

ESA CENTENNIAL PAPER

Dynamic interactions of ecohydrological and biogeochemical processes in water-limited systems

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Citation: Wang, L., S. Manzoni, S. Ravi, D. Riveros-Iregui, and K. Caylor. 2015. Dynamic interactions of ecohydrological and biogeochemical processes in water-limited systems. *Ecosphere* 6(8):133. <http://dx.doi.org/10.1890/ES15-00122.1>

Abstract. Water is the essential reactant, catalyst, or medium for many biogeochemical reactions, thus playing an important role in the activation and deactivation of biogeochemical processes. The coupling between hydrological and biogeochemical processes is particularly evident in water-limited arid and semi-arid environments, but also in areas with strong seasonal precipitation patterns (e.g., Mediterranean) or in mesic systems during droughts. Moreover, this coupling is apparent at all levels in the ecosystems—from soil microbial cells to whole plants to landscapes. Identifying and quantifying the biogeochemical “hot spots” and “hot moments”, the underlying hydrological drivers, and how disturbance-induced vegetation transitions affect the hydrological-biogeochemical interactions are challenging because of the inherent complexity of these interactions, thus requiring interdisciplinary approaches. At the same time, a holistic approach is essential to fully understand function and processes in water-limited ecosystems and to predict their responses to environmental change. This article examines some of the mechanisms responsible for microbial and vegetation responses to moisture inputs in water-limited ecosystems through a synthesis of existing literature. We begin with the initial observation of Birch effect in 1950s and examine our current understanding of the interactions among vegetation dynamics, hydrology, and biochemistry over the past 60 years. We also summarize the modeling advances in addressing these interactions. This paper focuses on three opportunities to advance coupled hydrological and biogeochemical research: (1) improved quantitative understanding of mechanisms linking hydrological and biogeochemical variations in drylands, (2) experimental and theoretical approaches that describe linkages between hydrology and biogeochemistry (particularly across scales), and (3) the use of these tools and insights to address critical dryland issues of societal relevance.

Key words: climate change; drylands; ecohydrology; ESA Centennial Paper; evapotranspiration; hysteresis; isotope; modeling; stochastic.

Received 3 March 2015; revised 25 April 2015; accepted 28 April 2015; **published** 7 August 2015. Corresponding Editor: D. P. C. Peters.

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Editors' Note: This paper was commissioned by the members of the Ecosphere Editorial Board to commemorate the ESA Centennial celebration.

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INTRODUCTION

Water is the essential reactant, catalyst, or medium for most biogeochemical processes and thus acts as a regulator of element cycling in the biosphere, enhancing or inhibiting biological activity depending on its availability. Changes in soil water have long been recognized as drivers of microbial and plant activities. Due to the nature of rainfall events, soil moisture increases rapidly, generating a pulse in water availability that affects hierarchically all ecosystem compartments, with large effects on both microbial and plant-driven biogeochemical processes (Noy-Meir 1973, Schwinning and Sala 2004). The first study investigating the *steady-state* relation between soil water and soil biogeochemical cycling dates back to the 1920s, showing how ammonification and nitrification increase with soil moisture until further wetting starts inhibiting aerobic activity (Greaves and Carter 1920). Later studies highlighted the *dynamic* nature of microbial responses to drying and wetting, resulting in disproportionately large peaks in soil carbon dioxide (CO₂) flux after wetting of dry soils, a phenomenon termed the “Birch effect” (Birch 1958). Today, the Birch effect has been recognized as a ubiquitous pattern driving both carbon (C) and nitrogen (N) pulses in various ecosystems (Austin et al. 2004, Jarvis et al. 2007, Boriken and Matzner 2009). Studies on plant water relations also date back to the early 20th century. The realization that stomata regulate gas exchanges (Brown and Escombe 1900) and that their movement is linked to soil moisture through water flow in the whole soil-plant-atmosphere continuum (van den Honert 1948) stimulated research on plant responses to water stress (e.g., Hsiao 1973). The dynamics of recovery after drought are far less studied. Evidence suggests that after prolonged dry periods there is no immediate response to a moisture pulse (e.g., in terms of photosynthetic rate) as in the case of heterotrophic respiration, but rather plant activity resumes slowly, often through cascading effects at the whole ecosystem scale (Huxman et al. 2004, Schwinning and Sala 2004). Both microbial and plant responses to moisture pulses provide good examples of the close coupling between hydrological and biogeochemical processes, which occur across a range of

spatial and temporal scales (Fig. 1).

This coupling is particularly evident in drylands. Drylands are regions with relatively low precipitation, long dry spells (e.g., dry seasons) and frequent occurrence of water scarce conditions, resulting in mosaics of vegetated and bare patches. Drylands are typically located in areas of prevalent divergence in the patterns of atmospheric circulation, in arid continental regions, on the leeward side of mountain chains, or in the proximity of cold ocean surfaces (Wang et al. 2012a). The drylands definition is often based on total annual precipitation being low relative to potential evapotranspiration (*ET*). To this end an aridity index (AI), defined as the ratio between precipitation and potential *ET*, is used to classify drylands as regions where the AI is smaller than 0.65 (e.g., sub-humid dryland, semi-arid dryland).

Drylands cover 40% of the earth’s terrestrial surface with over 2 billion inhabitants (Wang et al. 2012a). These are areas of critical concern as land degradation is occurring at an alarming pace and is affecting over one-third of the global population, compounding with other social problems especially in the developing world (MEA 2005, Wang et al. 2012a). Climate change, population pressure and recurrent disturbances have rendered many dryland systems highly susceptible to ecosystem degradation. Ecosystem degradation contributes to a dramatic decline in the productivity of croplands and rangelands worldwide (Reynolds et al. 2007), threatening food security and environmental quality. Hence understanding the coupled hydrological and biogeochemical processes in drylands is motivated by our increasing need to design novel solutions for water resource management, to explain and predict ecosystem degradation, evaluate degradation control strategies, and to analyze the effect of changing climate and anthropogenic activities on dryland systems. In addition to drylands, the coupling between hydrological and biogeochemical processes also appears evident in areas with strong seasonal precipitation patterns (e.g., Mediterranean and seasonally-dry tropical regions), and in mesic systems during droughts (Lohse et al. 2009, Thompson et al. 2011, Moyano et al. 2013, Vico et al. 2014). Therefore, understanding the connections between hydrological and biogeochem-

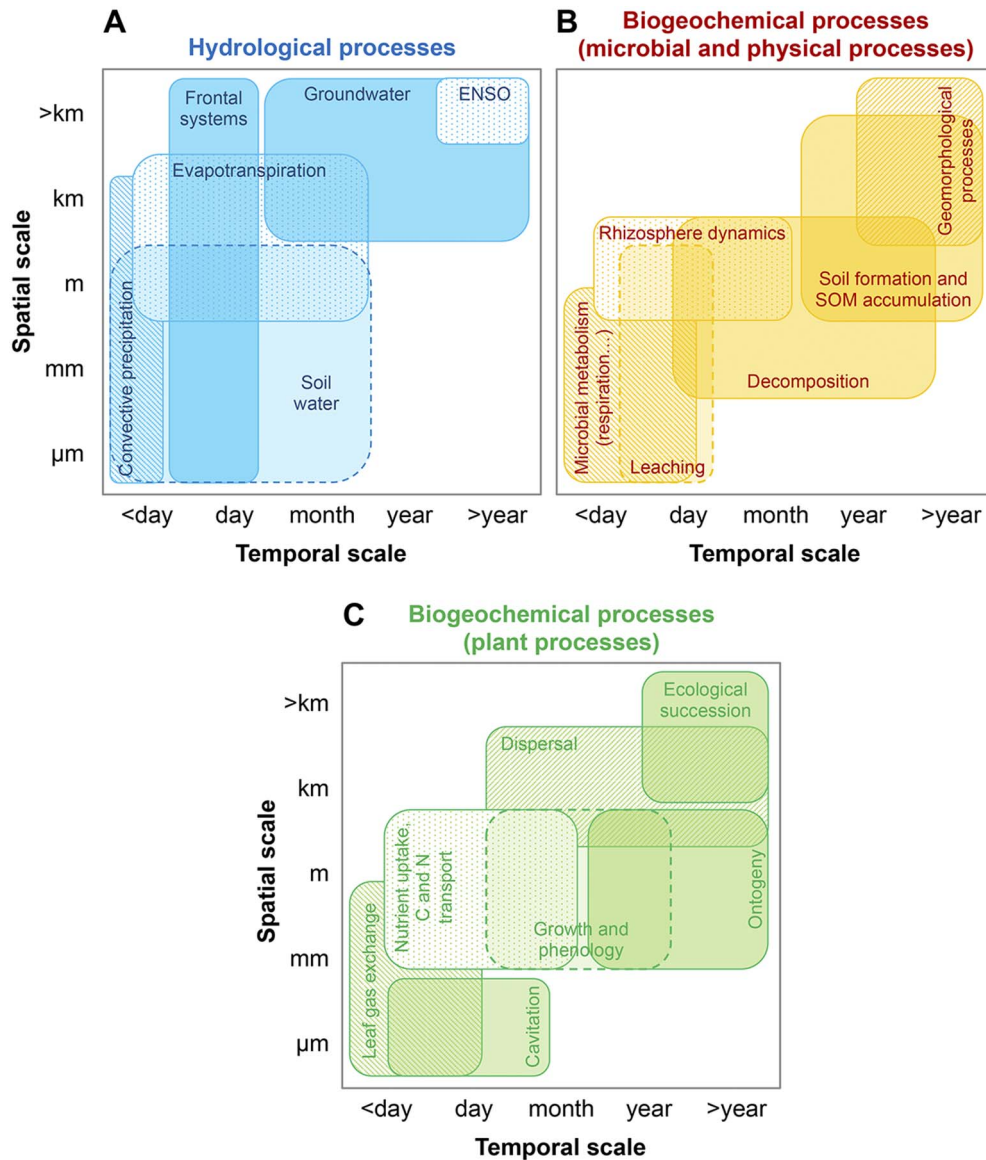


Fig. 1. The spatio-temporal scales of different hydrological processes (A) and biogeochemical processes: microbial and physical processes (B) and plant processes (C).

ical processes in water-limited systems can be translated to other systems under water-stressed conditions.

The most striking feature of the hydrological and biogeochemical connection is that the rainfall pulses driving the biogeochemical reactions (e.g., mineralization rate change after rainfall events) occur at the time scale of hours to days. However, hydrological-biogeochemical linkages caused by such short events propagate at much longer time

scale (Schwinning and Sala 2004). For example, the linkage between drought and water quality typically occurs at the time scale of months to years, even though the underlying pulse responses occur at the time scale of hours to days. Intensive agriculture in the US Midwest has been linked to degradation of water quality in the Mississippi River basin, including augmentation of fertilizer export (Davis et al. 2014), eutrophication of surface waters (Alexander et al. 2000),

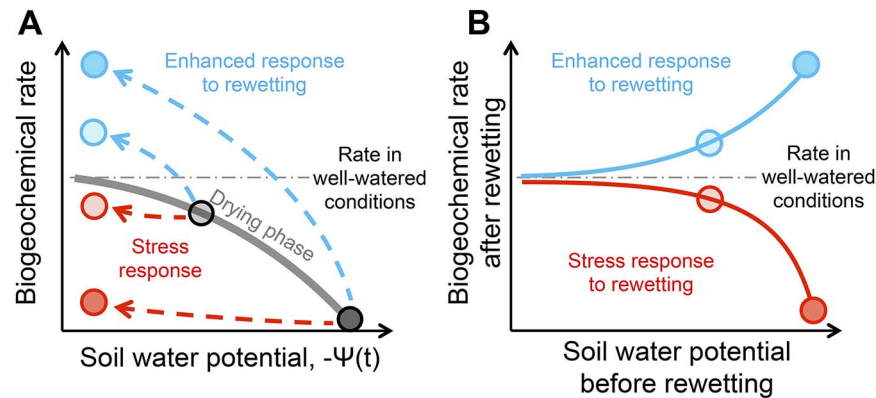


Fig. 2. Conceptual representation of biogeochemical responses to changes in soil water availability (in terms of water potential). (A) Declining biogeochemical rate as the soil becomes drier (grey curve) and subsequent response to rewetting (dashed arrows); red and blue arrows respectively indicate stress and enhanced responses: the former is typical of plant responses, whereas the latter is characteristic of microbial responses (analogous to Birch effect). (B) Rewetting from different levels of water potential leads to varying degrees of stress or enhancement (circles with different color and shading refer to the same points in both panels).

proliferation of nuisance algae (Michalak et al. 2013), and expansion of the hypoxic zone in the Gulf of Mexico (Turner and Rabalais 2003). These impacts may be intensified by droughts followed by rainfall pulses that drive rapid biogeochemical reactions with long-lasting consequences.

Besides the temporal connections, the coupling of hydrological and biogeochemical processes is apparent at all levels in the ecosystems—from soil microbial cells to whole plants to landscapes. Fig. 1 shows the various time scales of both hydrological processes and biogeochemical process and demonstrates the interaction of these processes over multiple spatio-temporal scales. Ecosystem fluxes such as net C exchange, and soil C and N mineralization rates are most easily affected by hydrological variations—often according to organism-specific trajectories (Fig. 2). However, other ecosystem properties that are less affected by individual moisture pulses (e.g., soil organic C pools) could still respond to hydrological variations in the long term. For example, using stable isotope as a tracing technique, a recent study showed that soil C contributions from C_3 and C_4 plants is mediated by mean annual rainfall in African savannas (Wang et al. 2009b).

There are several key reasons to study the interactions between hydrological and biogeochemical processes in water-limited systems: (1)

such interactions are recognized as significant in water-limited systems and there is growing interest in the scientific community to quantify and model these processes at different scales; (2) understanding the interactions is fundamental in solving/mitigating real world issues such as water quality, climate change and land degradation; and (3) the information is scattered in different disciplines and a holistic (interdisciplinary) perspective is required to integrate them. To this end, we aim at synthesizing the current understanding of the interactions of vegetation dynamics, hydrological and biochemical processes, complementing and updating previous extensive reviews on this topic (Noy-Meir 1973, McClain et al. 2003, Austin et al. 2004, Schwinning and Sala 2004, Borken and Matzner 2009). This article will examine the extent to which biogeochemical hot spots and hot moments can be characterized and predicted by essential hydrological phenomena across spatio-temporal scales, and discuss three opportunities to advance research in this area: (1) improved quantitative understanding of mechanisms linking hydrological and biogeochemical variations in drylands, (2) experimental and theoretical approaches that describe linkages between hydrology and biogeochemistry (particularly across scales), and (3) the use of these tools and insights to address critical dryland issues of societal relevance.

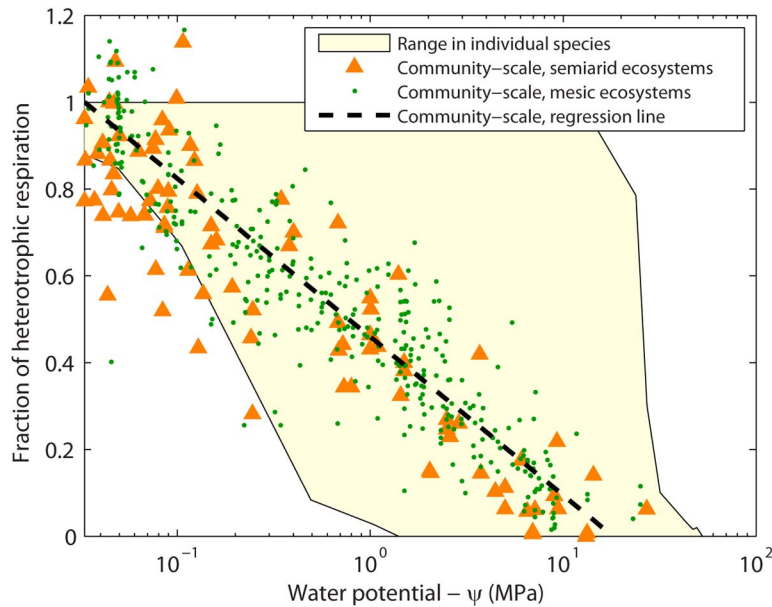


Fig. 3. Comparison between responses of individual microbial species and soil microbial communities from contrasting environments to changes in soil water availability, expressed as soil water potential. The range of species-level responses is enveloped between curves for sensitive and resistant organisms: in (A), *Pseudomonas* spp. (Lennon et al. 2012) and *Xeromyces bisporus* (Williams and Hallsworth 2009), respectively. Community-level data for respiration are from several sources, listed in Manzoni et al. (2012) and Moyano et al. (2012); only respiration-moisture curves that were well characterized at their drier end are shown.

MECHANISTIC UNDERSTANDING OF LINKED BIOGEOCHEMICAL AND HYDROLOGICAL PROCESSES IN DRYLANDS

Microbial responses

Microbial responses to moisture variations differ greatly between the drying and wetting phases (Fig. 2). Primarily these differences depend on the speed of these processes—drying is slower than rewetting and therefore is more conducive to gradual metabolic and physical changes. During soil drying, both matric potential and osmotic potential become more negative, causing a gradual decline in microbial activity through various mechanisms (Fig. 3). Unlike plants, active-growing soil microorganisms do not have water impermeable layers (e.g., in plant roots) and their membranes are semipermeable. Therefore their internal water potential equilibrates with the external medium, forcing them to decrease osmotic potential in the cell to avoid dehydration and maintain turgor (Griffin 1981, Potts 1994). Microbes may do so through the import or synthesis of compounds such as amino

acids, carbohydrates and inorganic solutes (Borken and Matzner 2009, Warren 2014). These compounds (or osmolytes) are often low molecular weight organic molecules that do not interfere with cellular processes, or ions that are more effective osmotic regulators but may cause metabolic impairment (Potts 1994, Boot et al. 2013). Using osmolytes to maintain turgor is effective only in a certain water potential range for at least two reasons. First, excessive osmolyte concentrations (especially ionic osmolytes) cannot be tolerated by all organisms. Second, as the soil dries, C and N substrates needed to synthesize osmolytes become less available, because their diffusivity decreases. As a consequence, it is possible that microbes become substrate-limited before being water-stressed (Boot et al. 2013, Manzoni et al. 2014a). In these conditions, microorganisms need to become dormant, or will further dehydrate and die (Borken and Matzner 2009).

Different microorganisms produce different compounds and have different tolerance ranges. Bacteria tend to use nitrogenous osmolytes such

as amino acids and tertiary amines (e.g., glycine, betaine) while fungi typically use sugar alcohols (e.g., mannitol and trehalose) for survival (Csonka 1989, Boot et al. 2013). Bacteria live in water films and fungi are mostly in contact with water films through hyphae, therefore fungi tend to have higher drought tolerance than bacteria in natural environments (Freckman 1986). Despite the hypothesized need to maintain turgor through osmoregulation, no accumulation of osmolytes during drought has been reported in most (Williams and Xia 2009, Boot et al. 2013, Kakumanu et al. 2013), but not all studies (Warren 2014). These differences in osmolyte accumulation may be attributed to methodological issues (field vs. laboratory conditions) or could be related to accessibility of organic substrate to synthesize osmolytes, and it clearly requires further investigations.

The dynamics following rewetting are faster than during drying. Microbial reactivation is rapid, leading to a pulse in respiration within a day after rewetting, or slightly later in soils that have been dry for several months (Meisner et al. 2013). The origin of these pulses, initially noticed by Birch (1958), has yet to be clarified, but likely stems from multiple biological and physical processes. From the biological point of view, when osmolyte accumulation does occur, on wetting the dry soils, microorganisms need to dispose of their solutes quickly to equilibrate with the outside water potential and avoid lysis and death (Kieft et al. 1987). Thus, the speed of soil water potential increase after wetting is critical to characterize survival. Larger rain events and faster infiltration rate cause faster water potential increases, but other factors are also at play. For example, soil organic substances induce hydrophobicity, which increases with the duration of drying and slows down the water potential increase following wetting; additionally, extra cellular polysaccharides may buffer moisture variations (Borken and Matzner 2009, Kaiser et al. 2015). Such slow-down of water potential increase will give microorganisms more time to equilibrate with their surrounding environment, likely reducing rewetting stress (Halverson et al. 2000). It has been originally hypothesized that intracellular solutes being released into the extracellular environment and rapidly consumed are the origin of respiration

pulse (Halverson et al. 2000). Later, the mineralization of C stored in microbial biomass (Fierer and Schimel 2003), but not osmolyte C (Williams and Xia 2009), has been suggested as a driver of respiration pulses.

An alternative hypothesis to explain respiration pulses is based on the release of substrates that are un-accessible in dry soils. Physical processes associated with rewetting (e.g., aggregate disruption, organic matter redistribution) can in fact expose previously protected soil organic matter to microbial attack (Denef et al. 2001, Miller et al. 2005, Kaiser et al. 2015). Dissolved substrates continue to accumulate in dry conditions because the activity of extracellular enzymes declines slowly as soil moisture decreases. However, diffusivity becomes severely impaired as drying progresses, so that these solutes cannot be transported to microbes and used. Upon rewetting, solute transport resumes and microbes can exploit a large (albeit temporary) source of C and nutrients, fueling a large respiration pulse. This hypothesis is strongly supported by model predictions (Lawrence et al. 2009, Manzoni et al. 2014a), and experimental observations (Schimel et al. 2011, Guo et al. 2014, Kaiser et al. 2015). In reality, the mechanisms behind the wetting induced biogeochemical pulses are probably a combination of both biological and physical processes since the C and N pulses are triggered by wetting, but peak intensity and integrated magnitude are generally decoupled from soil moisture (Jenerette et al. 2008, Bowling et al. 2011).

While the mechanisms causing respiration pulses are debated, observations of these pulses under a range of laboratory and field conditions are becoming more common. Pulse sizes typically increase with the duration of the dry period (Xiang et al. 2008, Muhr et al. 2010, Harrison-Kirk et al. 2013, Meisner et al. 2013) (Figs. 2 and 4A), and with the intensity of the rewetting event (Tiemann and Billings 2011, Lado-Monserrat et al. 2014). Thus, pulses occur when the initial water potential level is below -1 MPa and tend to increase in intensity as the pre-wetting water potential becomes more negative (Fig. 4A). The respiration rate during the pulse can be one order of magnitude larger than respiration under constantly wet conditions, and pulses are sustained after repeated drying and wetting cycles

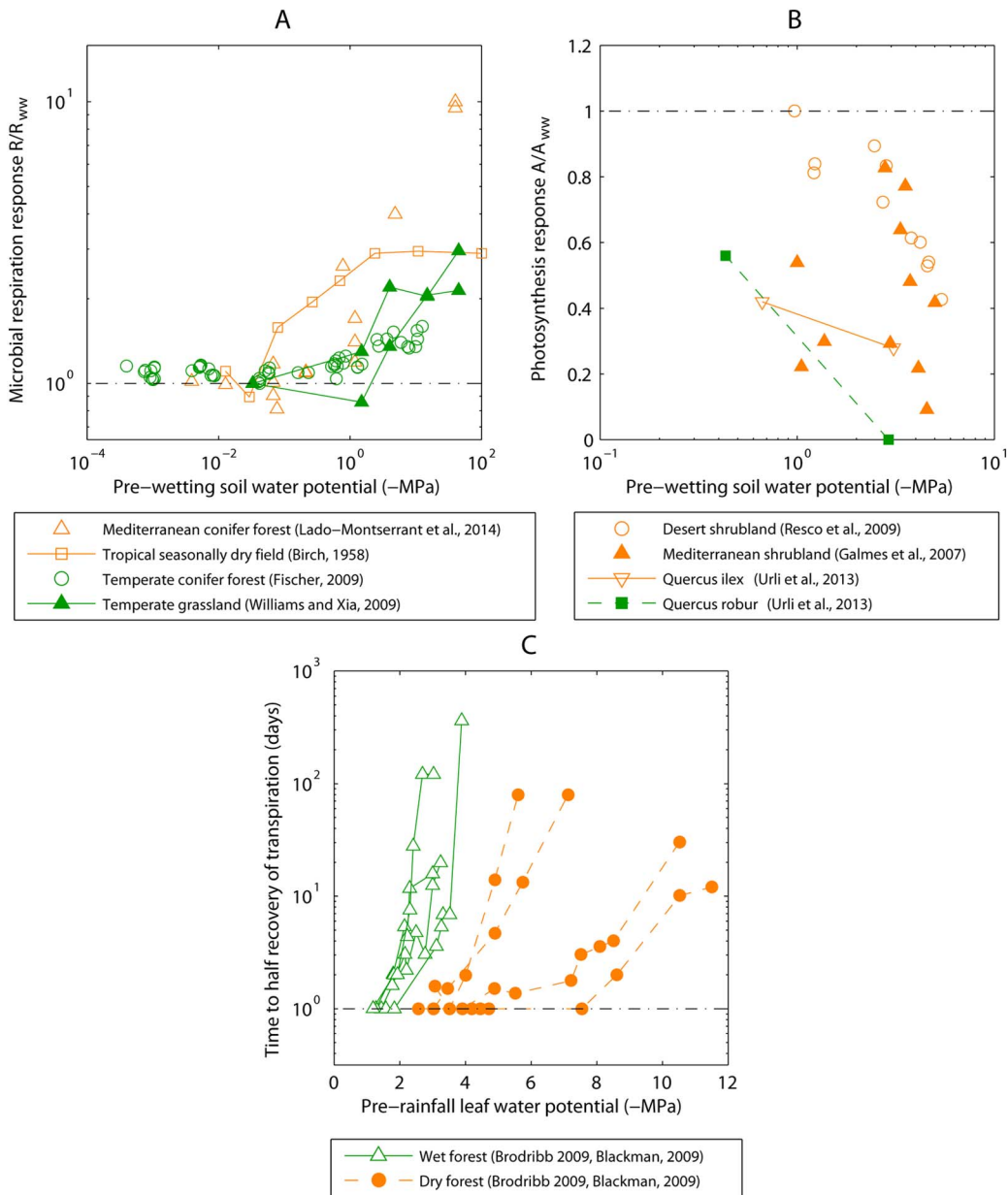


Fig. 4. Responses of vegetation and soil microbial biomass to rewetting, as a function of the soil or leaf water potential at the end of the dry period, in arid/semiarid (orange symbols) and mesic ecosystems (green). (A) Enhancement of soil respiration upon rewetting (Birch effect; expressed as respiration post-rewetting, R , over respiration in constantly well-watered conditions, R_{ww}) and (B) recovery of leaf-level photosynthesis after drying to different soil water potential levels (expressed as photosynthetic rate post-rewetting, A , over photosynthetic rate in constantly well-watered conditions, A_{ww}). (C) Time to reach half the pre-drought transpiration rate as a function of leaf water potential at the end of the dry period, in eight woody species from contrasting habitats. Several published sources provided soil respiration (Fischer 2009, Lado-Monserrat et al. 2014), leaf photosynthesis (Galmes et al. 2007, Resco et al. 2009, Urli et al. 2013), and transpiration recovery data (Blackman et al. 2009, Brodribb et al. 2010). The dot-dashed horizontal lines in (A) and (B) indicate a response ratio of one, i.e., no difference compared to moist conditions; in (C) it indicates a recovery time of one day, i.e., a rapid and full recovery. Note that the scales differ among the panels.

(e.g., Miller et al. 2005). After the respiration peak, a microbial growth pulse ensues, but not as intense as the respiration one (Göransson et al. 2013, Meisner et al. 2013).

In addition to the respiration pulses after moisture changes, continuous measurements of CO₂ flux demonstrate the existence of diel hysteresis between soil CO₂ concentrations and soil temperature (e.g., Riveros-Iregui et al. 2007), which is strongly dependent on soil moisture status across the growing season. The diel hysteresis can respond quite rapidly to precipitation inputs, especially during drought. This hysteretic behavior at depth varies in magnitude from one day to the next, and it appears to be independently mediated by photosynthetically active radiation (PAR) and soil temperature (Riveros-Iregui et al. 2007, Vargas and Allen 2008b). In dry soils, hysteresis is not readily observable at depth, likely because diffusivity is high and soil CO₂ sources are small. However, hysteretic behavior is propagated to the top of the soil surface and it is manifested and observed in measurements (Martin et al. 2012) or estimates (Riveros-Iregui et al. 2008, Vargas and Allen 2008a, Barron-Gafford et al. 2011) of surface soil CO₂ efflux. Furthermore, continuous measurements of the diel hysteresis in soil CO₂ dynamics (either at the soil surface or at depth) have also allowed for examination of the role of photosynthesis in regulating soil CO₂ efflux, including lag times of less than a day between peak solar radiation and peak soil CO₂ efflux rates (Liu et al. 2006, Vargas and Allen 2008b), which has been independently corroborated using both stable and radioactive isotopes (Bowling et al. 2002, McDowell et al. 2004, Carbone and Trumbore 2007) as well as spectral analysis (e.g., wavelet analysis) of above and belowground measurements (Heinemeyer et al. 2012). These hysteretic patterns thus indicate not only complex interactions between biogeochemical reactions and transport, but also between plants and soil microbes.

There are multiple uncertainty sources in explaining the microbial response to pulse events. Firstly, the uncertainty partially rises from the definition of the “control” conditions used to quantify the net or priming effect of drying and wetting on C and N mineralization (Borken and Matzner 2009). The “control” is

typically permanently moist (laboratory studies, as in Fig. 4A) or variably moist (field studies) during drying/wetting cycles. However, a permanently moist soil is not necessarily at the optimum soil moisture for C and N mineralization. The evaluation of natural or experimentally induced drying and wetting effects under field conditions is even more difficult. Under natural condition, drought is often introduced through rainfall exclusion experiments. Under such conditions, the control soil is subjected to natural changes in soil moisture and often apart from optimum soil moisture conditions. This explains why the priming effect is typically small when the moisture level of the control is at an optimum and the apparent priming effect will grow with decreasing moisture level in the control (Borken and Matzner 2009). All these uncertainties could interfere with the intrinsic priming effect and lead to misinterpretations. Secondly, the source of organic substrates (microbial vs. non-microbial) causing the microorganism responses to moisture pulses is under debate, as discussed above. Thirdly, microbial eco-physiology is one of the largest uncertainty sources. How soil microbes allocate the available substrates (e.g., to growth, osmoregulation, extracellular enzyme production) is far from understood. As a consequence, it is difficult to interpret observations such of respiration, growth, or carbon use efficiency (CUE), which integrate numerous processes. For example, microbial communities adapted to long-term drought showed increased CUE after rewetting (Göransson et al. 2013), but other studies show decreased CUE in soils subject to infrequent but large re-wettings (Tiemann and Billings 2011, Meisner et al. 2013).

Vegetation responses

Plants require a continuous flow of water to maintain leaf hydration, which in turn allows keeping stomata open and thus exchanging CO₂; transport nutrients to the growing tissues; maintain turgor essential for tissue expansion; provide water for all other physiological functions. Pulses in soil moisture, by altering soil water potential, affect the transpiration rate and therefore photosynthesis, structural integrity (turgor) and growth. Plant response to hydrological variations is typically slower or even in opposite direction compared with microbes (e.g.,

plants most often exhibit a short-term stress response, as in Fig. 2, and a long-term growth pulse). Long-term water availability (e.g., mean annual precipitation and soil moisture) determines vegetation structure and productivity (Rodríguez-Iturbe and Porporato 2004). To respond to shorter time scale water deficit (e.g., days to weeks), plants adopt two broad categories of long-distance signaling mechanisms (Wilkinson and Davies 2010). One mechanism exploits hydraulic signals, which are internal changes in water potential that propagate from one cell/organ to another (e.g., from roots in drying soil to leaves, Christmann et al. 2007). This hydraulic signal propagates according to the cohesion-tension theory (Dixon and Joly 1894, Honert 1948), that is, liquid water ascends plants in a metastable state under tension, following a gradient of decreasing water potential from the soil to the leaves. Pressure drops in the leaf thus trigger stomatal closure (Buckley et al. 2003).

While all plants respond to these passive hydraulic signals, only relatively modern lineages employ chemical signals derived from changes in the rate of transport of plant hormones and other chemical species from one cell/organ to another (Brodrribb and McAdam 2011). For example, soil drying can increase the synthesis and/or availability of the plant hormone abscisic acid (ABA) in the roots and this ABA is then transported in the xylem up to the shoots (Wilkinson and Davies 2002). An increase in vapor pressure deficit can also induce both ABA-based signaling and hydraulic change within the shoot (e.g., Tardieu and Davies 1992). Using a modeling approach, a recent study shows that simulations including both leaf water potential and foliar chemical signal concentrations regulation qualitatively reproduced transpiration of plants exposed to root zone drying, but the long-term effects of chemical signal concentrations regulation seemed negligible (Huber et al. 2014). This topic requires further investigation since previous laboratory and field observations suggest that epidermal water relations may act as a modulator of the responses of stomata to ABA (Tardieu and Davies 1992). During soil drying, not only gas-phase, but also liquid-phase conductance is reduced due to cavitation and embolism formation (Tyree and Sperry 1988). Water stress thus causes both lowered C uptake,

potentially leading to C starvation, and hydraulic damage, causing loss of water transport capacity for branches or whole trees (McDowell et al. 2008). Different drought response patterns are thus expected depending on plant water use strategies and the intensity and duration of water stress.

Plant dynamics upon rewetting are often characterized by a partial recovery compared to well-watered conditions (identified as ‘stress responses’ in Figs. 2 and 4), unlike microbial ‘enhanced responses’. This difference may be explained by the slower plant recovery after a dry period compared to soil microbes. In fact, the timescales of plant recovery lengthen as the degree of water stress damage increases, and are controlled by a suite of hydraulic traits (Blackman et al. 2009, Resco et al. 2009, Brodrribb et al. 2010, Urli et al. 2013). Re-hydration is quick, but gas exchanges resume in days to months after rewetting, and full recovery of hydraulic function may take years, leaving plants more vulnerable to subsequent droughts (Anderegg et al. 2013). A few species show enhanced growth rate after a rain, but only if the preceding drought was moderate (Brodrribb et al. 2010).

Hydrological variations can result in short-term variability in nutrient availability, and plants can respond to such changes in nutrient availability through physiological plasticity (i.e., dramatic change in root uptake kinetics) within the time scale of hours (Jackson et al. 1990, Wang et al. 2006). In the long-term, rainfall conditions can determine the nutrient abundance at one location. For example, previous studies show that mean rainfall amounts affect ammonium/nitrate ratios along rainfall gradients in both dry (Feral et al. 2003) and wet environments (Houlton et al. 2007). It has been shown that plants can adapt to these conditions by switching ammonium/nitrate uptake preference according to their long-term growing conditions (e.g., months to years) (Wang and Macko 2011). This is a good example of plant responses to longer-term biogeochemical variations driven by rainfall.

One challenge to study large-scale vegetation response to hydrological variation is the difficulty to quantify large-scale vegetation water use (i.e., transpiration, T). From the water management point of view, to efficiently use the limited water resources in drylands, plants need to

maximize the productive water loss (T) and minimize the unproductive water loss (evaporation from the soil, E) (Wang and D'Odorico 2008, Manzoni et al. 2014b). Meteorological-based methods to quantify large-scale ET measurements have become routine in recent years. However, separating E and T has always been a difficult task and various methods have been used to partition ET with large uncertainties (Wang et al. 2014). See *Modeling and observational advances. . . Quantifying large-scale vegetation water use* for a summary of some recent advances in partitioning ET .

Combined microbial and vegetation responses in the soil

The differentiation between microbial and vegetation responses are not immediately apparent for most biological processes (and associated observations). These include combined responses of both plant (autotrophic) and microbial (heterotrophic) processes in the transformation of C and nutrients in the soil. For example, processes responsible for the generation and flux of trace gases (e.g., soil CO₂ efflux or soil respiration) are commonly measured and represented as a deterministic function of soil temperature (e.g., Lloyd and Taylor 1994, Winkler et al. 1996), or as a function of coupled soil temperature-soil moisture dynamics (e.g., Riveros-Iregui et al. 2011, Moyano et al. 2013). Efforts have been made to incorporate stochastic precipitation pulses as drivers of this flux (e.g., Daly et al. 2008). While field studies directed at understanding the role of new water inputs on the separate contributions from plant and microbes exist (Hanson et al. 2000, Carbone et al. 2011, Suseela et al. 2012), the challenges in doing so are well accepted (Baggs 2006, Vargas et al. 2011). As a result, field studies more commonly investigate the combined responses of microbial and vegetation (e.g., Thomey et al. 2011, Vargas et al. 2012), thereby missing potentially important mechanisms.

The combined response of microbial and vegetation processes is often measured at spatial scales from the point to the landscape scale and at temporal scales from seconds to seasons to years, but these observations are commonly interpreted as single biological processes (e.g., ecosystem C uptake, ecosystem respiration). For

example, measuring the responses of leaf, soil, and ecosystem to a 25% increase in precipitation (via manipulation of precipitation) during the summer in the Chihuahuan Desert, researchers found that ecosystem C uptake and soil CO₂ efflux increased following individual watering events despite that measured stomatal conductance remained the same (Patrick et al. 2007). However, at the seasonal scale, water additions resulted in an increase in sequestration of atmospheric C and a decrease in soil CO₂ efflux (Patrick et al. 2007). While soil CO₂ efflux increased immediately after precipitation and for a few hours (~18 h), once the ecosystem entered an interpulse period and soil moisture decreased, rates of soil CO₂ efflux from wetted plots declined faster than in plots without water addition (Patrick et al. 2007). A more recent study demonstrated that soil processes at the landscape level exhibit bidirectional behavior in response to interannual water availability (Riveros-Iregui et al. 2012), because lowlands and wet areas of the landscape are favorable for autotrophic and heterotrophic transformation of soil C during dry years whereas uplands and dry areas of the landscape are more favorable during wet years. Both studies suggest a tight coupling between autotrophic and heterotrophic processes from the plot to the landscape level and across temporal scales from hours to seasons.

Numerous questions remain regarding the role of new moisture additions on regulating the combined response of plant and microbial activity in the soil and at the landscape level. For example, what is the role of new moisture pulses in modulating the coupling between photosynthetic activity, heterotrophic composition of soil organic matter, and soil CO₂ dynamics under varying antecedent conditions of soil moisture? Is there spatial covariability and temporal coevolution between C uptake (photosynthesis) and autotrophic (plant) or heterotrophic (microbial) respirations in the soil, and if so, does this covariability become more or less pronounced due to differing climate and hydrologic regimes? Opportunities exist to investigate the effects of moisture pulses in mediating temporal lags between photosynthetic activity and soil CO₂ dynamics under varying antecedent moisture conditions (e.g., Kuzyakov and Gavrichkova 2010). More studies are needed, espe-

cially using natural or artificial tracers across the plant-soil-atmosphere interface that allow for disentangling the role of new moisture inputs on concomitant soil CO₂ production and transport.

While efforts have rightly focused on furthering our understanding of soil CO₂ dynamics, many of the biotic and abiotic controls that influence soil CO₂ also influence other important greenhouse gases such as nitrous oxide (N₂O) and methane (CH₄). Soil water content is a strong mediator of not just the magnitude but also the bidirectional flux of both gases (Osaka et al. 2006, Itoh et al. 2007, Jungkunst et al. 2008, Karki et al. 2014). Soils are a net source of N₂O to the atmosphere; yet both N₂O uptake and consumption also occur in the soil (Ryden 1981, Schlesinger 2013). Similarly, CH₄ can be both produced and consumed in the soil (Rowlings et al. 2012, Yan et al. 2014). A quantitative understanding of the effects of water pulses on the bidirectional fluxes of both gases is needed, in particular at temporal scales that range from minutes to seasons.

COMPLEXITIES AND SCALE INTERACTIONS IN LINKED BIOGEOCHEMICAL AND HYDROLOGICAL PROCESSES IN DRYLANDS

Ecosystems are complex structures in which organisms at different trophic levels interact with a highly heterogeneous environment. Even under constant environmental conditions, interactions across species and trophic levels leads to dynamics at different time scales (internal or endogenous system dynamics). For example, ‘slow’ ecosystem compartments such as woody species change over long time scales compared to ‘fast’ compartments such as herbaceous vegetation. The variability of the environmental drivers in space and time contributes to the endogenous dynamics by adding exogenous (i.e., external) components. For example, prolonged wet periods may trigger major and long-lasting ecosystem changes, while a single rainfall event may cause short-term responses the consequences of which dissipate rapidly (Schwinning and Sala 2004). In addition to these endogenous and exogenous dynamics, responses to hydrological pulses can be classified based on how temporal and spatial scales interact. Typically, short-term

event such as localized thunderstorms have the strongest effects locally, whereas long-term events such as an unusually wet year have effects that span both small and large scales (Fig. 1).

Dynamics driven by internal factors

Even under stable environmental conditions, ecosystem components interact and often give rise to complex dynamics (Tilman and Wedin 1991, Manzoni and Porporato 2007). Understanding these dynamics is critical to disentangle climatic and endogenous drivers of an observed pattern, because endogenous drivers are the backbone of the ecosystem responses. External drivers can interact with the internal ones to create a wide range of responses, possibly shifting ecosystem trajectories from one attractor to another (Porporato and D’Odorico 2004, Ridolfi et al. 2011).

These internal dynamics may exhibit variation across a range of temporal scales, because different ecosystem components change at different scales. For example, a semiarid ecosystem responds to a fire event (which could be considered endogenous if strongly coupled to the fuel build-up [Anderies et al. 2002]) or rainfall after a prolonged dry period at scales ranging from hours (reactivation of soil microbes), to days (recovery of gas exchanges; germination from seed banks) to decades (recovery of woody vegetation). Even within an ecosystem compartment, response times may vary depending on the degree of acclimation and adaptation to dry conditions. For example, the time to recover hydraulic function after severe drought varies by two orders of magnitude depending on the plant community considered (Fig. 4). Species adapted to dry climates recover much faster than plants adapted to wet climates, for a given pre-wetting leaf water potential. Moreover, the sensitivity of recovery time to the pre-wetting state is higher in species adapted to wet conditions, suggesting a threshold-like response to drought leading to mortality, rather than a smooth response typical of drought resistance species.

Dynamics driven by external factors

Dryland ecosystems are prone to highly variable environmental perturbations, which trigger a range of responses at scales varying from hours to decades. These responses also

cascade through all the components of the ecosystem (Noy-Meir 1973, Schwinning and Sala 2004), thus exhibiting strong scale dependence. Typically, at larger (longer) scales, variations are smoother due to averaging effects in space and time. The dependence of moisture responses on the level of organization or the observation scale are particularly apparent when comparing community-level fluxes to the responses measured in isolated species or even organs in selected individuals. For example, the range of responses of microbial organisms to changes in water potential spans two orders of magnitude – yet, community-level responses are much narrower (Schwinning and Sala 2004, Manzoni et al. 2012) (Fig. 3). This narrowing or decrease in variance is due to both averaging effects and physical constraints that limit the response plasticity (Manzoni and Katul 2014).

After rainfall events, the decline in moisture is driven by both abiotic and biotic effects. Abiotic effects encompass deep percolation and evaporation, as well as atmospheric conditions setting the rate of potential *ET* (i.e., the maximum rate of soil moisture decline). The biotic effects are primarily controlled by the shape of the *T*-moisture curves, which depend on a suite of vegetation traits (Vico and Porporato 2008, Egea et al. 2011, Manzoni et al. 2014b). Therefore these curves should be interpreted as emerging properties of the internal dynamics in the plant-soil system, affected by plant functional traits and type (grasses, trees, shrubs), and by species adaptations. The declining part of the respiration pulses is instead mainly controlled by biotic processes—namely heterotrophic and autotrophic respiration—because abiotic processes such as gas diffusion are not limiting in dry soils.

Cross-scale connectivity

Hydrological connectivity is a system-level property that results from the linkages in the networks of water transport through the landscape, by which feedbacks and other emergent system behavior may be generated (Miller et al. 2012, Hunt et al. 2015). Ecosystem structure and function are critically dependent on the connectivity of ecohydrological and biogeochemical processes across time and space. Therefore, understanding connectivity will significantly improve our system predictions at larger scale

based on information from smaller scales (Peters et al. 2004). However, characterizing cross-scale connectivity is a challenge because most theories and modeling approaches are not applicable at multiple scales (with one exception, see the scaling relations derived by Hunt et al. 2015) and our understanding of cross-scale interdependencies of the processes controlling water fluxes from the soil to the plant and the atmosphere is still incomplete (Loik et al. 2004). Representing and synthesizing hydrological connectivity, from the point to the landscape scale, will require accounting for connections among hydrologic conditions, climate, vegetation, soil processes, and landscape morphology. Particularly, the topographic effects on water redistribution could enhance or inhibit hydrological and biogeochemical processes, creating biogeochemical hot-spots in the wettest locations (McClain et al. 2003). Therefore, taking topography into account could both improve our understanding of hydrological and biogeochemical linkages and provide an explanation for emerging spatial patterns (e.g., Adams et al. 2014). Moreover, topographic features and their spatial distribution are key to scale-up plot-based knowledge to the landscape level (e.g., Riveros-Iregui and McGlynn 2009, Vico and Porporato 2009, Riveros-Iregui et al. 2011).

Recent efforts have been focusing on better characterizing hydrological connectivity. For example, percolation theory has been used to quantify the size of hydraulically-connected soil patches in dry soils. Smaller patches (~10–100 μm) remain connected longer during drying, thus supporting residual microbial activity and explaining why microbial activity stops at the same water potential level (–15 MPa) in soils worldwide (Manzoni and Katul 2014). Over an even wider range of scales, Wang et al. (2012c) developed a conceptual framework for upscaling ecohydrological and biogeochemical processes using electrical circuit analogies. Exploiting Thévenin's theorem, any process that can be described by a linear electrical circuit analogy can be represented at larger-scales as a simplified Thévenin equivalent. The Thévenin equivalent behaves identically to the original circuit, so the mechanistic features of the model are maintained at larger scales. It is also possible to investigate how disruptions in micro-scale connectivity can

affect macro-scale processes. Even with these progresses, our understanding of the magnitude and dynamics of the cross-scale connectivity and how to characterize the connectivity is still rudimentary and significant efforts are required.

MODELING AND OBSERVATIONAL ADVANCES IN ADDRESSING THE HYDROLOGICAL-BIOGEOCHEMICAL INTERACTIONS

Mathematical or conceptual models can help disentangle the interactions among ecosystem components and their external drivers. Clearly, different modeling approaches are possible, depending on the context in which they are developed. Process-based models offer tools to examine how specific physical processes or ecosystem and organism properties affect the overall dynamics. Often the level of mechanistic detail and the spatial resolution are related to the time scale of interest (Jarvis and McNaughton 1986, Manzoni and Porporato 2009). As the scales are increased it may be necessary to reduce model detail and introduce stochastic components to surrogate processes at the smaller scales (Katul et al. 2007). Conceptually, process-based plant and microbial eco-physiological models can be scaled up to the ecosystem level by coupling them to models of water, C, nutrients, and energy flows in the soil and atmosphere, and by accounting for spatial heterogeneity (e.g., Fatichi et al. 2012). Long-term models describing successional dynamics, pedogenesis, geomorphology and evolution of other slower components can be further coupled to the plot-scale ecosystem models.

Modeling soil microbial eco-physiology

Traditionally, microbial responses to changes in soil moisture at the scale of a dry-down event have been described using rate modifiers that reduce the potential decay rate when water or oxygen are limiting (Bauer et al. 2008). These rate modifiers are often presented as empirical piecewise linear or nonlinear functions of soil moisture or water potential, and are calibrated against laboratory or field data (e.g., Fig. 3). Despite their ability to capture respiration trends during drying these functions do not provide a process-based representation of the underlying dynamics. Changes in respiration have also been

described by models based on changes in solute and oxygen diffusion rates, on the ground that the physical process of diffusion constraints C supply to the microbes in dry conditions and oxygen supply in wet conditions (Skopp et al. 1990, Schjonning et al. 2003, Davidson et al. 2012). These models assume that microbial dynamics equilibrate with the supply of C and oxygen, thus neglecting rapid changes that occur upon rewetting and the subsequent respiration pulses.

Process-based representations to capture these non-stationary dynamics have followed different approaches based on contrasting conceptual models of pulse mechanisms (either physiological or physical, or both). A hierarchy of models was developed to assess how different pool structure might affect the simulated pulse response (Lawrence et al. 2009). Including microbial biomass and enzyme pools was found to be important to correctly predict pulses. Notably, the presence of a soluble pool that accumulates C during drying (when microbial uptake is low, but extracellular enzymes are still active) and is used rapidly upon rewetting provided the needed mechanism for the respiration pulse (Lawrence et al. 2009, Manzoni et al. 2014a, Oikawa et al. 2014).

The eco-physiological responses of microbes to low water potential and C availability (both occurring in dry soils) are described in detail by some recent models, although with a focus on saline aquatic systems, laboratory settings, or C-limited conditions. Osmoregulation can be modeled using Van't Hoff equation, which links osmotic potential to solute concentration in microbial cells (Potts 1994). In turn, solute concentration and water content can be described by mass balance equations, accounting for uptake from the environment and inhibition effects of high salt concentrations on metabolism (Dotsch et al. 2008). Dormancy in response to lowered C supply is often described by switching functions that transfer a fraction of biomass from active to dormant state (Jones and Lennon 2010). A slightly different approach employs the concept of 'microbial activity', that is, a state variable tracking the metabolic status of microbial cells (Panikov 1996, Blagodatsky and Richter 1998). This activity state increases when substrate availability is high, thus up-regulating growth

and decay of microbes during periods of abundant resources. Similar concepts and mathematical formulations can be employed in soil biogeochemical models, after linking the transition to dormancy to soil water availability and the accumulation of osmolytes to the actual C supply to the microbial cells (Bär et al. 2002, Manzoni et al. 2014a).

These models can capture short-term dynamics at the event or dry-down time scales, but do not account for changes in microbial community composition following prolonged dry or wet periods. Conceptually, these changes could be described by evolving traits (Wallenstein and Hall 2012), that is, in a modeling framework that allows parameters encoding organism physiology evolving through time. This evolution can be regulated through explicit description of competing microbial populations, so that the community-level traits vary as a consequence of changes in the relative abundance of different phenotypes (Allison 2012, Resat et al. 2012, Kaiser et al. 2014). How this changes are coordinated with altered plant community composition over successional time scales is still largely unexplored from a modeling perspective.

Modeling plant eco-physiology

Models of plant eco-physiological responses to soil water changes are typically constructed around coupled equations for water transport, transpiration, and CO₂ assimilation that predict gas and energy exchanges over sub-daily time scales and at the leaf level. Leaf-scale processes are integrated to the canopy level and to daily and longer scales through plant growth models, which in turn can be coupled to plant competition models at successional time scales (Manzoni et al. 2013a). This hierarchy of models at different scales allows bridging rainfall event- and dry-down scales to seasonal- and climatic-scales, spanning the whole spectrum of responses to wet periods of different intensity and duration.

Water transport in plant tissues is generally described using an electrical analogy as a catenary process in which water follows a gradient of declining water potential from the soil to the leaves, crossing resistances representing different plant tissues (van den Honert 1948, Tyree and Sperry 1988, Bohrer et al. 2005, Wang et al. 2012c). This formalism allows estimating

leaf water potential and thus describe mechanistically changes in stomatal conductance (Buckley et al. 2003). Simpler models are based on empirical relations between stomatal conductance and photosynthetic rate or environmental conditions (reviewed by Damour et al. 2010). Alternative models employ the concept of optimal control, assuming that stomatal regulation maximizes CO₂ assimilation for a given water loss through transpiration (Cowan and Farquhar 1977), which leads to increased water use efficiency as soil becomes drier (Manzoni et al. 2013b and references therein). The assimilation rate is generally expressed as a function of photosynthetic capacity (a set of traits related to C fixation reactions) and leaf internal CO₂ concentration, which is in turn controlled by stomatal conductance and the atmospheric CO₂ concentration (Farquhar and Sharkey 1982). Because both photosynthetic capacity and stomatal conductance are parameterized as decreasing during soil drying, modeled assimilation rates also decline with soil moisture (Vico and Porporato 2008, Egea et al. 2011). These coupled water transport and C assimilation models critically depend on numerous parameters the detailed description of which is beyond the scope here. Importantly, however, these parameters represent mathematically specific traits that are often measured.

These trait-based, short-term models have been used to explore how different plant features determine emerging properties such as the transpiration-soil moisture and photosynthesis-soil moisture relations at the daily time scale (Daly et al. 2004a, b, Egea et al. 2011, Manzoni et al. 2014b). By linking aggregate parameters such as the moisture levels at incipient stomatal closure and at wilting, and the transpiration rate under well-watered conditions, to specific traits, these models bridge the gap between process-based representations and eco-hydrological models based on those aggregate parameters (e.g., Laio et al. 2001, Porporato et al. 2001).

Similar to soil microbial models, plant gas exchange and growth models typically assume constant eco-physiological traits. As such they link environmental conditions (soil moisture in particular) to plant activity with a one-to-one relation, neglecting carry-over effects of particular stress events (Fig. 4) and long-term changes in

vegetation characteristics, such as after prolonged dry or wet periods. For example, to our knowledge there are no process-based models explicitly accounting for recovery of photosynthetic capacity after a drought event, whereas some models address the recovery of xylem function (Vesala et al. 2003), but not the carry-over effects sometimes occurring over several years (Anderegg et al. 2013). At longer time scales, changes in traits due to species selection can be described through optimality approaches that explore a range of possible phenotypes and select the trait combinations that allow maximum fitness (Schwinning and Ehleringer 2001, Everard et al. 2010, Manzoni et al. 2014b). Plant mortality following drought events is particularly complicated to describe, since it results from multiple exogenous and endogenous factors, which only some recent works are attempting to disentangle (Parolari et al. 2014).

Quantifying large-scale vegetation water use

As we discussed in *Mechanistic understanding ... Vegetation responses*, one major challenge to study vegetation response to hydrological variation is the difficulty to quantify vegetation water use across scales. Multiple methods and techniques have been developed, including lysimeters (e.g., Fritschen et al. 1973, Allen et al. 1991), large tree potometers/transpirometers (e.g., Knight et al. 1981), ventilated chambers (e.g., Greenwood and Beresford 1979), whole tree chamber (Ryan et al. 2000), sap flow measurements, as well as radio isotope (e.g., tritium; Kline et al. 1970, Waring and Roberts 1979) and stable isotope approaches (e.g., deuterium; Calder et al. 1986) that trace whole plant transpiration. These plant-scale measurements require upscaling to the ecosystem/landscape level. Both bottom-up and top-down methods have been used to estimate plant water use at larger spatial scales. Bottom up methods involve the scaling up of individual plant measurement (e.g., chamber measurements, sap flow measurements) by considering a representative sample of individuals, whereas top-down approaches measure total ET (e.g., eddy-covariance method) and seek to partition its contributing components. Separating E and T is a difficult task and all the methods used to this aim contain large uncertainties (Wang et al. 2014). Among other methods, stable

isotopes of water provide a promising tool to separate E and T , as they carry distinct isotopic signatures. To assess ET partitioning using stable isotopes, three isotopic end members need to be quantified: the isotopic composition of ET (δ_{ET}), T (δ_T) and E (δ_E). Recent efforts have focused on developing, refining and assessing estimation methods of all three components (Wang et al. 2009a, Good et al. 2012, Soderberg et al. 2012, Wang et al. 2013). Particularly, by employing a mass balance approach for both isotopes and water vapor inside the leaf chamber, Wang et al. (2012b) developed a new framework to directly and continuously monitor δ_T . This method is not only important to assist ET partitioning, but also useful in physiological studies to capture the fast δ_T responses to radiation variations—a goal that previous approaches could not achieve (Wang et al. 2012b).

Techniques for fine-resolution observations of the hydro-biogeochemical interactions

One constraint for observing detailed hydrological and biogeochemical coupling is the limitation of continuous monitoring of biogeochemical fluxes at fine temporal and spatial resolution. In the last 10 years, the emergence of new technology, namely solid-state soil sensors, has improved the monitoring of the effects of water pulses on soil CO_2 dynamics, allowing for detailed examination at temporal scales that were difficult to observe in the past (Tang et al. 2003). High-resolution measurements are required to capture highly variable fluxes and pools. Field comparisons of solid-state soil sensors with traditional, discrete soil chambers have been useful to reveal information on the behavior of soil CO_2 efflux from hourly to seasonal time scales. For example, studies that have used both techniques show good agreement under periods of low soil water content and no rainfall; however, the good agreement disappears during or immediately following rainfall events as small as 1 mm in magnitude (Fig. 5). This discrepancy between techniques is important because it reveals systematically different responses in the CO_2 dynamics in the soil at depth (measured with solid-state sensors) and at the top of the surface (measured with the soil chamber), which would not have been revealed without fine-resolution observations. It has been

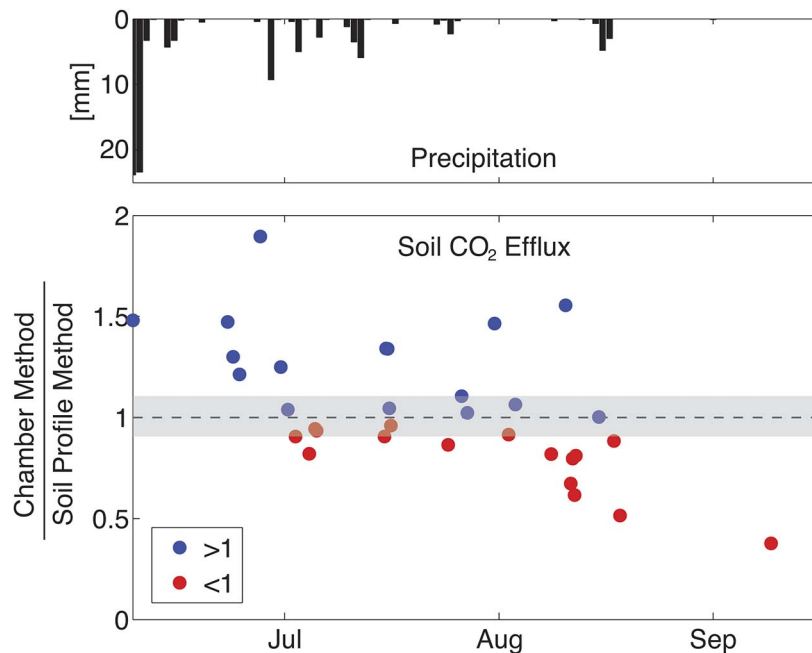


Fig. 5. (Top) Precipitation measurements over a growing season in a semi-arid, coniferous forest. (Bottom) Field comparison (ratio) between solid-state soil probes and a traditional soil chamber techniques to estimate surface soil CO₂ efflux. These measurements suggest that the soil CO₂ efflux at the soil surface is likely to be overestimated by more than 50% during and following rainfall. Shaded area represents agreement by both techniques within 10% of one another. See Riveros-Iregui et al. (2008) for additional details.

suggested that new water inputs can cause a CO₂ burst in soil gas phase immediately following precipitation due to rapid gas displacement in the pore space (Unger et al. 2010), followed by enhanced biological activity (Cable and Huxman 2004). Thus, it is likely that the burst observed and measured with soil chambers at the top of the soil surface is the result of a physical displacement of soil gas (i.e., soil CO₂ transport) that does not fully capture the enhancement in biological activity at depth (i.e., soil CO₂ production). While it has been suggested that microbially-induced CO₂ production can increase as early as 3 hours following rainfall (Blazewicz et al. 2014), questions remain regarding the relative increase of both soil CO₂ transport and soil CO₂ production following moisture additions. The findings of Fig. 5 do not imply that one technique performs better than the other, but rather that these techniques are largely complementary and should be used in tandem to assess the drivers of CO₂ production and transport in soils. Future studies should

focus on the use of fine-resolution techniques to examine the response of both above and below-ground processes across varying moisture states.

THE SOCIETAL IMPORTANCE OF UNDERSTANDING LINKED BIOGEOCHEMICAL AND HYDROLOGICAL PROCESSES IN DRYLANDS

Human dimension of dryland degradation

Human activities have a profound influence on the function of dryland ecosystems. Drylands worldwide have experienced rapid population growth in the past few decades creating additional demand for land and water resources, in particular for food and energy production. Further, many areas are experiencing extreme water scarcity resulting from unsustainable exploitation of resources (e.g., groundwater), political instability, and uncertainty induced by changing climate. On the one hand, the limited (or depleting) water resources are often the centerpieces of intense competition from the food and energy sectors. On the other hand, the

energy and food sectors are interdependent as energy production is often water intensive, and agriculture is both water and energy intensive. In many cases transporting water to end-use areas occur at the expense of energy. Hence, a holistic approach considering “food-energy-water nexus” is increasingly becoming a critical part of water policy decisions in dryland regions of the world (Bazilian et al. 2011).

Globally, human-induced land degradation is a major environmental issue affecting both the availability of land and water resources vital for food and energy production. The environmental and socio-economic-political effects of dryland degradation involve a complex interplay of biophysical and anthropogenic factors acting at different spatial and temporal scales (Geist and Lambin 2004). Due to the extent of degradation, its control is expected to improve quality of life in drylands. Human-induced land degradation, typically initiated by changes in land management, is associated with the intensification of either agricultural or livestock production. The increased stress on crop and rangelands is often manifested as an increase in soil erosion, nutrient decline, biodiversity loss, and soil salinity (D’Odorico et al. 2013). Dryland communities often depend on livestock-based farming systems for survival, increasing the pressure on scarce grazing resources (vegetation and water). The low productivity of croplands may drive rural agrarian communities to increase the stocking rate of grazing animals above the carrying capacity, leading to rapid degradation. Climatic changes, urbanization and large-scale energy development have also accelerated the degradation rates (MEA 2005, Hernandez et al. 2014). Often the biophysical and anthropogenic drivers of ecosystem degradation are interrelated. The rapid deterioration of livelihoods in rural areas induced by ecosystem degradation, in combination with political instability, may result in large-scale human migrations with socio-economic and political consequences (Glantz 1988). Understanding the interactions between ecohydrological and biogeochemical processes that affect the fate of water and nutrients are critical to improve our understanding of land degradation dynamics and to model responses of vulnerable ecosystems to management decisions.

Hydro-biogeochemical interactions and dryland degradation

Biogeochemical processes are strongly influenced by vegetation acting in concert with abiotic factors (e.g., hydrologic and aeolian processes). On the one hand, vegetation affects the spatial distribution and cycling of water and nutrients by altering soil structure, microbial biomass and microclimate. On the other hand, vegetation types and patterns in arid and semi-arid regions are maintained by the interaction of hydrological (moisture, sediment transport) and biogeochemical processes. Rapid changes in vegetation pattern is often considered a sign of environmental change or ecosystem degradation (Kefi et al. 2007). The vegetation changes are accompanied by biogeochemical alterations in drylands such as substantial changes in C and N dynamics. Interactions between sediment transport processes and vegetation are known to impact the functional types, density and patterns of vegetation (Ravi et al. 2009, D’Odorico et al. 2013). The selective removal and redistribution of nutrient-rich fine sediments determines the conditions favorable for the establishment and survival of different vegetation functional types, through their impact on the soil moisture regime and soil biogeochemical processes (Fig. 6). In fact, hydrological and aeolian transport processes in dryland ecosystems are responsible for creating and maintaining the observed heterogeneities in soil and nutrient redistribution (Schlesinger et al. 1990, Ravi et al. 2007). The heterogeneity in resource and vegetation distribution determines the spatial distribution of hydrological properties such as infiltration, runoff and soil moisture (Bhark and Small 2003, Eldridge et al. 2014). In turn, vegetation impacts sediment transport by altering soil moisture, surface roughness and sediment trapping efficiency. These interactions can lead to the formation of areas of “hydrologically enhanced plant productivity”, a common characteristic of many arid and semi-arid landscapes (Ludwig et al. 2005, Puigdefabregas 2005). The examples of the vegetation-sediment transport interactions are well documented in drylands including the formation and expansion of coppice dunes, and the ring pattern formation in certain grass species (Ravi et al. 2008, Ravi et al. 2009). Disturbances, natural or anthropogenic, can impact the sediment transport-vegetation

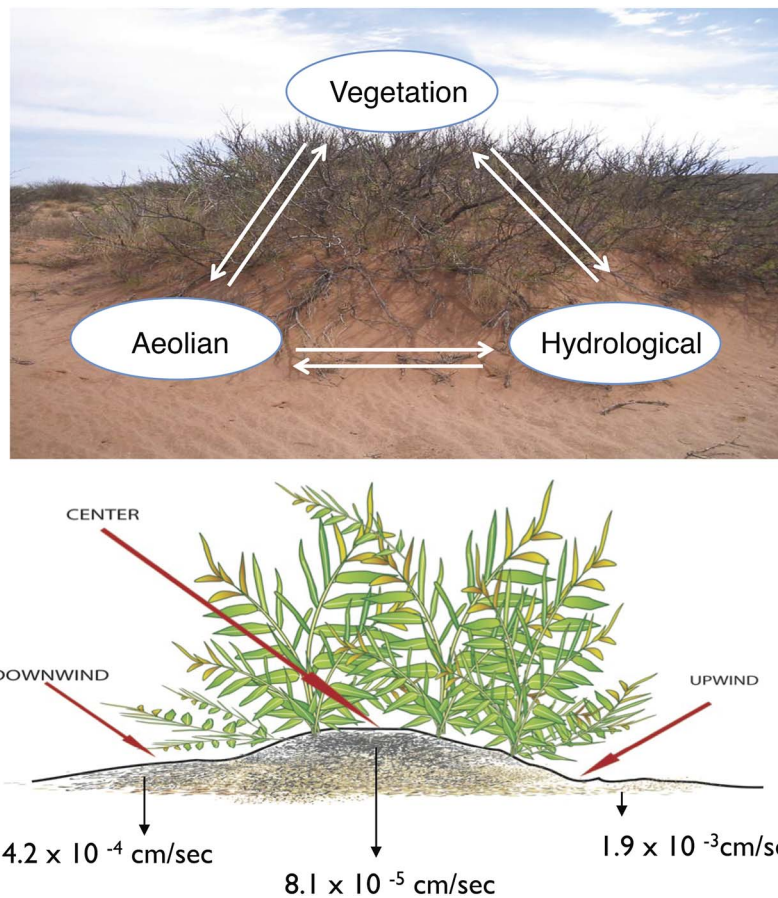


Fig. 6. Vegetation-sediment transport interactions in the formation and expansion of coppice dunes (modified from Ravi et al. 2007). Differential rates of removal and deposition of nutrient-rich fine soil particles by wind and water results in differential distribution of soil hydrological properties (e.g., unsaturated hydraulic conductivity values in the figure) and vegetation patterns.

interactions at different scales (Breshears et al. 2003, Ravi et al. 2009). Hence understanding the feedbacks among soil erosion processes, vegetation dynamics and disturbances are critical to quantify the biogeochemical responses of drylands to changing climate and management scenarios.

The interactions among vegetation, sediment transport and disturbances are thought to play a major role in ecosystem changes and degradation in drylands and there is a growing interest to address them collectively (Schlesinger et al. 1990, Ravi et al. 2009, Ravi et al. 2010). Major vegetation transformations in drylands such as woody plant encroachment and exotic grass invasion and the associated land degradation, highlight the role of vegetation disturbance-soil

erosion feedbacks (Ravi et al. 2009, Ravi et al. 2010). These rapid vegetation shifts are considered to be “transformative changes” with ecohydrological, biogeochemical and socioeconomic impacts (Turnbull et al. 2012, Wilcox et al. 2012, D’Odorico et al. 2013). The changes are often manifested through alterations soil moisture, runoff, rooting depth, *ET*, sediment transport, nutrient cycling and disturbance (e.g., fire) regimes. The impacts of vegetation transformations cannot be generalized, as in many cases the long term impacts of these changes on ecosystem functions are site-specific. In many drylands that are in a transition state (e.g., shrub-to-grass or grass-to-shrub), the changes in ecosystem functions can thus be explained and predicted in terms of spatial and temporal distribution of soil

resources, and the associated soil erosion-vegetation feedbacks, which are explained in the earlier section.

SUMMARY AND LOOKING FORWARD

This synthesis highlights the many ways in which hydrological and biogeochemical processes are coupled in water-limited ecosystems. This synthesis is fueled by the increasing need to understand and predict these interactions to address grand future challenges (e.g., climate change, water scarcity, food security). In the past few decades, research has moved away from disciplinary limitations and has evolved towards integrating ideas towards achieving a holistic framework. There is an ever-growing interest in the scientific community to quantify and model ecohydrological and biogeochemical interactions at different spatial and temporal scales, as the interactions are recognized as major drivers of ecosystem processes in water-limited ecosystems. This synthesis focuses on three opportunities for advancing coupled hydrological and biogeochemical research in these systems. First, we discussed quantitative understanding of mechanisms linking hydrological and biogeochemical variations. We focused on the mechanisms of microbial and vegetation responses, discussed the challenge and feasibility to separate them, and highlighted the inherent dynamical complexities. Second, we synthesized the advances in experimental and theoretical approaches that describe these hydrological and biogeochemical linkages. Third, we discussed applying these insights to address critical dryland issues such as land degradation and food-water-energy nexus.

Several areas deserve more attention. First, cross-scale interaction has been recognized to improve our system predictions at larger scale based on information from smaller scales. However, characterizing cross-scale connectivity from soil pores to landscapes is a challenge because theories and modeling approaches are in their infancy and cross-scale interdependencies (or invariance) of multiples processes are largely unknown. Second, the concepts of “hot spots” and “hot moments” are inherently focused on a dichotomy between extreme and mean environmental conditions (McClain et al. 2003); however, small spatial- and temporal-scale variation in

abiotic conditions is the norm in water-limited systems. Therefore, in closing, a better characterization of the fine scale abiotic variation (from soil pores to topographic features) and its effects on macroscopic ecosystem dynamics will be required to advance our understanding of ecohydrological and biogeochemical interactions.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for their supportive comments and constructive critiques. The manuscript benefits from the intellectual exchange between L. Wang and Heather Throop on related topics. L. Wang acknowledges partial support from the U.S. Department of Agriculture (2014-51130-22492) and U.S. National Science Foundation (IIA-1427642). S. Manzoni acknowledges partial support from the U.S. National Science Foundation (DEB-1145875/1145649). S. Ravi acknowledges partial support from the U.S. National Science Foundation (EAR-1451518). D. RIVERS-Iregui acknowledges support from the U.S. Department of Agriculture (2012-67019-21711).

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