

Review

Frameworks on Patterns of Grasslands' Sensitivity to Forecast Extreme Drought

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Received: 23 July 2020; Accepted: 30 August 2020; Published: 23 September 2020



Abstract: Climate models have predicted the future occurrence of extreme drought (ED). The management, conservation, or restoration of grasslands following ED requires a robust prior knowledge of the patterns and mechanisms of sensitivity—declining rate of ecosystem functions due to ED. Yet, the global-scale pattern of grasslands' sensitivity to any ED event remains unresolved. Here, frameworks were built to predict the sensitivity patterns of above-ground net primary productivity (ANPP) spanning the global precipitation gradient under ED. The frameworks particularly present three sensitivity patterns that could manipulate (weaken, strengthen, or erode) the orthodox positive precipitation–productivity relationship which exists under non-drought (ambient) condition. First, the slope of the relationship could become steeper via higher sensitivity at xeric sites than mesic and hydric ones. Second, if the sensitivity emerges highest in hydric, followed by mesic, then xeric, a weakened slope, flat line, or negative slope would emerge. Lastly, if the sensitivity emerges unexpectedly similar across the precipitation gradient, the slope of the relationship would remain similar to that of the ambient condition. Overall, the frameworks provide background knowledge on possible differences or similarities in responses of grasslands to forecast ED, and could stimulate increase in conduct of experiments to unravel the impacts of ED on grasslands. More importantly, the frameworks indicate the need for reconciliation of conflicting hypotheses of grasslands' sensitivity to ED through global-scale experiments.

Keywords: ANPP; climate extreme; diversity; ecosystem; global change; historical drought; precipitation

1. Introduction

Grassland is one of the major terrestrial ecosystems worldwide. It is distributed across a wide range of climates, elevations, and soil types [1,2]. Grassland delivers fodder for herbivores, renders aesthetic values, serves as biodiversity reservoirs, controls erosion, regulates climate (e.g., carbon sequestration) [3,4] and many more. These functions are naturally dependent on climate dynamics [3,5,6], and they respond in diverse ways to the natural climate variability, as well as currently intensifying human-driven climate change [7]. Hence, the complexity of management, conservation and/or restoration of these natural ecosystems requires a robust understanding of the underlying mechanisms governing their response to the dynamics of climate [8].

Precipitation is an essential driver of most terrestrial ecosystem processes [9]. It is widely regarded as the primary abiotic factor limiting most ecosystem functions (e.g., above-ground net primary productivity (ANPP), diversity) in grasslands [5,10–14]. Meanwhile, global climate models have predicted the occurrence of unprecedented extreme drought (ED) conditions at the end of this

century [15,16]. These ED conditions are expected to be statistically rare or unusual drought episodes far beyond the climax of historical record of droughts in any region of the world [17,18]. The ED could be rare within seasons or multi-year drought periods and could alter natural grasslands beyond that of typical interannual climate variability [9,17,19–21]. This may lead to severe loss of dominant life forms, species re-ordering, or shifts in plant community composition, triggered by disruptions in the interconnected complex ecological processes (e.g., nutrient cycling; Figure 1). The magnitude of the ecosystem alterations would largely depend on the period and magnitude of the ED events, stage of plants' growth cycle [22], the severity of changes, and resistance or recovery capacity of ecosystems after ED events [8,23]. With these uncertainties threatening the efficient delivery of ecosystem services, there is need for an in-depth understanding of how global or regional natural grasslands will respond to the ED [17,24,25].

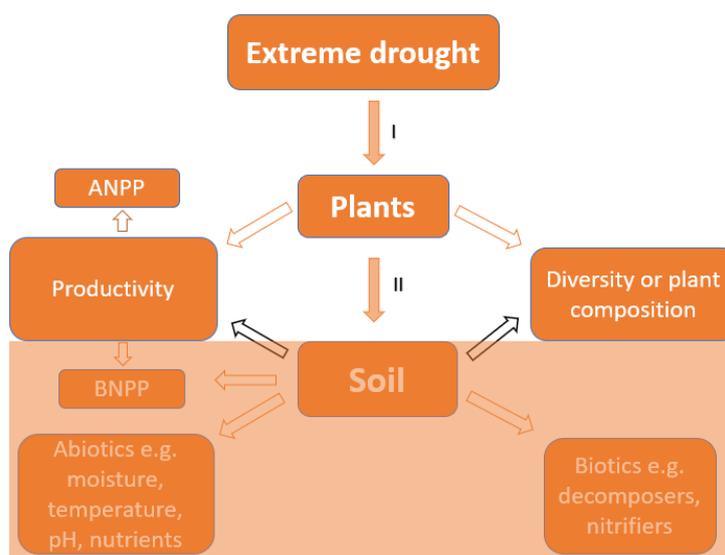


Figure 1. Conceptual diagram of how extreme drought could broadly impact grassland structure and functions. Extreme drought (ED) events could directly affect plants through decline in above-ground net primary productivity (ANPP), loss of diversity, or change in plant composition (filled brown arrow I and open brown arrows from the Plants). The ED could directly affect soil activities by altering soil microbial diversity, composition, and processes (filled brown arrow II), or indirectly through the loss of plant cover (filled brown arrow II) that could expose the soil to moisture loss, and inhibit the belowground net primary productivity (BNPP), activities of soil microbes, nutrient cycling, and others (opened brown arrows from the Soil). There is possibility of negative feedback effects of ED on the diversity and ANPP of drought-resistant plants that tolerate drought through belowground traits (opened black arrows from the Soil). Highlighted segment of the diagram represents the rhizosphere. Source: Author (Taofeek O. Muraina).

Certainly, previous investigations which were initiated following unusual or extreme drought events [17,26,27] have significantly created a strong background of the likely response patterns of grasslands to extreme climate changes [17]. The recent predictions of future ED events have also birthed the use of rainout shelters to impose and study ED effects on ecosystem functions across a wide range of ecosystems [9,20,24,28–32]. However, these studies are still unevenly distributed around the world [24], with differences in drought levels, many findings on single-site effects, and few comparisons of responses between sites [9,31–35]. They are yet to give a clear and broad pattern of how the essential functions of grasslands (e.g., ANPP, species diversity) spanning global precipitation or aridity zones (Table 1) could respond to a uniform extreme drought, e.g., ~80% growing season precipitation reduction. Therefore, for thorough understanding of the patterns and mechanisms underpinning

grassland response to future ED, there is need for wide adoption and implementation of multisite coordinated experiments with similar drought treatments [36] and measurement protocols [20,36–39].

Table 1. Grassland classification along precipitation or aridity gradient.

| Grassland Class | Precipitation Zones | AI (MAP/MPET) | MAP (mm yr ⁻¹) | Global Land Cover (%) |
|-----------------|---------------------|---------------|----------------------------|-----------------------|
| Xeric | Extreme-arid | <0.05 | <100 | 7.5 |
| Xeric | Arid | 0.05–0.2 | 100–250 | 12.1 |
| Mesic | Semi-arid | 0.2–0.5 | 250–600 | 17.7 |
| Mesic | Dry-subhumid | 0.5–0.65 | 600–1200 | 9.9 |
| Hydric | Humid | >0.65 | >1200 | 39.2 |

This table and information therein were adapted from [2,5]. AI = aridity index; MAP = mean annual precipitation; MPET = mean annual potential evapotranspiration.

In anticipation of more experiments and/or expansion of the existing ones that would address these gaps, conceptual frameworks could be built from the synthesis of literature to explain possible trends that will guide and/or aid general understanding of the response patterns of grasslands to ED. The sensitivity patterns can be studied through well-documented ecological precipitation–productivity relationship which is fundamental to management of grassland ecosystems [40]. Here, I propose frameworks for predicting the possible sensitivity—declining rate of an ecosystem function in response to the ED—patterns of ANPP spanning global precipitation gradient. The frameworks were particularly built to understand how the sensitivity of ANPP of natural grasslands spanning global precipitation zones (Table 1) could manipulate (weaken, strengthen, or erode) the orthodox positive precipitation–productivity. Thus, for the purpose of this study, the global grasslands were classified into three broad groups (xeric, mesic, and hydric) based on global aridity levels (Table 1; [2]). To allow a comparable assessment of the global-scale sensitivity, the frameworks (Figure 2) were generally built on four assumptions. First, it was assumed that the magnitude of the ED would be relatively uniform across the precipitation (or aridity) gradient. Second, the magnitude of sensitivity would be relative to the historical record of ANPP in every grassland. Third, the means of ANPP naturally differ across the gradient under ambient conditions. Lastly, the magnitude and direction of the relationship (slopes) would be contingent upon the sensitivity levels of the xeric and hydric grasslands. In the following sections, I present the existing hypotheses on possible patterns of grasslands’ sensitivity to extreme drought; develop frameworks depicting the sensitivity patterns; review mechanisms and dynamics that could support each framework; and make recommendations on how to reconcile the contrasting hypotheses.

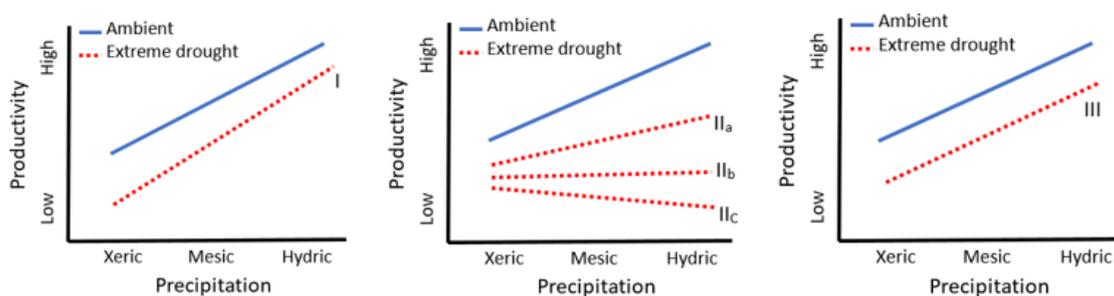


Figure 2. Hypothetical frameworks of extreme drought (ED) effects on the precipitation–ANPP relationship. (I) The slope of the relationship found under ambient condition could become steeper via higher ANPP sensitivity to the ED at xeric sites than mesic and hydric ones. (II) If the ANPP sensitivity emerges highest in hydric, followed by mesic, then xeric, a reduced slope, flat line, or negative slope may emerge. (III) If the sensitivity is strikingly similar across the precipitation gradient, the slope would remain as it was under the ambient condition. Source: Author (Taofeek O. Muraina).

2. How Will Extreme Drought Impact Productivity of Grasslands?

Ecologists often project the future status of the structure and processes of the earth system via earth system models [41,42]. Such models typically encompass land models which forecast the future state of terrestrial ecosystems [41]. For this reason, productivity, which is a key function of terrestrial ecosystems, and particularly the precipitation–productivity relationship, are part of the evaluation indices for the efficiency of the land models [41,42]. To date, there is consensus that strong positive correlation exists between precipitation and ANPP [10,29,40,43–45]. This is because photosynthesis, which is the main mechanism for plant growth and productivity, strongly couples with water [46]. However, intensified water deficits can manipulate this relationship [29,47,48] given that all grasslands are open to water stress [49]. For instance, reports have shown that the current dwindling seasonal distribution of precipitation, in both size and frequency [50], causes divergent sensitivity of ANPP across different grasslands [27,44]. As extreme drought looms in some regions of the world in the future [16,17,41,51], prior understanding of how ANPP may be affected are now much required [17,27].

There exist two contrasting hypotheses suggesting opposing sensitivity patterns along the precipitation gradient. The first hypothesis (A) holds that precipitation is less of a limiting resource in hydric and mesic grasslands, unlike in xeric ones (Table 1). Thus, this hypothesis suggests that the highest sensitivity would occur in xeric followed by mesic, then hydric [9,43]. The alternative hypothesis (B) suggests a reverse sensitivity ranking (hydric > mesic > xeric) because xeric grasslands, unlike mesic and hydric ones, are characterized by high aridity and should be constituted by drought-tolerant plant species [52–54]. These xeric plants are known to be drought-tolerant because they maintain their aerial growth and photosynthetic activities under low plant water potentials without xylem cavitation [54–56]. In other words, the second hypothesis proposes relatively minimal sensitivity in grasslands experiencing naturally high aridity prior to the ED (low aridity index grasslands; Table 1).

2.1. Frameworks of Sensitivity Patterns

Given the known dependence of plant productivity on precipitation, and in line with the two aforementioned opposing hypotheses (A and B) and intuition, there are three possible patterns (Figure 2) of sensitivity with which ED could manipulate the positive precipitation–ANPP relationship. Each of the three patterns depend on which grassland class along the precipitation gradient would experience higher and least sensitivity to drought. Any of these patterns could emerge because all natural grasslands are open to the potential ED-driven reduction of soil water availability, high evapotranspiration, decrease in soil microbial activities, poor nutrient mineralization and availability, and inhibition of nutrient uptake (Figure 1; [22,57–61]). However, the coping mechanisms of different species that constitute every grassland will largely determine the magnitude of their sensitivity [62]. Generally, plants tolerate drought via non-mutually exclusive hydraulic and photosynthetic adjustments [63]. For instance, stomatal could adjust carbon assimilation regimes and transpiration rate to achieve optimal productivity and prevent desiccation during drought [63]. Plants can also cope with ED by increasing the rates of absorption and translocation of water from root to other organs [49]. Whichever grassland class (xeric, mesic, or hydric) is dominated by plants that have the wherewithal (one or more drought-tolerance traits), and in which the coping mechanisms supersede, would experience less sensitivity than others. Therefore, the sensitivity could be higher in xeric, than the mesic and hydric sites as depicted in framework I (Figure 2; left panel; slope I); or unfold in opposite directions as illustrated in framework II (Figure 2; middle panel; slopes IIa–c); or a strikingly similar sensitivity occurs across the gradient (framework III; Figure 2; right panel; slope III).

2.1.1. Framework I

If the precipitation–ANPP relationship evolved in consonance with the first hypothesis (hypothesis A), the ANPP of xeric grasslands would exhibit greater sensitivity to ED, compared with mesic or hydric ecosystems [9,27,43], and the positive slope of the relationship would become steeper or strengthened

(Figure 2; left panel; slope I). One possible mechanism that could promote this framework I is the existence of positive precipitation–species richness relationship [64–69] and the fact that ANPP is a cumulative of all species in a particular ecosystem. If higher precipitation promotes species richness and ANPP across the precipitation gradient, it is expected that the xeric and mesic grasslands would possess less species richness and ANPP compared with hydric. Therefore, it can be inferred, that hydric (and mesic) grasslands stand a higher chance of possessing a pool of species with diverse drought-tolerance traits that would lessen their sensitivity to drought than the xeric ones [23,26,70,71]. For example, the hydric ecosystems may have higher number of plants with greater root length density for capturing soil water from the deeper soil depth [72–75], plants that would maintain photosynthesis through dehydration-tolerance of lamina and osmotic adjustment [55,76], or C4 and CAM (crassulacean acid metabolism) plants that subsist under water deficit [49,77]. The virtue of high species richness in hydric and mesic could also avail them the possession of those species that can switch from C3 to CAM metabolism to survive a prolonged ED [49,78]. Apart from drought-tolerance traits, community dynamics like species re-ordering, changes in species composition [79,80], and species asynchrony [1,81–85] are more likely in diverse communities and could minimize sensitivity in hydric grasslands than others. For instance, drought might trigger a shift in the competition for resources, structure, and abundance within highly diverse communities by favoring drought-tolerant subordinate species that would compensate for a possible higher sensitivity of the ED-intolerant dominant species [33,86]. This implies that species-rich ecosystems, unlike the species-poor ones, have a higher chance of possessing more subordinates and more rare species that may be more tolerant to ED and lessen the productivity loss by the dominants.

Indeed, the emergence of this framework I would contradict the notion that plant communities in drylands may be more tolerant to the effects of ED [53,87]. However, it may be that the unprecedented intensity of the ED would force the majority of the supposed drought-tolerant plants in drylands to exhibit drought-avoiding traits, thereby resulting to drastic reduction under ED. As ED avoiders, they could shed leaves, close stomata, redirect stored resources for increased below-ground productivity [88,89], and use more water from greater soil depths [90] to prevent eventual death and promote efficient recovery after drought events [55]. Monitoring of the mortality rate during drought and recovery rate in post-drought period could reveal whether those xeric ecosystems are only dominated by drought-tolerant species, or species with both drought-avoiding and drought-tolerance traits [25,74].

2.1.2. Framework II

If the sensitivity patterns emerge according to the second hypothesis (B), the xeric grasslands with high aridity (low AI) would exhibit a less response to ED than the less arid ones (mesic and hydric) [53,91]. As such, a weakened slope of the relationship (Figure 2; middle panel; II_a), flat line (II_b), or negative slope (II_c) would emerge. Emergence of a flat line or negative slope suggests that drought would have eroded the advantages that higher precipitation confers on grasslands in low aridity regions over those in high aridity regions. Any of the three patterns (slope II_a-c) in this framework II could unfold if the following conditions hold: (1) the supposed drought-tolerant plants are mainly domicile in xeric grasslands, and they could tolerate ED as they do for the non-extreme inter-annual water stress that characterize their ecosystems; (2) the mesic and hydric grasslands either have relatively negligible or no drought-tolerant species that could mitigate sensitivity as the xeric ones. In this case, plants in xeric grasslands could adjust and lessen sensitivity via higher allocation of assimilates to roots for enhanced water uptake from the deeper part of the soil [92,93], storage of water in shoots, reduced leaf area, and stomata opening at nights when transpiration is lower for CO₂ capturing [49]. Similarly, there will be lesser sensitivity in xeric grasslands if all plants, or those that contribute the substantial proportion of their ANPP, exhibit partial stomatal opening, while those in the mesic and hydric grasslands exhibit total stomatal closure under ED. Hence, partial stomatal opening that permits certain level of CO₂ uptake, photosynthesis, and minimal transpiration [49] would maintain a certain level of

ANPP, while stomatal closure in plants without drought-tolerant traits (e.g., deep root) would lead to higher sensitivity and eventual mortality. Alternatively, any of the patterns in this framework II could emerge if higher soil evapotranspiration rate, persistent high water-use, and non-closure of stomata of plants [94,95] force greater depletion of soil moisture, hydraulic failure, and eventual mortality of plants in hydric grasslands. Moreover, the usually less productive xeric grasslands, perhaps due to plants' adaptation to the dry conditions via conservative water-use [49], would experience less sensitivity than others if they experience lower soil evapotranspiration rate or lower soil moisture depletion [94].

Non-rainfall water (NRW) deposition is another phenomenon that could mitigate drought effects (sensitivity) [96,97] in grasslands. The NRW events, such as fog, dew, hoar frost, and water vapor adsorption, occur without rainfall [96,98], and plants could utilize them through foliar/canopy [99–101] or shallow root uptake [96]. Plants with rough and permeable leaves [100], and higher leaf area index have higher chance of capturing more NRW that could aid drought tolerance [97]. Persistence of this phenomenon under ED could promote efficient stomata conductance, reduce transpiration, increase carbon assimilation [96,102–105], and maintain production [106]. Despite the wide reportage of occurrence of NRW deposition in ecosystems [104,107], studies eliciting direct evidence of their ecological impacts on grassland functions—e.g., positive effect of dew on ANPP [100]—are extremely rare. Most previous studies suggest that contribution of NRWs to annual precipitation varies across sites and climate zones [104]. Groh and colleagues, for instance, found that dew and hoar frost contributed about 4.2–6% of the total annual precipitation, and 16.1% of total monthly precipitation in drier months across two grasslands [104]. In semi-arid areas of Madagascar, dew contributed about 19% of average annual rainfall of which 41% occurred during dry months [105]. Baier [108] reported that dew constitute 2% of the average annual rainfall in semi-arid climatic conditions of South Africa. These variations in the intensity of NRW events can influence differential sensitivity to extreme drought amongst grasslands across global aridity zones (Table 1). Moreover, the reports that dew contributes more to water budgets through its higher frequency and duration in arid areas than in humid areas [109] suggests that NRWs are high in xeric than mesic and hydric. Consequently, it is argued that if indeed the hypothesis of a lesser sensitivity in xeric grasslands would be true [53], higher intensity or efficient-use of NRW events should be one of the underlying factors conferring higher drought tolerance on plants in xeric sites [110]. Thus, it can be hypothesized that framework II could prevail under ED, if higher intensity of NRWs deposition and presence of plants that can efficiently capture/utilize them prevail in xeric grasslands than the mesic and hydric. With that, the xeric would experience a less sensitivity than the mesic and the hydric grasslands.

2.1.3. Framework III

Here a new hypothesis (C) is proposed that the three classes of grassland across the precipitation gradient could exhibit relatively similar sensitivity to the ED. This similar sensitivity across the gradient would result to a downward shift in the relationship, with little or no significant change in the slope (Figure 2, right panel; slope III). It is noteworthy that this hypothesis, unlike the previous two frameworks, has no scientific precedence, but it is not naturally impossible. For instance, this third hypothesis may ensue when the aforementioned potential conditions and adaptation traits that might confer a lesser sensitivity to hydric (in framework I) and xeric (in framework II) grasslands concurrently confer similar levels of low sensitivity to both grassland classes. One important mechanism that might bring about this relatively similar sensitivity is the extremely high similarity (or extremely low dissimilarity) in ecophysiological trait composition (e.g., drought-tolerant traits) amongst grasslands across the precipitation gradient [111]. This homogenization of ecophysiological traits is attainable through the increasing conscious and unconscious human movement of species into regions beyond their historical biogeographic realms [112,113]. So, the proposed framework III could ensue, when some species that are characteristically drought-tolerant and native to xeric grasslands spread into, naturalize,

and proliferate in mesic and hydric grasslands [114,115] prior to ED events and become the dominant species under ED.

3. Conclusions

Now that current and future hydrological changes threaten grassland ecosystems in relation to the efficient delivery of their services [17,36], ecologists are currently faced with hurdles to predict how ecosystems will respond to these escalating climate changes [36]. As biodiversity conservation, productivity management programs, and sustainability policies vis-à-vis future occurrences on natural ecosystems depend on the predictive knowledge of extreme drought events, I herein provide insights and foresights to probable models with which grasslands might respond to the ED. Drawing from previous reports, hypotheses, and thoughts, I systematically built frameworks of possible shifts in the magnitude and direction of the precipitation–ANPP relationship for understanding how the ED may impact regional or global natural grasslands. Although the proposed frameworks may not be exhaustive, or exhibited as stated per se, they could stimulate the required attentions of ecologists and agroecologists, and provide background knowledge on possible differences or similarities amongst grasslands in response to forecast ED. The frameworks particularly highlight the pressing need for comprehensive studies that would reconcile the aforementioned contrasting sensitivity hypotheses and elicit all possible mechanisms underlying eventual sensitivity pattern under predicted ED conditions. Prior understanding of how the ED impacts grasslands, and how the mechanisms could vary from xeric to mesic and hydric grasslands, would guide grassland managers in designing and applying appropriate management programs for different natural grasslands based on their peculiarities. I am aware that adequate understanding and reconciliation of the conflicting hypotheses of grasslands' sensitivity addressed herein demands global-scale standardized experiments in which extreme drought of the same magnitude is imposed over a long time. Therefore, I recommend wide adoption and implementation of existing global-scale extreme drought studies (e.g., Drought-Net. Available online: <https://drought-net.colostate.edu/>; accessed on 26 August 2020) to aid substantial spread across the global precipitation gradient and provision of solutions to herein highlighted knowledge gaps.

Funding: This research was funded by NATIONAL KEY R&D PROGRAM OF CHINA, 2017YFA0604802 and NATIONAL NATURAL SCIENCE FOUNDATION OF CHINA, 41320104002.

Acknowledgments: I profoundly appreciate Qiang Yu of IARRP-CAAS, Beijing for his guidance and provision of financial support for this publication. I also thank Saheed O. Jimoh of Grassland Research Institute of CAAS, Hohhot, and Suleiman K. Bello of King Abdulaziz University, Jeddah for their invaluable comments on the idea and draft that birthed this final manuscript.

Conflicts of Interest: The author declare no conflict of interest. The funders had no role in the design, writing, or the decision to publish the manuscript.

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