). Drought and grazing alter plant community composition and habitat structure. These vegetation changes influence positive and negative responses of wildlife (Benkobi and others 2007, Knowles 1986, Uresk 1990). For example, black-tailed prairie dog towns expand when vegetation cover and biomass decrease (Cincotta and others 1988, Uresk 1987), whether influenced by grazing or drought. Severe drought in North Dakota resulted in significant declines of a number of grassland-nesting bird species owing to nest abandonment, reduced nesting success, and a truncation of the nesting season in mid-June (George and others 1992). In early seral communities, small mammals and birds that prefer low vegetation structure and bare ground are more abundant, whereas those that prefer taller vegetation and litter are more abundant in higher seral vegetation communities (Agnew and others 1986, Fritcher and others 2004). Thus, sustained drought would shift bird and small mammal communities to favor those associated with early seral habitats. In prairie woodlands, drought and grazing reduce regeneration of trees and shrubs (Uresk and Boldt 1986), which in turn alters the bird and small mammal communities (Rumble and Gobeille 1998, 2001, 2004) toward species associated with early seral vegetation. Shrub-nesting bird populations may lag in response to loss of herbaceous understory vegetation if the shrub structure remains (Wiens and Rotenberry 1985).

Most, if not all, birds feed on or consume insects when the physiological needs of reproduction or early growth of young are high. Insect abundance is highly related to biomass of herbaceous vegetation (Healy 1985, Ramobo and Faeth 1999, Rumble and Anderson 1997, Wenninger and Inouye 2008). The amino acids that occur in birds reflect those of the insects they consume (Hurst and Poe 1985)—they are what they eat. Birds that are not able to consume enough insect protein do not develop properly or die (Johnson and Boyce 1990). Abundance and biomass of insects in south-central Wyoming exhibited significant correlations with grass and forb cover.[1] Drought in 2012 affected nest

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[1] Personal communication. Mark Rumble, Research Wildlife Biologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Rapid City, SD 57702.

productivity and chick survival of greater sage-grouse (*Centrocercus urophasianus*) (Schreiber 2013) and insect abundance was significantly lower than in 2011 when nest productivity and chick survival was greater.

Lek counts in south-central Wyoming made each year from 2011 through 2013, showed approximately a 15-percent decline in the maximum male attendance the year following the drought of 2012 (see footnote 1). Low precipitation and high temperatures had negative effects on recruitment, survival, and population growth of sage-grouse populations in Nevada (Blomberg and others 2012), and precipitation the preceding spring influenced sage-grouse nesting success (Holloran and others 2005). Vegetation responses to precipitation (e.g., taller grass) is associated with greater nest success of sage-grouse (Herman-Brunson and others 2009, Holloran and others 2005, Kaczor and others 2011a) and is selected for by sage-grouse broods (Kaczor and others 2011b). Brood success of sage-grouse is associated with greater insect abundance and vegetation communities with high cover of herbaceous vegetation (Harju and others 2013).

Increased prevalence of severe drought increases the chances that local sage-grouse populations are extirpated (Aldridge and others 2008). Drought also tends to concentrate sage-grouse around water where they may be susceptible to West Nile Virus (Naugle and others 2004). Sage-grouse are not unique in their response to drought. Gambel's quail (*Lophortyx gambellii*) populations fluctuate considerably in direct response to increases and decreases in precipitation and in response to food availability from forb seeds (Gullion 1960). Pheasant populations in South Dakota demonstrate a quadratic relation to precipitation; low populations are associated with drought and extremely wet conditions (Runia 2013). Regions of South Dakota where the 2012 drought was considered exceptional or extreme showed population declines of 12–13 percent, whereas populations in regions where drought was moderate to severe only declined 2 percent (Runia 2013). Plains sharp-tailed grouse (*Tympanuchus phasianellus jamesi*) populations also decline in association with heat stress and low precipitation during June (Flanders-Wanner and others 2004), and it has long been known that nesting success by sharp-tailed grouse increases when height-density of grassland vegetation increases from 5 to 20 cm (Prose 1987).

Drought Interactions With Other Disturbances and Stressors

Grasshopper Outbreaks

Rangeland and grassland ecosystems worldwide are prone to periodic outbreaks of native insect herbivores. The most common and noticeable insect outbreaks in western North America involve grasshoppers (Orthoptera), which contribute significantly to the structure and function of grasslands and other rangelands (Branson and others 2006). Grasshopper outbreaks can have severe economic impacts on the grazing industry, especially during periods of drought when available forage is already scarce (Hewitt and Onsager 1983). Climate, especially drought, is thought to play a key role in outbreaks of grasshoppers and other insect species on rangelands, but the underlying mechanisms are poorly understood (Capinera and Horton 1989, Gage and Mukerji 1977, Kemp and Cigliano 1994, White 1976). Drought can have both direct effects on the growth and survival of insects and also indirect effects via changes in food quality and susceptibility to disease.

Non-severe drought and warm temperatures generally have a positive effect on grasshopper populations. Warm, dry weather in winter and early spring can lead to increased survival, early egg hatch, and faster population growth; warm, dry weather in the fall can extend the life of females and allow them to produce and lay more eggs (Joern and Gaines 1990, Kemp and Sanchez 1987). Moreover, grasshoppers often prefer to feed on drought-stressed plants, partly due to drought-induced changes in plant chemistry (Bernays and Lewis 1986, Haglund 1980, Lewis 1982). Drought could further promote grasshopper populations by reducing incidence of disease, especially due to fungi as many fungi require moisture (Hajek and St. Leger 1994, Streett and McGuire 1990). However, extreme or prolonged drought can negatively affect grasshoppers through desiccation (especially eggs) or by killing their food plants (Farrow 1979, Joern and Gaines 1990, Mukerji and Gage 1978). Therefore, short-term, less-severe droughts can increase grasshopper outbreaks, but longer term, severe droughts will likely have a strong negative effect on grasshoppers and rangeland/grassland biodiversity in general (Kemp and Cigliano 1994, Tilman and El Haddi 1992).

Invasive Species

Droughts are predicted to accelerate the pace of invasion by some nonnative plant species into rangelands and grasslands (Abatzoglou and Kolden 2011, Everard and others 2010, Ford and others 2012, Runyon and others 2012). One route by which drought promotes plant invasions is through increased movement of hay across State lines to feed livestock in drought-affected areas (Conn and others 2010). Drought conditions can also exacerbate invasions by favoring invasive species over native species. For example, invasive saltcedar (*Tamarix ramosissima*) is more drought tolerant than co-occurring native species, and its capacity to invade is predicted to increase with drought (Cleverly and others 1997). In California, it has been argued that invasive grassland species tolerate drought-like conditions better than native species and that drought was a contributor to the invasion of annual species into California grasslands (Corbin and D'Antonio 2004, D'Antonio and Vitousek 1992, Everard and others 2010, Jackson 1985). However, Funk and Zachary (2010) found no differences in physiological responses to drought of three native versus three invasive species in southern California, suggesting that not all invasive species will be favored. Conversely, invasive species could be negatively affected by drought; for example, some have attributed drought to a recent decline in spotted knapweed (*Centaurea stoebe*) in western Montana grasslands [but biological control could have played a role, see discussion in Ortega and others (2012)].

Drought can also promote plant invasion indirectly by modifying the environment to favor nonnative species. For example, opportunities for invasion are created when drought kills native plants leaving open niches and bare ground (Breshears and others 2005). This was apparently the case following the Dust Bowl of the 1930s which resulted in increases in nonnative plant abundance (Weaver and Albertson 1936, 1939).

Drought is also an important contributor to the invasive annual grass–wildfire loop that threatens ecosystems not adapted to fire [e.g., cheatgrass (*Bromus tectorum*) forms a positive feedback with fire in parts of western North America's sagebrush biome] (Abatzoglou and Kolden 2011, D'Antonio and Vitousek 1992). In this self-perpetuating cheatgrass–fire loop, drought increases the frequency of wildfires (Abatzoglou and Kolden 2011), and burned sites are more likely to be invaded by nonnative plants, especially annual grasses (Balch and others 2013). Drought-induced fire also threatens to convert Sonoran Desert ecosystems to monocultures of nonnative plants such as buffelgrass (*Pennisetum ciliare*) and Lehmann lovegrass (*Eragrostis lehmanniana*) (Finch and others 2012).

Not only can drought affect invasions by nonnative plants, but it can also affect the tools used to manage them. The effectiveness of both herbicides and biological control can be altered by drought. To be effective, herbicides must be taken up through the leaves and stems of actively growing, green plants (Ashton and Crafts 1981). Herbicides applied to the foliage during periods of drought are usually much less effective than those applied when moisture is adequate (Bussan and Dyer 1999, Kogan and Bayer 1996). This is because many plant responses to drought—including reduced growth, closed stomata, thickened waxy cuticle, and increased pubescence—can reduce the uptake or translocation of herbicides (Kogan and Bayer 1996). For example, Morrison and others (1995) found that drought stress reduced translocation of herbicides and control of Russian knapweed (*Acroptilon repens*), a problematic rangeland weed in the Western United States. Therefore, our ability to manage invasive plants using herbicides could be reduced during periods of drought.

There is also some evidence that drought can alter the effectiveness of biological control of invasive plants. Historically, drought stress in plants was thought to benefit plant-feeding insects (Mattson and Haack 1987), which suggested that drought could benefit biocontrol using insects. However, a meta-analysis by Huberty and Denno (2004) found that continuous drought stress in plants negatively affected many insect herbivores, suggesting that biocontrol efficacy could generally be reduced by drought. Few studies have explicitly examined the effect of drought on biocontrol. Corn and others (2007) report that drought had little effect on the impact of the root weevil *Cyphocleonus achates* on spotted knapweed (*Centaurea stoebe*). However, Ortega and others (2012) found that the impact of *C. achates* on spotted knapweed was negated by drought conditions. Shishkoff and Bruckart (1996) found that drought stress has no effect on damage to yellow star-thistle (*Centaurea solstitialis*) caused by the rust fungus *Puccinia jaceae* in the laboratory. More research is needed to better understand how drought will affect biological control, an important management tool of rangeland invasive plants.

Wildfire and Drought

In the Unites States, more than 80 percent of all wildfires are started by humans. Lightning strikes are another common cause for natural wildfires (National Wildfire Coordinating Group Fire Investigation Working Team 2005). Recent increases in fire activity in some parts of the World have been attributed to climate change (Gillett and others 2004, Kasischke and Turetsky 2006, Pinol and others 1998, Westerling and others 2006). U.S. ecoregions with increasing trends in the number of large fires and total fire area also displayed increasing trends in drought severity (Dennison and others 2014). The incidence of large fires and extent of area burned have increased across the Western United States. Fire activity trends were most significant in southern and mountain ecoregions. Increased fire in these ecoregions coincided with increased drought severity (Moritz and others 2012). Under extended drought condition, wildfires are getting bigger, and more fires are starting earlier in the year. Since 1984, the area burned by the West's largest wildfires—those of more than 1,000 acres—increased by about 87,700 acres per year, and the areas where fire has been increasing the most are areas where drought has been worsening (Dennison and others 2014).

Climate change can indirectly affect rangeland vegetation by altering fire regimes. Increasing fire frequency leads to a replacement of fire-sensitive plant species with those that are more fire-tolerant (Nelson and Hu 2008). Most wildfires in the Western United States occur during the hottest, driest portion of the year (Westerling and others 2006), and the size of the area burned during any single year is correlated with the current drought condition (i.e., PDSI) and with wetter-than-normal conditions in May and August of the previous year (Polley and others 2013). In grass- and shrub-dominated ecosystems, fires are largest when unusually wet summers (during which fine fuels accumulate) are followed by dry conditions that enhance fuel flammability and ignition (Littell and others 2009). Fire activity is projected to increase considerably in the Western United States as the climate becomes both warmer and drier (Pechony and Shindell 2010, Polley and others 2013).

The largest U.S. grassland region is the Great Plains, a vast area of prairie, agriculture, and rangelands extending from the Dakotas through Iowa, Nebraska, Kansas, Oklahoma, and parts of Texas, and including the eastern parts of Montana, Wyoming, Colorado, and New Mexico (Bagne and others 2012). Fire is an important feature of many Great Plains rangelands, and its frequency, intensity, and seasonality are likely to be affected by changes in climate, productivity, and species composition. Fire was an important factor in maintaining grass dominance in the more productive rangelands of the eastern Great Plains. In more recent times, the removal of fire and/or changes in its seasonality, along with rising CO_2, have encouraged woody plant encroachment in many of these productive rangelands (Morgan and others 2008).

Indeed, woody encroachment has emerged as the dominant threat to grassland ecosystem services in the Great Plains (Engle and others 2008). In areas of long-term juniper encroachment, fires have shifted from frequent, grass-driven surface fires that vary in flame length (range ≤ 0.1 m to well over 3.4 m) (Finney and others 2011) to infrequent, juniper-driven crown fires that consistently exhibit extremely long flames (>14 m) and are of increasing societal concern (Twidwell and others 2013). Such alterations to the fire regime and fire suppression potential are important contributors to the recent rise in housing losses, suppression costs, and human injuries and deaths resulting from wildfires in the Great Plains (Tidwell and others 2013). Predicted changes in precipitation patterns are likely to encourage more frequent and intense fires in the future, with increased winter precipitation driving early-season plant growth, and warmer, drier summers desiccating vegetation, thus increasing the probability of fire (Morgan and others 2008).

A chief concern in the arid and semiarid rangelands of the Western United States is the rapid conversion of shrublands and desert into annual grassland through the spread of invasive annual grass species and the negative impacts this conversion will have on wildfire regimes, surface hydrology, and loss of critical habitat for threatened and endangered species (Abatzoglou and Kolden 2011, Bradley and Mustard 2005, Brooks and Esque 2002, Brooks and others 2004, Mack 1981, Wilcox and Thurow 2006). Over the past three decades, there has been a significant increase in the abundance and extent of invasive annual grass species in the Southwest, including cheatgrass across the Great Basin Desert, red brome (*Bromus rubens*) across the Mojave Desert, and buffelgrass across the Sonoran Desert (Betancourt 2007, Bradley and Mustard 2005, Brooks and Esque 2002). This change, along with a change in climate, has coincided with an increase in the number of large fires and area burned across the arid and semiarid Western United States (Brooks and

others 2004, Westerling and others 2006, Whisenant 1990). For example, in the Great Basin, fires were found to be more likely to start in cheatgrass than in other vegetation types, and cheatgrass is associated with increased fire frequency, size, and duration. As sites burn, more and more of the sites are likely to become cheatgrass grasslands, thus increasing their future probability of burning (Balch and others 2013). Also, elevated cheatgrass biomass following El Niño events is strongly linked to increased risk of fire during the following years' summer (Balch and others 2013). Future projections of climate change suggest that the Western United States is likely to become warmer and have greater precipitation variability, which could increase or decrease cheatgrass fire probability depending on how much warmer temperatures influence moisture availability. In general, evidence suggests that observed changes in climate have assisted in the spread of invasive annual grasses across western U.S. deserts both directly through changes in temperature and precipitation and indirectly through their influence on wildfire (Abatzoglou and Kolden 2011). For example, increased temperature and reduced humidity during spring and summer associated with recent protracted drought conditions since 2000 have doubled the frequency of extreme fire danger in the Sonoran Desert, resulting in an earlier start and lengthening of the fire season (Abatzoglou and Kolden 2011, Weiss and others 2009).

Pinyon-juniper woodlands—the third largest vegetation type in the West—characterize many Rocky Mountain and Intermountain rangelands and are vitally important for biodiversity, aesthetics, and commodity production (Mitchell and Roberts 1999, West 1999). Extreme drought conditions have characterized the American Southwest during the past decade, causing widespread mortality in pinyon-juniper woodlands. While comparably low precipitation levels have occurred at other times in the past century, rising temperatures have accompanied the latest drought, increasing water stress on vegetation and triggering increases in bark beetle-caused mortality. Drought-related outbreaks in bark beetles have killed pinyon pines on over 12,000 km^2 in the Southwest (Breshears and others 2005, Floyd and others 2009, Shaw and others 2005). The current severe, regional drought is providing the dry conditions necessary for extensive wildfire activity.

Historical fire rotation for pinyon-juniper woodlands has been estimated across the Unites States. Studies report very long fire rotations—for example, 410 years

in Barrett Canyon of central Nevada (Bauer 2006), 480 years in southern California (Wangler and Minnich 1996), 400–600+ years on the Uncompahgre Plateau in western Colorado (Shinneman and Baker 2009), and 400+ years on Mesa Verde in southwestern Colorado and on the Kaiparowits Plateau of southern Utah (Floyd and others 2004, 2008; Romme and others 2009). An upsurge of large fires (>400 ha) in forested landscapes throughout much of the Western United States began in the mid-1980s (Westerling and others 2006). Increasing trends in large fire frequency and total area burned are particularly noticeable in regions having extensive pinyon-juniper woodlands (e.g., the Southwest and the northern Great Basin). For example, a greater proportion of the pinyon-juniper woodland on Mesa Verde, Colorado, burned in the decade between 1995 and 2005 than had burned throughout the previous 200 years (Floyd and others 2004, Romme and others 2009). A combination of canopy fuel build-up during two wet decades before 1995 and the current drought conditions resulted in unprecedented fire activity (six large wildfires between 1996 and 2003) when compared with the reference period 1700–1900 (Floyd and others 2004).

Given the very long fire rotations that naturally characterize pinyon-juniper woodlands, it has not yet been determined whether the recent increase in frequency of large fires occurring in this vegetation type represents genuine directional change related to changing climate or fuel conditions, or whether it is simply a temporary episode of increased fire activity, comparable to similar episodes in the past. Ultimately, the suite of current and upcoming broad-scale environmental changes including warming temperatures, increasing tree densities in some areas, and expansion of fire-promoting species, such as cheatgrass, may all interact to dramatically increase the amount of burning in pinyon-juniper and other vegetation types over the next century (Romme and others 2009).

In the near term, the most consistent increases in fire activity occur in biomes with already somewhat warm climates (Moritz and others 2012). However, as the Arctic warms, wildfire may become increasingly important even within the coldest of all terrestrial eco-systems: tundra (Joly and others 2012). Tundra covers over 5,000,000 km^2 of the Arctic (Walker and others 2005), including a large portion of Alaska. Warmer and drier summers are associated with greater area burned in Alaska (Duffy and others 2005). The effects

of climate change are already apparent in the Arctic (Callaghan and others 2004, IPCC 2007). Mean annual temperatures have increased by 2–3 °C in the region in recent decades, with larger increases apparent during the winter months (Hinzman and others 2005, Joly and others 2012, Stafford and others 2000).

Climate change impacts on the habitats of Arctic land mammals are predicted to be severe (Lawler and others 2009) and have already been implicated in the decline of caribou (*Rangifer tarandus*) populations there (Vors and Boyce 2009). Mechanisms by which climate change may negatively impact caribou include increased frequency of wildland fire on winter ranges (Joly and others 2012). Although wildfires occur during the summer, they negatively impact caribou winter range. Migratory caribou rely heavily on tundra plants to sustain them through the winter months, and these plants can take 50 or more years to recover after wildland fires consume them (Joly and others 2012). Tundra has the potential to re-burn much more quickly than boreal forests, so warmer summer conditions could lead to additional fires (Joly and others 2009).

Effects of Drought on, or in Combination With, Human Uses and Practices

Drought Impacts on Livestock, and Forage Yield and Availability

Drought and livestock grazing are two major drivers of rangeland structure and productivity within the Great Plains. No geographic location is immune to the wide-ranging social and economic impacts of drought (Riebsame and others 1991). The Great Plains were historically grazed by bison until settlement in the 19th century when cattle were introduced as the major livestock. Ungulate grazing often leads to an increase in spatial heterogeneity and species diversity (Adler and others 2001, Bakker and others 2003a). However, grazing severity and timing largely determine the effect of ungulate grazers on rangelands.

Rangeland drought management is influenced by both historical perceptions and the drought class framework of the manager. Vegetation reports of the early explorers in the 19th century depended on the year observations were made (Coupland 1958). Early settlers expected productive lands and were accustomed to the more predictable and dependable precipitation patterns of the Eastern United States. Therefore, initial farming and ranching practices failed to accommodate the abiotic

and biotic changes associated with a highly variable climate and the combined effects of periodic drought and livestock grazing. Although current land managers have gained more experiential knowledge in these arid environments, management decisions in response to drought are still affected by the first perceptions of the early settlers. In recent years, unsustainable rangeland use has exacerbated the effect of drought, causing more land managers to experience financial hardship and perceive that meterological drought is increasing in frequency (Thurow and Taylor 1999). Land managers are encouraged to plan proactively for drought and maintain flexibility in rangeland management by diversifying livestock operations and types of land use (Coppock 2011, Kachergis and others 2014, Thurow and Taylor 1999).

Depending on intensity and frequency, grazing and drought independently can adversely impact the ecology and management of rangeland ecosystems by reducing plant cover and forage availability, reducing root growth, shortening the season of forage production, and exposing the soil to erosion (Vallentine 1989). However, because grazing and drought often occur at the same time, identifying the relative contribution of grazing and drought to these impacts is a difficult task requiring long-term monitoring (Fuhlendorf and others 2001). While the effects of grazing can occur relatively quickly to produce obvious contrasts, droughts often emerge slowly with cumulative effects that merge gradually into a catastrophic event (Riebsame and others 1991).

The separate and interactive effects of drought and grazing on rangeland vegetation can also be amplified by a variety of direct and indirect factors. For example, the broad-scale effects of drought are locally modified by variation in soil and topography (slope and aspect, which interact to influence water infiltration and runoff) and soil moisture retention. Often, the effects of drought are first observed on hilltops and ridges, followed by side slopes, and then depressions and valleys. South-facing slopes are impacted more than north-facing slopes, especially at higher latitudes (Coupland 1958, Weaver and others 1935). Concentrated and continuous grazing causes soil compaction that reduces water infiltration and increases surface erosion, thus exacerbating the effects of drought (Vallentine 1989). Droughts are also frequently accompanied by high populations of grasshoppers and accumulations of wind-blown soil particles, which can develop into drifts up to 3 feet deep (Coupland 1958, Weaver and Albertson 1940).

Grazing effects can produce a significant and somewhat predictable directional change in vegetation composition and productivity, which is primarily augmented directly by water stress and secondarily by additional factors that accompany drought. Water stress and grazing have been considered convergent selection pressures that involve the periodic reduction of biomass (Koerner and Collins 2014, Milchunas and others 1988). Consequently, plant traits selected due to a reduction in biomass by one driver, such as grazing, can enhance plant survival when exposed to other drivers, such as drought. Semiarid grassland communities with a long evolutionary history of grazing are dominated by relatively short-statured, grazing-tolerant, rhizomatous or stoloniferous grasses that compete primarily for soil resources (Milchunas and others 1988). In semi-arid grasslands, grazing before and during drought has little impact on community composition and structure (Heitschmidt and others 1999.)

By contrast, in sub-humid grasslands where mid- and tall-grasses must compete for light, grasses are not as tolerant of grazing because growth of the aboveground canopy is primarily vertical. Therefore, depending on the grazing evolutionary history, grazing in more mesic grasslands would have moderate to large effects on composition and canopy structure (Milchunas and others 1988). However, during droughts prior to settlement, free-ranging grazers (e.g., bison) would have either died and/or migrated out of the impacted area (Heitschmidt and others 1999). Consequently, grazing and severe drought may have not occurred together historically in some rangeland ecosystems, except possibly for short periods of time.

Relative contributions of drought and grazing to biomass reduction and shifts in vegetation composition within a rangeland may shift between mesic and more arid rangelands. In mesic tallgrass prairies, grazing and fire had a greater effect on community structure than precipitation (Koerner and Collins 2014). However, in the semi-arid northern Great Plains, climatic variation had a greater effect on vegetation composition and production than grazing intensity (Biondini and others 1998, Olson and others 1985). Semi-arid and arid grasslands of the Western United States are noted for their small (<5 mm) rainfall events and intervening dry periods (Loik and others 2004). Although small rainfall events may not contribute measurable increments in biomass, they are able to increase leaf water potential and help sustain physiological activity between larger rainfall events (Sala and Lauenroth 1982). Reduction in the occurrence of small rainfall events during drought may explain the greater sensitivity of more arid grasslands to precipitation than grazing. In sagebrush steppe, both drought and grazing independently reduce perennial grass and forb cover (Anderson and Inouye 2001; West 1983, 1988). Although dominant shrubs such as big sagebrush can be affected by drought, they are affected to a lesser degree than grasses and increase in relative abundance within the shrubland community (Pechanec and others 1937, West 1983).

Rangeland response to the effects of drought and/or grazing was exemplified by observational studies conducted before, during, and following the 1930s extreme drought in the Great Plains (i.e., the Dust Bowl) [see Weaver (1954) and references there-in, Pechanec and others (1937)]. Severe drought substantially reduced plant cover and forage availability. Continuous grazing at almost any level during severe drought can adversely impact rangeland structure and function. Heavy grazing can have the greatest impact and substantially increase the length of the recovery period (Albertson and others 1957). With low vegetative cover and high winds that usually accompany drought, the potential for soil erosion is high. Despite the negative long-term impacts, grazing during drought was a common practice used to maintain livestock herds until favorable conditions returned (Weaver 1954).

The directional, selective influence of grazing on vegetation is especially prominent in heavily grazed, mixed-grass prairies. Prolonged heavy grazing can simultaneously decrease grass basal area and increase plant density (Briske 1991 and references there-in). Grazed sites with a high density of plants with small basal areas may be subject to higher drought-induced mortality compared to a lower density of plants with larger basal areas in lightly and moderately grazed grasslands (Albertson and others 1957, Fulhlendorf and others 2001). A high density of plants with small basal areas may serve as a valuable indicator of pending compositional changes during drought conditions (Fuhlendorf and others 2001). During the drought of the 1930s, drought-induced plant mortality under heavy grazing increased the amount of bare soil, which was often quickly colonized by Russian thistle (*Salsola kali*) (Albertson and others 1957).

Moderate grazing also influences the long-term directional change of vegetation that is magnified by drought, but to a lesser degree than heavy grazing (Coupland 1958). Actually, reductions in basal area

during periodic droughts were sometimes less in moderately grazed grasslands compared to ungrazed grasslands (Coupland 1958, Weaver and Albertson 1936). Weaver and Albertson (1936) attributed the higher basal area observed in moderately grazed pastures compared to lightly and ungrazed pastures to grazing-induced increases in drought-resistant species such as blue grama and buffalograss. However, buffalograss is more sensitive to drought than blue grama, which often becomes the dominant species during periodic droughts. On the other hand, buffalograss has the ability to rapidly produce new stolons once favorable conditions return. If the drought is not severe or prolonged, then moderate grazing also allows the less drought-resistant species to persist. However, during prolonged, severe drought, the drought-sensitive mid-grasses will suffer high mortality (Coupland 1958). Post-drought vegetation recovery was always slower on sites dominated exclusively by blue grama compared to sites with a combination of blue grama and buffalograss (Albertson and Weaver 1944). Consequently, blue grama was important for protecting the soil during drought, while buffalograss was important for recovery following the drought.

Vegetation recovery following drought is generally proportional to the intensity of grazing before, during, and after the drought (Albertson and Weaver 1944). Weaver (1954) described several cases where livestock were sold during the drought of the 1930s because of severe shortages of forage. Because of economic hardships (including The Great Depression), producers were unable to re-stock their pastures with livestock for several years. Therefore, many rangelands damaged by combinations of grazing and drought were rested, especially heavily grazed pastures where forage was reduced very early in the drought cycle. In this context, rangeland recovery during a severe drought was more rapid than recovery during a short-term drought event where herds of cattle were maintained during and immediately following the drought (Weaver 1954).

In general, moderately grazed, mixed-grass prairie can recover fairly quickly from moderate (Coupland 1958) and severe drought (Albertson and Weaver 1944). Vegetation recovery on heavily grazed grasslands with few remnants of the pre-drought vegetation remaining and considerable bare soil will include several years of an annual weed stage, which will substantially delay recovery of native perennial grasses. If dry conditions return during the post-drought recovery, the annual weed stages could persist for several years (Albertson and Weaver 1944). In contrast, sagebrush shrublands that have transitioned from a sagebrush-native perennial grass mixture to a heavily shrub-dominated community remain in this stable state even after grazers are excluded for multiple years (West and others 1984).

Few perennial grass seeds persist in the soil for more than 5 years, with the seeds of some species living <1 year (Baskin and Baskin 1998). Consequently, recovery of perennial grasses from drought and/or grazing is dependent upon stem recruitment from belowground meristematic tissue (the bud bank sensu Harper 1977; Benson and Hartnett 2006). Weaver and Albertson (1936) reported that with the return of normal precipitation following the 1930s drought, western wheatgrass (*Pascopyrum smithii*) rapidly expanded into areas of bare soil created by the drought. Because the drought had significantly reduced (eliminated) opportunities for sexual reproduction, the rapid expansion of western wheatgrass most likely occurred through vegetative growth via the bud bank. A few small precipitation events during drought may play a significant role in maintaining the viability of bud banks through extreme dry conditions (Sala and Lauenroth 1982).

As individual drivers, drought and grazing can have a similar effect on rangelands. In combination, the relative contributions of drought and grazing to the response and recovery of a rangeland strongly depend on the severity of each driver and the climate and dominant vegetation of the rangeland. Although effects of drought and grazing on rangeland community structure and function continue to be documented, a more mechanistic understanding of the impact of drought and grazing should be sought. Understanding how drought and grazing alter factors such as nutrient availability or the bud bank will provide land managers with more tools to respond to joint drought and grazing issues.

Effects of Drought on Restoration Success

Ecological restoration encompasses a variety of management actions intended to restore or repair degraded ecosystems. Degradation can range from minor deviations of vegetation structure and community composition from a desired state, to complete denudation of vegetation, soil loss, and associated disruption of ecosystem function (Allen 1995, Bainbridge 2007, SER 2004). Many U.S. rangelands have been dramatically altered by intensive uses such as agriculture, mining, military operations, and

vehicular traffic (Bainbridge 2007). Other grasslands and shrublands remain intact but have been degraded to various degrees by overgrazing or mismanagement, often resulting in depletion of forage and encroachment by woody plants (Archer and others 2011). Invasive exotic species are also a serious problem in many areas (Brown and others 2008, Sheley and others 2011).

Different types of restoration are applicable to different circumstances. Grazing management, prescribed fire, herbicides, and mechanical treatments such as mowing and chaining may be used to selectively reduce undesirable species (Archer and others 2011, Briske and others 2011, Fuhlendorf and others 2011, Vallentine 1989). If desirable species are not present in sufficient quantity to recover on their own, active planting (seeding or transplanting) may be necessary (Bainbridge 2007, Hardegree and others 2011). On severely degraded sites, soil remediation or topsoil replacement may be required (Pinchak and others 1985, Schuman and others 1985).

The ultimate goal of full-scale ecological restoration is to reestablish functioning ecological communities resembling those that existed prior to intensive human disturbance (SER 2004), as illustrated by longstanding efforts to restore native prairies in agricultural regions of the U.S. Midwest (Rowe 2010). In other settings, site integrity and productivity are the primary goals, and the terms rehabilitation or reclamation are applicable (SER 2004); for example, reclamation of surface mine disturbances (OSM 1997), rehabilitation following wildfire on Federal lands (Beyers 2004), and rehabilitation of agricultural lands in the Conservation Reserve System (Baer and others 2009). Although nonnative plants have a long history of use for rehabilitation and reclamation in the United States, current policies encourage use of native species on Federal lands (Johnson and others 2010a, Richards and others 1998) and some sites previously planted with nonnatives have been targeted recently for restoration with natives (Bakker and others 2003b, Hulet and others 2010, Wilson and Gerry 1995).

Because of the critical role of water in plant establishment, growth, and survival, restoration plantings are directly impacted by drought conditions. Insufficient precipitation has been invoked to explain suboptimal plant establishment for many restoration plantings in grassland and shrubland systems (Bakker and others 2003b, Bleak and others 1965, Fehmi and others 2014, Glenn and others 2001, Hulet and

others 2010, Ratzlaff and Anderson 1995). If low plant establishment is accompanied by intensive soil disturbance (e.g., seeding using rangeland drills), there may be a risk of increased erosion by wind (Miller and others 2012) or water (Pierson and others 2007), as well as impacts to preexisting plants (Ratzlaff and Anderson 1995). Even in cases where plant establishment is initially successful, plantings may later die back during drought years (Bleak and others 1965, Currie and White 1982).

Although drought conditions are a disadvantage for plantings, they can be advantageous for plant control to the extent that water deficits make undesirable plants more susceptible to mechanical treatments, herbicides, or fire. For example, control of crested wheatgrass (*Agropyrum cristatum*) by clipping or herbicides has been shown to work better under drier conditions (Bakker and others 2003b, Hansen and Wilson 2006). The effectiveness of foliar herbicides may be reduced under drought conditions because of poor translocation following application (Vallentine 1989), although this differs by herbicide and plant species (Abbott and Sterling 2006, Lauridson and others 1983, Morrison and others 1995, Roche and others 2002). Soil herbicides require water for dissolution and soil penetration and are thus likely to be less effective during drought (Vallentine 1989).

The use of prescribed fire as a restoration tool during drought requires special considerations. In desert grasslands encroached by mesquite, drought conditions may make prescribed fire difficult to implement because of insufficient fine herbaceous fuel (Britton and Wright 1971, Teague and others 2010, White and Loftin 2000). In other settings where fuel is more abundant, it may be especially dry during drought, and this combined with low air humidity can make fires explosive and difficult to control (Ralphs and Busby 1979).

Narratives of escaped prescribed fires frequently include drought as a contributing factor, leading to loss of control and ensuing damage (Brunson and Evans 2005, Earles and others 2004). Furthermore, the effects of prescribed fires may be different during drought compared to wetter years. Increases in light, higher temperatures, and nutrient inputs to soils that represent positive effects of fire under high moisture conditions could become detrimental when soil moisture is low (Augustine and others 2010, Bremer and Ham 1999, Teague and others 2008, Whisenant and others 1984).

Depending on the seasonal incidence of drought conditions, optimal dates for prescribed burning might also differ compared to normal years. Burns intended to control certain species or groups (e.g., annual weeds, cool-season grasses) by burning during their active stage (Adkins and Barnes 2013, Anderson and others 1970, DiTomaso and others 2006) might be constrained by smaller windows of opportunity due to early onset of dormancy. On the other hand, if the purpose of burning can be met during the dormant stages (Brockway and others 2002, Ford and Johnson 2006), then the window of time for burning may be longer during drought. Benefits of prescribed fire ultimately depend on vegetation regrowth, which may be diminished if drought occurs during the post-fire period. Ladwig and others (2014) found that drought conditions delayed expected grass recovery following prescribed fire in a Chihuahuan Desert grassland, and that effects of burn timing (spring, summer, and fall) were short-lived due to the overriding influence of the drought.

Increasing Rangeland Ecosystem Resilience to Drought

Adaptive Strategies for Managing Livestock

Land managers and livestock producers must periodically cope with and adapt to drought, both in the short term and in the long term. Adaptive strategies can vary regionally, but appropriate measures must be taken to provide adequate recovery of vegetation to ensure proper ecological function and economic returns. Greatest success will be achieved with careful planning of strategies to employ before, during, and after droughts. Some adaptive responses to drought include:

- Reducing stocking rate to allow plant recovery

- Using fencing and other developments to manage livestock distribution

- Using drought-resistant feed crops

- Using drought-adapted stock

- Adjusting season of use

- Diversifying ways for economic gain

- Implementing deferred grazing system

- Developing, restoring, or reclaiming water

- Providing shade structures for livestock

- Reducing the time livestock graze a specific pasture/unit/paddock

- Increasing the time or rest between periods of grazing

- Testing new techniques for responding to drought

The most obvious and arguably the single most important strategy for adapting to drought is reduction in stocking rate because plants that have been overgrazed or cropped too frequently are less able to recover after drought (Hart and Carpenter 2005). Conservative and flexible stocking rates enable maintenance of proper amounts of residual forage. Where droughts are relatively common, breeding stock should only represent 50–70 percent of the total carrying capacity (Hart and Carpenter 2005). Grazing time in pastures can also be reduced, as an action or in combination with other actions, such as supplemental feeding and reducing number of livestock. In addition, ranchers can first sell stocker cattle as a means of herd reduction during drought to protect the breeding herd so that re-stocking after recovery is easily accomplished. Another technique for coping with drought is use of fencing, salt, water development, and strategic herding to increase uniformity of use. Likewise, some animals inherently make more uniform use of the landscape than others, suggesting that selective breeding can preemptively aid drought adaptation (Howery and others 1998).

As a last measure, supplemental forage can be used to augment the sparse forage that drought conditions induce; however, use of supplemental forage can potentially exacerbate the problem by maintaining an unsustainable number of animals. In addition, animals will likely continue to use greener, more-palatable rangeland vegetation even if ample supplemental feed is supplied. From a herd-management or economic perspective, consideration should be given to selling animals before they have lost excessive weight and weaning calves earlier than normal which reduces forage demand (Howery 1999). Additionally, nonproductive animals or animals with low fertility rates should be culled first during drought periods.

Since economic returns and ecological integrity are linked to vegetative resources, careful consideration of vegetation conditions is required, during and after droughts in concert with herd management adaptations.

In this vein, extra monitoring is prudent to ensure that forage yields and ecological integrity can be maintained in the future. Extra rest periods can aid recovery while ranges are recovering after a drought. The timing of grazing also becomes a critical factor in determining recovery after a drought. For example, use of ranges when nondesirable species are green and palatable and deferring grazing until perennial species have produced seed can aid recovery. However, this generalization does not always apply as it may be more advantageous to utilize perennial grasses during the early vegetative stages but prior to the booting phase, emphasizing the importance of planning and monitoring before, during, and after drought.

Regardless of the strategies used, adaptation to and recovering from drought requires careful planning before, during, and after for maximum effectiveness. Moreover, the single most important outcome that can be controlled by management is selecting an appropriate and flexible stocking rate.

Adjusting Restoration Practices Under Drought Conditions

Drought conditions generally pose constraints for restoration practices such as planting or prescribed burning (see previous section). Such practices might best be deferred during periods following extended drought or preceding predicted drought conditions. However, postponing a restoration project may not be satisfactory in situations where policy, funding, logistics, or other concerns favor immediate action. In such cases, restoration practices can be implemented but modified in ways that compensate for limited soil moisture (e.g., irrigation, water catchments) or use alternative techniques to achieve the desired outcome (e.g,. mechanical treatment instead of prescribed fire).

If a decision is made to use prescribed fire during a drought, it should be done with careful planning and precautions. As reported by Guse (2009), The Nature Conservancy successfully carried out a ca. 730-ha prescribed burn during extreme drought conditions in southern Texas, noting that the drought provided an unprecedented opportunity to restore shrub-invaded grasslands. The success of the operation was attributed to extensive commitments of resources (reportedly 2-3 times the minimum required number of firefighters and water delivery systems), by assuring that firefighters were well trained and equipped, and implementing burns in incremental, manageable stages over a period of 9 days (Guse 2009).

During periods of drought, it may be best to focus restoration efforts on removal of undesirable plants as opposed to planting treatments. In reference to native grassland restoration in the northern Great Plains, Bakker and others (2003b) recommended that crested wheatgrass control measures be undertaken during drier years while seeding of native species take place in wetter years. In the Great Basin, juniper removal by mastication (shredding) can be beneficial for herbaceous species by both releasing competitive water use of the woody overstory and enhancing soil moisture beneath shredded debris (Young and others 2013).

If planting is deemed necessary during a drought year, a variety of strategies and techniques can be employed to increase the probability of successful plant establishment in the short term and species persistence in the long term. Plant materials should be carefully selected to ensure that the species and ecotypes are adapted to drought conditions, especially during the establishment phase, and are resilient if drought is episodic or long-term climate change is projected. The ability to rapidly extend roots downward into the soil is an important trait for seedlings facing a soil drying front (Abbott and Roundy 2003). Equally important is the capacity of seeds to remain dormant until soil moisture is sufficient to sustain seedling growth (Biedenbender and others 1995, Frasier and others 1987). Larger seeds will likely have greater capacity to endure water limitations during the critical establishment phase compared to smaller seeds (Hallett and others 2011, Leishman and Westoby 1994). In addition, larger seeds are better able to emerge when buried beneath soil, and can thus be planted at depths where they are buffered from surface soil moisture fluctuations (Carren and others 1987, Monsen and Stevens 2004, Montalvo and others 2002).

As seedlings become larger, they tend to become less sensitive to moisture fluctuations, hence, it may be advantageous to transplant seedlings (or even fully grown plants) rather than attempting to establish plants from seed. Transplanting has been found to be effective for establishing shrubs and forbs in water-limited environments, especially if transplants are hardened off prior to planting and provided with supplementary water afterwards (Anderson and Ostler 2002, Bainbridge 2007, Glenn and others 2001, Grantz and others 1998a, Holden and Miller 1995, Watson and others 1995). The use of water-holding materials such as sepiolite clay and hydrogels in root plugs of transplants may enhance their survival in dry soils (Chirino and others 2011, Minnick and Alward 2012).

Irrigation can be helpful for restoration plantings, although it may be untenable for large restoration projects or remote sites where transport is an issue and water sources are distant (Anderson and Ostler 2002). Its feasibility is perhaps highest when restoring abandoned agricultural sites with an existing irrigation infrastructure. Roundy and others (2001), Chambers and others (2014), and Porensky and others (2014) demonstrated benefits of sprinkler irrigation for restoring abandoned agricultural fields in western deserts, although Banerjee and others (2006) noted problems with this approach due to weed proliferation and accumulation of salinity in the soil from low-quality irrigation water. Alternative irrigation techniques such as drip-lines, wicks, and clay pots can be used to direct water toward specific plants and/or deeper horizons (Bainbridge 2007). Precipitation data from weather stations near restoration sites have reportedly been used to determine how much irrigation water to supply (i.e., to ensure that total monthly water matches amounts recorded during years with average to above-average moisture) (Anderson and Ostler 2002, Bashan and others 2012, Belnap and Sharpe 1995, Hall and Anderson 1999). The importance of watering during the appropriate season was highlighted by Allen (1995), who found that summer irrigation did not compensate for lack of springtime moisture when seeding purple needlegrass (*Stipa pulchra*), a cool-season grass, at a summer-drought environment in California.

Beyond direct irrigation, a variety of measures can be implemented to enhance or conserve existing water supplies at restoration sites. By placing seed at the bottom of furrows, drill seeding enhances precipitation capture for seedling establishment, and the effect can be amplified by deepening the furrows (Monsen and Stevens 2004). In a similar manner, pitters and imprinters can be used to create micro-catchments that capture and concentrate water (Bainbridge 2007, Dixon 1995, Holden and Miller 1995). Edwards and others (2000) found that catchments of 4–25 m^2 improved establishment for many, but not all, shrub species tested at a Mojave Desert site. Because ponded water appeared to adversely affect some species planted in catchment bottoms, they recommended planting on the berm in cases where the soil has low infiltration (Edwards and others 2000).

Other treatments aim to improve soil infiltration or water-holding capacity. Deep ripping reportedly improves water-holding properties of the soil, as well as making soil more accessible to plant roots (Brown

and others 2008, Montalvo and others 2002, Schmidt and Belford 1994). Short-term intensive trampling by livestock has reportedly increased infiltration on crusted sandy loam soils (Roundy and others 1992). On recently burned sites, soil water repellency is a common problem that could potentially be mitigated through tillage or the application of wetting agents (Madsen and others 2012a, 2012b). Mulches made from materials such as straw, gravel, wood chips, and shredded brush may be helpful for moderating soil temperatures and reducing evaporative water loss from the soil surface (Bainbridge 2007, Eldridge and others 2012, Nyamai and others 2011, Winkel and others 1995, Young and others 2013). However, Belnap and Sharpe (1995) concluded that dry straw mulch was not helpful for plant establishment in a cold desert environment with sandy soils having poor water-holding capacity. They hypothesized that the mulch absorbed water that would otherwise have been available to plants, and that by concentrating water near the soil surface, plants were triggered to germinate at times when deeper water supplies were not actually present to sustain them. Fehmi and Kong (2012) drew similar conclusions upon finding that mulching led to lower seeded plant establishment on very coarse-textured soils (very gravelly sands). Mulches may also be problematic if they are applied too thickly and thereby have an inhibitory effect on seedling emergence (Dodson and Peterson 2010, Winkel and others 1995).

In areas receiving snow, snow fences can be placed upwind of plantings to increase soil moisture through the accumulation of snowdrifts (Greb 1980). David (2013) described snow fences constructed and arranged so as to maximize snow capture for sagebrush establishment on abandoned natural gas pads in Wyoming. Stubble from winter-sown annual crops has been used to capture snow on agricultural land in the northern Great Plains (Greb 1980), although its effects may be negligible in areas with low snowfall and shifting wind patterns (Hart and Dean 1986).

Because of water limitations during droughts, it may not be possible to establish plants at desired densities even when applying the strategies described earlier. Resources might thus best be focused on the most favorable sites, such as drainages or areas of naturally occurring snowdrifts (Meyer 1994), which could later serve as centers for vegetation spread. In situations where rapid plant establishment is desired for soil stabilization, as in post-fire rehabilitation on public lands (Beyers 2004), greater emphasis could be placed on physical erosion control measures as opposed

to revegetation treatments. Runoff and sediment loads from recently burned slopes can be reduced independent of vegetation by applying straw, bark, or wood shred mulch (Fernandez and Vega 2014; Groen and Woods 2008; Robichaud and others 2013a, 2013b) or constructing erosion barriers such as contour trenches (Robichaud and others 2008). Wind erosion and dust emissions from burned areas have been reduced using wind fences, dispersed barriers (e.g., plastic cones), and mechanical soil furrowing applied perpendicular to prevailing winds (Grantz and others 1998a, 1998b). Recently developed soil aggregating agents (He and others 2008, Liu and others 2012, Orts and others 2007, Stabnikov and others 2013) might also prove useful for erosion control in certain settings.

Given the cyclical nature of drought, some years will likely be much better for restoration plantings than others (Holmgren and Scheffer 2001), and to the degree that favorable years can be predicted, they should be utilized to initiate plant communities that will be able to withstand subsequent periods of drought. Plant materials selected for restoration plantings should ideally be adapted, collectively if not individually, to the full range of conditions expected over time at the planting sites. If some species are better adapted for higher moisture and others for drier conditions, shifts from one group to the other may help protect communities from extreme fluctuations in biomass during drought cycles (Richardson and others 2010, Seabloom 2007, Tilman 1996, Tilman and Downing 1994). Accordingly, over-reliance on one or few species in restoration plantings can increase their susceptibility to drought perturbations in comparison to more diverse plantings, although diversity in and of itself may not be advantageous if the species do not complement or compensate for each other in some way (Carter and Blair 2012, Seabloom 2007). Complementary/compensatory traits relevant to restoration of grasslands and shrublands include functional type (e.g., grass versus shrub versus forb), leaf phenology (e.g., evergreen versus drought-deciduous; cool- versus warm-season), drought dormancy strategy (e.g., seeds versus buds), rooting depth, water-use efficiency, and responsiveness to changes in water availability within the soil profile (Carter and others 2012; Munson 2013; Schwinning and others 2002, 2005; Volaire and others 2014; Weaver and others 1935). Mariotte and others (2013) found that competitiveness of dominant grassland species declined during drought, allowing drought-resistant subordinate species to assert greater dominance. The subordinates in turn reduced the degree to which the dominants declined, apparently through facilitative interactions in the soil environment (Mariotte and others 2013).

Techniques for restoring species diversity in grasslands and shrublands are continually being evaluated and improved. Seeding equipment such as the rangeland drill, originally designed for seeding a limited class of large-seeded grasses, has been modified over time to handle a greater diversity of seed types that can be planted at different depths (Monsen and Stevens 2004, Vallentine 1989). The difficulty of establishing subordinate forbs in the presence of competitive dominant prairie grasses has prompted strategies involving seeding rate adjustments and allowing forbs to establish prior to interseeding with grasses (Kindscher and Fraser 2000) or seeding subordinate and dominant species in separate patches (Dickson and Busby 2009).

Genetics-Based Strategies To Manage for Drought Resilience

Strategies to manage for drought resilience in grassland, shrubland, and desert ecosystems need to incorporate an understanding of the genetics of drought tolerance in plants (Khasanova and others 2013), how adaptive responses to drought vary within and between plant species (Cony 1995), and how natural selection operates on drought tolerance traits both before and after management practices are put into effect (Kulpa and Leger 2013). In this section, we explore the ecological genetics of drought tolerance in arid-land plants and discuss current management strategies that incorporate genetic information in drought resilience and how these practices might evolve in the face of rapid global change.

Ecological genetics of drought tolerance—Drought tolerance in plants can be defined as persistence through periods of low water availability (Passioura 1996). A suite of traits that increase water-use efficiency by decreasing water loss and/or water use through morphological and physiological means, or shift phenology and dormancy to avoid water stress can contribute to drought tolerance (Chaves and others 2003, Reich and others 2003). Underlying these traits is an array of genetic and developmental pathways that control the timing of seed germination, plant growth, and reproduction; the development of morphological structures, such as leaf shape and lignification; and physiological processes, including protein synthesis and recycling, carbon uptake, and osmotic adjustment (Chaves and others 2003, Ingram and Bartels 1996, Peñuelas and others 2013).

Traits that have positive effects on plant survival and reproduction under drought stress are considered adaptive and will be favored by natural selection in drought-prone environments (Ackerly and others 2000). Because the climatic factors leading to drought stress vary substantially through both time and space (Cook and others 2004, McKee and others 1993) and interact with physiological processes and life history in complex ways, plant species will generally exhibit a combination of traits that contribute to drought tolerance (Reich and others 2003). Also, because species often persist in a variety of climatic conditions, populations are likely to be adapted to local water availability conditions (Heschel and others 2002), which will lead to intraspecific variation in drought tolerance across the species range.

Climate change is likely to increase the severity and frequency of droughts (Cook and others 2004); therefore, plant populations that currently persist in arid and semi-arid ecosystems are likely to face increasing selective pressure to evolve more robust drought-tolerance traits or face local extirpation (Aitken and others 2008). With recent climate change, some plant species have undergone rapid evolution due to increased drought stress (Franks and others 2007). However, as rates of change increase, conditions may shift too rapidly for most species to evolve rapidly enough (Aitken and others 2008). The rate of evolutionary response of plant populations to increased drought severity and frequency will also depend on a number of species and population-specific constraints (Ackerly and others 2000), including: (1) available genetic variation—populations with low genetic variation in important drought-tolerance traits will be less likely to keep pace with changing conditions; (2) life history traits—species with complex mating systems, such as those that depend on specific pollinators, or species with longer generation times, such as trees and shrubs, may be more vulnerable to environmental shifts; and (3) genetic correlations between selected traits—when selection acts in different directions on multiple traits that are linked through developmental, physiological, or genetic pathways, populations will be less likely to evolve.

Ecological genetics and management strategies—An understanding of the ecological genetics of drought tolerance can help managers practice "evolutionarily enlightened management" in drought-prone ecosystems (Ashley and others 2003). In particular, efforts to conserve plant communities in situ will benefit from genetic vulnerability assessments that take into account a population's adaptive match to its

current environment, its rate of evolutionary response as climates shift, and possible constraints on its further evolution as conditions continue to change. Plant populations that demonstrate adaptive mismatches, slow evolutionary rates, or numerous evolutionary constraints will require more attention and resources than populations that do not face these challenges.

Restoration efforts will also benefit from a genetic approach. The use of seed sources that are adapted to environmental conditions at a restoration site is widely recommended, because these plants are more likely to establish and reproduce (Lesica and Allendorf 1999). Plants from nearby sources are more likely to have adaptive advantages than more distant sources because they are likely to have evolved in similar environments and be related to local ecotypes. In addition, nearby seed sources may be less likely to cause genetic swamping, where genotypes of local remnants are replaced by introduced genotypes, or outbreeding depression, where hybridization with local remnants leads to a loss of fitness through the disruption of locally adapted gene complexes (Hufford and Mazer 2003).

Artificial selection for drought tolerance—One way to use genetic information in wildland drought management strategies is through artificial selection for drought tolerance. Indeed, since the later part of the 20th century, greater attention has been directed at selecting for drought tolerance in wildland restoration species (Johnson and Asay 1993). Delayed stress onset, a type of drought resistance in agricultural crops developed through genetic engineering, has not yet been developed or applied in rangeland or forest ecosystems (Lawlor 2013). Assessment of drought tolerance in wildland species is often more challenging than in agricultural species because plants are rarely grown in conditions that approximate their source environments, and often little is known about their molecular genetics. Therefore, a suite of measurable phenotypic traits, such as rapid seedling emergence, root development, specific leaf area, and water-use efficiency, have generally been used to assess potential drought tolerance in wildland plant breeding programs (Johnson and Asay 1993).

It is important for managers to understand the selection criteria of a germplasm release before using it in restoration projects, particularly in drought-prone plant communities. In the Western United States, artificial selection for drought tolerance has primarily been performed on nonnative grasses that are common

components of post-fire stabilization seedings (Asay and others 2003), though some programs have used drought tolerance as a selection criterion in the development of native plant releases (Jensen and others 2012, Mukherjee and others 2011). Most native plant releases have been selected for high growth rates and seed production (Asay and others 2003), which can lead to high fitness at some wildland sites, but may be counter-productive to success in drought-prone environments (Kulpa 2010). For example, Kulpa and Leger (2013) studied the squirreltail (*Elymus elymoides* ssp. *Californicus*) Toe Jam Creek accession (Jones and others 2003, 2004) in two post-fire seedings with very low establishment success; they found that the surviving populations had undergone extreme directional selection for smaller plant and seed size, as well as earlier flowering phenology. These traits have been associated with drought tolerance in many plant species, but ran counter to the initial traits of the Toe Jam Creek accession, which was selected for release because of its high biomass and seed size. This mismatch may have contributed to the low success rate of the plantings.

Seed transfer guidelines, drought tolerance, and assisted migration—Seed transfer guidelines are useful in identifying seed sources that are likely to be well adapted to a given transplant location (Campbell 1991, Ying and Yanchuk 2006). The use of seed transfer guidelines dates back to the 1920s in North American forestry, when foresters recognized large differences in hardiness and growth of trees with different geographic origins (Bates 1928, Thrupp 1927). Tree seed transfer guidelines were initially based on variation in climatic zones within a species range (Haddock 1962), and they have been updated as genetic information from common garden studies has become more available (Campbell 1986, St. Clair and others 2005). In the past decade, managers and researchers have recognized the usefulness of seed transfer guidelines in the restoration of nonforest communities, particularly in arid and fire-prone environments (Erickson 2008; Johnson and others 2004, 2010a), and seed transfer guidelines have been developed for grass (Erickson and others 2004, Johnson and others 2010b, St. Clair and others 2013), forb (Johnson and others 2013), and shrub (Horning and others 2010) species in the intermountain west.

While seed transfer guidelines do not focus on drought tolerance per se, they do delineate climatic zones where populations of a given species are likely to be adapted, which can be useful in finding seed sources that can

persist in arid conditions (Ying and Yanchuk 2006). In addition, species-specific guidelines are developed using multivariate analyses of common garden data on climatically based adaptive traits (Campbell 1991), and these data allow researchers to find traits that correlate with specific environmental conditions. For example, St. Clair and others (2013) found that in bluebunch wheatgrass (*Pseudoroegneria spicata*), leaf length-to-width ratio (measure of length adjusted leaf narrowness) was highly correlated with annual heat moisture index (a measure of aridity). This makes sense because narrower leaves are less likely to suffer from water loss in stressful conditions due a lower number of exposed stomata. To help refine seed source selection decisions, research is needed to identify populations with traits that contribute to drought tolerance.

Assisted migration, a management strategy where organisms are translocated from sites with suboptimal environmental conditions to sites with more optimal conditions, may become integral to conservation strategies as the rate of climate change increases (Peters and Darling 1985). Assisted migration can encompass a broad range of goals, from minimizing loss of biodiversity to preventing extinction, and operate at a range of spatial scales, from local to continental (Williams and Dumroese 2013). Seed transfer guidelines, because they determine transfer distances that avoid maladaptation (Johnson and others 2004) and can be re-projected using models of expected future environmental conditions (Thomson and others 2010), will play an integral role in the planning of assisted migration efforts under global change.

Conclusions

To conclude, drought has significant ecological impacts—both direct and indirect—on native rangeland plant species, including effects on their physiology, growth, reproduction, physiognomy, and abundance. Drought also impacts rangeland ecosystem functioning and resilience through impacts on water availability, soil integrity, habitat, wildlife populations, livestock, and humans. Drought influences the likelihood and dynamics of other stressors and disturbances such as insect outbreaks, invasive species, wildfire, and human land uses. Drought often requires adjustments in methods for managing livestock and restoring plant communities. Managing and restoring native plant communities resilient to drought and climate change involves matching seed sources and adaptive traits to appropriate environmental and climatic conditions. Seed transfer

guidelines and assisted migration techniques are being developed to aid managers in need of restoration tools in the face of drought and climate change.

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