

Incorporating Biogeochemistry into Dryland Restoration

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Dryland degradation is a persistent and accelerating global problem. Although the mechanisms initiating and maintaining dryland degradation are largely understood, returning productivity and function through ecological restoration remains difficult. Water limitation commonly drives slow recovery rates within drylands; however, the altered biogeochemical cycles that accompany degradation also play key roles in limiting restoration outcomes. Addressing biogeochemical changes and resource limitations may help improve restoration efforts within this difficult-to-restore biome. In the present article, we present a synthesis of restoration literature that identifies multiple ways biogeochemical understandings might augment dryland restoration outcomes, including timing restoration around resource cycling and uptake, connecting heterogeneous landscapes, manipulating resource pools, and using organismal functional traits to a restoration advantage. We conclude by suggesting ways to incorporate biogeochemistry into existing restoration frameworks and discuss research directions that may help improve restoration outcomes in the world's highly altered dryland landscapes.

Keywords: degradation, restoration or remediation, biogeochemistry, drylands, nutrient cycling

Restoring degraded drylands is a critical challenge

for the twenty-first century. Drylands, defined by an aridity index below 0.65 and including hyper arid, arid, semiarid, and subhumid regions (Middleton and Thomas 1992), cover 45% of the Earth's land surface (Pravalié 2016) and are home to more than 2 billion people (Safriel et al. 2005). Precise estimates are difficult, but at least 20% of drylands are considered degraded (Reynolds et al. 2007a, Safriel 2009, Bestelmeyer et al. 2015), which we define as a persistent reduction in ecological productivity, biodiversity, and ecosystem services, such as soil conservation, water regulation, and forage (Safriel et al. 2005) due to land-use practices and climate change. Although the problem of dryland degradation is widely recognized (United Nations 2011), the ability to restore productivity and ecosystem services to degraded drylands has been poor (James et al. 2013); for example, seed germination and seedling survival can be as low as 5%–10% after seeding in some dryland types (Kildisheva et al. 2019).

Dryland restoration is challenging because aboveground and belowground biomass are constrained by low overall precipitation, high climate variability, and low soil fertility (Safriel et al. 2005). When degradation causes changes in the biomass or distribution of ecological communities, such as in some cases of woody-plant encroachment (Puttock et al. 2014) or annual plant invasion (Miller et al. 2012), an ecosystem's ability to retain resources (e.g., soil nutrients,

moisture, native plant seeds) can be reduced (but see Archer et al. 2001, Maestre et al. 2009). This reduced capacity to retain resources can result in a feedback of resource loss that is difficult to reverse (Bestelmeyer et al. 2015). When this feedback is occurring, it is often very challenging to meet restoration goals (Monaco et al. 2012, Svejcar and Kildisheva 2017), such as returning plant and soil crust cover and soil stability (Antoninka et al. 2016, Fick et al. 2020, Havrilla et al. 2020).

In the present article, we explore the possibility that the discipline of biogeochemistry may help advance restoration goals and outcomes within dryland restoration. Biogeochemistry is defined as the biologic, geologic, and chemical processes that dictate the composition of an environment (Schlesinger and Bernhardt 2013). The simplifying principle that underlies biogeochemistry is that, within a given ecological state, essential requirements for chemical elements such as carbon (C), nitrogen (N), and phosphorus (P) are unchanging; therefore, by tracking their quantities, fluxes, chemical conversions, and ratios, constraints can be identified that lead to system-level understanding. For example, ecologists have long understood that multiple resources can limit rates of ecosystem processes such as plant growth (Rietkerk and van de Koppel 1997), whereas basic stoichiometric requirements can limit the distribution and abundance of producers, consumers, and decomposers (Güsewell 2004, Schmidt et al. 2016, Leroux

et al. 2017). Although some of these concepts have been applied to restoration ecology (Suding et al. 2004), there is an opportunity to further incorporate biogeochemical understandings into dryland restoration frameworks and actions.

Biogeochemistry has the potential to help improve dryland restoration outcomes for several reasons. First, recent biogeochemical insights in drylands have illuminated important biogeochemical principles relevant to restoration (figure 1). For example, although water limitations have received the most attention in explaining productivity in drylands, other limiting resources, such as nutrients, are increasingly being recognized as important drivers in dryland productivity, species composition, and ecological processes (Austin 2011, Eskelinen and Harrison 2015). Second, biogeochemical approaches may offer insight into the difficult issue of restoration timing. Correctly timing dryland restoration efforts so they coincide with both periods of prolonged soil moisture (Hardegee et al. 2012) and nutrient availability for target organisms may aid restoration outcomes such as plant or biocrust germination and establishment (figure 2). Third, biogeochemical insights provide the opportunity to examine organismal traits that can be used and manipulated to affect biogeochemical cycling in a restoration setting. For example, the use of N-fixing biocrusts or plants can be used to increase soil N availability when increasing primary production is the restoration goal (Evans and Ehleringer 1993).

For these reasons, incorporating a biogeochemical perspective into restoration frameworks and actions has the potential to improve restoration outcomes (but see Maestre et al. 2006); however, an examination of studies covering these topics is lacking. In the present article, we present a summary of the restoration literature that addresses biogeochemistry in degraded drylands and examine dryland biogeochemical research in a restoration context. From the literature, we identified four primary ways that restoration action addresses biogeochemistry in degraded regions: timing restoration around resource cycling and uptake, connecting heterogeneous landscapes, manipulating resource pools, and using organismal functional traits to a restoration advantage. Within each of these categories, we provide examples of how these tactics have been used in restoration and how new insights in biogeochemistry may relate to restoration action.

Timing around resource cycling and uptake

Timing restoration actions around precipitation events or periods of prolonged soil moisture is an effective way to increase plant regeneration or survival in drylands (Abbott et al. 2003), such as during monsoonal El Niño events in the US Southwest or projected times of increased or reliable soil moisture in other regions (Holmgren and Scheffer 2001, Hardegee et al. 2018). Restoration actions planned in accordance with water availability can increase the establishment of native seeds (Shriver et al. 2018), influenced

vegetation recovery trajectories (Copeland et al. 2018), and may aid in the establishment of inoculated biological soil crust (biocrust; Young et al. 2019, Fick et al. 2020)—surface-dwelling photosynthetic communities that support primary production and soil stabilization in drylands (Chaudhary et al. 2009, Darrouzet-Nardi et al. 2015).

However, timing restoration action so that it occurs during periods when water and other resources are available is a strategy that has not received much attention, despite its potential impact on restoration outcomes (Seastedt and Knapp 1993, Blair 1997). Precipitation events can be decoupled from photosynthesis, N transformations, and organic matter inputs that stimulate biological responses in drylands. This decoupling is likely because of a temporal lag in nutrient cycling following precipitation pulses or a differential response to precipitation from plant or microbial functional types (Schwinning and Sala 2009, Winkler et al. 2020). During precipitation events or periods when water is less limiting, a rapid drawdown in soil nutrients can occur as plants capitalize on moisture to acquire important resources. This drawdown in nutrients may change the limiting resource from water to nutrients over relatively short time periods (Seastedt and Knapp 1993). These patterns, combined with data suggesting strong nutrient controls over dryland systems (Hooper and Johnson 1999, James et al. 2005), point to the need to plan around the availability of other limiting resources in addition to water availability when attempting to establish and maintain vegetation and biocrust communities.

Alternatively, planning restoration actions around times when resources are naturally limiting may be an effective strategy for reducing biomass of annual invasive species. For example, in the southwestern United States, nutrient limitation for exotic cheatgrass (*Bromus tectorum* L.) occurs during the late winter and early spring, although water limitation occurs during late spring and fall (Miller et al. 2006). In a restoration context, lowering the availability of nutrients (e.g., by adding C to stimulate microbial immobilization of N) at times when invasive species are already nutrient limited or adding soil amendments that alter soil chemistry, such as calcium dichloride and zeolite, may reduce the likelihood of increased invasion, although the effectiveness may vary with factors such as soil type and precipitation (Newingham and Belnap 2006). Planting native annual plants that reduce soil resource availability at the same time exotic annual plants are seeking the resources represents a potential restoration practice that uses a biogeochemical mechanism. Furthermore, data suggests that some bunchgrass species, which are common restoration target species, and have a stronger growth response to nitrate (NO_3^-) over ammonium (NH_4^+ ; Monaco et al. 2003), providing an opportunity to target N additions or sequestration strategies toward specific plant types, however, these patterns may not hold across systems (James et al. 2008). Although we know N can increase plant growth in drylands (Yahdjian et al. 2011), further research determining whether, how, and when different forms of N or other

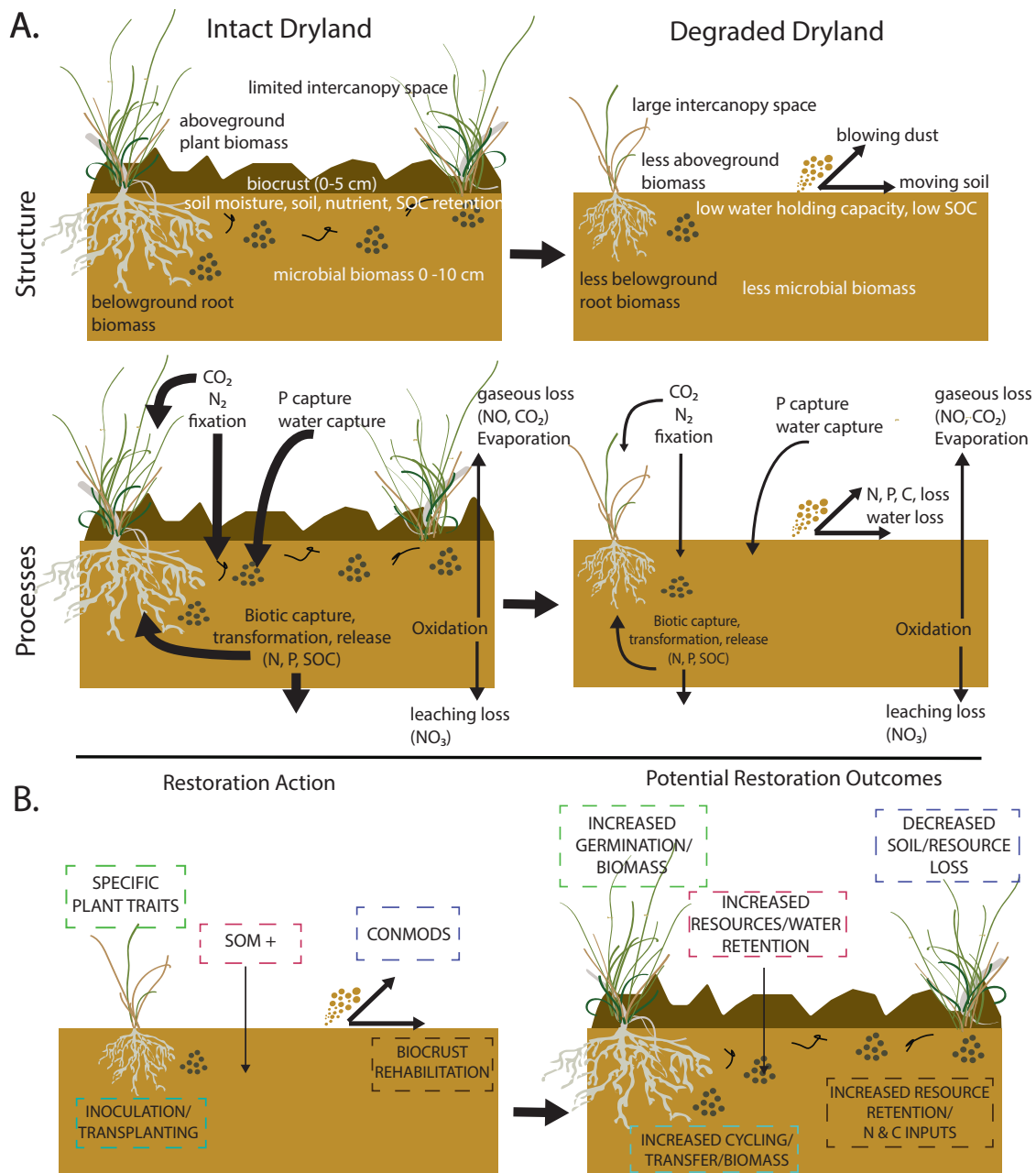


Figure 1. Diagram depicting general biogeochemical properties within some dryland types. (a) The left panel is an example of a semiarid grassland in the absence of recent severe disturbance, which we are calling “intact.” On the right is an example of the same dryland after degradation, which we define as a reduction in productivity and ecosystem services due to land-use practices or climate change. The biogeochemical components change noticeably from the intact to degraded state and involve changes in the structure (biomass pools and organismal types) and processes (degree of nutrient, carbon, and water retention, loss, and capture). The arrow widths indicate hypothesized differences in the amount of nutrient and carbon cycling occurring and the amount of water capture or loss. Generally, degradation decreases biomass, amounts of cycling, and soil moisture retention. (b) The left panel is an example of restoration actions that can be applied to degraded drylands to jumpstart biogeochemical processes when water is available, such as adding soil organic matter (SOM +), using plant traits that allow for higher rates of germination and establishment, (specific plant traits), transplanting vascular plants and inoculating with soil microorganisms (inoculation or transplanting), adding biocrust propagules back onto the soil surface (biocrust rehabilitation), and changing resource connectivity (conmods). On the right are the potential biogeochemical outcomes of those restoration actions. Throughout this review, we highlight the importance of spatial and temporal components, multiple limitations, and organismal traits related to each restoration action and how they may increase the likelihood of the biogeochemical outcomes shown in the figure.

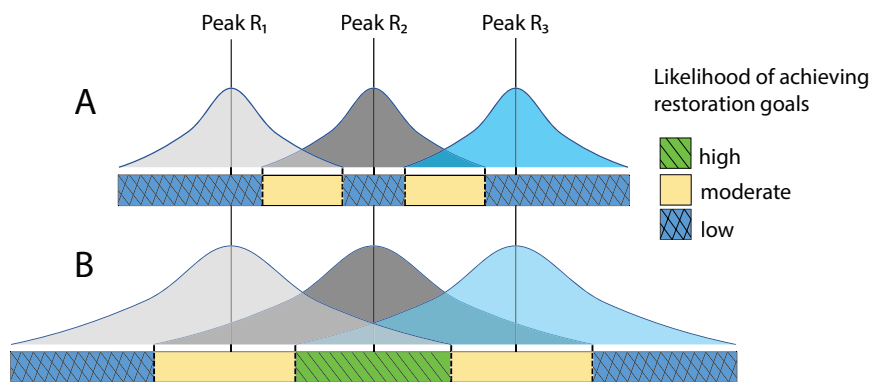


Figure 2. Drylands can be limited by multiple resources that are heterogeneous across space and over time. (a) In areas in which the availability of limiting resources, such as water, nutrients, or organic carbon (shown as R_1 , R_2 , and R_3), have limited overlap, achieving restoration goals such as increased productivity and ecosystem functioning may be more difficult (indicated as low). (b) When restoration actions increase the duration or magnitude of multiple limiting resources, the likelihood of achieving restoration goals is greater (indicated as high). For example, restoration actions that add resources such as nutrients and mulch can increase resource retention and create more overlap in resource availability when soil moisture becomes available. In addition, restoration actions that collect resources, such as ConMods, can maintain resources, such as soil nutrients, creating more overlap during periods of prolonged soil moisture.

limiting resources affect restoration outcomes could provide more biogeochemically informed management options.

The timing and asynchrony of resource limitations is likely going to be more pronounced under climate change, with the potential to make dryland restoration more difficult in the future. For example, concentrations of soil organic C and total N are expected to decrease with aridity, whereas the concentrations of inorganic P are expected to rise (Delgado-Baquerizo et al. 2013). This decoupling in biogeochemical cycles is attributed to the predominant role of water and biological processes on concentrations of soil organic C and N and the predominant role of rock weathering on P concentrations. Nonlinear changes in resource availability in drylands may shift the balance of limiting resources and require additional interventions through time in the form of resource additions, such as organic matter, or resource retention methods, such as small barrier structures that serve as connectivity modifiers (ConMods; Okin et al. 2015). Predictive models that forecast multiple resource fluctuations (soil moisture, N, C, and P) under a more arid climate could aid in restoration planning and could allow practitioners to plan ahead to restore dryland ecosystems so that they are more resilient to future fluctuations in resources availability (Bradford et al. 2018).

Connecting heterogeneous landscapes

Heterogeneity, at both large and small scales, is a defining characteristic of drylands (Bestelmeyer et al. 2006). Within drylands, plant canopies are often discontinuous

and soil properties vary widely from microsites to landscapes (Buxbaum and Vanderbilt 2007). With this heterogeneity come differences in soil nutrient and water content, retention, and cycling rates at multiple scales that may help or hinder restoration efforts (Prober et al. 2002, Valladares and Gianoli 2007). In some cases, restoration action seeks to turn heterogeneous landscapes into more homogeneous landscapes in which resources are spread evenly over an area. This type of intervention can combat resource accumulation in specific areas, as in the case of shrub islands that concentrate nutrients and organic C under shrubs and leave interspaces bare (Schlesinger et al. 1996). Inserting physical barriers that collect wind- and water-borne organic matter is a longstanding restoration tactic to reduce resource loss and maintain an even spread of resources (Ludwig and Tongway 1996). Implementing physical barriers, such as ConMods or straw checkerboards can interrupt connected pathways that remove litter and topsoil (Li et al. 2006,

Rachal et al. 2015) and change nutrient content at the retention point (Jacobs 2015). These types of interventions have been effective at increasing plant and biocrust establishment and germination across a variety of settings (Fick et al. 2016, Peters et al. 2020).

Increasingly, restoration tactics are using background heterogeneity at a variety of scales to augment restoration action and outcomes. One such tactic is the use of restoration islands. Restoration islands are nucleated sites that require high management inputs but serve as areas of high biodiversity and functioning that can radiate out into larger areas or be connected over time (Hulvey et al. 2017). Targeting soil types, textures, and microsites that have desirable soil nutrient and water cycling characteristics in addition to other important abiotic variables such as soil depth, slope, aspect, and solar radiation levels (Breshears et al. 1997) may help practitioners plan where and when to create restoration islands. Soil characteristics were shown to strongly affect revegetation outcomes in a restored sagebrush ecosystem in Wyoming, in the United States, where soil-related variables correctly predicted revegetation performance on 82.4% of plots (Boyd and Davies 2012). Similarly, initiating restoration in depressions or vegetated areas that create physical breaks across a landscape and accumulate resources, such as plant litter or soil moisture through run-on, may increase plant regeneration (Field et al. 2012, Havrilla et al. 2020). These types of approaches may allow practitioners to take advantage of the landscape-scale resource redistribution

and accumulation patterns that occur during dryland degradation (Schlesinger et al. 1990).

Heterogeneity associated with soil characteristics can also influence biocrust community presence and function (Belnap et al. 2003, Pietrasiak et al. 2011). Using background soil heterogeneity to determine where to introduce biocrust propagules may be a tool for successfully reintroducing these important ecosystem engineers (Bowker et al. 2006). Evidence suggests that soil textures, nutrient availabilities, and water-holding capacities interact to influence biocrust species presence and, ultimately, function (Williams et al. 2013, Bowker et al. 2016). For example, some biocrust types can develop more rapidly on fine fraction soils (smaller than 125 micrometers) than on coarse fraction soils (Rozenstein et al. 2014), and some biocrust species may favor specific soil micronutrients (Bowker et al. 2005). Considering these variables during restoration planning may help with the establishment of biocrust communities.

An important consideration when using background heterogeneity to plan restoration action is the influence of increasing aridity on the relationships between soil characteristics and nutrient cycling. The relationships between soil properties, N mineralization, and net primary production can change over aridity gradients. For example, soil texture's influence on N mineralization can diminish under very arid conditions because of small soil C and N pools across soil textures but increase in semiarid conditions and subhumid conditions where soil C and N pools are larger and the differences between N turnover are greater between soil textures (Austin et al. 2004). The ways in which these background biogeochemical processes may change under a future climate is an important consideration when attempting to restore plant and biocrust communities in specific locations.

Manipulating resource pools

Most forms of dryland degradation redistribute resource pools (Yates et al. 2000, Michaelides et al. 2012). In a restoration setting, whether to add nutrients or bind nutrients will depend on the ecological transition that has occurred and the ultimate restoration goal. Efforts to reintroduce nutrients to increase plant productivity in drylands have been met with mixed outcomes. Although adding N in the form of fertilizer can increase primary production (Yahdjian et al. 2011), N-specific additions can increase the dominance of undesired annual species that quickly capitalize on higher nutrient levels (Chen et al. 2017) or decrease plant species diversity (Suding et al. 2005).

The addition of organic C can have multiple applications in dryland restoration. When the restoration goal is to reduce invasive species cover, restoration projects have used C-rich soil amendments (e.g., sawdust, sugar) to reduce nutrients—specifically, N—by immobilizing nutrients within soil microbes, making them less available to exotic plants (Bleier and Jackson 2007, Perry et al. 2010, Morris and Barse, De 2013). However, this approach varies in effectiveness

depending on the form of C, as well as the characteristics of the site and plant traits (Vasquez et al. 2008). In addition, sucrose addition can reduce biocrust lichen and moss cover and biocrust species richness (Chiquoine et al. 2020). When the restoration goal is soil moisture retention, adding organic C amendments, such as mulch, can increase the percentage volumetric water content and soil roughness by increasing microtopography, resulting in higher infiltration and lower rates of soil erosion (Eldridge et al. 2012, Hueso-Gonzalez et al. 2018). However, the degree to which mulch influences soil moisture can depend on the amount of mulch added, with lower mulching rates having the smallest effect (Jordán et al. 2010).

The application of organic amendments to soils, such as sewage sludge or manure, can increase plant productivity, retain soil moisture, increase soil microbial community biomass, and increase soil stability (for a meta-analysis, see Gravuer et al. 2019). However, the effect of the amendment on soil properties can vary widely depending on the amendment origin (for a review, see Hueso-Gonzalez et al. 2018). Like fertilizer additions, organic amendments run the risk of increasing undesirable or invasive plant species through increased nutrient availability (Martínez et al. 1997, Hanke et al. 2015) and may also reduce biocrust survival due to burial (Chiquoine et al. 2016). The possibility for undesirable outcomes with amendment additions, such as an increase in invasive annual plant species, highlights the need for site-specific amendment application strategies. Tailored strategies can take into account amendment type, minimum effective doses, and the possibility of using low-N amendments to reduce invasive species presence but maintain increases in plant productivity (Hueso-Gonzalez et al. 2018, Gravuer et al. 2019). Restoration outcomes may be improved through a greater understanding of the interactions between the timing, form, and amount of amendments to add to a site and their interactions with climate. Site-specific amendment recommendations attained through modeling may represent an effective way to achieve restoration goals, such as increased primary productivity and biodiversity.

Examining less frequently used amendments may be useful for manipulating specific soil properties. For example, gypsum and urea showed promise in increasing plant biomass and restoring desired soil properties such as N availability and pH in a postmining site (Bateman et al. 2019). The latter property can influence plant composition during restoration because of the limited pH tolerance of some plants and can contribute to the binding or release of essential nutrients (Costantini et al. 2016). However, benefits of these amendments decreased with water scarcity. More research is needed to determine the efficacy of these amendments as drylands continue to become more arid under climate change.

There is a clear need to better predict ecological responses to nutrient inputs in drylands on the basis of the mixed outcomes of resource additions in restoration. Beneficial

future research directions include testing for thresholds of N addition or comparisons of N forms (organic N versus NH_4^+ versus NO_3^-) that could improve restoration objectives, such as biodiversity, without increasing undesired species (Bai et al. 2010). Furthermore, addressing relationships between precipitation, temperature, and nutrients in a restoration context will become more important as precipitation regimes change and aridity increases (Grossiord et al. 2018). A meta-analysis of N fertilization studies found that both water and N limit primary production in drylands, but at different times of the year, with the effect of N becoming smaller as annual precipitation decreases (Yahdjian et al. 2011). Building from these types of insights will be useful in dryland areas in which N deposition is increasing, allowing managers to begin to predict how N deposition may change plant composition and soil communities under future climates (Fenn et al. 2003, McHugh et al. 2017) and how this could affect restoration options and outcomes.

Using organismal functional traits

Plant functional traits (e.g., height, specific leaf area, seed mass) can be used to predict plant performance and measure outcomes of restoration actions (Clark et al. 2012). Across ecosystems, incorporating plant functional traits into restoration planning and predictions represents an important and growing component of ecological restoration. For example, in some mesic grasslands, traits such as competitive ability, vegetative growth, and seed bank persistence can be determinants of restoration success (Pywell et al. 2003). Efforts to match plant functional traits to environmental and biogeochemical variables in dryland settings is a potential way to maximize revegetation success (Balazs et al. 2020).

Identifying and understanding how plant functional traits affect biogeochemical cycling is an underexplored area of trait-based research (Bardgett 2017). In a degraded Mediterranean site, species with deep roots, low leaf to total photosynthetic area ratios, and N-fixing bacteria associations had the highest survival rates in nutrient poor soils, which was attributed to the species' abilities to maximize resource uptake (Padilla et al. 2009). In southeastern Australia, the plant species *Themeda australis* suppressed soil NO_3^- concentrations and the presence of exotic annual species by producing low N litter and having high N capture through extensive root systems with year-round activity (Prober and Lunt 2009). Across geographic locations, leaf traits such as growth rate, specific leaf area, and tissue strength can affect decomposition and subsequent soil C and nutrient cycling, whereas root traits such as root length density, root depth, and specific root length can influence C inputs into soils, microbial biomass, and resource retention through reductions in erosion (see review in Bardgett 2017). Furthermore, efforts relating specific plant traits to nutrient cycling in dryland systems can provide practitioners with a greater understanding of how plant traits are going to affect restoration outcomes. Terrestrial biogeochemical and dynamic vegetation models could help these efforts by

providing more links between plant traits and soil processes. However, these biogeochemical responses to plant traits are predicated on seedling survival, which currently represents a bottleneck in dryland restoration (James et al. 2011) and has been attributed to a lack of understand of plant seed traits such as dormancy and germination and their relationship with climate (Kildisheva et al. 2019).

Considering biological traits outside of plant species can also be beneficial. Specific traits within biocrust species can be used to achieve desired biogeochemical outcomes in dryland restoration (Mallen-Cooper and Eldridge 2016, Mallen-Cooper et al. 2020). For example, many species within biocrust communities can fix N (Torres-Cruz et al. 2018) and capture airborne macro- and micronutrients through dust more readily than others (Belnap 2003, Lan et al. 2012), potentially increasing nutrient or C availability within soils (Evans and Ehleringer 1993, Barger et al. 2016). Restored cyanobacterial biocrusts can sequester C in mine waste soils (Muñoz-Rojas et al. 2018) and the composition and stage of development within some biocrust community types can alter albedo and, ultimately, the energy balance for a given area, a trait that influences soil temperature and feedbacks to local climate (Couradeau et al. 2016, Rutherford et al. 2017). Similar to selecting plant species traits, biocrust traits may be a valuable tool to enhance C sequestration, increase nutrient capture and cycling, and create microclimates to promote resource retention during restoration.

The manipulation of subsurface soil organisms and their functional traits to achieve specific restoration outcomes remains complex. Inoculating with arbuscular mycorrhizal fungi or other growth-promoting microorganisms to increase nutrient acquisition is an established practice in dryland restoration (Bashan and de-Bashan 2010, De-Bashan et al. 2012). However, outcomes can vary with the origin of the soil organisms (native or commercial varieties) and the response variables measured (Caravaca et al. 2003, Chaudhary et al. 2019). For example, mycorrhizal addition can improve plant growth but does not always improve soil quality (Alguacil et al. 2003). Important to note is that the fungal or microbial consortia associated with dryland plants are not well categorized, and many root-associated fungi show strong plant preferences, implying that adding arbuscular mycorrhizal fungi generalists to soils may not be a one-size-fits-all approach for plant success (Klironomos 2003). Most mutually beneficial mycorrhizal associations are locally adapted, and inoculation with nonlocalized fungi may affect soil microbial community composition and may hinder restoration goals (Schwartz et al. 2006).

When transplanting vascular plants or growing plants from seed, inoculating with native soil microorganisms may increase plant establishment and growth when compared with controls (Jeffries and Barea 2001, Requena et al. 2001), particularly in a warming and drying climate (Remke et al. 2020). This can be achieved through transplanting native soil into pots or transplant areas, providing a

potentially cost-effective and low-consequence solution for practitioners. There are, however, many outstanding biogeochemical questions related to the relationship between vascular plants, associated soil microbes, and their functions, including questions about when microbes immobilize nutrients (Gallardo and Schlesinger 1995), when microbes move from mutualists to parasites within plants (Johnson et al. 1997), and which conditions best prime microbial activity (Blagodatskaya and Kuzyakov 2008). Answering these questions in a restoration context could bolster our ability to restore with advantageous soil organisms, in correct proportions, and at opportune times.

Relating functional traits across organisms may be important to achieving desired restoration outcomes. For example, plant traits that result in low-quality litter, such as low specific leaf area, can increase the growth of fungi relative to bacteria, slowing rates of nutrient cycling and increasing nutrient retention (Bardgett 2017), which is a common goal in dryland restoration. Restoration actions that seek to restore both biocrust and plants may want to account for the complex interactions between plant traits and biocrust traits. Biocrusts can be either a facilitator or competitor of plant species, depending on plant traits and biocrust community types (Zhang et al. 2016). For example, plants without N-fixing symbionts exhibited a more positive response to biocrusts presence than plants with N-fixing symbionts (Havrilla et al. 2019). Considering how traits within plants, biocrusts, and soil microorganisms interact to influence biogeochemical cycling and specific restoration goals is an underexplored and potentially important area of research.

Incorporating biogeochemistry into dryland restoration

In the present synthesis, we examined restoration action that addresses biogeochemistry in four primary ways: timing restoration around resource cycling and uptake, connecting heterogeneous landscapes, manipulating resource pools, and using organismal functional traits to a restoration advantage. Our overall conclusion is that specific restoration actions within each category show strong potential for achieving restoration goals, including planning restoration around periods of resource availability and cycling, using restoration islands and connectivity modifiers, adding fertilizer or organic amendments, and using trait-based restoration approaches. Another key insight is that each of these actions should be implemented in the context of resource availability at specific locations and should take into consideration resource changes through time. Because resource availability is often asynchronous in drylands, synchronizing resource availability to benefit plant and biocrust communities may be an important restoration action. Although it is complex, this type of multiresource planning may help increase resource overlap, reduce the likelihood of limitations, and aid in the establishment of plant and biocrust species.

Currently, multiple frameworks exist to help plan restoration actions and predict restoration outcomes. These

include state and transition models, as well as quantitative models based on processes and mechanisms driving restoration outcomes (Reynolds et al. 2007b, James et al. 2013, Okin et al. 2015, James and Carrick 2016, Svejcar and Kildisheva 2017). Biogeochemical insights, specifically ones that aid in synchronizing multiple resources through time and across locations, may help to augment these frameworks in useful ways. For example, insights into temporal considerations and colimitation may be effectively incorporated into frameworks that address propagule dispersal and generation, plant establishment, and biocrust restoration. The temporal and spatial components of nutrient and C availability that influence plant demographic transitions can be included alongside more traditionally considered drivers, such as water and propagule availability, in restoration action. As another example, state and transition models can further incorporate soil nutrient dynamics into ecological site descriptions (Duniway et al. 2016), given the increasing evidence that drylands are often limited by nutrients. Practices that time restoration action around precipitation events, such as El Niño events in the Southwest United States (Holmgren and Scheffer 2001) can also consider manipulating additional limiting resources while planning around soil moisture availability. Adaptive and anticipatory management and concepts within “pre-restoration,” or planning restoration with future climate in mind, could incorporate biogeochemical concepts, such as colimitations or specific plant traits, when planning for increase aridity and precipitation uncertainty (Butterfield et al. 2017, Bradford et al. 2018, Shriver et al. 2018).

Research directions for incorporating biogeochemistry into dryland restoration

Despite the benefits of incorporating biogeochemistry into restoration frameworks and actions, there are clear gaps in our understanding of dryland biogeochemistry that need to be addressed. These important research gaps include gaining more comprehensive understandings of colimitations over space and across time, understanding interactions between limiting resources and increasing aridity, predicting plant and soil community outcomes of resource additions, and determining organismal functional traits that affect nutrient availability. Although most empirical research in this synthesis focused on manipulating resource pools and organismal traits, fewer experiments examined preexisting and manipulable temporal and spatial components into research questions, such as the seasonality of restoration or using naturally occurring pockets of high resources to begin restoration action. There is a need for more experiments addressing these questions, because the limited data suggests planning around areas and times of increased resource and soil moisture availability may be a determining factor in dryland restoration outcomes. Hypotheses such as the transient maximum hypothesis support this assertion by demonstrating that biotic responses—or a lack thereof—can often be explained by shifts in multiple limiting resources over time

and across space (Seastedt and Knapp 1993, Blair 1997). Future research questions that integrate these concepts with iterative hypothesis testing and report “negative” restoration outcomes could go far in advancing our understanding of biogeochemistry in a restoration setting. In addition, concerted efforts by ecosystem ecologists to incorporate restoration components into experiments would advance understandings in both disciplines.

Many outstanding questions surround how dryland ecosystems will respond to climate change. Climate driven changes in ecosystem structure such as vegetation composition (Allen et al. 2010), biocrust cover (Ferrenberg et al. 2015), and insect and mammal distributions (Ye et al. 2018, Eldridge et al. 2020), will result in functional changes to ecosystem, such as changes in resource cycling and distribution (de Graaff et al. 2014). The novel functional ecosystems that emerge will become the baseline for predicting and gauging restoration outcomes, because concepts such as ecological reference states lose meaning under new climate regimes (Harris et al. 2006). To inform restoration action and predict restoration success, it will be essential to understand how ecosystem processes and functions affected by climate change will alter biogeochemical cycling. Specifically, long-term manipulative experiments that examine cover change and functional responses are necessary to understanding, managing, and restoring this rapidly changing biome (de Graaff et al. 2014).

Conclusions

There is an increasing need to restore productivity and ecosystem functions in global drylands. Integrating biogeochemistry into dryland restoration could be a key to achieving a variety of targeted restoration outcomes. The need to restore drylands will only grow as global change accelerates (Ye et al. 2019). Dryland regions are expected to expand over the next century (Huang et al. 2015) and face the continued pressures of climate change, accelerated land use, and species invasions (Hoover et al. 2019). The limited capacity to effectively restore dryland regions implies the need to explore new approaches to returning desired function and productivity to these socially, economically, and ecologically important regions (Reynolds et al. 2007b). Finally, the difficulties of restoring drylands and the widespread changes in basic biogeochemical structure that accompanies degradation highlights the need for sustainable use and conservation within dryland regions. These types of efforts, in addition to an increased understanding of the processes and functions occurring within intact and degraded drylands, are necessary to reduce degradation and negate the need for perpetual restoration of these valuable ecosystems.

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