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Restoring biogeochemical properties in drylands and exploring functional roles of biological soil crust

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RESTORING BIOGEOCHEMICAL PROPERTIES IN DRYLANDS AND EXPLORING FUNCTIONAL ROLES OF BIOLOGICAL SOIL CRUST

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Dedication

This dissertation is dedicated to all my incredible mentors, my husband Zach, and semi-arid ecosystems

RESTORING BIOGEOCHEMICAL PROPERTIES IN DRYLANDS AND EXPLORING FUNCTIONAL ROLES OF BIOLOGICAL SOIL CRUST

by

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Abstract

Degradation in dryland regions is a persistent and accelerating problem. Though the mechanisms that initiate and maintain dryland degradation have been well studied, restoring productivity and function to degraded dryland ecosystems remains difficult. Here, I present three chapters that address gaps in our understanding of dryland functions and our ability to restore them. I begin by examining how dryland restoration research has addressed altered biogeochemical cycling in drylands and how to expand current understandings of dryland biogeochemistry into restoration. I then present two chapters that explore mechanistic and quantitative understandings of the contribution of biocrusts to soil nutrient cycling both now and under altered precipitation regimes. Taken together, this dissertation contributes to highlighting the overlap between biogeochemical research in drylands and efforts to restore altered biogeochemical landscapes within degraded regions.

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Chapter 1: Introduction

The ecological significance of drylands, defined as hyper-arid, arid, semi-arid, and subhumid regions, has long been overlooked (Hoover et al. 2019). Ecological processes within drylands influence inter- and intra-annual global net primary production (Ahlstrom et al., 2015; Poulter et al., 2014), global nitrogen cycling and NO emissions (Porada et al. 2014; Weber et al. 2015), and energy balance at small (Rutherford et al. 2017) and large scales (Zhao et al. 2018). Yet our ability to understand these cycles is limited by a lack of mechanistic and quantitative understandings of ecological processes in drylands and their relationships with precipitation (Collins et al., 2014). Especially lacking are mechanistic understanding of nutrient cycling within soil surface communities known as biological soil crusts (biocrusts), which can be a dominant form of groundcover in many dryland types (Belnap and Gardner 1993). Basic questions surrounding nutrient pool size, transfer, and cycling within and below the top few centimeters of soil remain unanswered (Ferrenberg et al., 2017; Rudgers et al., 2018; Throop and Belnap, 2019).

These gaps in understanding are made apparent by our inability to restore altered biogeochemical cycles in degraded dryland regions (Copeland et al., 2017; Schlesinger et al., 1990). Despite global initiatives to reverse dryland degradation (Cowie et al. 2018), more than 20% of dryland areas are degraded (Reynolds et al. 2007b). While water limitation is undoubtably a main culprit in slow recovery rates within drylands (Noy-Meir 1973), the altered biogeochemical cycles accompanying degradation may also play a role in limiting restoration success (Austin 2011). Landscape transitions and subsequent degradation can redistribute nutrient pools spatially (Schlesinger et al. 1996), alter the form and quantity of litter inputs (Throop and Archer 2007), change connectivity pathways over which resources move (Okin et

al. 2015), alter albedo (Rutherford et al. 2017), and redistribute functional species (Bowker, 2007), all of which need to be addressed during dryland restoration. Until there is greater insight into the mechanisms that maintain cycles, fluxes, and functions in drylands and a better incorporation of those insights into restoration action, our ability to restore desired biogeochemical cycling in degraded regions will likely remain limited (Copeland et al., 2017; Winkler et al., 2018; Young et al., 2019).

Here, I present three chapters that address the highly altered biogeochemical landscapes within drylands. I predominantly focus on biocrust and how these diminutive communities can have large impacts on soil fertility (Ferrenberg et al. 2018). Biocrusts can influence surface soil fertility through their roles as soil stabilizers (Chaudhary et al. 2009), CO_2 fixers (Darrouzet-Nardi et al. 2015; Sancho et al. 2016), and contributors of nitrogen (N) via N_2 fixation (Barger et al. 2016; Torres-Cruz et al. 2018). Biocrusts can also regulate soil microbial communities through the creation of a 'cyanosphere' which facilitates nutrient and C exchange between phototrophs and heterotrophs (Baran et al. 2015; Couradeau et al. 2019a; Nelson et al. 2021), in addition to contributing to the movement of nutrients through the soil, possibility through microbial connections (Green et al. 2008; Aanderud et al. 2017; Carvajal and Coe 2021), and by providing nutrients to plants, as shown through isotopic labeling (Mayland and McIntosh 1966; Stewart 1967). Contributions from biocrust have the capacity to be particularly significant in ecosystems notable for their low soil organic matter reservoirs, high oxidative potential, and overall low levels of soil fertility (Collins et al. 2014).

Chapter 1 explores how dryland restoration practices have incorporated biogeochemistry. Historically, there has been very little overlap between the fields of biogeochemistry and restoration (e.g. Milton et al. 1994; James et al. 2013; James & Carrick 2016; Whitford 2001).

However, due to the nature of degradation in drylands, which is strongly tied to changes in nutrient availability and feedbacks therein, there may be great utility in uniting these two fields of research. Further, as the negative impacts of global change are increasingly felt by society, there is an increasing need to restore ecologic functions related to biogeochemical cycling in ecosystems around the globe (Cowie et al. 2018; Ye et al. 2019). In this chapter, we review areas where restoration actions have addressed altered biogeochemical processes in drylands. We suggest additional ways that insights into altered carbon, nitrogen, and phosphorus cycles and fluxes can be incorporated into restoration action.

Chapter 2 focuses on biocrust within a semi-arid desert on the Colorado Plateau. Biocrusts occurring on the Colorado Plateau have been widely characterized (e.g., Anderson, Harper, & Holmgren, 1982) making this location ideal for further inquiry into biocrust ecology. The different types of biocrusts that co-occur here, namely lightly-pigmented cyanobacterial crusts, darkly-pigmented cyanobacterial crusts, and moss dominated crust, are considered three of the dominant biocrust types within the region and represent a loosely-characterized developmental trajectory (Belnap 2003a). This chapter focuses on the contributions of these three different biocrust types to sub-surface soil fertility and microbial activity and quantifies biocrust contributions both at the soil surface and below the soil. Importantly, climate change and accelerated land-use is converting biocrust type from darkly pigmented and moss crust types to lightly pigmented crust types (Reed et al. 2012; Ferrenberg et al. 2015). This conversion highlights the need to quantify the contributions of each crust type to nutrient dynamics in this system so we can predict how those contributions might change with shifting cover types.

Chapter 3 asks how precipitation frequency and amount controls ecosystem processes in drylands. While precipitation is a dominant factor in ecological functions and processes (Collins

et al. 2014), our ability to understand or predict how variation in precipitation amount and frequency influence things such as biomass accumulation and nutrient cycling is limited (Schwinning et al. 2004). These insights are especially important for managing and restoring biocrusts, which can experience mortality with changes to precipitation patterns (Reed et al. 2012; Maestre et al. 2013; Ferrenberg et al. 2015). This chapter explores the response of two common biocrust types to a gradient in frequency and magnitude of precipitation in a mesocosm experiment. We explore both the ways in which biocrust organisms respond to variations in precipitation and also the biogeochemical consequences for the soil beneath the biocrust. These findings have direct implications for our ability to predict biotic response to the increased precipitation variability expected under climate change (Schwinning et al. 2008; Maestre et al. 2012).

Taken together, this dissertation explores the biogeochemical mechanisms behind dryland functions, such as biocrust C uptake and nutrient cycling, and asks how we can use the knowledge of those mechanisms to restore degraded regions. The research presented here can aid in the efforts underway by the United Nations during this decade on ecological restoration (2021-2030) and help provide more mechanistic understandings for how to restore this important biome.

Chapter 2: Incorporating biogeochemistry into dryland restoration

Restoring degraded drylands is a critical challenge for the 21st century. Drylands, defined by an aridity index below 0.65 and comprising hyper-arid, arid, semi-arid, and sub-humid regions (Middleton and Thomas 1992), cover 45% of the earth's land surface (Pravalie 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 (Safriel et al. 2005; Reynolds et al. 2007b; Bestelmeyer et al. 2015), which we define as a persistent reduction in ecological productivity, biodiversity, and ecosystem services, such soil conservation, water regulation, and forage (Safriel et al. 2005) due to land use practices and climate change. Though the problem of dryland degradation is widely recognized (United Nations Environmental Management Group 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 is 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 occurs, 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 (Faist et al. 2019; Fick et al. 2020; Havrilla et al. 2020).

Here, 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; thus, 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 like plant growth (Rietkerk and van de Koppel 1997), while basic stoichiometric requirements can limit the distribution and abundance of producers, consumers, and decomposers (Güsewell 2004; Schmidt et al. 2016; Leroux et al. 2017). While 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 2.1). For example, while 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 (Hardegree et al. 2012) and nutrient availability for target organisms may aid restoration outcomes such as plant or biocrust germination and establishment (Figure 2.2). *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).

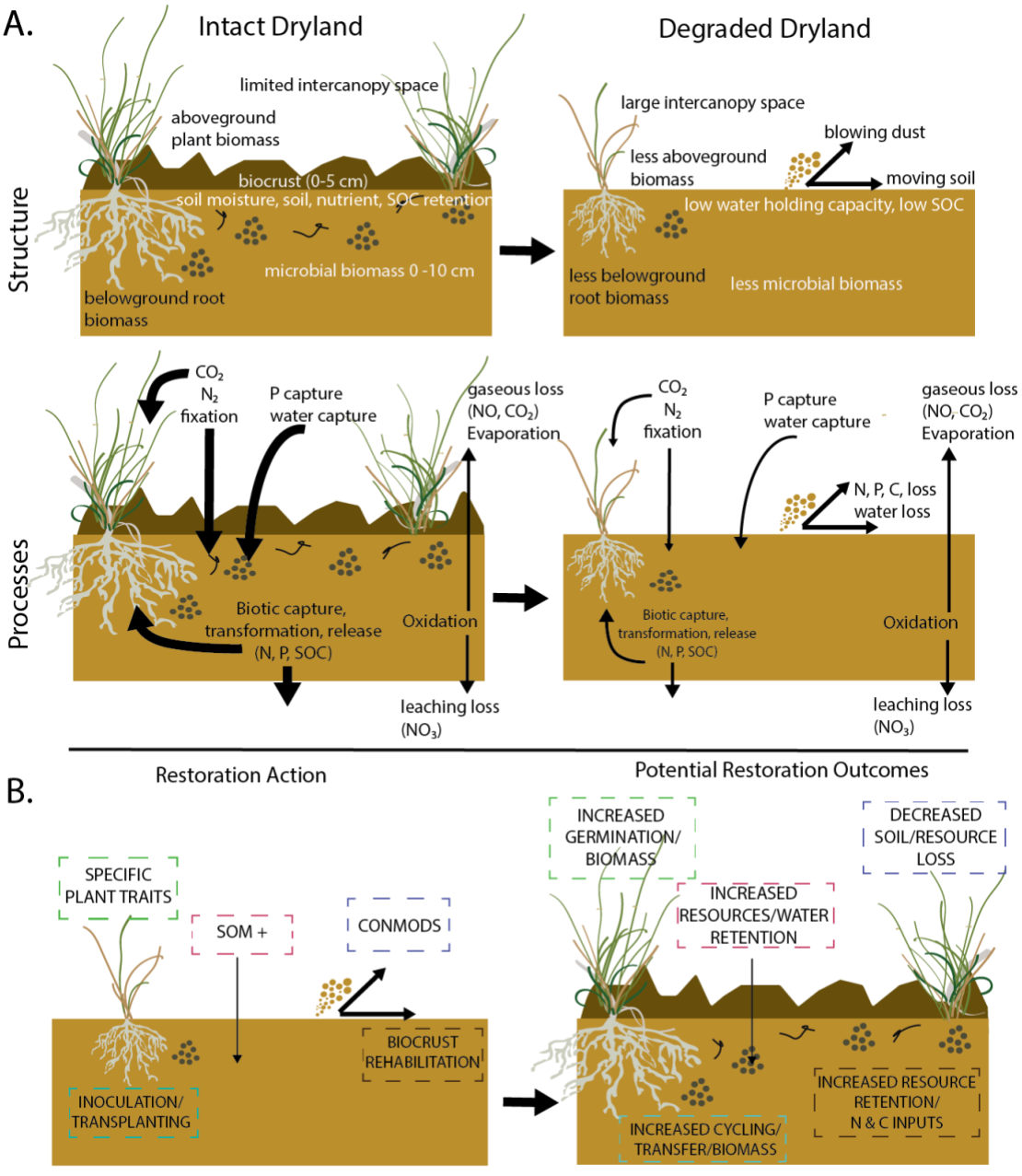

A.
Intact Dryland
Degraded Dryland
Structure
limited intercanopy space
aboveground plant biomass
biocrust (0-5 cm)
soil moisture, soil, nutrient, SOC retention
microbial biomass 0 -10 cm
belowground root biomass
large intercanopy space
blowing dust
less aboveground biomass
moving soil
low water holding capacity, low SOC
less belowground root biomass
less microbial biomass
Processes
CO2 N2 fixation
P capture water capture
gaseous loss (NO, CO2) Evaporation
Biotic capture, transformation, release (N, P, SOC)
Oxidation
leaching loss (NO3)
N, P, C, loss water loss
B.
Restoration Action
Potential Restoration Outcomes
SPECIFIC PLANT TRAITS
SOM +
CONMODS
BIOCRUST REHABILITATION
INOCULATION/ TRANSPLANTING
INCREASED GERMINATION/ BIOMASS
DECREASED SOIL/RESOURCE LOSS
INCREASED RESOURCES/WATER RETENTION
INCREASED RESOURCE RETENTION/ N & C INPUTS
INCREASED CYCLING/ TRANSFER/BIOMASS

Figure 2.1 A diagram depicting the general biogeochemical properties within some dryland types. In A, the left panel is an example of a semi-arid 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, C, and water retention, loss, and capture). 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. In part B, the left panel is an example of restoration actions that can be applied to degraded drylands to jump-start 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 and affect biogeochemical processes, transplanting vascular plants and inoculating with soil microorganisms, adding biocrust propagules back onto the soil surface, and changing resource connectivity. 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 here.

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. Here 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: (1) timing restoration around resource cycling and uptake, (2) connecting heterogeneous landscapes, (3) manipulating resource pools, and (4) 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.

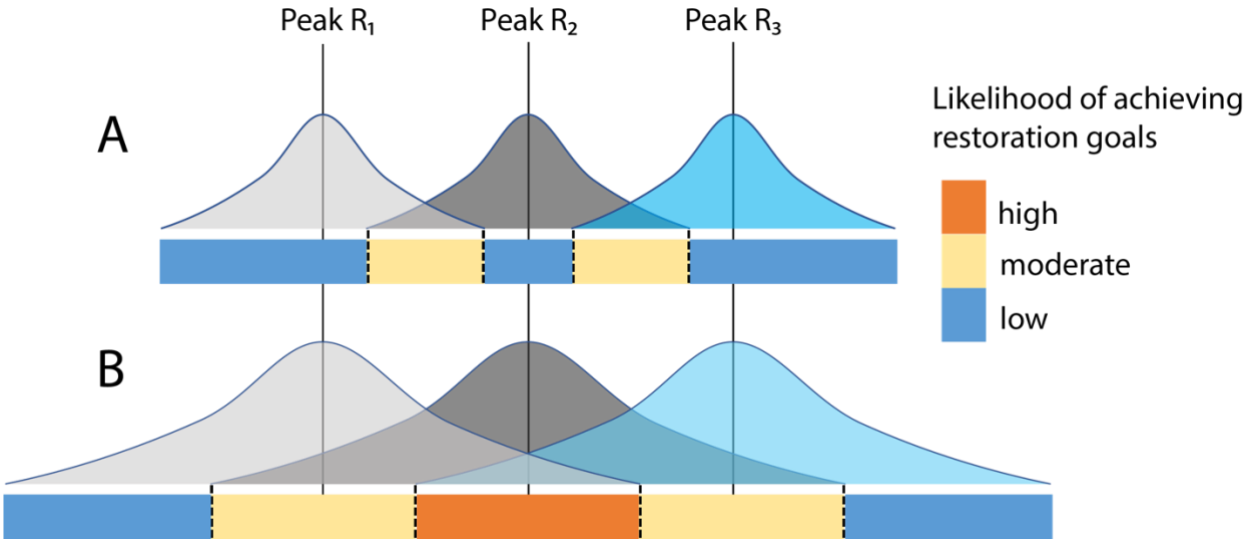


Figure 2.2 Drylands can be limited by multiple resources whose availability is heterogenous through space and time. (A) In areas where limiting resources, such as water, nutrients, or organic C (shown as R_1, R_2, and R_3), have limited overlap, achieving restoration goals such as increased productivity and ecosystem functioning may be more difficult. (B) When restoration actions increase the duration and/or magnitude of multiple limiting resources, the likelihood of achieving restoration goals is greater. For example, restoration actions that add resources like nutrients and mulch can increase resource retention and create more overlap in resource availability when soil moisture becomes available. Additionally, restoration actions that collect resources, such as ConMods, can maintain resources, such as soil nutrients, creating more overlap during periods of prolonged soil moisture.

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 U.S. Southwest or projected times of increased or reliable soil moisture in other regions (Holmgren and Scheffer 2001; Hardegree 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. 2019b; 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 due to a temporal lag in nutrient cycling following precipitation pulses and/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 US, nutrient limitation for exotic cheatgrass (*Bromus tectorum* L.) occurs during the late winter and early spring, while 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 $CaCl_2$ 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. Further, 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 towards specific plant types, however, these patterns may not hold across systems (James et al. 2008). While we know N can increase plant growth in drylands (Yahdjian et al. 2011), further research determining if, how, and when different forms of N, or other 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 while 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, both at large and small scales, is a defining characteristic of drylands (Bestelmeyer et al. 2006). Within drylands, plant canopies are often non-continuous and soil properties vary widely from microsites to landscapes (Buxbaum and Vanderbilt 2007). With this heterogeneity comes 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 homogenous landscapes where 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. 2015b) 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, U.S., 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 2003a; 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 (< 125µm) than on coarse fraction soils (Rozenstein et al. 2014) and some biocrust species may favor specific soil micronutrients (Bowker et al. 2000).

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 due to small soil C and N pools across soil textures but increase in semiarid conditions and sub-humid 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. While 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, thus 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). Additionally, 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 percent 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 (see meta-analysis by Gravuer et al. 2019). However, the effect of the amendment on soil properties can vary widely depending on the amendment origin (see review in 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 like N availability and pH in a post-mining site (Bateman et al. 2019). The latter property can influence plant composition during restoration due to 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 based on 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 vs. NH_4^+ vs. NO_3^-) that could improve restoration objectives, like biodiversity, without increasing undesired species (Bai et al. 2010). Further, 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 where 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 (height, specific leaf area, seed mass, etc.) 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 like 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, while 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). Further 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 et al. 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 sub-surface soil organisms and their functional traits to achieve specific restoration outcomes remains complex. Inoculating with arbuscular mycorrhizal fungi or other growth-promoting micro-organisms 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/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 non-localized 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 to 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 around 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

This synthesis examined restoration action that addresses biogeochemistry in four primary ways: (1) timing restoration around resource cycling and uptake, (2) connecting heterogeneous landscapes, (3) manipulating resource pools, and (4) 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. While complex, this type of multi-resource 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 2016a; 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 co-limitation 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 US (Holmgren and Scheffer 2001) can also consider manipulating additional limiting resources while planning around soil moisture availability. Adaptive and anticipatory management and concepts within "prestoration", or planning restoration with future climate in mind, could incorporate biogeochemical concepts, such as co-limitations or specific plant traits, when planning for increase aridity and precipitation uncertainty (Copeland 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: (1) gaining more comprehensive understandings of co-limitations over space and across time; (2) understanding interactions between limiting resources and increasing aridity; (3) predicting plant and soil community outcomes of resource additions, and (4) determining organismal functional traits that affect nutrient availability. While most empirical research in this synthesis focused on manipulating resource pools and organismal traits, fewer experiments examined pre-existing 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, since 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 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. Additionally, 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, as concepts such as ecological reference states loose 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 impacted 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).

CONCLUSION

There is an increasing need to restore productivity and ecosystem functions in global drylands. Further 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. 2019b). 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. 2007a). 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.

Chapter 3: Vertical movement of soluble carbon and nutrients from biocrusts to subsurface mineral soils

INTRODUCTION

Within drylands, productivity and function can be co-limited by water, nutrients, and organic carbon (C) (Austin 2011). Understanding the pathways through which nutrients and organic C enter and are retained within dryland soils is therefore essential for understanding ecosystem processes in this expansive biome (Hartley et al. 2007; Rudgers et al. 2018). Yet, we have a limited understanding of how common soil surface communities in drylands, known as biological soil crusts (biocrusts), are biogeochemically connected with the mineral soil below (deeper than 2 cm) (Barger et al. 2016). Biocrusts contain varying levels of lichens, mosses, cyanobacteria, fungi, algae and other macro- and micro- organisms often occurring in successional stages (Chamizo et al. 2012). These biocrusts can influence surface soil fertility through their roles as soil stabilizers (Chaudhary et al. 2009), CO_2-fixers (Darrouzet-Nardi et al. 2015; Sancho et al. 2016), contributors of nitrogen (N) via N_2 fixation (Barger et al. 2016; Torres-Cruz et al. 2018), and regulators of soil microbial communities (Baran et al. 2015), in addition to contributing to plant nutrients, as shown through isotopic labeling (Mayland and McIntosh 1966; Stewart 1967). Contributions from biocrust have the capacity to be particularly significant in ecosystems notable for their low soil organic matter reservoirs and overall low levels of soil fertility (Collins et al. 2014).

One mechanism through which nutrients and C move from biocrusts into the mineral soil is downward transport during and following pulsed precipitation events (Barger et al. 2016). Water leached through the biocrust layer can carry with it ammonium (NH_4^+) (Maier et al. 2014; Porada et al. 2014), nitrate (NO_3^-) (Barr 1999), biogenic phosphorus (P) (Johnson et al. 2005),

and a wide variety of metabolites (Baran et al. 2015; Swenson et al. 2018). However, studies of the chemical makeup and the fate of biocrust-sourced dissolved compounds are rare, and contradictions exist within the literature as to biocrusts' contribution to subsurface soil nutrients and organic matter. In some cases, biocrusts have been shown to increase the levels of subsurface nutrients and organic C, such as inorganic N (Barger et al. 2016; Ferrenberg et al. 2018), while in others, subsurface nutrients and organic C were similar beneath biocrusts types and bare ground (Guo et al. 2008; Delgado-Baquerizo et al. 2013; Moreira-Grez et al. 2019). Further, biocrust communities are comprised of different morphological groups and species, which can differ across desert and soil types (Colesie et al. 2016) and along successional gradients within a given area (Housman et al. 2006), with consequences for the amounts and forms of compounds leached into subsurface soil (Johnson et al. 2005; Tucker et al. 2020).

Biocrust-derived leachate may also influence subsurface microbial communities, with implications for nutrient retention and gaseous release from mineral soil layers, as seen with leaf litter in other ecosystems (e.g., Cleveland et al. 2010). Exudates from biocrust can structure soil microbial communities and soil food webs adjacent to biocrusts (Baran et al. 2015). However, the extent to which leachate influences deeper soil microbial communities is unclear. Microbial operational taxonomic units (OTUs) below biocrusts can be similar across different biocrust and soil types (Steven et al. 2013a; Moreira-Grez et al. 2019), with the notable exception of moss crust, which can have higher microbial biomass and community diversity in the mineral soil below the moss compared to earlier successional, cyanobacteria-dominated biocrust stages (Delgado-Baquerizo et al. 2015; Bao et al. 2019) possibly due to the large amounts of organic C released from moss crusts, which can structure microbial communities (Baran et al. 2015). The variability in resource inputs from different biocrust types and differences in the microbial

communities below biocrust types underscore the likelihood of varying levels of connectivity between the biocrust layer and the mineral soil below. Connectivity between the biocrust and the microbial communities and functions in the mineral soil layer has implications for microbial nutrient turnover, resource storage, and CO_2 respiration in both the short and long term (Cleveland et al. 2010).

Here, we present a novel experimental design that sought to assess biocrusts' connectivity with mineral soil using multiple successional stages of biocrust. Specifically, we examined lightly pigmented, darkly pigmented, and moss dominated biocrust that represent a generalized gradient of succession in our study system from least to most developed (Belnap et al. 2003). Lightly pigmented cyanobacterial crusts are early colonizers and are generally dominated by the cyanobacterial *Microcoleus vaginatus* (Belnap 1993). Darkly pigmented crusts, generally dominated *Microcoleus vaginatus* and *Scytonema* spp., (Couradeau et al. 2016) and moss dominated crusts are considered more developed, later successional forms of biocrust. Darkly pigmented cyanobacteria crusts generally have high rates of N fixation and microbial biomass while darkly pigmented and moss crusts have high rates of C fixation when compared to lightly pigmented crusts (Housman et al. 2006). For this experiment, we located an area with a relatively homogenous sandy soil type and assessed the differences in connectivity between the three biocrust successional stages and the mineral soil below. We addressed the following questions: (1) What compounds are leached from the biocrust layer during wet-up events and do the compounds differ among biocrust types? and (2) Do compounds leached from the different biocrust successional stages regulate short-term microbial activity in sub-surface soils? In addressing these two questions, this experiment lends insight into the role of dissolved resources moving from biocrusts into the mineral soil and the short-term consequences of these inputs for

heterotrophic respiration, with implications for a larger understanding of nutrient and C cycling in dryland soils.

2. MATERIAL AND METHODS

This study consisted of three complementary components that each assessed soil or leachate associated with different biocrust successional states on the Colorado Plateau, USA. These three components consisted of a field assessment of nutrient and C content in *in-situ* biocrust and the below-biocrust mineral soil, a laboratory assessment of potential leachate chemistry, and a soil incubation with biocrust leachate. Biocrust types consisted of an early successional, lightly pigmented cyanobacterial biocrust (i.e., likely dominated by *Microcoleus vaginatus,* (Garcia-Pichel et al. 2013)**,** a mid-successional darkly pigmented cyanobacterial biocrust (likely dominated by *Microcoleus vaginatus and Scytonema* spp., (Couradeau et al. 2016), and a mid to late successional moss dominated biocrust (dominated by *Syntrichia caninervis*). Biocrust samples were collected in January 2017 in a 25 m^2 area of semiarid desert outside of Moab, UT (38°41' 02.31" N, 109°43'11.60" W, 1,529 m above sea level). The soil type was visually homogenous, with the soils characterized as a well-drained, fine sandy loam on average 86 cm deep in the Begay-Sazi-Rizo complex. Soils in the region are generally alkaline, pH ranged from 7.26-7.84 in the biocrust layer and 7.67-8 in the mineral subsoil. The ecological site was a Four-Wing Saltbush, semidesert. Parent material was alluvium and eolian deposits derived from sandstone. The three different successional stages were co-occurring within the 25 m^2 area. The co-occurrence of different biocrust successional stages was likely due to past physical disturbance, potentially the historic presence of cattle, which disturb biocrusts in discrete patches and can leave other patches intact. However, the site was visually undisturbed during biocrust collection.

2.1 Assessment of biocrust and mineral soil in the field

To determine the *in-situ* extractable C and nutrient concentrations both within and below the different biocrust types, we collected biocrust samples using a 10 x10 cm metal square core down to 2 cm depth. A flat metal sheet was slid under the square core to remove the biocrust (n = 10 for each crust type). On the exposed soil in the 10 x 10 cm area, we took three 2.54 cm diameter cores of soil to a depth of 8 cm (2-10 cm below crust surface), which were combined into one sample (n = 10 for each crust type). We sieved the soil through a 4 mm sieve, removed roots and visible organic matter, and homogenized before subsampling for extractions.

To determine total C and N concentrations, we dried a subset of each sample at 60 ℃, ground the samples, and measured for total C and N on an elemental analyzer (Elementar Vario Micro Cube, Elementar Inc., Langenelsbold, Germany). The samples represent both the inorganic and organic C pools, as carbonates were not removed. Because the samples were from relatively uniform soil, the carbonate would likely be similar across samples, thus comparisons between total C most likely represent changes in total organic C. To determine the pigment concentrations of lightly and darkly pigmented biocrust samples, we extracted chlorophyll *a* (Chl_a) and scytonemin (Scy) with 90 % acetone for 12 hours in the dark at 4 ºC after being finely ground (Castle et al. 2011). The supernatant was decanted, and pigment concentrations were measured spectrophotometrically (GENESYS 10S UV-VIS, Thermo Scientific, Waltham, MA) at 665 nm and 394 nm for Chl_a and Scy, respectively. The equation to convert the A_{665} value to [Chl_a] was taken from Ritchie 2008 and conversion of the A_{394} values to [Scy] was performed as in Garcia-Pichel and Castenholz 1991. We measured organic matter concentrations of the lightly pigmented, darkly pigmented, and moss biocrusts by loss-on-ignition of an oven-dried (105 ℃)

sample in a muffle furnace at 550 °C for 4 hrs (Davies 1974); (ThermoScientific Thermolyne, Waltham, MA, USA).

We extracted inorganic N pools, NH_4^+ and NO_3^-, using 2 M KCl and fresh soil. The soil slurry was shaken for 1 hour then allowed to settle overnight (Robertson et al. 1999). Inorganic N concentrations (NH_4^+ and NO_3^-) were quantified colorimetrically using the indophenol blue method for NH_4^+ and using a Cd-column reduction followed by the Greiss-Ilosvay method for NO_3^- on a Smartchem 200 Discrete Autoanalyzer (Unity Scientific, Milford, MA). Soil PO_4^{3-} was extracted using Olsen's method, with a 0.5 M $NaHCO_3$ solution and a shaking time of 16 hrs (Olsen 1954). Soil extractable PO_4^{3-} and microbial PO_4^{3-} concentrations were quantified using a modified ascorbic acid molybdate analysis (Kuo 1996) on a Smartchem 200 Discrete Autoanalyzer (Unity Scientific, Milford, MA). Limit of quantification was 0.02 mg PO_4^{3-}-P/l for all P measurements. Microbial C, N, and P concentrations were estimated with a chloroform cell lysis method by adding 1 ml of amylene-stabilized $CHCl_3$ to soil in a 125 ml flask that was stoppered with neoprene and allowed to sit in the dark for 16 hr before being ventilated and extracted with 0.5 M K_2SO_4 (for microbial biomass C and N, (Brookes et al. 1985; Beck et al. 1997) or 0.5 M $NaHCO_3$ (for microbial biomass PO_4^{3-}) and shaken for 1 hr (Weintraub et al. 2007). Microbial biomass C, N, and P were calculated as the amount extracted from nonfumigated soil subtracted from the amount extracted from fumigated soil. No microbial biomass correction factors were applied (Weintraub et al. 2007). All extracts were filtered through Whatman #1 filter paper (GE Healthcare, Chicago, IL). Extractable organic C and total dissolved N were extracted with 0.5 M K_2SO_4, shaken for 1 hr (Weintraub et al. 2007). Extractable organic C, total dissolved N, and microbial biomass C and N were analyzed on a Shimadzu TOC-V_{CPN} with the TNM-1 attachment (Shimadzu Corporation, Kyoto, Japan).

Determining the concentrations of the biomass, nutrient, and C concentrations both within and below biocrusts provides a point-in-time assessment of biologically available pools in the field.

2.2. Assessment of leachate chemistry

On the same day and at the same site as the collections described above, we collected intact cores of each biocrust successional state (n = 15 for each stage), 2 cm deep and 4.6 cm in diameter. We returned the cores to the laboratory and used them to determine the nutrient concentrations of potential leachate from different biocrust successional states over a four-week period. Once in the lab, we used a razor blade to carefully scrape the subsoil from the biocrust. The subsoil could be differentiated from the biocrust layer by the lack of cohesion between soil particles and the lack of visible cyanobacterial filaments or rhizomes. Because the crust layer varies in thickness, specifically between successional stages, the biocrust thickness was different for each sample and ranged from 6 mm – 12 mm for lightly and darkly pigment cyanobacterial crusts and 10 mm – 15 mm for moss. We seated the cores in plastic cylinders that were open on the top and had mesh screen on the bottom. Below the mesh screen was a second cylinder with a layer of marbles resting on top of a second layer of mesh screen. The marbles were to ensure sediment did not pool on the bottom of the mesh, to control the flow of leachate during extractions, and to improve connectivity for liquid movement between the mesh layers (Figure 3.1).

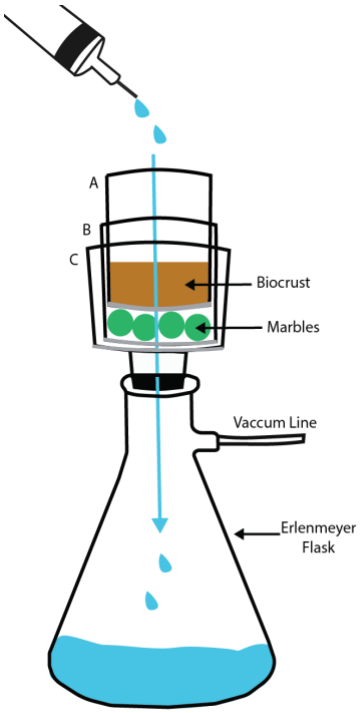


Figure 3.1. The collection system used to collect leachate from biocrusts. Biocrusts were placed in a plastic cylinder (A), that was open on the top with a 1.18 mm mesh screen (shown in grey) at the bottom. Cylinder A was placed within a second plastic cylinder (B) open on the top and with a layer of marbles resting on a mesh screen (represented in grey). Marbles were used to ensure sediment did not pool over the filter. Cylinders A and B were placed in a Buchner funnel (C) with a 55 mm Whatman #1 filter on the bottom. Watering treatments were administered across the biocrust using a syringe. Water moved through cylinders A and B and through the funnel and filter into an Erlenmeyer flask. Water was pulled through the system using vacuum filtration and immediately collected and frozen until analysis.

Once a week for four weeks, we added 30 ml of deionized water to lightly pigmented and darkly pigmented crusts, 35 ml of deionized water to moss crusts, and 25 ml to blank controls that did not have any biocrust but maintained all other aspects of the infrastructure. These

volumes corresponded to 15-21 mm of rainfall and were chosen to ensure enough liquid moved through the sample and was available for C and nutrient analyses. Differences in watering amount were accounted for in the final µg/ml calculations. After allowing the liquid to saturate the biocrust and move downward with gravity for 10 minutes, we placed the biocrust cores onto a vacuum filtration system to pull remaining liquid through the biocrust system and we collected the liquid in vials below the samples. We analyzed the collected liquid leachate for NH_4^+, NO_3^-, PO_4^{3-}, extractable organic C and total dissolved N as described above. The concentrations in the leachate were summed across the four time points to compare across biocrust types. To examine differences in the nutrients within leachate and the nutrients with the soil crust layer between biocrust types, we standardized nutrients "lost" in leachate to those occurring in the biocrust layer using the equation: ((sum nutrient leached)/(nutrient amount in biocrust)) × 100

To assess metabolites in the leachate, we combined leachate from each sample across the four-time points of the experiment and then compiled three replicates from the same biocrust type together into one sample, so that the total number for each biocrust type was $n = 3$. We did this to ensure we had enough sample to perform the analysis. The relative concentrations of key metabolites were profiled using normal phase liquid chromatography (Merck SeQuant ZIC-HILIC column, 150_1 mm, 3.5 mm, 100 Å) coupled to an Agilent 6520 ESI-Q-TOF at the Lawrence Berkeley National Laboratory (Sparks et al. 1996). For metabolomics, approximately 30 ml liquid leachate were lyophilized (FreeZone 2.5 Plus, Labconco) and resuspended in 200 µl methanol containing internal standards (5-50 µM of ^{13}C-^{15}N Cell Free Amino Acid Mixture, Sigma). Samples were vortexed for 20 seconds, filtered through 0.2 µm centrifugal filters and placed into LC-MS vials for analysis. LC-MS data were acquired using an Agilent 1290 LC stack with a HILIC column (Merck SeQuant ZIC-HILIC column, 150_1 mm, 3.5 mm, 100 Å)

coupled to a Q Exactive Orbitrap MS (Thermo Scientific). Metabolites were identified using the Metabolite Atlas and verified based on exact mass and retention time (< 1 min difference) and MS/MS fragmentation spectra matching to known standards. Differences between relative amounts of metabolites were determined by normalizing the peak area for each metabolite to the high peak value across biocrust types. A two-way ANOVA and Tukey HSD test at an alpha level of < 0.05 was used to indicate the normalized metabolite amounts that differed significantly between biocrust types.

2.3 Assessment of CO_2 flux and microbial biomass after leachate addition

To answer our question exploring the relationship between leachate and microbial activity, we conducted a soil incubation experiment where we added leachate from each biocrust successional stage (collection described in 2.2. above) to the mineral soil collected from beneath biocrusts in a full-factorial design. Specifically, mineral soil samples from the same site described above were collected in July 2019 from beneath lightly pigmented cyanobacterial, darkly pigmented cyanobacterial, and moss dominated biocrusts were given leachate collected from each of the crust types ($n = 3$ for each below-crust soil–leachate pairing). We collected mineral soil by removing the 0-2 cm layer of lightly pigmented, darkly pigmented, and moss-dominated biocrusts using a 10 x 10 cm square core and collected soil beneath by taking 3, 4.6 cm diameter cores at a depth of 2-5 cm. For our incubation, we added 15 g of the below-biocrust mineral soil to 120 ml gas-tight glass Mason jars fitted with rubber septa and brought the soil to 50 % of water holding capacity (around 2 ml per sample) with leachate. We sealed the jar for 24 hours and then used a syringe to mix and collect 8 ml of headspace without exposing the headspace to the atmosphere. We analyzed CO_2 concentration of the headspace using a benchtop infrared gas analyzer (IRGA; CA-10, Sable Systems International, North Las Vegas, NV). Soil

respiration rate was calculated as μmol CO_2 g^{-1} hr^{-1}. Before and after the 24-hr incubation we extracted the samples for microbial biomass C concentration assessment as described above.

2.4 Statistics

We checked the data for normality and homogeneity of variance and found that many of the response variables were non-normal and heteroscedastic. We used permutational ANOVAs, which do not assume data normality or homogeneous variance, to determine how strongly response variables differed across biocrust successional states. We conducted a pairwise permutational test to determine how different the response variables were from one another among the biocrust successional states. The permutational ANOVAs was conducted using the package 'VEGAN' in R (Oksanen et al. 2019) and the permutational pairwise test was conducted using the package 'pairwiseAdonis' in R (Arbizu 2017). We also calculated the differences in the magnitudes among the crust types for each response variable. The differences in magnitude are reported as ratios such as $\bar{X}_{light} : \bar{X}_{dark}$ where $\bar{X}_{light}$ is the mean of the lightly pigmented cyanobacterial biocrusts for a given variable and $\bar{X}_{dark}$ is the mean of the darkly pigmented cyanobacterial biocrust for the same variable. The data were non-negative, showed some degree of log normality and contained zeroes. As such, we calculated 95 % confidence intervals for the ratios using a maximum-likelihood method designed for data with these features (Zhou and Tu 2000). Confidence intervals not containing 1 are considered statistically significant for $H_0 = 1$, which would correspond to a 1:1 ratio, or no difference among crust types (likelihood ratio test; (Zho and Tu 1999; Zhou and Tu 2000). The calculations were conducted using the package 'treateffect' in R (Darrouzet-Nardi, 2020). To compare relative intensify of detected metabolites, we created a heat map using the function "heatmap.2" in the package "gplots

v3.1.1" in R and the hierarchical clustering with the package used the complete argument in the "hclust" function (Figure 3.3).

3. RESULTS

3.1 Characterization of biocrust successional states

The Chl_a and Scy concentrations were higher in darkly pigmented cyanobacterial, mid-successional biocrusts than in the early successional lightly pigmented cyanobacterial biocrusts (Figure 3.2). Chlorophyll *a* concentrations were 5.5 times [4.11, 7.45; 95 % CI] as high in darkly pigmented as in lightly pigmented cyanobacterial crusts (p = 0.001, F = 143.84). Scytonemin concentrations were 9.8 times [6.24, 15.5; 95 % CI] as high in darkly pigmented as in lightly pigmented cyanobacterial crusts (p = 0.001, F = 90.70). The percent organic matter increased across biocrust successional states (p = 0.001, F = 59.78), increasing 2.3 times [1.87, 2.67; 95 % CI] from lightly pigmented biocrust to darkly pigmented cyanobacterial crust (p < 0.001), and then 1.8 times [1.52, 2.34, 95 % CI] from darkly pigmented cyanobacterial to moss dominated biocrust (p < 0.001)

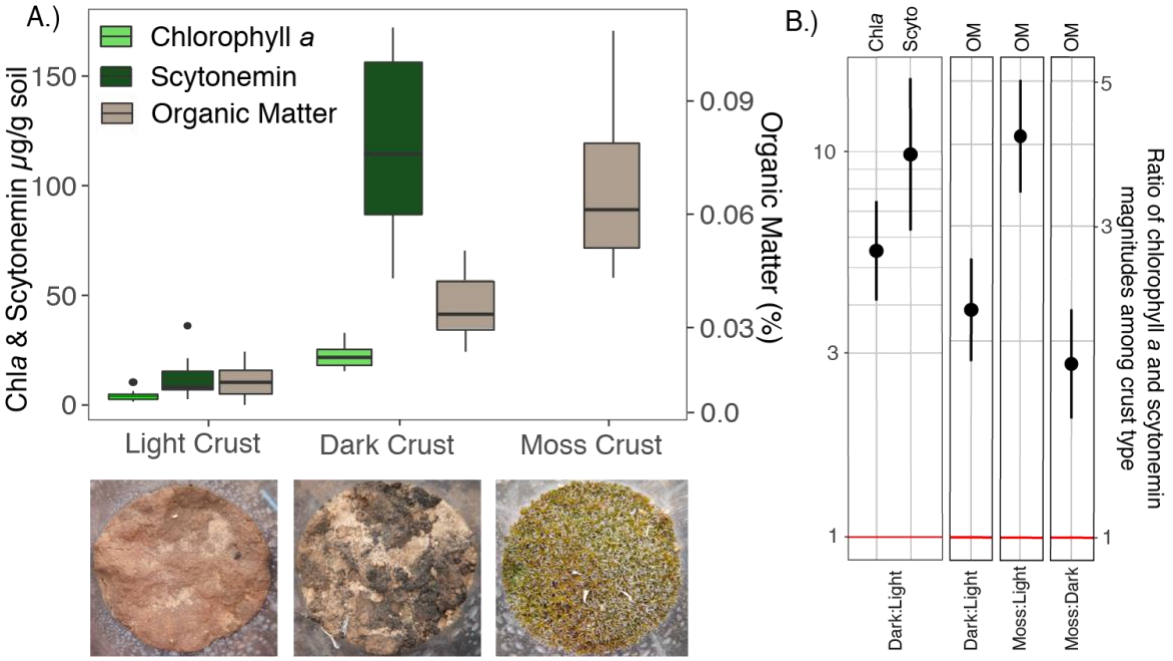


Figure 3.2. A.) The amount of chlorophyll *a* and scytonemin in µg per g of soil in lightly-pigmented and darkly-pigmented cyanobacterial crusts and the percent organic matter in all three biocrust types pictured in the figure (chlorophyll *a* and scytonemin were not measured in moss-dominated crusts). Early successional lightly pigmented cyanobacterial biocrusts are likely dominated by *M. vaginatus,* mid to late-successional darkly pigmented cyanobacterial biocrust are likely dominated by *Scytonema* spp., and a mid to late successional moss-dominated biocrust are dominated by *S. caninervis*. B.) Ratios with 95 % confidence intervals among biocrust successional stage comparing chlorophyll *a*, scytonemin, and organic matter concentration. Each point and associated confidence interval shows the magnitude of the ratio shown on the horizontal axis (e.g., dark:light). For example, Chl *a* was 5.5 times higher in dark crusts than in light crusts, with a confidence interval of [4.11, 7.45]. Confidence intervals were calculated based on the maximum likelihood method in Zhou and Tu (2000) for the ratio of two means in lognormally distributed data containing zeroes. Confidence intervals not containing 1 would be considered statistically significant.

3.2 Nutrients and organic C

3.2.1 N concentrations

Generally, N concentrations in the biocrust layer were higher within darkly pigmented cyanobacterial and moss biocrusts than in lightly pigmented cyanobacterial crusts (Figure 3.3 A., B., C.). For example, total soil N and extractable NH_4^+ concentrations were around twice as high in darkly pigmented cyanobacteria and moss dominated biocrusts than lightly pigmented cyanobacterial crusts (NH_4^+ dark:light = 2.6 [1.99, 3.42; 95 % CI], moss:light = 2.8 [1.91,4.45; 95 % CI]) (% Total N dark:light = 1.92 [1.56, 2.37; 95 % CI], moss:light = 2.26 [1.73, 2.93; 95 % CI]). Extractable NO_3^- concentrations were the exception, with NO_3^- values highest in the

darkly pigmented cyanobacterial crust and similar in the other two crust types (p = 0.011, F = 3.61). The ratio of total C to total N was 1.2 times [1.12, 1.42; 95% CI] as high in lightly pigmented cyanobacterial crusts than in moss crusts and 1.3 times [1.2, 1.48; 95% CI] as high than in darkly pigmented crusts (Figure 3.3A).

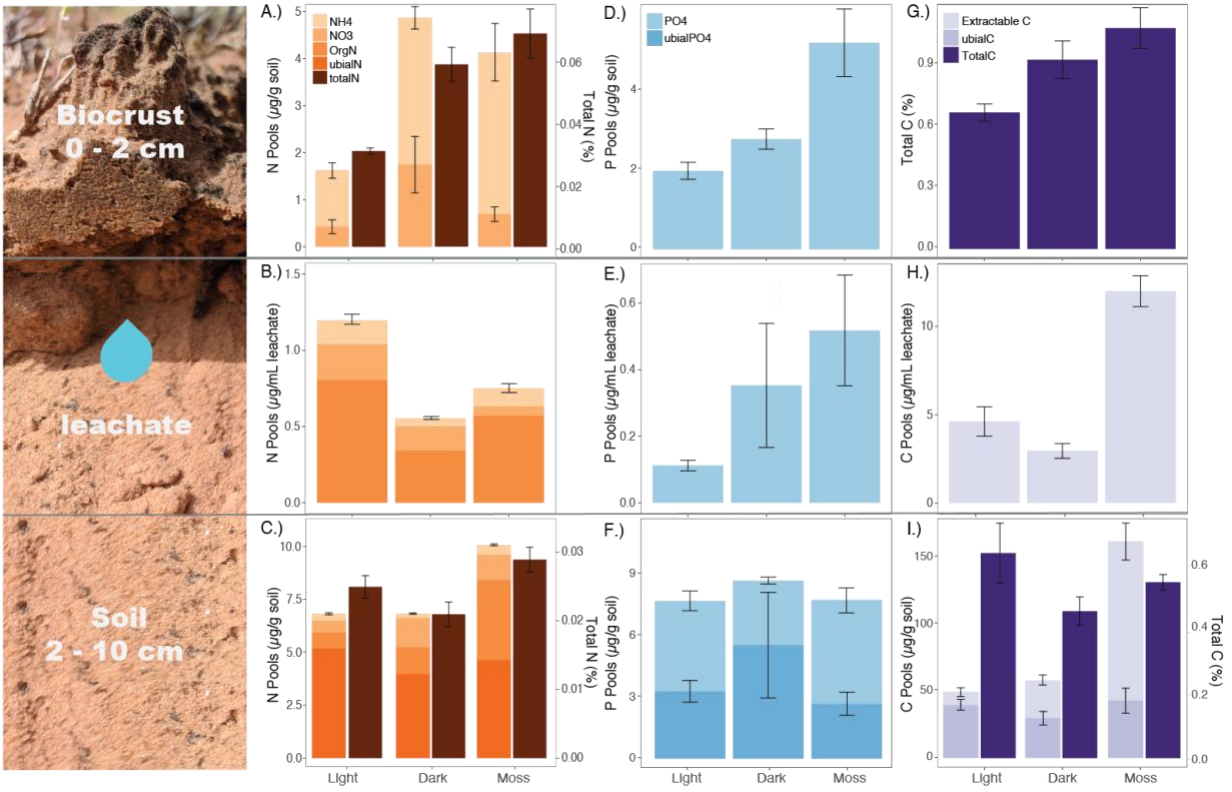


Figure 3.3. Nutrient and organic C concentrations in the biocrust (0-2 cm) layer, in leachate from biocrusts, and in the soil layer (2-10 cm) for lightly pigmented cyanobacterial, darkly pigmented cyanobacterial, and moss biocrusts. A).). N concentrations (µg/g biocrust) and total percent N in the biocrust layer B). N concentrations (µg/ml leachate) in the crust leachate. Overlapping error bars were removed to prevent confusion (NO_3^-: light SE ± 0.022, dark SE ± 0.023 moss SE ± 0.018) TDN: light SE ± 0.14, dark SE ± 0.06, moss SE ± 0.07). N concentrations (µg/g soil) in the mineral soil layer (2-10 cm). Overlapping error bars were removed to prevent confusion (NO_3: light SE ± 0.19, dark SE ± 0.27, moss SE ± 0.14), (TDN: light se ± 0.16, dark se ± 0.14, moss se ± 0.48), (microbial N: light se ± 0.54, dark se ± 0.62, moss se ± 0.96). PO_4^{3-} concentrations (µg/g biocrust) in the biocrust layer E). PO_4^{3-} concentrations (µg/ml leachate) in the crust leachate F). PO_4^{3-} (µg/g soil) and microbial PO_4^{3-} (µg/g soil) in the mineral soil layer (2-10 cm). G). Total soil C (%) in the biocrust H). Extractable C µg/ml in leachate. I) Extractable organic C (µg/g soil), microbial biomass C (µg/g soil), and total soil C (%) in the mineral soil layer (2-10 cm). Error bars represent SE.

For the leachate, total dissolved N concentration was highest in lightly pigmented cyanobacterial crusts compared to moss or darkly pigmented cyanobacterial biocrusts, with the latter having the lowest N concentration overall. For example, total dissolved N was 2.34 times [1.34, 3.92; 95% CI] as high in leachate from the lightly pigmented cyanobacterial crusts as it was from darkly pigmented cyanobacterial crusts ($p = 0.02$), while NO_3^- concentrations were 3.98 times [2.27, 6.97; 95 % CI] as high in lightly pigmented cyanobacterial biocrusts as it was in moss crusts ($p < 0.001$). When comparing the N leached from the biocrust to the N found in the biocrust layer, lightly pigmented cyanobacterial crusts lost more NH_4^+ (13.04%) and NO_3^- (55.25%) relative to the amount within the biocrust layer, than either the moss (NH_4^+ = 3.54,

NO_3- = 8.74) or darkly pigmented cyanobacterial crust (NH_4^+ = 1.77, NO_3- = 9.02). The ratio of extractable total dissolved organic C to total dissolve N in leachate grew substantially larger along the successional gradient, with the C:N ratio 4.3 times [3.56, 5.31; 95% CI] greater in leachate from mosses than leachate from lightly pigment cyanobacterial crusts and 1.7 times [1.09, 2.73; 95% CI] greater than leachate from darkly pigment cyanobacterial crusts (Figure 3.3B).

There were few generalizable patterns for N forms within the mineral soil beneath the biocrust, and the overall patterns of N concentrations in the soil layer did not reflect those in the biocrust layer or its leachate. The largest differences were seen in the extractable NO_3^- and total dissolved N concentrations in the soil, which were lower beneath lightly pigmented cyanobacterial crusts compared to below darkly pigmented and moss crusts. While the extractable NH_4^+ concentrations in the soil were 1.5 [1.08, 2.15; 95 % CI] times higher below lightly pigmented crusts and 2.2 [1.56, 3.04, 95 % CI] times higher below moss crusts than below darkly pigmented cyanobacterial crusts (Figure 3.3C).

3.2.2 P concentrations

The extractable PO_4^{3-} concentrations in the biocrust layer increased from lightly pigmented to darkly pigmented cyanobacterial to moss crusts (p = 0.002, F = 10.16) (Figure 3.3D). The PO_4^{3-} in the leachate had a similar pattern to extractable PO_4^{3-} in the biocrust layer, but the variation among the biocrust successional states was large (p = 0.16, F = 1.99) (Figure 3.3E). The PO_4^{3-} concentrations in the soil layer below the biocrusts were about 1.5 times lower below darkly pigmented cyanobacterial crust compared with the other two crust successional states ([light:dark 1.4 [1.02, 1.79; 95% CI], moss:dark 1.62 [1.29, 2.03; 95% CI]), while

microbial PO_4^{3-} concentrations were similar in soils below all three crust successional states (p = 0.53, F = 0.94) (Figure 3.3F).

3.2.3 C concentrations

Extractable total dissolved organic C in the biocrust layer increased from lightly pigmented to darkly pigmented cyanobacterial to moss crusts (p = 0.004, F = 6.49) (Figure 3.3G). Organic C in the leachate from moss crusts was 2.5 times [1.7, 3.87; 95% CI] higher than lightly pigmented crusts and 4 times [3.01, 5.54; 95% CI] higher than darkly pigmented cyanobacterial crusts (Figure 3.3H). In the mineral soil below the biocrust, extractable total dissolved organic C and microbial C were much higher below moss crusts than below lightly and darkly pigmented cyanobacterial crusts. For example, total dissolved organic C was 11.6 times [5.14, 26.37; 95% CI] as high in moss than in lightly pigmented cyanobacterial crusts. Total percent C was similar across all biocrust types (p = 0.14, F = 2.18) (Figure 3.3I).

3.3 Metabolites in leachate

The LC-MS analysis showed a wide range of metabolites in the leachate from each biocrust successional state. Most of the metabolites were verified with authentic standards, and those that were not considered putative and not included in the list of present metabolites. Moss dominated crusts seemed to have the highest relative abundance of metabolites compared to lightly and darkly pigment crusts. Hierarchical clustering grouped lightly pigmented and darkly pigmented crusts together, separate from moss dominated crusts. Some, but not all, metabolites differed strongly between biocrust successional stage (Figure 3.4). Differences in relative abundance of metabolites did not follow clear patterns related to the biological classification of the metabolites. Many present metabolites were osmolytes (Figure 3.5). Of the five commonly recognized osmolytes found with the leachate (ectoine, proline, betaine, choline, and

trigonelline) only the relative abundance of betaine and choline differed strongly between successional stages. Betaine: moss:dark 3.49 [1.71, 7.12; 95% CI], moss:light 4.342 [1.13, 16.68; 95% CI], dark:light 1.24 [0.27, 5.7; 95% CI].

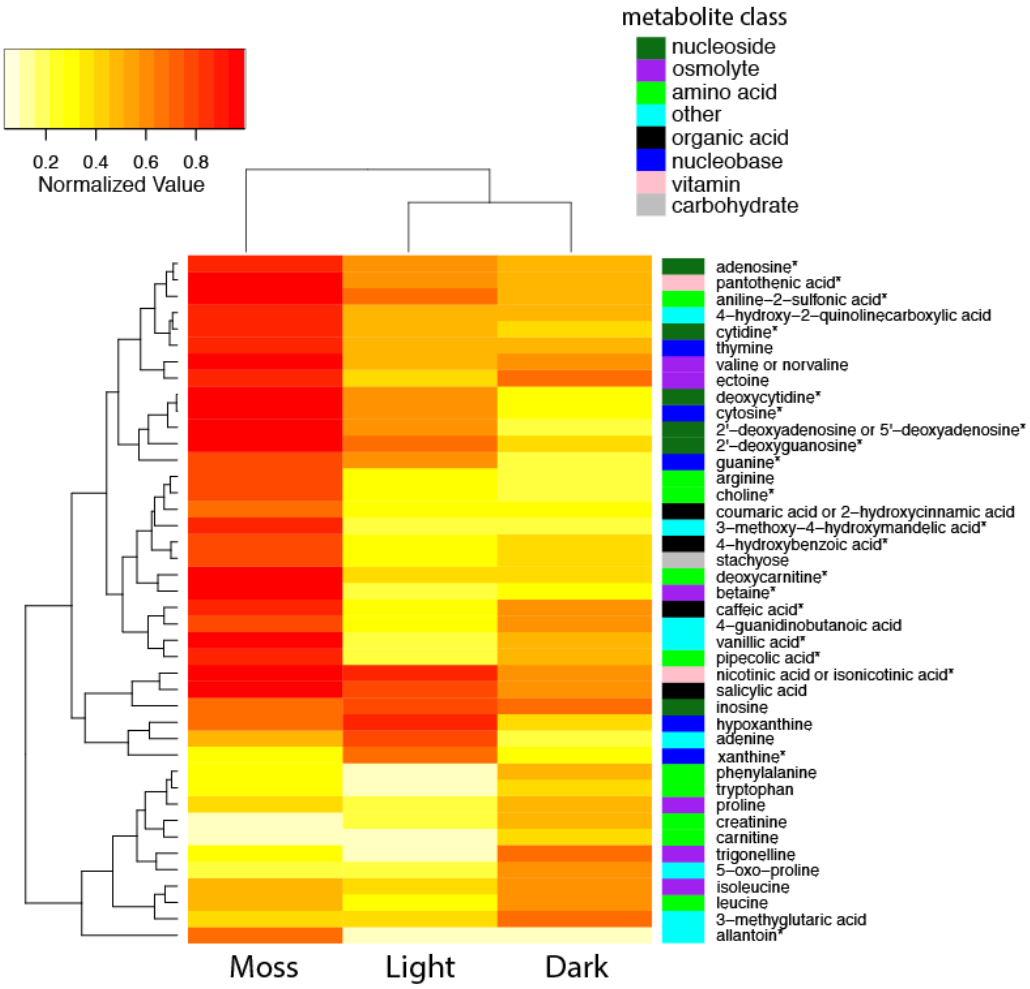


Figure 3.4. Comparison of relative intensity of detected metabolites from the three biocrust successional stages. Peak values were normalized to the large peak value for each metabolite across biocrust successional stages. 0 indicates the lowest relative abundance and 1 represents the highest relative abundance. The dendrogram on the left and top clusters similarly extracted metabolites based on hierarchical clustering and the heat map displays the intensity of metabolites normalized to the most intense peak within each row (metabolite). The heat map was created using the function "heatmap.2" in the package "gplots v3.1.1" in R and the hierarchical clustering with the package used the complete argument in the "hclust" function. * indicates metabolite intensities that are statistically different (based on an alpha level of 0.05) among the three biocrust types. Only confirmed metabolites were included.

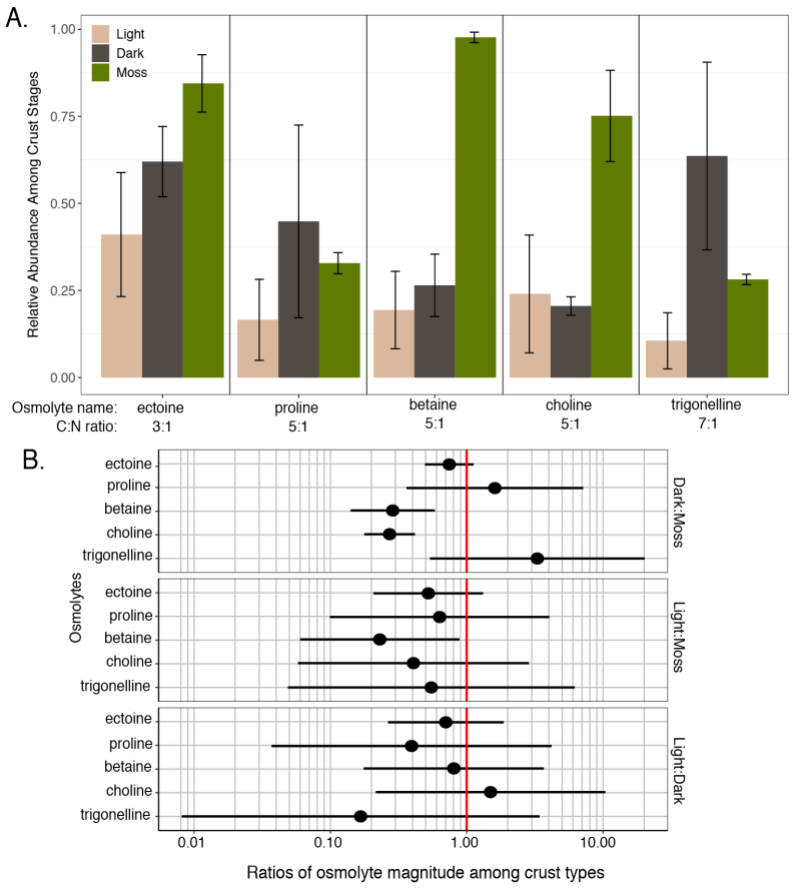


Figure 3.5. A. The normalized abundance between crust types of common, confirmed osmolytes found within the leachate in order of increasing C:N ratio. While comparisons across osmolyte types cannot be made, the order of magnitude of the average peak area across biocrust successional stages for each osmolyte is included to show potential differences in the quantity of the different osmolytes. B. Ratios with 95 % confidence intervals among biocrust successional stages for each osmolyte. Each point and associated confidence interval show the magnitude of the ratios shown on the horizontal axis (e.g., dark:moss). For example, proline was 1.6 times higher in dark crusts compared to moss crusts with a confidence interval of [0.36, 7.14]. Confidence intervals were calculated based on the maximum likelihood method in Zhou and Tu (2000) for the ratio of two means in lognormally distributed data containing zeroes. Confidence intervals not containing 1 would be considered statistically significant.

3.4 Soil respiration and microbial C

A full-factorial design crossing soils from beneath the different biocrusts with leachate collected from the different biocrusts revealed that CO_2 respiration changed significantly as a function of the successional state from where mineral soils were collected (p = 0.001, F = 54.440), but not as a function of the successional stage from where leachate was sourced (p = 0.452, F = 0.89) (Figure 3.6). Because respiration rates did not differ strongly among leachate sources on a given subsoil, we treated the four different leachates as replicates when examining the relationship between CO_2 respiration and subsoils. Soil CO_2 respiration rates were similar in soils collected from beneath lightly pigmented and darkly pigmented cyanobacterial crusts (p = 0.92) but were around 1.7 times higher in soils collected from beneath moss biocrust (moss:light = 1.76 [1.52, 2.04; 95 % CI], moss:dark = 1.74 [1.56,1.95; 95 % CI]; Figure 3.6). Microbial biomass C concentrations were also significantly different across mineral

soil types (p = 0.001, F = 38.03) but were similar among leachate treatments (p = 0.86, F = 0.24). We again treated leachate types as replicates within mineral soil types, since the differences among leachate types were small. Microbial biomass C was around 2.3 times higher in mineral soil beneath darkly pigmented cyanobacterial and moss crusts than below lightly pigmented crusts (dark:light = 2.28 [1.93, 2.7; 95 % CI], moss:light = 2.31 [1.87, 2.85; 95% CI]). Mineral soil collected beneath lightly pigmented cyanobacterial crust had the highest soil respiration to microbial biomass C ratio (activity : biomass = 0.102) compared to darkly pigmented crust soil (activity : biomass = 0.045) and moss crust soil (activity : biomass = 0.077). Note that the microbial biomass in the incubation experiment were distinct from the *in-situ* microbial biomass measurements and not comparable due to the differences in timing and method of collection.

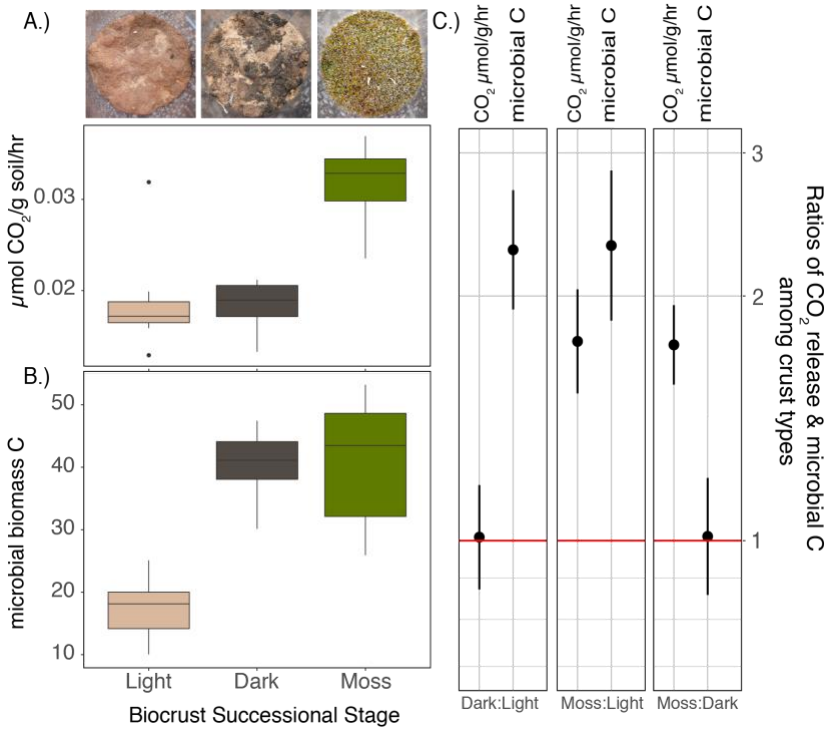


Figure 3.6. A). Respiration rates (μmol CO_2/g dry soil/hr) of soils collected from beneath the three biocrust successional states during a 24 hr incubation B). Changes to microbial biomass C concentrations within mineral soil collected from beneath the three different biocrust successional states after a 24 hr incubation. Vertical bars on the boxplots represent median values and the vertical lines represent minimum and maximum values. C). Ratios with 95 % confidence intervals among biocrust successional stages for soil CO_2 respiration (CO_2 μmol/g/hr) and microbial biomass C. Each point and associated confidence interval show the magnitude of the ratios shown on the horizontal axis (e.g., dark:light). For example, soil CO_2 respiration rates were 1.76 time higher in the soils beneath moss-dominated crusts compared to lightly-pigment crusts with a confidence interval of [1.52, 2.04]. Confidence intervals were calculated based on the maximum likelihood method in Zhou and Tu (2000) for the ratio of two means in lognormally distributed data containing zeroes. Confidence intervals not containing 1 would be considered statistically significant.

4. DISCUSSION

Here, we explored the connectivity between biocrusts and the subsurface mineral soil. We found that biocrusts released a wide range of nutrients and organic C compounds during leaching events and that the concentrations of C, N, and P in leachate differed widely among the three biocrust successional stages, as did the degree to which the resources accumulated in the 2-10 cm soil layer (Figure 3.3). Further, we found that leachate concentration did not appear to affect short-term microbial CO_2 fluxes in mineral soil (Figure 3.6) as it has in other ecosystem types (e.g., Cleveland et al. 2010). Instead, the provenance of mineral soil, with regard to which biocrust successional state occurred on the surface where the soil was collected, was the main

driver of differences in CO_2 flux, suggesting a longer-term effect of biocrust type on sub-surface microbial respiration. Overall, we observed that the degree of connectivity between biocrusts and the mineral soil depends on the biocrust successional stage, and the resource being considered, and that changes to successional stage may have significant influence on the biogeochemical connectivity between biocrusts and mineral soil.

4.1 Nutrients and organic C in biocrust leachate

The patterns in leached nutrients and C varied among biocrust type and element. For example, lightly pigmented cyanobacterial crusts lost the most N in leachate of the three biocrust types. This finding is surprising, given the dominant species of this area's lightly pigmented crusts, *M. vaginatus*, is not a N-fixer; although, N fixation by free-living organisms tightly associated with *M. vaginatus* is common, these rates are typically relatively low (Steppe et al. 1996; Belnap 2003b). However, its known that cyanobacteria secrete a large fraction of their photosynthate into their surrounding environment (Baran et al. 2015; Thomazo et al. 2018), and there is emerging evidence for a 'cyanosphere,' in which the pioneering soil cyanobacteria, *M. vaginatus,* concentrates N-fixing bacteria around cyanobacterial bundles through organic C exudation (Couradeau et al. 2019). Our results build on these findings to suggest the early-successional cyanosphere is less able to retain N than later-successional cyanobacterial communities, and notably, that this cyanobacterial-dominated biocrust loses more N relative to the N it stores in the biocrust layer. Similar patterns of N loss in leachate, including large amounts of organic N loss, were observed in a separate experiment examining leached N from lightly and darkly pigmented biocrusts collected on the Colorado Plateau (Johnson et al. 2005). The ability of darkly pigmented crusts to retain more N and C than lightly pigmented crusts suggests structural and/or species differences between lightly and darkly pigmented biocrusts

that allows microbial communities within darkly pigmented cyanobacterial biocrusts to better retain resources. This could be related to the more complex species compositions that bind and resorb nutrients (Garcia-Pichel and Belnap 1996; Garcia-Pichel et al. 2001; Couradeau et al. 2019) and suggests another differences among the three biocrust types is the ability to retain nutrients, specifically N. Our findings suggest lightly pigmented biocrusts maintain lower C and nutrient stocks and are less able to maintain soil fertility in the 0-2 cm soil layer than later successional crust types. But, surprisingly, may promote N fertility in deeper soil layers disproportionate to their N stocks, as indicated by the larger amounts of N leached downward from the surface.

The large stoichiometric differences in the leachate (for example, the large differences in C:N between lightly and darkly pigmented cyanobacterial crust leachate) likely influences the ultimate fate of the leachate, as well as the microbial communities that utilize and recycle it. Nutrients and organic C in leachate may be resorbed, taken up by vascular plants, fungi, archaea, or other bacteria, flushed to deeper soil layers, rapidly oxidized, or transformed and lost in gaseous form (Barger et al. 2016), all of which could be influenced by changes in leachate stoichiometry. Here, the dissolved C:N ratio in leachate doubled between successional stages, suggesting that disproportionate amounts of dissolved organic C are being released into the soil below late-successional crusts relative to N, likely structing the complex communities found there (Baran et al. 2015) but leading to a larger potential for N limitation in soils below late-successional crusts. Because biocrust types are anticipated to change under global change scenarios (Ferrenberg et al. 2015; Reed et al. 2016) these stoichiometric differences in biocrust leachate, as well as the connectivity among biocrust types and mineral soil, is important for understanding the fate of these nutrients and C in transitioning drylands (Reed et al. 2012;

Maestre et al. 2013; Ferrenberg et al. 2018). Further, changes in precipitation patterns and increasing aridity will likely influence the degree of connectivity between biocrust and the mineral soil. This is due to the predominant role of precipitation in controlling the downward movement of water (Collins et al. 2014) and therefore the degree to which the biocrust and subsoil are connected. Less precipitation or smaller precipitation events may decrease the degree to which biocrust contribute to subsoil nutrients.

The metabolite content in leachate also varied among biocrust successional stages. The large amounts of organic C found in leachate from moss crusts is similar to other studies examining biocrust leachate (Zhao et al. 2016) and contained a correspondingly large concentration and diversity of metabolites. Osmolytes, specifically betaine, choline, ectoine, trigonelline, and proline, were found in leachate from each biocrust type and most commonly in moss crusts. There is evidence that these osmolytes are essential components of the desiccation and rehydration of biocrusts (Swenson et al. 2015). The long list of other metabolites detected, including amino acids, nucleotides, nucleobases, sugars, and vitamins, suggests additional functions related to microbial activity. Metabolites are important components of microbial food webs within biocrusts, with heterotrophs specializing in specific metabolites released from cyanobacteria as substrates (Baran et al. 2015). The differences in metabolite content from different biocrust types is likely related to the different complexities and structures within each biocrust type. For example, extracellular polymeric matrixes (EPM) released as microbially-produced exopolysaccharides from biocrusts can bind and capture metabolites, helping to retain them in the biocrust layer (Swenson et al. 2018). Different amounts of EPM in the three crust types (Rossi et al. 2018), as well as the large amounts of organic C derived from tissue and rhizomes of moss crusts (Dümig et al. 2013), may help explain differences in leachate metabolite

content. Future work quantifying the various metabolites and directly comparing concentrations of the observed metabolites with microbial activity would further our understanding of these pools and their role in microbial activity in the soils below biocrust.

4.2 Nutrient pools within and below biocrusts

The nutrient and organic C concentrations of the 2-10 cm soil layer did not strongly reflect the concentrations of the biocrust layer or the leachate, with the exceptions of moss crusts, which leached large amounts of total dissolved organic C and had high total dissolved organic C pools in the mineral soil (Figure 3.3). Some studies have observed a difference in nutrient and C pools below biocrusts (Guo et al. 2008; Barger et al. 2013) while others have not (Beraldi-Campesi et al. 2009; Brankatschk et al. 2013; Moreira-Grez et al. 2019; Yang et al. 2019) reflecting a lack of consensus on the degree of connectivity between biocrusts and the mineral soil below. This is not entirely surprising, as nutrient pools can change dramatically through time and, because they represent the net effect of multiple inputs and types of uptake/loss (Hart et al. 1994), they may not correlate with inputs or be dissimilar across crust types at a given time point. For example, in a separate experiment conducted on the Colorado Plateau, soil NO_3^- concentrations in the 0-10 cm soil layer almost doubled between winter and spring, while resin-extractable NO_3^- decreased around 17 times during the same time period (Zelikova et al. 2012). A separate study measuring 2 – 5 cm below lightly pigmented and darkly pigmented cyanobacterial crust on the Colorado Plateau did not observe large differences in inorganic N amounts among crust types over time (Barger et al. 2005). To more fully explore connectivity between biocrusts and the mineral soil, more studies examining resource pools within the biocrusts and mineral soils across time are needed.

4.3 Microbial CO_2 flux from sub-crust soils

Nutrients leached from the different biocrust types did not change short-term heterotrophic activity in sub-surface soils (Figure 3.6). This was unexpected, as we did see significant differences in leachate chemistry across biocrust successional states (e.g., total dissolved organic C concentrations were more than twice as high in leachate from late successional moss dominated biocrust than in either of the earlier successional states) and as both microbial respiration and biomass responded to differences in leachate concentrations in other ecosystems (Qiu et al. 2005; Cleveland et al. 2006). While we observed short-term responses here, it is possible we would see larger differences with longer incubation times. Soil respiration rates in the mineral soil were relatively low compared with other systems, reinforcing the notion that subsurface soils have lower microbial activity (Miralles et al. 2012). When looking at the role of biocrust community type, the higher respiration rate coming from below the moss biocrusts suggests a longer-term influence of crust leachate on sub-surface microbial activity. The large amounts of organic C leached from moss crusts and the large total dissolved organic C pools found in the mineral soil below moss crusts may serve as an easily accessible source of C for heterotrophs in the mineral soil when water is available. These findings suggest a longer-term influence of moss crust on the mineral soil and microbial cycling (Dümig et al. 2013), namely through the accumulation of organic C in the soil over time, with consequences for the amount of C being released from dryland soils.

5. CONCLUSION

The vertical movement of soluble C and nutrients from the biocrust layer to the mineral soil may be one of the main mechanisms through which biocrusts contribute to mineral soil fertility. Here, we observed that the degree of connectivity between biocrusts and the mineral soil

depends on the biocrust type and the resource being considered. The contrasting findings in the literature as to the role biocrusts play in providing fertility to the deeper soil layers further highlights how differences in biocrust type, element, soil depth, seasonality, and water inputs can change the degree of connectivity between biocrusts and deeper soils. This study adds to our understandings of how different biocrust types and deeper mineral soil exchange fertility and provides nuance to the outcomes of nutrients and C cycling along successional gradients in dryland regions. Future studies manipulating multiple abiotic variables, such as soil texture and precipitation amounts, would further our understanding of connectivity and allow for improved predictions of large scale biocrust contributions to the mineral soil.

Chapter 4: Physiological and biogeochemical responses of biocrust to a wide range of precipitation frequencies and amounts

INTRODUCTION

Precipitation pulses dictate ecological activity in drylands (Collins et al. 2014a). Ecological processes, such as biomass accumulation, nutrient and carbon cycling, are either directly or indirectly tied to precipitation pulses, which typically occur as isolated rainfall events or a series of rainfall events punctuated by periods of dryness (Noy-Meir 1973; Westoby et al. 1989; Collins et al. 2014). The degree to which ecological processes respond to precipitation pulses is controlled by the length of time moisture remains available in the soil, the depth that soil moisture penetrates, the frequency of precipitation, and the physiological and morphological characteristics of the organism (Schwinning et al. 2004b; Schwinning and Sala 2009). Understanding these controls is a necessary step to predicting the ecological outcomes of altered precipitation patterns and higher temperatures anticipated under climate change (Maestre et al. 2016). However, our ability to disentangle these controls and predict ecological responses remains limited.

Many of the questions examining how dryland organisms respond to precipitations pulses have been tested using vascular plants (Schwinning and Ehleringer 2001). However, fewer studies have focused on biological soil crusts (biocrusts), which are diminutive communities of primary producers that grow on the soil surface between vascular plants and can be a dominant form of groundcover in many drylands (Ferrenberg et al. 2017). Biocrusts are comprised in varying degrees of desiccation-tolerant lichens, mosses, cyanobacteria, algae, and fungi (Belnap 2003a). Biocrusts contribute to C and N fluxes (Barger et al. 2006; Darrouzet-Nardi et al. 2015; Weber et al. 2015) and can increase soil fertility in surrounding soil (Barger et al. 2016). Like

vascular plants, differences in biocrust physiology, morphology, and pulse utilization strategies (i.e., how quickly rehydration occurs, when photosynthesis begins, etc.) can dictate biocrusts' response to precipitation pulses and the biogeochemical outcomes. However, unlike vascular plants, biocrusts are entirely reliant on the water status of the immediate soil surface (Schwinning and Sala 2009). The frequency and duration of soil surface wetting, rather than the absolute amounts of precipitation, therefore likely influences ecological responses in biocrusts more so than in vascular plants.

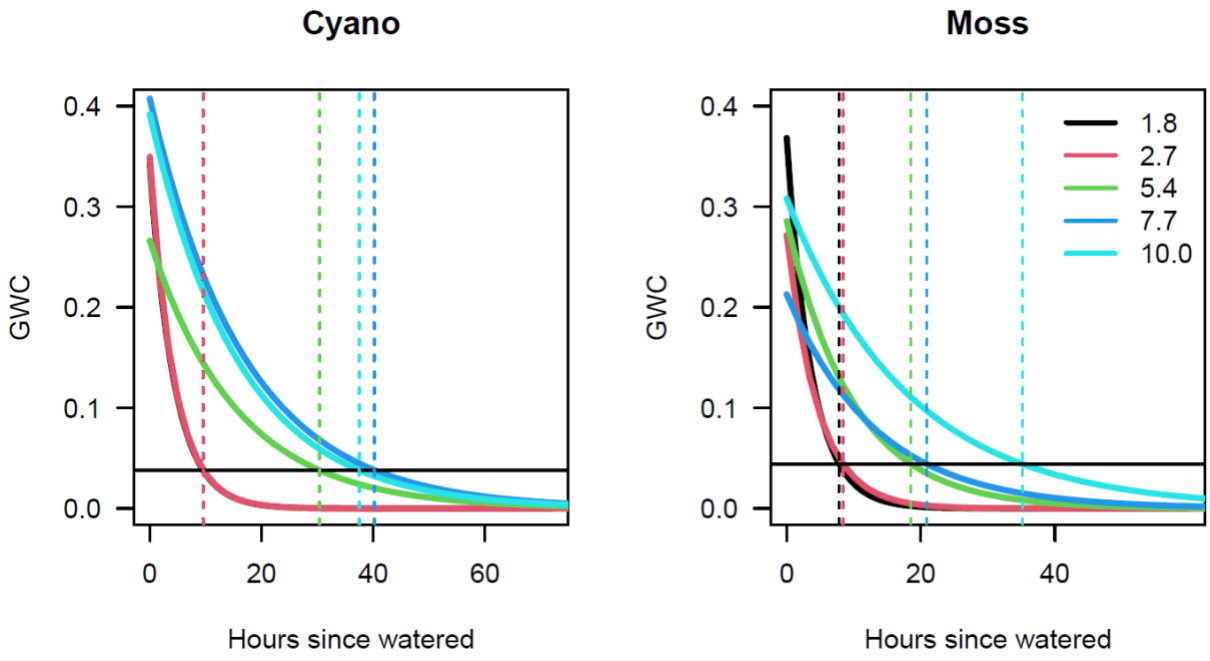
The ways in which biocrusts respond to changes in frequency and duration of precipitation can change with biocrust type. In moss-dominated biocrusts, small, frequent precipitation pulses can result in moss mortality due to carbon starvation (Coe et al. 2012; Reed et al. 2012) while cyanobacteria-dominated crusts can have decreased chlorophyll *a* content and shifts in cyanobacterial species composition under delayed or altered precipitation patterns (Steven et al. 2013b; Fernandes et al. 2018). The different responses to variations in precipitation size and frequency by different biocrust types is likely tied to their ability to utilize precipitation pulses. Biocrusts dominated by cyanobacteria can rapidly respond to precipitation during brief periods of hydration and rapidly reenter desiccation (Garcia-Pichel and Belnap 1996). For example, metabolism activity within *Microcoleus vaginatus*, a common cyanobacterial species, responds rapidly to precipitation while simultaneously showing evidence of cellular preparation for dehydration (Rajeev et al. 2013). This rapid response is also true of moss biocrusts, which can rehydrate and fix carbon 10-30 minutes following water addition (Coe et al. 2014). However, moss crusts require more water to achieve a positive carbon balance than cyanobacterial dominated crusts (Reed et al. 2012; Strong et al. 2013; Zhang et al. 2018), and also need more

water to reach maximum net photosynthesis compared to cyanobacterial and lichen biocrust types (Tamm et al. 2018).

These different responses to variation in precipitation can also have larger biogeochemical consequences which likely differs with biocrust type. Darkly pigmented cyanobacterial crusts fix more N than moss crusts (Housman et al. 2006; Barger et al. 2016) and communities of N-fixing heterotrophs living within cyanobacterial crusts can exude N into the cyanosphere through secretion (Couradeau et al. 2019, Nelson et al. 2021). Cyanobacterial crusts therefore typically have larger N pools and may also lose more N into the soil below biocrusts during watering events (Johnson et al. 2005). When precipitation timing and frequency was altered, moss mortality induced by carbon starvation changed N pools in the soils beneath mosses, increasing pools of NO_3^- relative to NH_4^+ with consequences for N retention in soils (Reed et al. 2012; Young and Reed 2017). Our understanding of additional biogeochemical consequences to changes in precipitation, particularly organic C and P pools and the effects of stoichiometric changes, are limited.

The importance of biocrust to dryland ecosystem function and biocrusts' utility as a model study system (Bowker et al. 2014) lends it to asking questions about the factors controlling dryland organismal response to precipitation pulses. Here, we sought to determine how moss-dominated biocrusts and darkly-pigment cyanobacterial biocrusts respond to a gradient of pulse size and frequency and the biogeochemical consequences of those responses. In a green-house mesocosm, we administered deionized water in varying amounts and frequencies to darkly pigmented cyanobacterial crusts and moss-crusts while keeping the overall amount of water the same for a four-month period (Figure 4.1). At the end of the experiment, we measured biological and physiological responses within the two biocrust types, as well as CO_2 flux and soil

nutrient content. Our primary goals were to assess: 1. how these common biocrust types respond biologically and physiologically to a gradient of precipitation pulses and frequencies, 2. if there is an optimal pulse size and frequency for biocrust carbon uptake and 3. how differences in pulse size and frequency influence biocrust nutrient inputs into the surrounding soil. We hypothesized substantial differences in moss physiological responses, C flux, and nutrient contributions with variations in watering amounts and frequency, while anticipating a muted response of darkly-pigmented cyanobacterial crusts due to differences in how the two crust types utilize precipitation pulses. We hypothesized a threshold of water amount and frequency, over which moss crusts perform better, and a decline in nutrient retention at high watering amounts for both crust types, due to nutrients being flushed from the biocrust into deeper soil layers.



Watering (mm)	*Cyano threshold time (hours) (mean +/- s.d.)*	*Moss threshold time (hours) (mean +/-, s.d.)*
1.8	9.5 +/- 0.24	7.8 +/- 0.17

2.7	9.6 +/- 0.15	8.4 +/- 0.22
5.4	30.4 +/-1.4	18.6 +/- 0.61
7.7	40.3 +/- 0.82	20.9 +/- 0.85
10	37.5 +/- 0.64	35.2 +/- 1.1

Figure 4.1. Gravimetric water content (GWC) is the standardized water content determined from surface moisture probes. Hours since water was determined by determining when wetness periods started in the data set, and then counting upwards until water content fell below the wetness threshold for at least 50 sequential readings. The horizontal line represents the detectable wetness threshold for each crust type. The vertical lines represent the duration of detectable wetness based on where the dry down curves intersect the wetness threshold. The table shows the mean number of hours +/- s.d. that each treatment remained wet after a watering treatment.

METHODS

We collected darkly-pigmented cyanobacterial crust likely dominated by *Microcoleus vaginatus* and *Scytonema* spp., (Couradeau et al. 2016) and moss crust samples consisting of *Syntrichia caninervis* down to 10 cm depth from within a quarter mile area outside of Moab, UT, USA (38° 38'07.87" N, 109° 46 30.36" W). Samples were collected in 10 cm diameter and 10 cm deep plastic collars that maintained the soil column and biocrust surface intact. The soil type was a fine sandy-loam and the ecological site description was Utah Juniper, blackbrush (USDA Web Soil Survey). We brought the biocrust samples to a greenhouse attached to the Southwest Biological Science Center in Moab, Utah, USA.

After a one-week period, we began to administer watering treatments on the crust samples. We added the following volumes and frequencies of deionized water: 1.8 mm three days a week, 2.7 mm two days a week, 5.4 mm one day a week, 7.7 mm every week and a half and 10 mm every two weeks over a three-month period. We had $n = 5$ replicates per treatment. The mean precipitation amount was 70 mm per area and was equal to the mean upper quartile range of rainfall over a four-month period from April – July 2009-2016.

Inside the greenhouse, we monitored photosynthetically active radiation (PAR) using an Apogee Instruments Quantum Sensor SQ-215. Greenhouse temperature was measured using a Campbell Scientific Model 108 (CS-108) where the temperature probe shielded by vented, white polyvinyl housing to prevent direct infrared absorption. Relative humidity (RH) was measured using a Campbell HMP35C sensor. We also collected environmental data from the Mesowest website (https://mesowest.utah.edu/) that records data from a climate station less than a quarter mile away from our greenhouse site (station ID: MOAB). These data were used to compare the greenhouse conditions with ambient environmental conditions.

In order to monitor the amount of time the samples remained wet, we measured soil moisture to a depth of ~ 2 mm every 10 minutes for the duration of the experiment in three replicates of each treatment using soil moisture probes described in Howell et al. (2019). Briefly, the probes measured water content of the biocrust layer based on calculated of conductance from 2, 3 mm long copper electrodes. Sensor insertion caused almost no damage to the biocrust and cover less than 1 cm^2 surface area. Mopro sensor data were calibrated from units of siemens to gravimetric water content using the approach described in Howell et al. (2019). Because the mesocosm structure was different from the calibration samples, we additionally rescaled the calibrated gravimetric water content with maximum and minimum wetness specific to each pot

using the ‘rescale’ function in R package ‘pracma’ (Borchers 2019). Thus, the shape of the curve was determined by the laboratory calibrations, and the scale by the maximum and minimum water content of each sample.

We used the R package ‘drc’ to fit dry down curves to our surface moisture data (Ritz et al. 2015). Analysis indicated that a 3-parameter exponential decay model with the lower asymptote specified as the lower water content measured in our data set fit the data better than either a two-parameter exponential decay function, or a 3-parameter exponential decay function with no lower limit specified ($p<0.01$). The exponential decay model indicates that both cyanobacterial and moss crust dried similarly rapidly at 1.8 and 2.7 mm rainfall (Figure 4.1) Cyanobacterial crust remained detectably wet longer than moss crusts after 5.4 and 7.7 mm rainfall and both crust types remained wet for >35 hours after 10 mm rainfall (Figure 4.1).

To examine the physiological responses of moss crusts to differences in watering frequency and amounts, we measured the maximum photochemical quantum yield of PS II (Fv/Fm), the effective photochemical quantum of PS II (Y(II)), and non-photochemical florescence quenching (NPQ) on dark-adapted moss crust at 30 minutes and 120 after watering. These photosynthetic parameters have been shown to change with watering amounts and light with *Syntrichia caninervis* (Ekwealor et al. 2020). After giving moss crusts their treatment water amount, we placed a DLC-8 Dark Leaf Clip on the surface of the moss crust then placed the sample under a cardboard box to dark-adapt the sample. The samples remained under the box for 30 minutes, after which they were removed and measured using a MINI-PAM II (Heinz Walz GmbH, 2018). A script was run with actinic light of photosynthetic flux density before and after the actinic light.

In order to see how precipitation pulses and frequency influence CO_2 exchange, we measured net soil exchange (NSE; Darrouzet-Nardi 2015), respiration (R), and gross primary production (GPP) at the end of the experiment on all samples. NSE was measured using a custom-made transparent chamber (that sealed over the mesocosm and attached to a LI-8100A Automated Soil Gas Flux System (Li-Cor Inc, Lincoln, NE, USA) (Figure 4.2). R was measured in the dark using 10 cm Survey Chambers. CO_2 fluxes were calculated using Li-Cor File Viewer software by the linear fit to the water-corrected CO_2 concentration change over a 2.5-minute period following a 30-s dead band. GPP was calculated as the difference between NSE and R. This calculation was chosen to ensure that fluxes into the atmosphere were positive, where R has a positive sign, GPP has negative sign, and NSE is either be positive or negative, depending on whether more CO_2 is being taken up or released from the mesocosm.

Figure 4.2. Transparent soil CO_2 exchange chamber designed for the experiment. Chamber is made out of clear polycarbonate and attached to a LI-8100A Automated Soil Gas Flux System (Li-Cor Inc, Lincoln, NE, USA). The base of the dome was screwed into the mounting piece of the Li-Cor that fits over a ~10 cm diameter container. Dome was made by Stressed Skin Design, Inc, Grand Junction, CO

To determine the effect of different precipitation pulses and frequencies on pigment concentrations of darkly-pigmented biocrust samples, we extracted chlorophyll a (Chla) and scytonemin (Scy) with 90 % acetone for 18 hours in the dark at 4 ºC after being finely ground with agate stone mortar and pestle(Castle et al., 2011). The supernatant was decanted, and pigment concentrations were measured spectrophotometrically (Synergy H1 Hybrid Plate Reader, Biotek, Winooski, Vermont, USA) at 665 nm for Chla and 384, 663, and 490 nm for Scy. The equation to convert the A665 value to [Chla] was taken from Ritchie et al (2007) and to convert the A384, A663, and A490 nm values to [Scy] was taken from Garcia-Pichel and Castenholz (1991).

To understand the influence of moisture pulses on soil nutrients at the end of the experiment, we took one 0 – 5 cm soil cores with the mesocosm and measured inorganic N pools, NH_4^+ and NO_3^-, using 2 M KCl on fresh soil sieved through 2 mm wire mesh. For the moss samples, we removed the aboveground moss tissue from the soil cores. The soil slurry was shaken for 1 hour then allowed to settle overnight (Robertson et al. 1999). Soil PO_4^{3-} was extracted using Olsen's method, with a 0.5 M $NaHCO_3$ solution and a shaking time of 16 hrs (Olsen 1954). Total dissolved organic C and N were extracted with 0.5 M K_2SO_4, shaken for 1 hr (Weintraub et al. 2007). We also placed anion and cation resin strips beneath each biocrust in the

larger mesocosm experiment to examine accumulated nutrients through time. Resin strips were extracted in 20 mL of 2 M KCl. All extracts were filtered through Whatman #1 filter paper (GE Healthcare, Chicago, IL). A subsample of fresh soil was removed to assess soil %C and N via elemental analysis (Elementar Americas, Mt. Laurel, NJ).

Inorganic N concentrations (NH_4^+ and NO_3^-) were quantified colorimetrically using the indophenol blue method for NH_4^+ and using a Cd-column reduction followed by the Greiss-Ilosvay method for NO_3^-. Soil extractable PO_4^{3-} and microbial PO_4^{3-} concentrations were quantified using a modified ascorbic acid molybdate analysis (Kuo 1996). All colorimetric reactions were performed on a Smartchem 200 Discrete Autoanalyzer (Unity Scientific, Milford, MA). Extractable organic C and total dissolved N were analyzed on a Shimadzu TOC-V_{CPN} with the TNM-1 attachment (Shimadzu Corporation, Kyoto, Japan).

Statistics were performed using R. Data were checked for normality and, when non-normal, the data were transformed to achieve normality. We conducted a two-way ANOVA and Tukeys HSD to assess differences in response variables between treatments. We also calculated the differences in the magnitudes among response variables. The data were non-negative, showed some degree of log normality and contained zeroes. As such, we calculated 95% confidence intervals for the ratios using a maximum-likelihood method designed for data with these features (Zhou and Tu 2000). Confidence intervals not containing 1 are considered statistically significant for $H_0 = 1$, which would correspond to a 1:1 ratio, or no difference among crust types (likelihood ratio test; Zho and Tu 1999; Zhou and Tu 2000). The calculations were conducted using the package 'treateffect' in R (Darrouzet-Nardi, 2020).

RESULTS

Greenhouse Climate

Maximum temperature in the greenhouse ranged from an average of 30 °C in April to 40°C in July which is similar to maximum outdoor air temperature (Figure 4.3). Relative humidity (RH) ranged peaked at 49% in April, which was about 6% higher than relative humidity outside of the greenhouse.

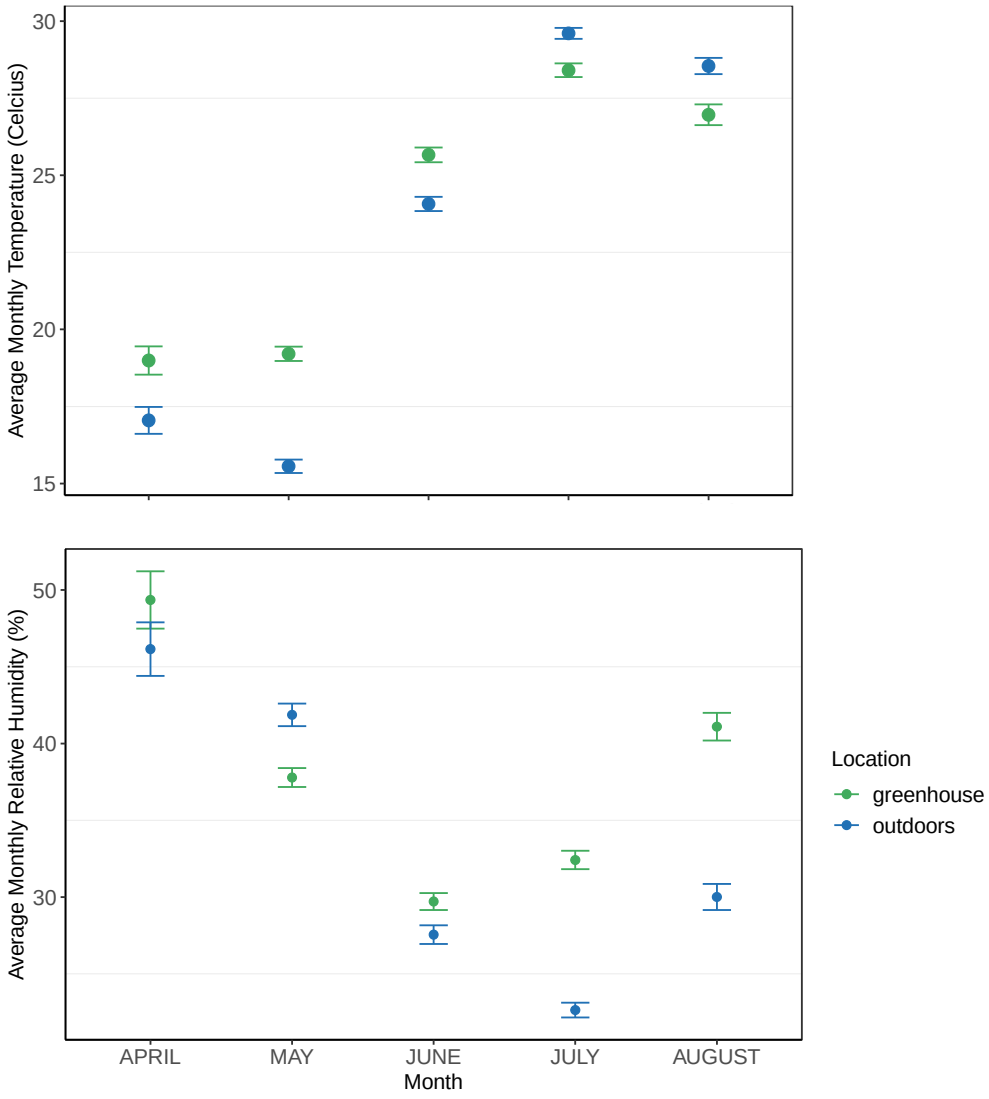


Figure 4.3. Average monthly temperature and average monthly relative humidity in the greenhouse and at the outdoor weather station adjacent to the greenhouse for the course of the experiment. Error bars represent SE.

Volumetric Water Content

The administered watering treatments were reflected in the 0 – 0.5 cm volumetric water content. The duration of wetness for each watering event increased linearly from the smallest watering treatment to the largest (Adjusted R^2 = 0.64, p-value = >0.001) while the cumulative amount of time spent wet over the four-month experiment was the same for each treatment (Adjusted R^2 = -0.04, p-value = 0.58).

Biological & Physiological Measurements

Chlorophyll *a* and scytonemin content in the darkly-pigmented crusts were similar across watering treatments at the end of the experiment (F = 1.47, p-value = 0.25). Fv/Fm values, the maximum potential quantum efficiency of Photosystem II, were similar across watering treatments for moss crusts at both 30 minutes after watering (F = 1.31, p-value = 0.3) and 120 minutes after watering (F = 1.06, p-value = 0.4). The Y(II), a measurement ratio of plant efficiency, of moss crusts was lower in larger watering treatment samples 30 minutes after watering (F = 4.17, p-value = 0.01), with Y(II) in mosses 13% less in the 10 mm watering treatment than the 1.8 mm watering treatment (10mm:1.8mm = 0.86 [0.77, 0.97; 95% CI]). Moss crust NPQ was higher in the larger watering treatment samples 120 minutes after watering (F = 4.43, p-value = 0.01), with NPQ at the 10 mm watering treatment 2.5 times more than the 1.8 mm watering treatment (10mm:1.8mm = 3.19 [1.25, 8.11; 95% CI]) (Figure 4.4).

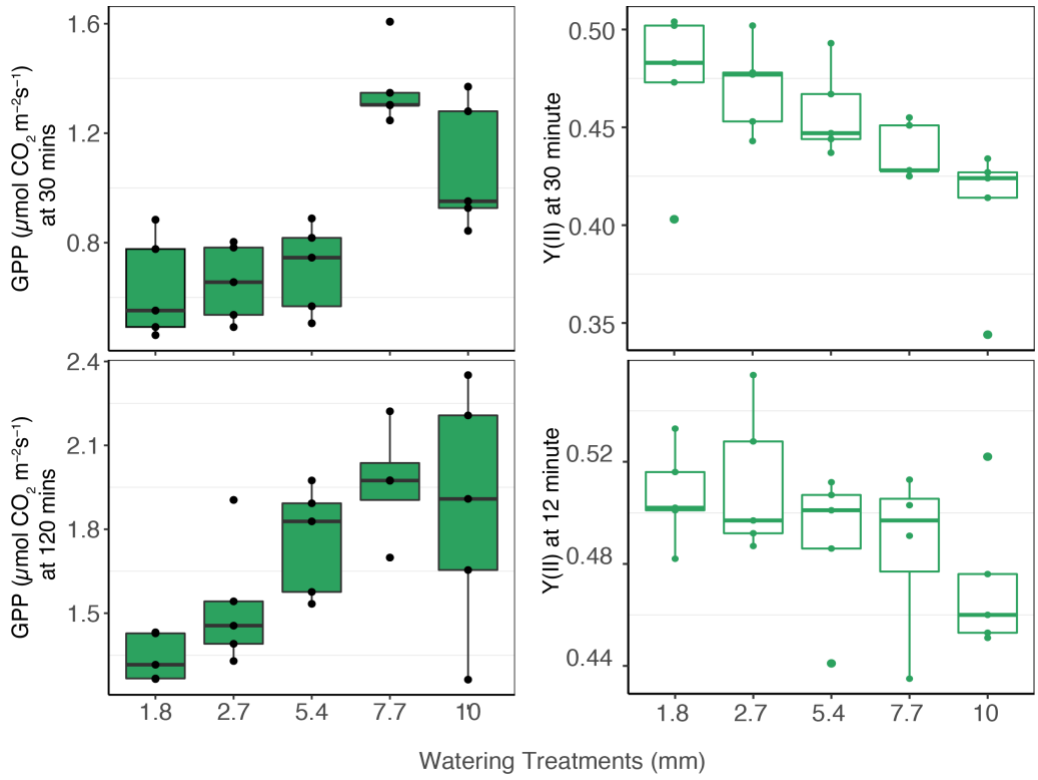


Figure 4.4. Left: Boxplots showing the average calculated GPP values for moss crusts 30 minutes (top row) and 120 minutes (bottom row) after watering. Right: Box plots showing Y(II) values at same time points. Vertical bars on the boxplots represent median values and the horizontal lines represent minimum and maximum values. Points are the values from the n = 5 samples.

Carbon Flux

Darkly-pigmented cyanobacteria crusts

Overall, the largest differences in CO_2 flux from darkly-pigmented crusts appeared between the smallest and the two largest watering treatments. Respiration in the 7 mm and 10 mm treatments were around 1.5 times as much as respiration values in the 1.8 mm watering treatments 120 minutes after watering (7.7mm:1.8mm = 1.39 [1.24, 1.57; 95% CI]) (30 minutes, F = 4.27, p-value = 0.01, 120 minutes, F = 5.39, p-value = 0.005). GPP was similar between the

1.8, 2.7, and 5.4 mm watering treatments at 30 minutes after watering, but CO_2 uptake amounts in 7.7 mm and 10 mm water treatments were almost twice as large (7.7mm:1.8mm = 1.86 [1.37, 2.53; 95% CI], 10mm:1.8mm = 1.69 [1.17, 2.43; 95% CI]) in the 7.7 mm and 10 mm treatments as the 1.8 mm treatments (F = 10.47, p-value = >0.001). At 120 minutes after watering, GPP in 10 mm water treatments was 1.5 times (10mm:1mm = 1.45 [1.24, 1.71; 95% CI]) as much as the 1.8 mm watering treatments but was generally similar all other across treatments (F = 3.39, p-value = 0.03). NSE was similar across all watering treatments at both 30 minutes (F = 2.31, p-value = 0.1) and 120 minutes after watering (F = 0.44, p-value = 0.78). NSE, Respiration, and GPP values in moss crusts were consistently 1.4 times as much as CO_2 fluxes in darkly pigmented cyanobacterial crusts (Appendix Supplemental Table 4.2) with the exception of NSE at 120 minutes after watering, which was similar between crust types ($t(44)=-0.75$, $p = 0.46$).

Moss crusts

Generally speaking, CO_2 flux measurements in moss crusts were similar between the 1.7, 2.7, and 5.4-mm watering treatments and then increased and leveled off at the 7.7 and 10 mm watering treatments. At 30 minutes after watering, moss crust respiration was similar between the 1.7, 2.7, and 5.4 mm watering events but then increased so that GPP at 7.7 mm was 1.5 times (7.7mm:5.4mm = 1.92 [1.52, 2.42; 95% CI]) as much as GPP at 5.4 mm, and remained similar at the 10 mm watering treatment (F = 16.91, p-value = >0.001) (Figure 4.4). Moss respiration increased mostly linearly from 1.8 mm to 10 mm watering treatments 120 minutes after watering (F = 22.38, p = >0.001) with respiration in 10mm treatments 1.6 times as much as respiration in the 1.8 mm treatments (10mm:1.8mm = 1.61[1.45, 1.78; 95% CI]). GPP was again similar between the 1.7, 2.7, and 5.4 mm watering events and increased to where GPP in the 7.7. mm and 10 mm treatments were around 1.5 times (7.7mm:5.4mm = 1.92 [1.52, 2.42; 95% CI],

10mm:5.4mm = 1.5 [1.14, 2.02; 95% CI]) as much as the 5.4 mm treatment watering treatments 30 minutes after watering (F = 16.473, p = >0.001). However, at 120 minutes differences in GPP were only apparent between the 1.8 mm watering events and the 7.7 and 10 mm watering events, which were around 1.8 times as high (7.7mm:1.8mm = 1.86 [1.37, 2.53; 95% CI]) (F = 4.62, p-value = 0.009). NSE was similar between watering treatments 30 minutes after watering (F = 1.3416, p-value = 0.2892) but the 10 mm watering treatment was around 2 times as much as the 1.8 mm (10mm:1.8mm = 2.33 [1.54, 3.5; 95% CI]) and 2.7 mm watering treatment 120 minutes after watering. and 2.7 mm treatments (10mm:2.7mm = 2.69 [1.6, 4.5; 95% CI]) (F = 5.855, p-value = 0.003).

Nutrients

Darkly-pigmented cyano crusts

Nutrients in the soil below darkly pigmented cyanobacterial crusts were largely similar between watering treatments. The one exception is NO_3-, where soil under the 7.7 mm watering treatment had 4 times (7.7mm:1.8mm = 3.95 [2.27, 6.9; 95% CI]) as much NO_3- than the soil under the 1.8 mm treatment (F = 2.66, p-value = 0.06) (Figure 4.5). While not statistically significant at an alpha level of 0.5 due to the large amount of variability, the average amounts of NO_3^- collected on resin strips at the 10 mm watering treatments were 5 times (10mm:1.8mm = 5.26 [2.19, 12.62; 95% CI]) as much as NO_3^- on resin within the 1.8 mm watering treatment (F = 1.88, p-value = 0.15) (Figure 4.5). The amounts of NH_4^-, TON, PO_4^{3-}, NPOC, %N & %OC in the soil remained consistent across watering treatments (Appendix Supplemental Table 1). Percent N in the biocrust was twice (0-0.5cm:0.5-5cm = 2.05 [1.66, 2.52; 95% CI]) as much as %N in the soil beneath (t(68)=-5.2, p-value = >.001). The concentrations of PO_4^{3-} in moss crust was over 1.5 times (moss:cyano = 1.6[1.34, 1.98; 95% CI]) as much as the

concertation's in darkly pigment crusts NPOC was 2.4 times (NPOC moss:cyano = 2.38 [1.84, 3.06; 95% CI]) as high. Concentrations of NO_3^-, NH_4^-, and %C were similar between biocrust types (Appendix Supplemental Table 1).

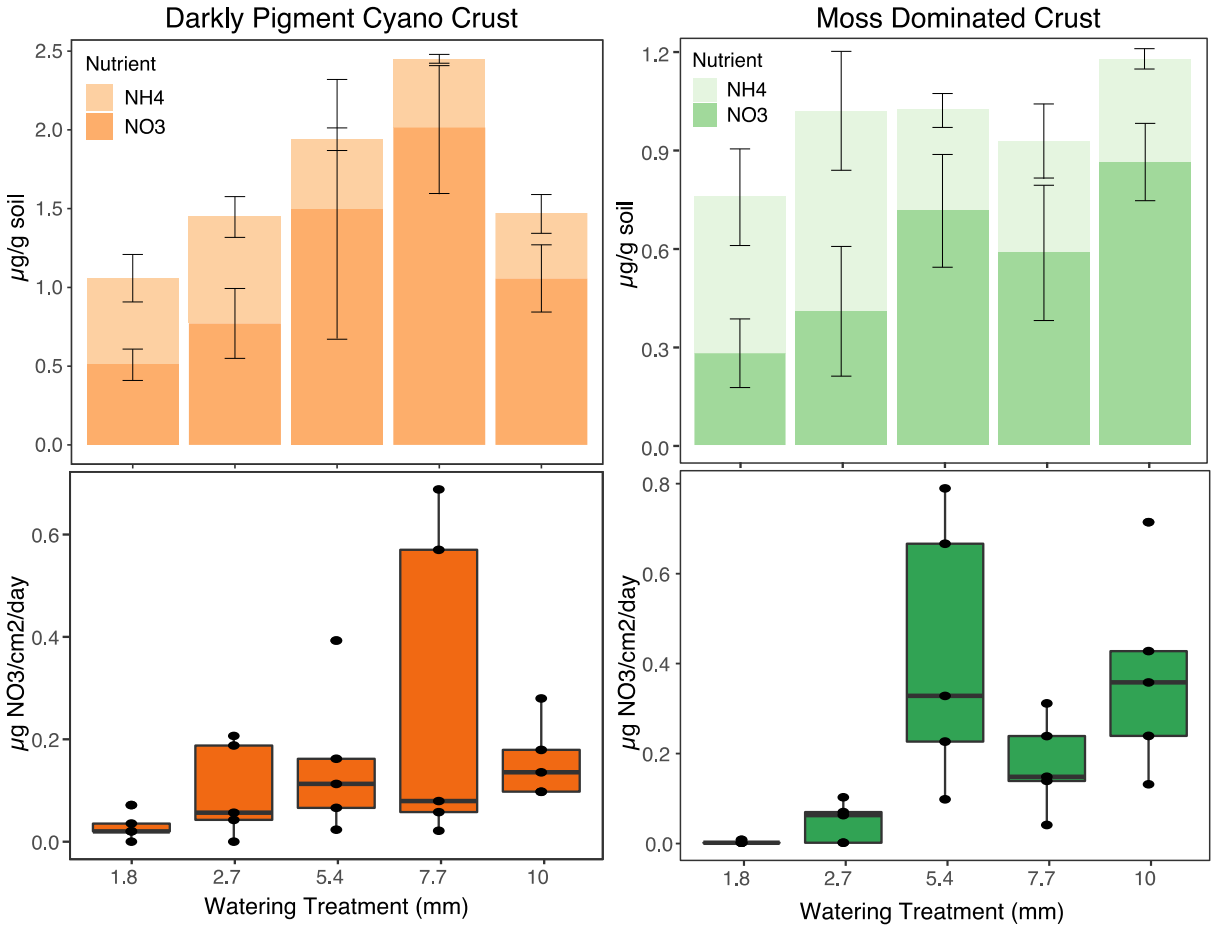


Figure 4.5. Top panel: Average values for extracted NO_3^- and NH_4 from the soil beneath cyanobacterial crusts (left panel) and moss crusts (right panel) after 4 months of watering treatments. Error bars are standard error. Bottom panel: Boxplots showing accumulated NO_3^- amounts on resin strips below cyanobacterial crusts (left panel) and moss crusts (right panel). Vertical bars on the boxplots represent median values and the horizontal lines represent minimum and maximum values. Points are the values from the n = 5 samples.

Moss crusts

Nutrients within and below moss crusts were also relatively similar between watering treatments. The main exception was NO_3- amounts collected on resin strips below the moss crusts, which were near 0 µg/cm^2/day at the 1.8 mm and 2.7 mm watering treatments, then increased to around 0.3 µg/cm^2/day at the 5.4 mm watering treatments and remained similar at 7.7 and 10 mm watering treatments (F = 12.81, p-value = >0.001). %N in the moss was around 1.2 times (0-0.5:0.5-5 = 1.18 [1.03 ,1.36; 95% CI]) as much as %N in the soil beneath (t(44) = -2.12, p-value = 0.04). The amounts of NH_4-, TON, PO_4^{3-}, NPOC, %N & %OC in the soil remained consistent across watering treatments (Appendix Supplemental Table 1).

DISCUSSION

Understanding how the biological constituents of drylands respond to variation in precipitation amount and frequency is essential to anticipating ecological responses in this pulse-dominated biome (Ferrenberg et al. 2015). Here, we examined two common biocrust types and hypothesized substantial differences in their responses to variation in precipitation due to different pulse-utilization strategies and the presence of precipitation thresholds that determine functional responses. While the two biocrust types did respond differently to alterations in precipitation, the differences were not as large as anticipated. Instead, it appears that within a

greenhouse setting, both biocrust types can utilize varied precipitation pulses in such a way that their performance and biomass maintenance (measured as Fv/Fm in moss crust, chlorophyll *a* in darkly-pigmented crust, and CO_2 flux in both crust types) does not dramatically change under a gradient of pulse sizes and varied frequencies. Similarly, nutrient contributions in the 2-5 cm soil below the biocrust were surprisingly similar across biocrust types and watering amounts, with the exception of nitrate which showed noticeable differences across treatments. Below we explore the trends we observed, many of which point to mechanisms that enable biocrusts to maintain performance and biomass under highly varied precipitation patterns, and the consequences for nutrient contributions to the soil.

Carbon-Use Strategies

Contrary to our hypothesis, we did not observe large increases in moss or cyano-crust net C uptake from the small frequent to large infrequent watering events. In fact, net soil exchange (NSE) values in moss and cyanobacteria crusts were positive (meaning more C was respired than taken up) and similar across watering treatments and crust type. This is likely due to the mesocosm design, which included biocrusts as well as the 10 cm soil column below. The intact soil column would have contained respiring heterotrophs (Darrouzet-Nardi et al. 2015), therefore a positive NSE may not represent a negative C balance for the moss and cyanobacterial crusts. Calculated GPP values, however, do provide some insights into how precipitation frequency and amounts may have influenced biocrust C fluxes. In our experiment, calculated GPP values along the gradient of watering amounts and frequencies demonstrated a threshold-like pattern between 5.7 mm and 7.7 mm watering events. Calculated GPP was similar within each crust type between the 1.8 – 5.4 mm frequent watering treatments, then increased at the 7.7 mm less frequent watering treatment and remained similar at 10 mm infrequent events. This step-wise increase

suggests a threshold between 5.4 and 7.7 mm of water, over which calculated GPP is greater, and also suggests a leveling off of GPP around 7.7 mm of water. We propose that this leveling-off can be partially explained by the legacy of watering frequency on moss and cyanobacterial photosynthesis, which we explore below.

The length of desiccation can affect the speed at which photosynthesis can restart after a precipitation event (Proctor et al. 2007). Shorter desiccation times result in faster activation of photosynthesis in both cyanobacterial and moss crusts (Potts 1999). Processes such as non-photochemical quenching (NPQ), a photoprotective mechanism that decreases quantum efficiency of photosynthesis (Müller et al. 2001; Ruban 2016; Malnoë 2018), can take hours to days to relax and for photosynthesis to resume at pre-desiccation levels (Ekwealor et al. 2020). Here, we saw evidence of reduced photosystem II efficiency and NPQ in less frequent watering treatments, despite these treatments have the largest pulse sizes and remaining wet the longest. This reduced efficiency may have contributed to the leveling off of CO_2 uptake within the largest watering event. Just as frequent, smaller precipitation events have been shown to reduce the capacity for carbon uptake (Reed et al. 2012), infrequent watering events also appear to limit carbon uptake in the short term. However, within our experiment, neither moss or cyanobacterial crusts showed signs of stress or C starvation within their tissue over 4 months of the watering treatments, suggesting the variety of photosystem responses to water frequency and timing we observed are sufficient to maintain a positive C balance over multiple months.

Unlike other studies examining small frequent watering events in biocrust mosses, we did not see evidence of stress or mortality in our small, frequent watering treatment. In previous studies, smaller watering events were shown to make biocrust susceptible to net C losses, where respiration exceeded uptake (Coe et al. 2012). Over time, this net C loss led to evidence of stress

and mortality within mosses in multiple studies (Reed et al. 2012; Maestre et al. 2013; Zhang et al. 2018). To achieve a positive C balance, moss crusts are thought to need around 2 mm of water (Reed et al. 2012; Zhang et al. 2018) while cyanobacterial crusts are thought to need over 1.5 mm (Strong et al. 2013). Despite administering frequent, 1.8 mm events, we did not see any evidence of stress within the moss samples. One explanation for these divergent results is the higher levels of humidity, and therefore less evaporative demand, experienced by mosses during the course of our experiment. While temperatures within the greenhouse were similar to the ambient outdoor temperature, humidity in the greenhouse was higher in the months of July and August than outdoor humidity. This reduced evaporative demand likely lengthened the period of available soil moisture for crusts when compared to other experiments that administered small frequent watering events outdoors (Reed et al. 2012; Zhang et al. 2018). These differences suggest that the threshold under which moss mortality occurs is not at a particular water amount, but instead a soil moisture duration threshold which is controlled by the evaporative demand from the atmosphere. Within our experience, 1.8 mm of water that was retained for 7 hours appears to be enough water to maintain a positive C balance over the course of the experiment.

Nutrient-dynamics and ecosystem responses

Despite providing substantially different volumes of water, we saw few differences between watering treatments in the concentrations of inorganic C, organic C, NH_4^+, and PO_4^- in the soil beneath moss and cyanobacterial biocrust at the end of the experiment. This was surprising, as the duration of wetting is thought to be a main determinant in the amount of nutrient cycling and accumulation that can occur within biocrust (Morillas and Gallardo 2015). The one exception was NO_3^-, which showed a pattern of increasing concentration in the soil beneath moss and cyanobacterial crusts from the small frequent watering events to the large

infrequent events. NO_3^- is the most mobile form of N and is a product of N fixation that occurs within cyanobacterial crusts (Stewart 1970). Our results suggest more NO_3^- is being moved downward into the soil profile with progressively larger watering events. Interestingly, the NO_3^- concentrations beneath cyanobacterial crusts decreased under the highest, most infrequent watering treatments (10 mm), which may indicate that the NO_3^- is being moved further into the soil profile (>5 cm) than we measured. Within our experiment, 7.7 mm of water administered once a week appears to move the most N from cyanobacterial biocrust into the soil. Because biocrust can be the main contributor of N to dryland systems (Evans and Ehleringer 1993; Barger et al. 2016), understanding how precipitation amounts and frequencies interact to control N fixation and accumulation within biocrust, and deeper soil layers is necessary for anticipating changes to N availability (Barger et al. 2016). Here, we see evidence that smaller, frequent watering events move little to no NO_3^- into the soil below biocrusts while large, infrequent watering events may move NO_3^- into soil layers > 5 cm deep.

CONCLUSION:

Like all desert life, biocrusts have a range of adaptations that make it possible for them to survive in harsh environments. Within this experiment, the variations we administered in precipitation amounts and frequencies did not push the biocrust organisms outside of their physiological capacity or largely alter biogeochemical cycling within biocrust mesocosms. Instead, both darkly pigmented cyanobacterial crusts and moss crusts appear to have mechanisms that allow for the large variations in precipitation we administered, including non-photochemical quenching and the ability to rapidly respond to precipitation. These findings emphasize the need to continue to undercover the underlying mechanisms that determine biocrusts response to

changes in precipitation so that we are better able to understand the consequences of a rapidly changing climate.

Chapter 5: Conclusion

Dryland restoration is exceedingly difficult due to the myriad ecological and biogeochemical changes associated with dryland degradation (Schlesinger et al. 1990; Peters et al. 2006). In this dissertation, I examined biogeochemical changes that accompany degradation and explored ways to reverse it. Additionally, I offered new insights into the role of biocrust in contributing to soil fertility, and how those contributions may change with climate change. Below, I present multiple conclusions about our ability to restore drylands and the role of biocrusts in maintaining and restoring ecological functions in dryland settings, including 1. The need to understand the biogeochemical make up of novel states 2. The role of biocrust in subsoil fertility 3. The challenges associated with biocrust restoration 4. The need for a dryland-specific field of ecological restoration.

THE NEED TO UNDERSTAND THE BIOGEOCHEMICAL MAKE UP OF NOVEL STATES

State-changes within drylands make restoring to a previous ecological state difficult if not impossible (Bestelmeyer et al. 2015). State changes are processes that include changes in connectivity (e.g. Okin et al. 2015; Rachal et al. 2015), shifts in species dominance (e.g. D'Odorico et al. 2012), soil loss (e.g. Belnap et al. 2009; Duniway et al. 2019), invasion by non-native species (e.g. D'Antonio & Vitousek 1992; Belnap & Phillips 2001), and interactions therein (e.g. Ravi et al. 2010). With these changes comes concomitant changes in biogeochemical cycles that have been explored from small (Breshears 1998; Belnap and Sherrod 2008; Throop and Archer 2008) to large (Ridolfi et al. 2008; Barger et al. 2011) scales. As drylands expand due to climate change and degradation increases (Ye et al. 2019a) the occurrence of novel states will likely increase. Understanding how to manage these novel states will require an understanding of the biogeochemical processes that control biomass accumulation

and resource loss in these new ecological types. Within drylands, it may be beneficial to move away from attempts to restore ecosystems to a previous ecological state and instead spend resources in trying to figure out how to maintain desired ecological functions (i.e., soil stability, carbon sequestration, etc.) in novel states. This point is emphasized by the dismal rates of restoration success within drylands, which can be as low as 5% in some dryland types (James et al. 2011). The information presented in chapter 1 can be applied to novel ecological states and represents a way forward for understanding and managing the biogeochemical underpinnings of degraded drylands.

THE ROLE OF BIOCRUST IN SUBSOIL FERTILITY

Restoration requires an understanding of how biotic components are interacting to influence ecosystem functions (Temperton et al. 2004). However, our understanding of interactions between the two main primary producers in drylands, vascular plants and biocrusts, is limited (Zhang et al. 2016). Noticeably lacking is a clear understanding of the role of biocrust in providing available nutrients to vascular plants (Rudgers et al. 2018). Experimentation has shown that plants grown within biocrust have higher nutrient content in leaf tissue (e.g., Ferrenberg et al. 2018) and isotopic data has shown that N fixed by biocrust can end up in vascular plant tissue (Mayland and McIntosh 1966; Stewart 1967). However, the exact mechanisms through which biocrust-derived nutrients, namely N, are made available to plants remains unclear. Multiple studies have shown lateral movement of isotopically labeled N from biocrusts into plant tissue and, in some cases, the movement of labeled C from plants to biocrust (Green et al. 2008; Aanderud et al. 2017; Carvajal and Coe 2021). Fungal connections, namely dark septate-endophytes, have been proposed as the main mechanism through which N and C are being exchanged between biocrust and plants (Rudgers et al. 2018a; Dettweiler-Robinson et al.

2019). However, simultaneous lines of evidence are pointing to the existence of a 'cyanosphere' or area of nutrient exchange within the cyanobacteria dominated layer of biocrust (Couradeau et al. 2019a; Nelson et al. 2021). The exchange of metabolites within the cyanosphere between photoautotrophic cyanobacteria and heterotrophic microbes suggests that cyanobacteria are in a symbiotic relationship with N-fixing heterotrophs to provide C in exchange for N (Swenson et al. 2015; Baran et al. 2015). This relatively closed system of exchange calls into question the utility of long-distance fungal exchange of nutrients when the cyanosphere appears to produce enough C and N for cyanobacterial survival at the micrometer scale. However, the multiple and mounting lines of evidence for the rapid lateral transfer of N and C across the soil surface cannot be discounted and either represents a major undetected methodological flaw with isotope labeling or a yet unexplained mechanism moving N and C across the soil. In chapter 2, I explored the role of leachate in transferring nutrients and C into deeper soil layers. The downward movement of resources likely represents a main pathway through which biocrust-derived nutrients are entering the soil and being utilized by vascular plants. This pathway could also explain rapid transfer from biocrusts to plant tissue through root uptake during precipitation or experimental watering. However, this pathway does not appear to explain evidence of soil surface N transfer that has been shown in multiple studies (Carvajal and Coe 2021), excepting cases of evaporative demand pulling diffused leached label back up to the soil surface. To effectively answer these questions, a better understanding of the water dynamics within the soil matrix is required, as water is clearly a factor in translocation of nutrients, either through passive movement or through the activation of short or long-distance microbial transfer. Understanding the hydrologic mechanisms of nutrient translocation would allow for a better understanding of

the relationship between biocrust and plants, and how that relationship may change as precipitation patterns change in drylands (Schwinning et al. 2004).

THE CHALLENGES ASSOCIATED WITH BIOCRUST RESTORATION

The research presented in this dissertation, specifically chapters 2 and 3, can help inform the restoration of ecologically important communities of biological soil crust. Stabilizing and returning nutrients to desert soils is one of the main challenges associated with dryland restoration (Plaza et al. 2018). Because biocrusts act as effective soil stabilizers and provide C and N into the soil, there is considerable interest in restoring biocrusts in degraded regions (Antoninka et al. 2020). While there is large potential in the application of biocrust as a restoration tool (Bowker 2007) there have also been challenges and minimal success during biocrust restoration trials (Chandler et al. 2019; Young et al. 2019; Faist et al. 2019). The lack of successful propagation has been attributed to releasing propagules in the wrong season (Young et al. 2019) and unstable soil surfaces on which to establish biocrust propagules (Faist et al 2019). Instances where biocrust restoration has been successful have involved substantial habitat modifications (Fick et al. 2020), such as in the case of straw-checkboards in China (Li et al. 2006), and supplemental water (Xiao et al. 2015). The requirement of habitat modifications calls into question the utility of biocrust propagules as efficient tools for restoration. While a thorough meta-analysis exploring the variables that result in successful biocrust restoration is forthcoming, there are multiple insights that can be gleaned from the literature that may help improve biocrust restoration research.

One way in which biocrust restoration research could be improved is by standardizing a control. Most biocrust restoration experiments measure restoration success in terms of increase in biocrust cover, or a similar biomass metric, through time (e.g., Román et al. 2018). This

increase is typically compared to a control in which no biocrust propagules were added (e.g., Giraldo-Silva et al. 2020). While it is valuable to show that propagules can grow through time, there would also be utility in understanding the presence or function of biocrust compared to a pre-disturbance level or compared to some standardized metric of a desired functional response, such as a desired soil stability level. Further, when measuring chlorophyll *a* as a main determinant of biomass, there are clear methodological inconsistencies that allow for orders of magnitude more chlorophyll *a* being reported in some studies as opposed to others (e.g., Wang et al. 2009; Seiderer et al. 2017). Determining a single method for chlorophyll *a* determination would allow practitioners to set target chlorophyll levels when performing restoration and provide effective benchmarks with which to measure restoration success.

Adding biocrust propagules has been the main focus in biocrust restoration. However, the lack of consistent success with propagule addition calls into question whether propagule scarcity is the reason behind the lack of biocrust in degraded systems. Because biocrust species can propagate vegetatively (Tilman and Wedin 1991) and be dispersed through wind (Bowker et al. 2010), it seems unlikely that propagule scarcity is the main reason biocrusts aren't recovering. While considerable research has addressed the ways in which biocrusts are disturbed, namely trampling and climate change (Belnap and Gillette 1998; Ferrenberg et al. 2015), there is less research on the barriers to biocrust establishment. Further experimentation exploring these barriers, such as unstable soils, compacted soils, water limitation, nutrient limitation, and repeat disturbance at restoration sites, would likely aid in our ability to ameliorate the habitat so that natural recovery can take place or propagules can be effectively added.

While growing biocrusts in a greenhouse or lab setting and reintroducing it to the landscape represents an exciting way forward in biocrust restoration, there is considerably less

energy put into salvaging biocrusts on the landscape before a disturbance takes place (Tucker et al. 2020a). Salvaging biocrust may represent the best way forward in biocrust restoration, as transplanted biocrusts have had some of the largest success rates within biocrust restoration experiments (e.g., Chiquoine et al. 2016). The field of biocrust restoration would benefit from this cost-effective step, in addition to advocating for biocrust conservation where possible.

THE NEED FOR A DRYLAND-SPECIFIC FIELD OF RESTORATION.

The many challenges associated with dryland degradation and the many holes in our understanding of dryland function that have been outlined in this dissertation point to the need for a dryland-specific field of ecological restoration. Past modes of restoration that focus on references states and seeding are proving ineffective in the dryland biome (Bestelmeyer 2006; James et al. 2011). This challenge is increasingly being recognized and met with dryland-specific models of restoration, including state and transition models (Bestelmeyer et al. 2009), connectively models (Okin et al. 2015), quantitative dryland restoration models (James and Carrick 2016a), and socio-economic models (Reynolds et al. 2007b). However, modes of restoration that span organismal types and offer effective restoration tools are lacking (Collins et al. 2014a; Winkler et al. 2018b; Bradford et al. 2018). As drylands are expected to expand by around 23% by the end of the next century (Huang et al. 2015) there is a clear need for a more robust field of research that combines the fields of biogeochemistry, soil science, hydrology, sociology, and ecology to meet the unique challenges associated with aridification and accompanying degradation in the world's drylands.

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Appendix

Appendix Supplemental Table 4.1 ANOVA and Tukey HSD results of response variables of moss dominated crust (moss) and darkly-pigmented cyanobacterially dominated crust (cyano) between different watering treatments.

Column1	Type	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Treatment	p adj
Chlorophyll	Cyano	4	26.72	6.6801	1.4729	0.248	1.8-10	1.00
							1.8-2.7	1.00
							1.8-5.4	0.56
							10-2.7	1.00
							10-5.4	0.59
							2.7-5.4	0.74
							7.7-1.8	0.91
							7.7-10	0.89
							7.7-2.7	0.77
							7.7-5.4	0.16
Scytonemin	Cyano	4	18.28	4.5699	2.1934	0.107	1.8-10	0.85
							1.8-2.7	0.71
							1.8-5.4	0.08
							1.8-7.7	0.99
							10-2.7	1.00
							10-5.4	0.43
							2.7-5.4	0.60
							7.7-10	0.98
							7.7-2.7	0.91
							7.7-5.4	0.18
Fv/Fm at 30	Moss	4	0.009417	0.0023541	1.3077	0.301	1.8-10	0.78
							2.7-1.8	0.89
							2.7-10	0.27
							2.7-5.4	0.99
							2.7-7.7	1.00
							5.4-1.8	0.99
							5.4-10	0.53
							7.7-1.8	0.97

							7.7-10	0.41
							7.7-5.4	1.00
Fv/Fm at 120	Moss	4	0.00737	0.001842	1.057	0.405	10-1.8	1.00
							2.7-1.8	0.99
							2.7-10	1.00
							5.4-1.8	0.36
							5.4-10	0.54
							5.4-2.7	0.61
							5.4-7.7	0.68
							7.7-1.8	0.99
							7.7-10	1.00
							7.7-2.7	1.00
YII at 30	Moss	4	0.014411	0.0036028	4.1731	**0.013**	7.7-10	0.54
							5.4-10	0.10
							2.7-10	**0.02**
							1.8-10	**0.02**
							5.4-7.7	0.81
							2.7-7.7	0.41
							1.8-7.7	0.34
							2.7-5.4	0.95
							1.8-5.4	0.92
							1.8-2.7	1.00
YII at 120	Moss	4	0.0050886	0.00127214	1.598	0.216	1.8-10	0.34
							1.8-5.4	0.86
							1.8-7.7	0.79
							2.7-1.8	1.00
							2.7-10	0.22
							2.7-5.4	0.73
							2.7-7.7	0.65
							5.4-10	0.87
							5.4-7.7	1.00
							7.7-10	0.96
NPQ at 30	Moss	4	0.001766	0.0004415	2.3188	0.092	10-1.8	0.26
							10-2.7	0.77
							2.7-1.8	0.88
							5.4-1.8	0.13
							5.4-10	0.99

							5.4-2.7	0.54
							5.4-7.7	1.00
							7.7-1.8	0.17
							7.7-10	1.00
							7.7-2.7	0.62
NPQ at 120	Moss	4	0.0019614	0.00049034	4.4288	**0.011**	10-1.8	**0.01**
							10-2.7	0.20
							10-5.4	0.17
							10-7.7	0.97
							2.7-1.8	0.54
							2.7-5.4	1.00
							5.4-1.8	0.61
							7.7-1.8	**0.05**
							7.7-2.7	0.57
							7.7-5.4	0.51
Respiration at 30	Moss	4	3.1694	0.79236	16.906	#####	10-1.8	**0.00**
							10-2.7	**0.05**
							10-5.4	0.07
							2.7-1.8	0.17
							5.4-1.8	0.12
							5.4-2.7	1.00
							7.7-1.8	**0.00**
							7.7-10	0.24
							7.7-2.7	**0.00**
							7.7-5.4	**0.00**
Respiration at 120	Moss	4	3.9735	0.99337	22.378	#####	10-1.8	**0.00**
							10-2.7	**0.00**
							10-5.4	**0.01**
							10-7.7	0.56
							2.7-1.8	0.88
							5.4-1.8	**0.00**
							5.4-2.7	**0.03**
							7.7-1.8	**0.00**
							7.7-2.7	**0.00**
							7.7-5.4	0.31

NSE at 30	Moss	4	0.3432	0.085801	1.3416	0.289	10-1.8	0.39
							10-5.4	1.00
							2.7-1.8	0.36
							2.7-10	1.00
							2.7-5.4	1.00
							2.7-7.7	1.00
							5.4-1.8	0.43
							7.7-1.8	0.37
							7.7-10	1.00
							7.7-5.4	1.00
NSE at 120	Moss	4	0.3946	0.09865	5.855	**0.003**	1.8-2.7	0.96
							10-1.8	**0.01**
							10-2.7	**0.00**
							10-5.4	0.12
							10-7.7	0.33
							5.4-1.8	0.74
							5.4-2.7	0.37
							7.7-1.8	0.50
							7.7-2.7	0.21
							7.7-5.4	0.99
GPP at 30	Moss	4	2.06053	0.51513	16.473	#####	1.8-10	**0.01**
							1.8-2.7	1.00
							1.8-5.4	0.97
							1.8-7.7	**0.00**
							10-7.7	0.12
							2.7-10	**0.01**
							2.7-5.4	0.99
							2.7-7.7	**0.00**
							5.4-10	**0.03**
							5.4-7.7	**0.00**
GPP at 120	Moss	4	1.25	0.31252	4.62	**0.009**	1.8-10	**0.03**
							1.8-2.7	0.80
							1.8-5.4	0.12
							1.8-7.7	**0.01**
							10-7.7	0.98
							2.7-10	0.24
							2.7-5.4	0.61

							2.7-7.7	0.12
							5.4-10	0.95
							5.4-7.7	0.76
Respiration at 30	Cyano	4	0.7343	0.18356	4.266	**0.013**	10-1.8	**0.02**
							10-2.7	0.76
							10-5.4	0.37
							10-7.7	1.00
							2.7-1.8	0.15
							2.7-5.4	0.95
							5.4-1.8	0.45
							7.7-1.8	**0.02**
							7.7-2.7	0.82
							7.7-5.4	0.42
Respiration at 120	Cyano	4	1.028	0.256999	5.3861	**0.005**	10-1.8	**0.00**
							10-2.7	0.41
							10-5.4	0.68
							10-7.7	0.99
							2.7-1.8	0.22
							5.4-1.8	0.06
							5.4-2.7	0.98
							7.7-1.8	**0.01**
							7.7-2.7	0.69
							7.7-5.4	0.92
NSE at 30	Cyano	4	0.28055	0.070138	2.3114	0.095	7.7-1.8	1.00
							5.4-1.8	0.68
							10-1.8	0.72
							2.7-1.8	0.09
							5.4-7.7	0.81
							10-7.7	0.84
							2.7-7.7	0.14
							10-5.4	1.00
							2.7-5.4	0.64
							2.7-10	0.69
NSE at 120	Cyano	4	0.04111	0.010278	0.4389	0.779	10-1.8	0.74
							10-2.7	0.97

							10-5.4	0.98
							10-7.7	1.00
							2.7-1.8	0.97
							5.4-1.8	0.95
							5.4-2.7	1.00
							7.7-1.8	0.84
							7.7-2.7	0.99
							7.7-5.4	1.00
GPP at 30	Cyano	4	0.75027	0.187568	10.468	**1E-04**	1.8-10	**0.01**
							1.8-2.7	1.00
							1.8-5.4	0.88
							1.8-7.7	**0.00**
							10-7.7	0.83
							2.7-10	**0.02**
							2.7-5.4	0.95
							2.7-7.7	**0.00**
							5.4-10	0.07
							5.4-7.7	**0.00**
GPP at 120	Cyano	4	0.57259	0.143148	3.3893	**0.03**	1.8-10	**0.04**
							1.8-2.7	0.07
							1.8-5.4	0.15
							1.8-7.7	0.07
							2.7-10	1.00
							5.4-10	0.94
							5.4-2.7	0.98
							5.4-7.7	0.99
							7.7-10	1.00
							7.7-2.7	1.00
NH4	Moss	4	0.15122	0.037804	1.0849	0.392	1.8-10	0.92
							1.8-5.4	0.86
							1.8-7.7	0.89
							10-5.4	1.00
							10-7.7	1.00
							2.7-1.8	0.95
							2.7-10	0.57
							2.7-5.4	0.47
							2.7-7.7	0.50

							7.7-5.4	1.00
NO3	Moss	4	0.9959	0.249	1.816	0.168	10-1.8	0.17
							10-2.7	0.39
							10-5.4	0.97
							10-7.7	0.80
							2.7-1.8	0.98
							5.4-1.8	0.37
							5.4-2.7	0.69
							5.4-7.7	0.98
							7.7-1.8	0.69
							7.7-2.7	0.94
NH4	Cyano	4	0.0994	0.02485	0.846	0.512	1.8-10	0.92
							1.8-5.4	0.99
							1.8-7.7	0.99
							2.7-1.8	0.91
							2.7-10	0.47
							2.7-5.4	0.68
							2.7-7.7	0.67
							5.4-10	1.00
							5.4-7.7	1.00
							7.7-10	1.00
NO3	Cyano	4	0.98969	0.247423	2.6613	0.063	10-1.8	0.50
							10-2.7	0.89
							10-5.4	0.99
							2.7-1.8	0.95
							5.4-1.8	0.73
							5.4-2.7	0.99
							7.7-1.8	**0.04**
							7.7-10	0.60
							7.7-2.7	0.17
							7.7-5.4	0.38
NO3_resin	Moss	4	1.34262	0.33566	12.808	**<.001**	10-1.8	**0.00**
							10-2.7	**0.00**
							10-7.7	0.38
							2.7-1.8	0.61
							5.4-1.8	**0.00**
							5.4-10	1.00

							5.4-2.7	**0.00**
							5.4-7.7	0.28
							7.7-1.8	**0.01**
							7.7-2.7	0.20
NO3_resin	Cyano	4	0.2774	0.06935	1.879	0.154	10-1.8	0.31
							10-2.7	0.85
							10-5.4	1.00
							2.7-1.8	0.86
							5.4-1.8	0.45
							5.4-2.7	0.95
							7.7-1.8	0.13
							7.7-10	0.99
							7.7-2.7	0.57
							7.7-5.4	0.93
Total Organic N	Moss	4	21.05	5.2625	1.5237	0.235	10-1.8	0.19
							10-2.7	0.42
							10-5.4	0.58
							10-7.7	0.31
							2.7-1.8	0.98
							2.7-7.7	1.00
							5.4-1.8	0.91
							5.4-2.7	1.00
							5.4-7.7	0.99
							7.7-1.8	1.00
Total Organic N	Cyano	4	18.35	4.588	0.676	0.617	1.8-5.4	1.00
							1.8-7.7	1.00
							10-1.8	0.83
							10-2.7	1.00
							10-5.4	0.64
							10-7.7	0.82
							2.7-1.8	0.94
							2.7-5.4	0.82
							2.7-7.7	0.93
							7.7-5.4	1.00
PO4	Moss	4	1.963	0.49076	0.4387	0.779	1.8-7.7	1.00

							10-1.8	0.96
							10-5.4	1.00
							10-7.7	0.91
							2.7-1.8	0.88
							2.7-10	1.00
							2.7-5.4	1.00
							2.7-7.7	0.80
							5.4-1.8	0.98
							5.4-7.7	0.95
PO4	Cyano	4	0.935	0.2337	0.597	0.669	10-1.8	0.91
							10-2.7	1.00
							10-7.7	0.96
							2.7-1.8	0.93
							2.7-7.7	0.97
							5.4-1.8	0.67
							5.4-10	0.99
							5.4-2.7	0.98
							5.4-7.7	0.76
							7.7-1.8	1.00
NPOC	Moss	4	3.55	0.886	0.175	0.949	1.8-10	1.00
							1.8-2.7	1.00
							1.8-5.4	0.99
							1.8-7.7	0.95
							10-2.7	1.00
							10-5.4	0.99
							10-7.7	0.96
							2.7-5.4	1.00
							2.7-7.7	0.99
							5.4-7.7	1.00
NPOC	Cyano	4	3007.7	751.92	1.4682	0.253	1.8-5.4	0.96
							10-1.8	0.54
							10-2.7	0.97
							10-5.4	0.20
							10-7.7	0.55
							2.7-1.8	0.95
							2.7-5.4	0.68
							2.7-7.7	0.95

							7.7-1.8	1.00
							7.7-5.4	0.95
%N in soil 0-0.5	Moss	4	0.0009399	0.00023497	0.6831	0.612	1.8-2.7	0.89
							1.8-5.4	0.90
							1.8-7.7	0.90
							10-1.8	1.00
							10-2.7	0.74
							10-5.4	0.76
							10-7.7	0.75
							5.4-2.7	1.00
							5.4-7.7	1.00
							7.7-2.7	1.00
%N in soil 0-0.5	Cyano	4	0.00832	0.0020799	1.0022	0.43	1.8-2.7	0.99
							1.8-5.4	0.56
							1.8-7.7	0.74
							10-1.8	1.00
							10-2.7	0.99
							10-5.4	0.54
							10-7.7	0.72
							2.7-5.4	0.83
							2.7-7.7	0.94
							7.7-5.4	1.00
%N in soil 0.5-5	Moss	4	5892760	1473190	2.7512	0.057	1.8-10	**0.04**
							1.8-2.7	0.95
							1.8-5.4	0.61
							1.8-7.7	0.96
							2.7-10	0.17
							2.7-5.4	0.95
							5.4-10	0.49
							7.7-10	0.16
							7.7-2.7	1.00
							7.7-5.4	0.94
%N in soil 0.5-5	Cyano	4	0.0047402	0.00118506	2.6849	0.061	1.8-5.4	0.78

							1.8-7.7	0.99
							10-1.8	0.31
							10-2.7	0.34
							10-5.4	**0.04**
							10-7.7	0.16
							2.7-1.8	1.00
							2.7-5.4	0.74
							2.7-7.7	0.99
							7.7-5.4	0.95
%OC in soil 0.5-5	Moss	4	0.02864	0.007161	1.678	0.215	1.8-2.7	0.97
							1.8-5.4	0.74
							1.8-7.7	0.76
							10-1.8	0.85
							10-2.7	0.49
							10-5.4	0.38
							10-7.7	0.24
							2.7-5.4	0.90
							2.7-7.7	0.96
							7.7-5.4	0.99
%OC in soil 0.5-5	Cyano	4	0.070864	0.017716	0.8109	0.539	1.8-10	0.97
							1.8-2.7	0.99
							1.8-5.4	0.49
							1.8-7.7	0.70
							10-5.4	0.91
							10-7.7	0.98
							2.7-10	1.00
							2.7-5.4	0.89
							2.7-7.7	0.97
							7.7-5.4	0.99
%OC in soil 0.5-5	Moss	4	967.68	241.92	2.4777	0.079	1.8-10	0.34
							1.8-5.4	1.00
							2.7-1.8	1.00
							2.7-10	0.26
							2.7-5.4	0.98

							5.4-10	0.48
							7.7-1.8	0.79
							7.7-10	**0.05**
							7.7-2.7	0.93
							7.7-5.4	0.64
%OC in soil 0.5-5	Cyano	4	0.039792	0.0099481	1.1075	0.381	1.8-2.7	1.00
							1.8-5.4	0.99
							1.8-7.7	0.86
							10-1.8	0.84
							10-2.7	0.71
							10-5.4	0.56
							10-7.7	0.30
							2.7-5.4	1.00
							2.7-7.7	0.95
							5.4-7.7	0.99
%N in tissue	Moss	4	0.0026	0.000652	0.041	0.997	10-1.8	1.00
							10-2.7	1.00
							10-5.4	1.00
							10-7.7	1.00
							2.7-1.8	1.00
							2.7-7.7	1.00
							5.4-1.8	1.00
							5.4-2.7	1.00
							5.4-7.7	1.00
							7.7-1.8	1.00
%C in tissue	Cyano	4	7.183	1.7958	0.1215	0.973	10-1.8	0.98
							10-2.7	1.00
							10-5.4	0.98
							10-7.7	1.00
							2.7-1.8	0.99
							2.7-5.4	0.99
							2.7-7.7	1.00
							5.4-1.8	1.00
							7.7-1.8	1.00
							7.7-5.4	1.00

Appendix Supplemental Table 4.2. Comparisons of response variables for moss dominated (moss) and darkly-pigmented cyanobacterial dominated (cyano) crust types. Confidence intervals were calculated based on the maximum likelihood method in Zhou and Tu (2000) for the ratio of two means in lognormally distributed data containing zeroes. Confidence intervals not containing 1 would be considered statistically significant.

Response	Comparsion	effectsize	CI_lower	CI_upper
Respiration 30	moss:cyano	1.355717	1.209249	1.519926
Respiration 120	moss:cyano	1.339493	1.202004	1.492709
GPP 30	moss:cyano	1.344999	1.09198	1.656644
GPP 120	moss:cyano	1.392713	1.241673	1.562124
NSE 30	moss:cyano	1.365705	1.162578	1.604323
NSE 120	moss:cyano	1.117131	0.8708917	1.432992
NO3	moss:cyano	0.7110752	0.3206368	1.576949
NH4	moss:cyano	0.8072257	0.5920284	1.100645
PO4	moss:cyano	1.626803	1.392935	1.899937
NPOC	moss:cyano	2.381229	1.849907	3.065156
NO3 resin	moss:cyano	1.66	0.68	4.05

Vita

Kristina Young received a B.A. in Biology, emphasis in Botany from the University of Montana in 2010 and a M.S. in Forestry from Northern Arizona University in 2017 where she was a Wyss Scholar for Conservation of the American West. Kristina was a Graduate Research Assistant with Dr. Anthony Darrouzet-Nardi at the University of Texas El Paso. While there, she was chosen as a Compass Science Sentinel, a program recognizing emerging leaders at the intersection of science, communication, and policy. Kristina has published manuscripts on biological soil crust and restoration in *New Phytologist, Scientific Reports, Oikos, Restoration Ecology, American Journal of Botany, Ecological Applications,* and *BioScience.* Kristina also served as the founder and director of the Science Moab Engagement Initiative, a nonprofit science engagement organization based out of Moab, Utah.