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The complex relationship between precipitation and productivity in drylands

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Perspective

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Abstract

Drylands provide multiple essential services to human society, and dryland vegetation is one of the foundations of these services. There is a paradox, however, in the vegetation productivity–precipitation relationship in drylands. Although water is the most limiting resource in these systems, a strong relationship between precipitation and productivity does not always occur. Such a paradox affects our understanding of dryland vegetation dynamics and hinders our capacity to predict dryland vegetation responses under future climates. In this perspective, we examine the possible causes of the dryland precipitation–productivity paradox. We argue that the underlying reasons depend on the location and scale of the study. Sometimes multiple factors may interact, resulting in a less significant relationship between vegetation growth and water availability. This means that when we observe a poor correlation between vegetation growth and water availability, there are potentially missing sources of water input or a lack of consideration of other important processes. The paradox could also be related to the inaccurate measurement of vegetation productivity and water availability indicators. Incorporating these complexities into predictive models will help us better understand the complex relationship between water availability and dryland ecosystem processes and improve our ability to predict how these ecosystems will respond to the multiple facets of climate change.

Impact statement

Dryland vegetation plays a major role in multiple essential services provided to human society. Water is the most limiting factor for dryland vegetation growth. However, there is a paradox between dryland vegetation productivity and water availability: water is the most limiting resource in drylands, but we do not always see a strong relationship between precipitation and productivity. Such a paradox affects our understanding of dryland vegetation dynamics and hinders our capacity to predict dryland vegetation responses under future climates. In this perspective, we explore the possible causes of the dryland precipitation–productivity paradox. Understanding the causes will help us better understand the complex relationship between water availability and ecosystem processes, which can lead to improved predictions about how these globally important ecosystems will respond to the multiple facets of climate change in the future.

Introduction

Drylands are water-limited ecosystems generally defined by an aridity index (i.e., precipitation/potential evapotranspiration) less than 0.65. These ecosystems cover about 40% of the global land surface and provide multiple essential services to human society (Eldridge et al., 2011; Wang et al., 2022). Notably, drylands support 60% of global food production (Wang et al., 2022) and include the largest area of grazing land on earth (Maestre et al., 2022). Because water availability is considered to be the main limiting factor for dryland vegetation growth (Wang et al., 2022; Kannenberg et al., 2024), we would expect a strong relationship between the amount of water input (e.g., precipitation) and aboveground net primary productivity (ANPP) within a site over time or for multiple sites across a water availability gradient. Indeed, there are observations ranging from the plot to ecosystem scale in which this relationship holds (Epstein et al., 2006). However, there are many observations across different sites and scales where this relationship is weak or nonexistent (Fernández, 2007). Additionally, the precipitation–ANPP relationship is much stronger spatially than temporally (Sala et al., 2012; Knapp et al., 2017). Furthermore, other studies have shown that temperature can be a more important driver of ANPP than precipitation at the mesic end of the dryland gradient (Sasaki et al., 2023). Therefore, there is a paradox in the dryland water availability–ANPP relationship: water is the most limiting resource in drylands, but we do not always see a strong relationship between water availability and productivity. The lack of a strong relationship between water input and ANPP in drylands occurs not only in observations but also in modeling. For example, Reynolds et al. (2004) used a plant physiological model to simulate vegetation responses to different water inputs under a range of atmosphere and soil and plant conditions and then calculated correlations between vegetation growth and water inputs. They found these relationships to be relatively poor across the board (Reynolds et al., 2004). Such a paradox affects our understanding of dryland vegetation dynamics and hinders our capacity to predict dryland vegetation responses under a future, warmer climate with higher seasonal and interannual variation in precipitation. In this perspective, we explore the possible causes of the dryland water-ANPP complexities and their implications.

Methodology considerations

Uncertainties in representing dryland water availability

Precipitation versus soil water

Precipitation is the most commonly measured and widely used parameter to represent water availability in drylands. Precipitation is the major water input to terrestrial ecosystems and is straightforward to measure with a long history of field measurements globally. However, not all precipitation becomes available to plant growth due to runoff and evaporation. In fact, up to 95% of precipitation in drylands returns to the atmosphere through evapotranspiration (Wilcox and Thurow, 2006), with evaporation accounting for more than 50% of evapotranspiration in drylands (Lu et al., 2017). As such, the concept of effective precipitation has been introduced to refer to the precipitation component that is available to plant growth. Of course, plants do not directly use precipitation for their growth but instead mostly rely on soil water. Soil moisture is therefore the second most common parameter to represent dryland water availability. There is large spatial heterogeneity of soil water status in drylands, and soil moisture also varies with depth. It is therefore a challenge to accurately capture the status of soil moisture spatially and temporally. Furthermore, water movement in the soil–plant continuum is driven by the soil water potential gradient rather than by soil water content. As such, soil water potential would be a better parameter to represent soil water availability. However, soil water potential measurements are much less common relative to soil water content across global drylands and depth-varying data are even more scarce. Recently, drought indices, such as Palmer Drought Severity Index or Standardized Precipitation Evapotranspiration Index, have been used to indicate water availability (Jiao et al., 2021). These indices consider both water input (e.g., precipitation rather than soil water) and water demand (e.g., potential evapotranspiration) of a region, but they tend to have coarse spatial and temporal resolutions. Currently, there is no ideal indicator to represent water availability in drylands through the soil–plant–atmosphere continuum. It is important to keep these limitations in mind when examining the relationship between water availability and plant productivity using various water availability indicators.

Precipitation amount versus precipitation variability

Mean annual precipitation is often used as a surrogate for soil water availability in ecosystems. However, dryland productivity may respond not only to total precipitation but also to within-season variability in the size and frequency of rain events (Feldman et al., 2024). In drylands, the bucket model (Knapp et al., 2008) predicts that increased precipitation variability around the same mean annual precipitation will increase productivity because fewer, larger rain events lead to deeper infiltration and longer lasting soil moisture than frequent, smaller rain events. Although short-term experiments have validated this model (Heisler-White et al., 2009), long-term experiments find model predictions to be valid in drylands only when secondary limitations (e.g., nitrogen availability) are alleviated (Brown and Collins, 2024). Therefore, simplifying moisture inputs to annual totals will likely miss important characteristics of growing season rainfall, underestimate the role of nutrient availability and potentially weaken the relationship between water input and ANPP. Although projected changes in precipitation are still uncertain across many drylands, global warming is expected to increase precipitation variability (Thornton et al., 2014; Pörtner et al., 2022), highlighting the importance of considering within-season patterns of precipitation when modeling the relationship between precipitation and ANPP (Feldman et al., 2024).

Non-rainfall water and groundwater

Rainfall is the main source of soil water in most dryland ecosystems. However, other forms of water input to drylands include fog, dew and water vapor adsorption (Lopez-Canfin et al., 2022). These inputs could play a significant role in sustaining vegetation activities during rainless periods, and their impact could exceed rainfall in certain ecosystems (Wang et al., 2017). When we quantify the relationship between vegetation productivity and water availability, typically only rainfall amount is included, and non-rainfall water inputs are rarely considered. Ignoring the potential contribution of non-rainfall water could be partially responsible for the observed weak relationship between precipitation and ANPP within a site over time.

Besides non-rainfall water sources, in some dryland regions, groundwater may also be an important source to plants. Vegetation with deep rooting systems, such as riparian trees, has the capacity to utilize deep groundwater that is unavailable to herbaceous plants (Ding et al., 2017). As such, groundwater-dependent vegetation is less subject to short-term reductions in precipitation. However, prolonged droughts could significantly impact vegetation growth if groundwater availability declines. Also, even without a change in rainfall amount, extensive human groundwater extraction will reduce groundwater levels and could directly impact vegetation growth (Brunette et al., 2024). For such groundwater-dependent ecosystems, if only local precipitation is considered in the water input equation, the strength of the relationship between vegetation productivity and rainfall will be reduced.

Uncertainties in quantifying and representing vegetation productivity

At the plot scale, harvesting all aboveground herbaceous biomasses at the end of the growing season is considered to be the most direct and accurate way to estimate annual ANPP (Fahey and Knapp, 2007). For woody plants, allometric methods are typically used to estimate the aboveground biomass (e.g., Clark et al., 2001). Because these methods indirectly incorporate the loss of productivity by grazing, browsing or senescence, they may underestimate primary production. Furthermore, these plot-scale measurements require extensive replication to capture the strong small-scale heterogeneity of dryland vegetation.

At the ecosystem scale, vegetation productivity is often estimated from eddy covariance flux tower-based CO_2 measurements and is represented by gross primary production (GPP). Flux towers offer high temporal resolution measurements of GPP over relatively large ecological footprints (e.g., hundreds of meters to kilometers).

Tower-based GPP measurements are usually considered to be the gold standard to benchmark and validate the carbon cycle in land surface models. However, GPP is not a directly observable variable, and it is deduced from net ecosystem exchange (NEE) measurements using different methods partitioning NEE into GPP and total ecosystem respiration (e.g., daytime partitioning vs. nighttime partitioning) and considerable biases can occur in tower-based GPP estimates (Keenan et al., 2019). Ideally, GPP can be further partitioned into net primary production (NPP) if total ecosystem respiration can be partitioned into root and heterotrophic respiration. However, this is challenging to achieve for flux tower measurements and rarely done.

At very large spatial scales, remote sensing-based estimates of biomass are often a necessity. The Normalized Difference Vegetation Index (NDVI, an estimate of "greenness") is often used as a surrogate for vegetation productivity, but there are potential issues using NDVI to represent vegetation productivity in drylands. First, remote sensing data, especially satellite-based remote sensing data, often have a coarse spatial resolution (e.g., MODIS NDVI resolution is 500 m and Landsat NDVI is 30 m), which homogenizes local variability in vegetation production (e.g., trees, shrubs and herbaceous composition). Second, NDVI does not account for tissue loss by grazing or senescence and thus potentially underestimates vegetation production. That is why people often use peak NDVI or integrate multiple measurements over the growing season to minimize this bias. Other satellite-derived direct productivity indicators (e.g., MODIS GPP and NPP) generally perform poorly in drylands. This poor performance in drylands is related to the limited amount of dryland ground truth data used to calibrate and drive light use efficiency models (Smith et al., 2018). Our ability to constrain nearly every variable in the light use efficiency models, such as absorbed photosynthetically active radiation (APAR) by plant canopies or the efficiency at converting APAR to carbohydrates (ε), remains limited in dryland systems because of data scarcity as well as the structural and functional heterogeneities in many dryland ecosystems (e.g., sparse canopies, C_3/C_4 composition) (Smith et al., 2018). The use of solar-induced chlorophyll fluorescence (SIF) to estimate productivity has increased recently because it is directly linked to plant photosynthesis (Sun et al., 2023a, 2023b). However, currently, there are no direct SIF observations from satellites and all available satellite SIF products are from space missions that were designed to monitor atmospheric trace gasses. Satellite SIF data are therefore indirect estimates that build on a set of assumptions that are affected by a suite of factors including meteorology (Song et al., 2021). SIF measurements from towers or unmanned aerial vehicles could be one solution, but tower-based SIF measurements are still limited and lacking standardized processing and retrieval methods (Sun et al., 2023b). More importantly, it has been argued that SIF data availability and applications currently outpace the growth in the mechanistic understanding of SIF dynamics (Sun et al., 2023a).

Ecosystem process considerations

Lag effect between water input and vegetation response

Although water is the most limiting factor controlling ANPP in drylands, vegetation growth sometimes lags behind precipitation inputs both within and between years (He et al., 2021). During a growing season, peak rates of photosynthesis often occur several days after a rain event (e.g., Thomey et al., 2014) and depend on event size and duration of soil moisture (Vargas et al., 2012). This lag effect of precipitation on ANPP can be highly complex. Sala et al. (2012) hypothesized that the effects of dry years, for example, carried over to reduce ANPP the following year despite higher precipitation inputs because of structural, biochemical or compositional changes. Indeed, using flux tower data, Petrie et al. (2018) reported that the correlation between ANPP and precipitation in a given year was influenced by the sequence of prior conditions. For example, ANPP often increased with the length of multiyear wet periods, such that the importance of the amount of current-year precipitation declined. Others have shown that drought legacies reduce belowground bud banks and limit the capacity for vegetation to respond to increases in precipitation (Luo et al., 2023). These lagged responses obscure a strong relationship between vegetation productivity and water input rate or preclude its existence.

Nonlinear effect

Most previous studies primarily employed equation-based and linear approaches to investigate the relationship between water availability indicators (e.g., precipitation) and vegetation productivity. However, a nonlinear relationship could occur both spatially because more mesic or colder drylands are less water limited and temporally because other factors limit vegetation growth when water is plentiful (e.g., Hsu et al., 2012; Knapp et al., 2017; Rudgers et al., 2018). Based on long-term data from 48 grassland sites in Mongolia, Sasaki et al. (2023) applied an equation-free, nonlinear time-series analysis to examine the relationship between precipitation and vegetation productivity. The results are counterintuitive in that they found that productivity responded positively to annual precipitation in mesic regions but negatively in arid regions (Sasaki et al., 2023), likely due to lagged effects. Additionally, productivity responded negatively to interannual variability in precipitation in mesic regions but positively in arid regions (Sasaki et al., 2023), as has been demonstrated elsewhere both empirically (Cleland et al., 2013; Gherardi and Sala, 2019) and through modeling studies (Hou et al., 2021). These results indicate that the response of vegetation productivity to water availability may often be nonlinear and state dependent. Nonlinear responses, lag effects and state-dependent variables create multiple challenges for translating complex relationships into modeling frameworks that can effectively predict vegetation response to water availability under current and future climates.

Impact from non-water factors

Depending on locations and season, other meteorological factors such as temperature, relative humidity and vapor pressure deficit (VPD) could also play a role in moderating the relationship between ANPP and water availability (Novick et al., 2016; Knapp et al., 2024; Novick et al., 2024; Wright and Collins, 2024). For example, in the Namib Desert, vegetation growth is significantly impacted by temperature based on more than 20 years of satellite observations (Qiao and Wang, 2022). In this case, the temperature impact is negative, meaning that plant growth was reduced as the temperature increased, and temperature modulates the vegetation response to water availability. Given that temperature is increasing globally, but predicted changes in precipitation are spatially variable, more work is needed to address the potential interactions associated with coupled changes in both soil water and atmospheric demand across drylands. Besides meteorological factors, soil nutrients such as soil nitrogen and phosphorus availability play a significant role in affecting the relationship between ANPP and water availability in drylands (Yahdjian et al., 2011; Brown and Collins, 2024). For example, low soil nitrogen constrains the vegetation response to water availability in African savanna ecosystems (Wang et al., 2010). In addition to these physical factors, biological factors such as competition and herbivory (Maestre et al., 2022) could further moderate the relationship between ANPP and water availability.

Conclusion and looking forward

Although water availability is considered to be the strongest limiting factor governing primary production in drylands, we do not always find a linear relationship or even a strong positive relationship between water availability and vegetation productivity within a site over time (Knapp et al., 2017). This affects our capacity to predict future vegetation dynamics in drylands and to manage these ecosystems to enhance carbon sequestration. This is particularly important considering the increasing constraints on vegetation growth observed over the recent decades (Jiao et al., 2021). The underlying reasons are numerous depending on the location and scale of a study. Sometimes multiple factors may interact, resulting in a less significant and nonlinear relationship between vegetation growth and water availability. This means that when we observe a poor correlation between vegetation growth and water availability, there are likely missing sources of water input or demand (e.g., groundwater, non-rainfall waters, VPD) or we lack consideration of other important processes, such as lag effects, within-season rainfall variability, nutrient availability or nonlinear interactions. In some cases, weaker relationships could also result from error-prone measurements (e.g., ground-level measurements) and the representation of vegetation productivity and water availability (e.g., satellite proxies). Understanding and incorporating these complexities into predictive models will be challenging, but doing so will help us better understand the complex relationship between water availability and ecosystem processes in drylands. It will also improve our ability to predict how these globally important ecosystems will respond to the multiple facets of climate change in the future.

Data availability statement. There is no data in this study.

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Author contribution. L.W.: Conceptualization, funding acquisition and writing – original draft. S.C.: Writing – review and editing, contributing additional ideas and funding acquisition.

Competing interest. The authors declare no competing interests exist.

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