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On the Ground

- Rangeland managers actively focus on the potential to induce a shift in a site to an alternative state, but predicted changes in climate, particularly the likelihood of more extreme drought, necessitate reevaluating risks for alternative states.
- Rangelands will differ in their susceptibility to undergo state changes due to climate change in general and for droughts of the future, in particular, which may be hotter.
- Trees, shrubs, and grasses are expected to differ in their sensitivity to drought, with trees likely being most sensitive; this affects the likelihood for state changes in grasslands, shrublands, woodlands, and savannas.
- Considering these differences can help rangeland managers deal with the challenges of increasing drought that is forecast to occur with climate change.

Keywords: drought, state and transition, grassland, shrubland, woodland, savanna.

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Managing rangelands is challenging and will become more difficult as the frequency and intensity of climate extremes, such as drought, increases as forecasted with climate change. Rangeland management has advanced beyond reliance on assumptions of a predictable plant community moving back and forth between unstable (early successional) and stable (late successional) states. Rangeland managers now recognize the

potential for more pronounced, difficult-to-predict changes in vegetation dynamics that might not be directly or readily reversible. The broader framework for considering these more pronounced changes has been defined in terms of the different “states” that a rangeland site might fall into, which can vary over a set of site conditions, and the “transitions” that drive a change from one major vegetation state to another.¹

For fire and grazing, the potential to induce a shift in a rangeland to an alternative state under some conditions has been well documented and is a major priority of rangeland managers. However, there has been less emphasis on understanding the role of climate change and climate extremes as drivers of state transitions, in contrast to shorter-term changes in productivity and composition. This distinction is important given that the challenges associated with managing rangelands under climate extremes, such as drought, are likely to become greater due to climate change, as their magnitude and frequency are expected to increase with changes in precipitation patterns.² Moreover, because of warming trends, future droughts are likely to co-occur with higher temperatures than prior ones, independent of other factors affecting drought intensity and frequency. In the United States, heat waves have become more frequent and intense, especially in the west, and droughts in the southwest and heat waves everywhere are projected to become more intense.³ Changes in climate are increasing the likelihood for these types of extreme events.^{2,3} These climate change consequences need to be considered in the context of managing rangelands under drought.

In the present study we discuss the following:

1. The direct implications of drought under climate change for state transitions in rangelands and the indirect effects of the interaction of drought with other drivers of vegetation dynamics such as wildfire and pest or pathogen outbreaks;
2. Vulnerabilities of grassland, shrubland, woodland, and forest rangeland systems to state transitions with more extreme drought; and

- General considerations for managing rangelands to avoid undesirable state transitions as droughts become drier and hotter in the future.

Climate Change and Increasing Drought Extremity

An important aspect of developing and applying state and transition theory is to identify events that can drive a transition from one state to another as opposed to normal climate variability or management practices that cause variation within a given state. Extreme climate events (*sensu* Smith⁴), such as extreme droughts that elicit large and potentially irreversible ecological responses, are important drivers of state change. The mechanisms underlying these state changes are expected to be the mortality of dominant life forms, shifts in plant community composition, and/or establishment of novel life forms or species (Fig. 1). Each of these mechanisms is expected to elicit substantial responses that may play out over different time frames, with mortality-driven changes in composition and turnover of life forms (e.g., change from woody- to grass-dominated) potentially resulting in transitions to alternate states.

Although rangeland managers have been dealing with droughts for decades, warming conditions will result in droughts that are expected to be hotter on average than prior droughts.⁵ Moreover, changes in precipitation means and variability will result in more frequent and extreme droughts with respect to the long-term climate record.⁴ Indeed, many areas, such as the southwestern United States, are projected to become both hotter and drier; these combined conditions will likely increase frequency of extreme dry years as well as the intensity (or statistical extremity) of drought. Even small increases in average temperature can be important for

increasing drought intensity. First they can increase soil evaporation rates, leaving less water for plants.⁶ Second, they can increase physiologic stress on plants, reducing growth and even resulting in plant death under extreme conditions.^{5,6} Warmer temperatures increase atmospheric demand for water directly, leading to increased plant stress. As plant stress increases with increasing extremity of drought, plants can be pushed beyond their physiologic limits, resulting in mortality (Fig. 2), shifts in composition, and ultimately transitions to new states.

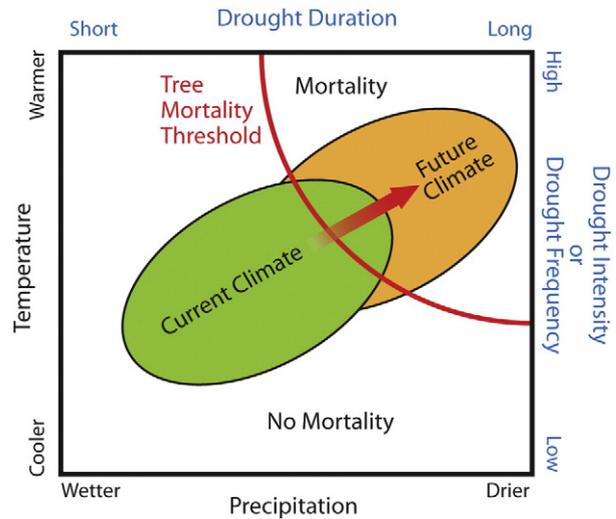


Figure 2. Conceptual diagram, showing range of variability of "Current Climate" parameters for precipitation and temperature, or alternatively for drought duration and intensity, with only a small portion of the climate "space" currently exceeding a species-specific plant mortality threshold. "Future Climate" shows increases in extreme drought and temperature events associated with projected global climate change, indicating heightened risks for drought-induced die off for current tree populations. This figure was developed for tree mortality, but can apply to shrub or grass mortality, although the mortality threshold for these different life forms likely differs (Figs. 3-4) (reproduced from Allen et al.⁵).

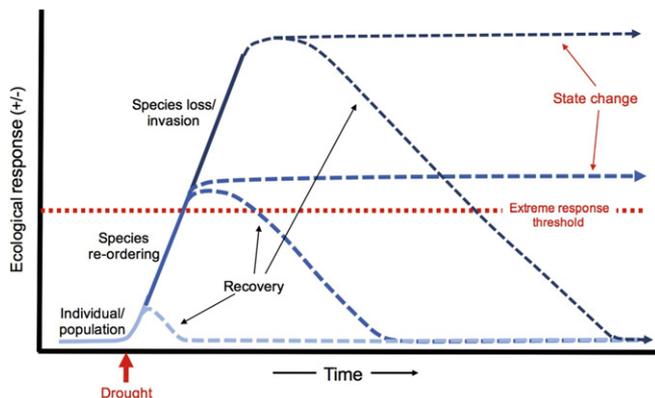


Figure 1. Processes that underlie state transitions with extreme drought. A drought that affects physiology and growth (individual-level responses) will have a smaller effect (positive or negative) on ecological processes (i.e., productivity) than one that results in large shifts in species abundances (species reordering), or in mortality of species or invasion by others. A state transition is likely to occur as a consequence of crossing an extreme response threshold (dotted red line) in which significant changes in abundance or loss of dominant life forms results in large ecological effects. These changes may be characterized by prolonged recovery or may lead to persistent state changes. Modified from Smith.⁴

More extreme droughts also may interact with other drivers of state transitions. Hotter and drier conditions can enable more intense wildfire, and also can alter the periods when fire might be most effectively prescribed as a management tool to maintain a given rangeland site. Pests and pathogens, especially those affecting woody plants, may become more pronounced during periods of drought. Protracted periods of drought leave soil conditions dry, which can, for example, result in increased wind erosion.⁷ Additionally, such dry soil may be susceptible to erosion associated with post-drought flooding, which is expected to become more intense in some areas as a result of climate change. These varied consequences of drought under climate change need to be considered in the context of rangeland states and transitions.

Another important aspect to consider relative to alternate states and potential transitions as a result of more extreme drought is the relative abundance of different plant life forms, such as grasses, shrubs, and trees, and their relative vulnerabilities to drier and hotter conditions. These dominant life forms can

differ in their sensitivity to drought, and as a result, the drivers and consequences of state changes can be different for grasslands, shrublands, and woodlands. Physiologically, the same characteristics that enable grasses to be resistant to grazing (e.g., growth from meristems at or below ground level; rapid responses to precipitation inputs) may enable them to be more resistant to more extreme drought events.⁸ Woody plants, however, are more sensitive to drought and can die due to a combination of hydraulic failure (loss of connectivity among the water flowing vessels), loss of carbon reserves, and/or the effects of pests and pathogens.^{5,9} Shrubs may be less sensitive than trees in part due to differences in physiology (many shrubs are more drought tolerant) and associated differences such as rooting patterns.⁸ Differences in sensitivity to mortality among life forms is not simply due to life cycle but rather reflects physiologic and morphologic differences among those life forms. Furthermore, fire is a key process for maintaining grasslands by limiting the establishment of woody plants, but it can kill some trees and shrubs, causing a shift from a woodland to a nonwooded state (which may be desirable or undesirable depending on the system and societal values). Thus, this disturbance could enhance the probability of transitioning to alternate states with more extreme drought. We next consider state–transition issues more specifically for grasslands, woodlands, and shrublands.

Contrasting Grasslands, Shrublands, and Woodlands or Savannas

In grassland systems, drier and hotter drought conditions drive reduced water availability but are unlikely to drive a state change (Fig. 3), unless the drought is so extreme as to trigger grass mortality, in which case an eroded state or an invaded state could result. In general, most temperate grasslands are

water-limited ecosystems with regard to forage production (above-ground net primary production [ANPP]), and plant community structure and composition varies strongly with geographic gradients in both temperature and precipitation. The sensitivity of NPP in grasslands to interannual variability in water availability is greater than in most other ecosystem types,¹⁰ and thus productivity responses to drought in grasslands can be substantial although also quite variable. For example, sensitivity in ANPP to the 2012 central US drought varied by twofold from desert grassland to mesic tallgrass prairie, with the former more sensitive than the latter.¹¹ In contrast, recent research suggests that warmer temperatures and even heat waves may have little direct effect on grassland.¹² Instead, it is the indirect effects of warming (greater evaporative demand and lower soil moisture) that can lead to even more extreme drought responses.

Rigorously assessing grassland responses to extreme drought is a challenge given the unpredictability of naturally occurring droughts. In a mesic grassland in Kansas, a 2-year extreme drought was imposed experimentally with both community and ecosystem responses and recovery documented.¹² After 2 years of a 66% reduction in growing season rainfall, ANPP was reduced to historic lows with both C4 grasses and C3 forbs responding strongly (–45% and –76%, respectively). Despite these large ANPP responses to extreme drought, when average levels of growing season rainfall were applied post-drought, complete recovery in ANPP occurred within 1 year. This recovery was entirely due to increased grass ANPP, as forb productivity remained reduced by 80% post-drought. Consistent with this functional response, community structure also was altered post-drought with an increase in relative grass abundance and a reduction in forbs, particularly the formerly codominant Canadian goldenrod (*Solidago canadensis*). This

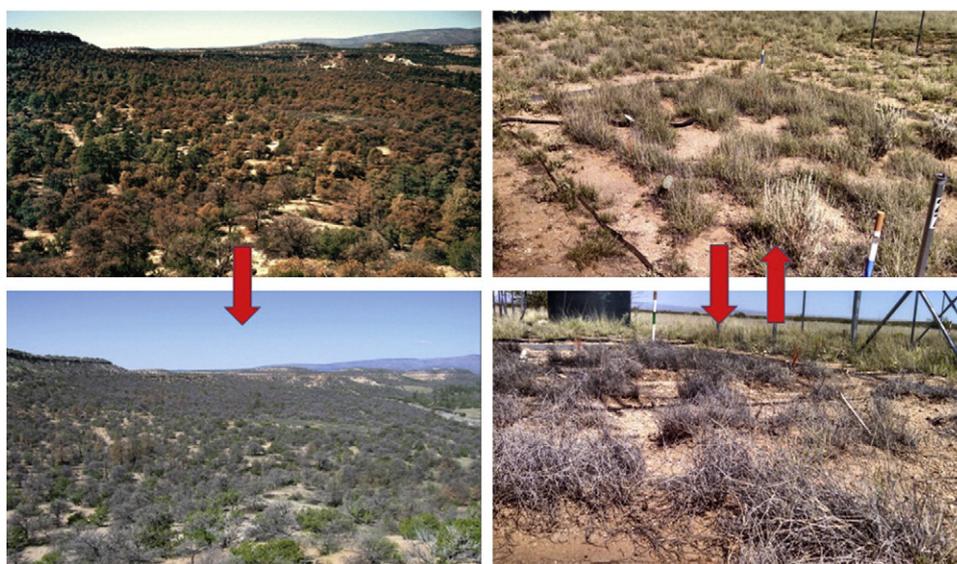


Figure 3. Effects of hotter drought vary by life form and associated rangeland types. Trees in semiarid woodlands (left) are vulnerable to mortality (Photos courtesy of C. D. Allen⁵), which can produce a shift to an alternate state, whereas grasses (right) may initially lose above-ground biomass but may be more likely to recover, preventing a state change (Photos courtesy of M. D. Smith).

particular forb has remained in low abundance in this community for 2 years post-drought, suggesting that mortality occurred and that such extreme droughts can elicit shifts in plant community structure without altering important ecosystem functions, such as ANPP or forage production.

In contrast to grassland systems, woodland and savanna systems are more likely to undergo a state transition in response to hotter, more extreme drought due to tree mortality, either in response to the drought, associated pests and pathogens, and/or due to wildfire effects (Fig. 3⁵). This sensitivity is highlighted in a recently developed metric for the southwestern United States, the Forest Drought Severity Index (FDSI¹³). The FDSI considers the precipitation inputs of prior months and more current conditions of the atmosphere—particularly the atmospheric demand associated with current humidity and temperature conditions. This one simple metric predicts changes in how green ecosystems are (measured with remotely sensed data for the Normalized Difference Vegetation Index), the temporal dynamics of large wildfires, and the patterns of large-scale tree die-off events. When trees from semiarid forest or woodland rangelands are lost in high proportions, the microclimate can be substantially altered and seed sources may be limiting. Consequently, a state change may occur in some systems that is a relatively long-term shift to a less wooded state.¹⁴ For example, very intense and severe wildfire may denude the system creating an eroding state. Less severe and or intense wildfire may induce a competitive release of understory herbaceous species.

Shrubland systems may have responses that differ from those of either grasslands or woodlands and savannas (Fig. 4). The woody plants in shrublands may be both more drought tolerant than trees and more resistant to damage from fire. Despite evidence that grasses are more resistant and resilient to severe drought than woody plants (especially trees), research suggests the potential for drought alone to cause a shift in shrublands toward grasslands once woody plants are established in the system. Although woody plant mortality does occur during

extreme drought in these systems, high mortality rates often are limited to larger tree species, leaving the shrub component of these systems intact.¹⁵ Shifts from shrublands to grasslands are most often the result of drought interactions with disturbance such as fire and not the result of drought dieback alone. Shrubs that have proliferated in many savannas and shrublands often are adapted to withstand long-term drought conditions.¹⁶ As a result, in areas with both grasses and shrubs, declines in grass cover often are observed as a result of prolonged severe drought, whereas shrub cover remains high. Indeed, recent experiments suggest that simply an increase in the frequency of drought years alternating with wet years will lead to reduced grass productivity and increased shrub growth.¹⁷ This creates the potential for woody plant encroached savannas to transition to less productive shrub-dominated communities with low grass cover and large amounts of bare ground.¹ These broad-scale shifts from perennial grass-dominated savannas to desertified woody plant and bare ground-dominated shrublands have been observed in perennial grasslands and savannas globally as a result of feedback between drought adapted woody plants and soil resources.

Management Challenges and Considerations

Rangeland managers should consider adapting existing management paradigms in ecosystems where more extreme drought is likely to initiate a shift to an alternative state. This is not the general case for grasslands. Managers should instead focus on state changes resulting from woody plant invasions owed to alterations of disturbance regimes (e.g., fire), because drier and hotter drought is not expected to trigger a change to a more desertified state. Instead, drought is associated with reductions in ANPP. Even under a utilitarian paradigm that emphasizes forage production as the sole resource objective, drought is considerably less of a threat to forage and livestock production than a state shift from grassland to woodland. This is important to recognize because considerable investments have focused on adaptations and control (e.g., fencing) to mitigate for short-term, first-order effects of drought over investments that prevent the decadal change from grassland to woodland causing long-term collapses in primary production in grasslands.

A very different approach is warranted in woodlands and savannas, which are vulnerable to alternative state change as a result of hotter droughts. Drought-induced tree die-off events are transforming multiple woodland, savanna, and forested rangelands. State changes resulting directly from drought can be difficult to prevent with interventions. In such instances, managers should consider where to promote greater functional diversity to increase resilience of forests to hotter drought and, in other cases, where to foster translocation of physiologically drought-tolerant species. Even greater potential for state change is expected as a result of how drought magnifies the severity of fire, pests, pathogens, and disease. Preventing the occurrence of these drivers has not succeeded in the past, and it is unlikely this trend will change in the future.

In contrast to the negative effects posed by more extreme drought, hotter and drier droughts will present isolated

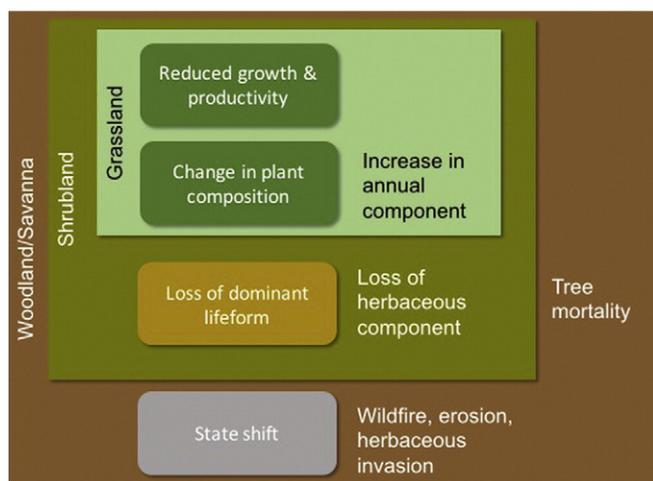


Figure 4. A proposed conceptual framework for considering how more extreme drought forecast with climate change may differentially impact rangeland types, based on life form types and their relative abundances.

opportunities to more effectively meet desired rangeland targets, particularly if managers can identify the potential to couple drought with rangeland interventions. For example, the combination of recent extreme droughts and high intensity fires has recently resulted in unprecedented mortality of multiple resprouting shrub species in two ecoregions of the southern Great Plains.¹⁸ Currently, managers avoid conducting fires in these conditions because they fall outside the conditions typically deemed acceptable. However, more frequent, extreme droughts have the potential to increase the probability with which fire can be used to more effectively meet woody plant mortality targets and facilitate community assembly toward a more desirable state.

Understanding the potential for state transitions in rangelands as a result of drought requires recognition that more extreme droughts and greater precipitation variability could potentially enable transitions to states previously not observed. This recognition will allow managers to identify opportunities to target drought conditions opportunistically and to adapt management practices to avoid undesirable transitions. Assessing transition probabilities and management options related to them requires differentiation between rangeland types—particularly with respect to woody plant component (grasslands vs. shrublands vs. woodlands and savannas, as well as related forested rangelands) with respect to how extreme a drought event is.

Conclusions

Reviewing rangeland responses to increasing drought extremity forecast with climate change provides several applicable insights:

1. Not all rangelands will be equally susceptible to such droughts—particularly with regard to their vulnerability to undergoing state changes;
2. The degree of woody plant abundance, and differences in mortality thresholds among growth forms, may be an attribute that helps explain differential vulnerability to state changes; and
3. Management in an era of change and uncertainty needs to be in tune with forecasted changes in external drivers (e.g., drought) and the relative differences in vulnerability among rangeland ecosystems to these drivers.

Managing rangelands in the context of alternate state theory will be a challenging but necessary approach to management in an era of rapid climate change.

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