The Interactive Role of Wind and Water in Functioning of Drylands: What Does the Future Hold?

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Feedback mechanisms between abiotic and biotic processes in dryland ecosystems lead to a strong sensitivity to interannual variations in climate. Under a future regime of higher temperatures but potentially increased rainfall variability, drylands are anticipated to experience changes in wind and water transport that will alter plant community composition and feedback on landscape connectivity. Here, we present a conceptual framework for understanding the coupling of vegetation productivity, aeolian transport, and hydrologic connectivity under anticipated changes in future climate, which suggests that a more extreme climatic regime will lead to more connected landscapes with attendant losses in soil, nutrient, and water resources. When enhanced connectivity triggers state changes, irreversible changes in ecosystem functioning can occur, with implications for the future of global drylands.

Keywords: precipitation, runoff, wind erosion, connectivity, deserts

rylands, comprising ecosystems with low water availability from hyperarid deserts to subhumid grasslands, cover more than 40% of the Earth's land surface and house more than 2 billion of the world's population, many of whom rely on the environment for subsistence needs (Reynolds et al. 2007). Compared with wetter regions, drylands are characterized by patchy vegetation with considerable bare mineral soil (e.g., D'odorico et al. 2006, 2007). The degree of connectivity, which is the ability of material to flow from one place to another on the landscape, is the result of the spatial arrangement of elements on the landscape (structural connectivity) and their interaction with the strength of the process causing movement (functional connectivity). Connectivity among bare patches is an important factor determining nutrient retention (e.g., Ludwig et al. 2002, 2007, Webb et al. 2012) and local transport by wind and water (e.g., Tengberg 1995, Wainwright et al. 2000, 2002, Dougill and Thomas 2002, Wang et al. 2008, Moreno-De Las Heras et al. 2010). At a longer range, connectivity affects export of the aeolian and fluvial material (e.g., Mahowald et al. 2005, 2008, Parsons and Abrahams 2009) that ultimately controls feedback loops between biotic and abiotic processes in drylands (e.g., Okin et al. 2009b, 2015; a note on usage: for simplicity, when structural connectivity is meant, the term will be used; connectivity alone will refer to functional connectivity).

Transport of sediment by both wind and water in deserts has been studied for several decades, but there is a dearth of understanding how these processes interact with one another in space and time (for some exceptions, see Al-Masrahy and Mountney 2015 and Schepanski et al. 2012). This is particularly true when considering dryland systems where vegetation has a strong role in determining structural, as opposed to functional, connectivity (Bracken et al. 2013). The purpose of this article is to discuss these interactions as driven by above ground net primary production, with implications for landscape changes resulting from transport processes. Here, we present a conceptual framework for the interactions between wind and water transport at the hillslope scale and vegetation productivity (at interannual timescales) as mediated by local precipitation. A recent review on fluvial processes in dryland rivers is available (Tooth 2011); therefore, this article focuses on hillslope processes.

The interactive roles of biotic and abiotic (wind and water) processes are especially evident in landscapes that have undergone ecosystem state change, a process that has been observed in drylands worldwide. An important example of this is the encroachment of woody vegetation into former grasslands to produce shrublands (Schlesinger et al. 1990). The shorter connected pathways in grasslands limit the transport of sediment by wind and water while the conversion to shrublands has made these landscapes more sensitive to precipitation variability (Mueller et al. 2007a,

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Table 1. Coefficients of variation (CV, standard deviation/mean) for wind and precipitation metrics for three stations in the arid southwest United States using hourly data from 1990 to 2017 (NOAA 2018). CV_{mean} is calculated using annual values from 1990 to 2017. CV_{max} is the value for the season (i.e., DJF, MAM, JJA, SON) with the highest CV during the time period from 1990 to 2017. The number-of-days metrics are meant to highlight the frequency of the stronger rain or wind events that could result in sediment transport. In all cases, the CV for wind-related metrics is less than the CV for water-related metrics. This is also true of individual seasons (not shown).

	Barstow, California		Las Vegas, Nevada		Lubbock, Texas	
	CV _{mean}	CV _{max}	CV _{mean}	CV _{max}	CV _{mean}	CV _{max}
Precipitation (total)	1.26	1.72	0.70	3.06	1.04	1.67
Wind Speed (average)	0.05	0.09	0.12	0.15	0.04	0.07
Number of days with more than 5 millimeters of precipitation	1.07	3.45	0.53	1.00	0.35	0.75
Number of days with winds of speeds more than 7 meters per second	0.06	0.31	0.42	0.71	0.14	0.45

2007b, Bergametti and Gillette 2010, Stewart et al. 2014). Although the application of the conceptual framework is not limited to the case of woody-plant encroachment into grasslands, these are well-studied drylands where these interactions are most evident.

Conceptual framework

In this section we describe a conceptual framework for the interplay of wind, water, and vegetation in arid landscapes, stressing the importance of the idea of connectivity in understanding these interactions.

Wind and water play different roles in the landscape. The most important difference between the functional roles that wind and water play within a landscape is that water serves as both a resource and as a medium of transport. As a means of transport, water is important ecologically because it drives erosion and nutrient losses or redistribution (Schlesinger et al. 1999, 2000). Wind does not serve as resource, although it does play important ecological functions in drylands, such as in affecting evapotranspiration rates (e.g., Dickinson 1984) and as an agent of seed dispersal (e.g., Peters et al. 2004b). As means for transport, both wind and water transport have been shown to be important abiotic processes that control the spatial distribution of soil resources (e.g., Wainwright et al. 1999, Li et al. 2008). This is critical because the joint distribution of soils and vegetation is one of the most-discussed aspects of shrub encroachments in drylands (Schlesinger and Pilmanis 1998), which is one of the most-discussed forms of land degradation in drylands. Fertile islands, resource-rich patches of soil centered on plants, both result from and enforce plant community change (Schlesinger et al. 1990) and are a key functional trait of drylands at the plant-interspace scale (Peters et al. 2007).

Wind and precipitation are ubiquitous factors affecting dryland ecosystems, but their importance varies on different spatial and temporal scales. Wind is present, to varying degrees, nearly every day, and although it can

fluctuate within and between days and seasons, it displays less variability than precipitation on annual and seasonal scales (table 1). The episodic nature of precipitation, on the other hand, results in greater variability on both daily and interannual timescales. From an ecosystem perspective, the consequence of this is that windy seasons are reliably so, whereas precipitation more often occurs at extremes of wet and dry. Although some arid regions have a reliable seasonality in precipitation, the duration and total amounts within the rainy season also vary significantly from year to year (Wainwright 2006).

Hydrologic connectivity. Interannual variations in precipitation constitute an important forcing for arid and semiarid regions that can elicit very different hydrologic responses depending on the overland flow and subsurface connectivity across a landscape. Hydrologic connectivity is defined here in terms of how water moves horizontally from upland hillslope (source areas) toward terminal location such as channels (e.g., Bestelmeyer et al. 2011). In dryland landscapes, hydrologic pathways present an opportunity for water losses into the subsurface, from the individual plant rooting zones up to the river reach scale (Gee and Hillel 1988, Goodrich et al. 2004). Vegetation cover plays an important role in controlling hydrologic structural connectivity, with the larger bare areas found between shrubs providing greater structural connectivity for overland flow, thus enabling greater runoff generation on shrub-dominated areas as compared with grass-dominated slopes (e.g., figure 1; Schlesinger et al. 1999, Bautista et al. 2007). Functional connectivity for hillslope-water movement is a function of this structural connectivity and the depth of flow, which is controlled by precipitation intensity and duration (Turnbull et al. 2008). Water travels farther and flows to or from more parts of the landscape for more intense or longer-duration rainfall events than for smaller events.

Overcoming subsurface losses to hillslope soils is essential for establishing hydrologic connectivity in a dryland

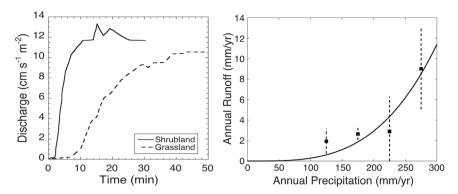


Figure 1. (Left) The results from field-scale rainfall simulations show that runoff generation also shows dependence on vegetation type and therefore on hydrologic connectivity (after Parsons et al. 2006). (Right) The threshold runoff production in channels ranging from 0.8 to 4.7 hectares over the period 2010-2016. The binaverage and standard deviation (bin size of 50 millimeters per year) of average annual runoff (R in millimeters per year) are normalized by upstream area as a function of annual precipitation (P in millimeters per year) from four flumes at the Jornada Experimental Range (JER) in south-central New Mexico, United States (Schreiner-Mcgraw and Vivoni 2017). Power-law regression of the form $R = 5.63 \times 10^{-8} P^{3.35}$, with $R^2 = 0.91$ when forced through origin.

landscape. While a large portion of water returns to the atmosphere via plant transpiration or soil surface evaporation (Seyfried et al. 2005, Newman et al. 2006), periods with above-average precipitation allow for enhanced overland flow and subsurface connectivity. For instance, figure 1 (right) shows the annual runoff as a function of annual precipitation at a mixed shrubland watershed described by Templeton and colleagues (2014). Runoff production occurs in response to individual storm events, primarily occurring during the wet summer season, through an infiltration excess mechanism (Schreiner-McGraw and Vivoni 2017). Runoff is a process described by a power-law relation with respect to precipitation. Annual precipitation amounts greater than approximately 250 mm per year lead to large increases in runoff production as hydrologic losses on hillslopes and in channels are exceeded. A similar type of type of threshold behavior (i.e., a certain amount of rainfall needs to be exceeded for runoff to be activated through connected overland flow pathways) exists along the entire hydrologic pathway from watershed source areas to closed basin playas (Mckenna and Sala 2016).

Connectivity for wind transport. Aeolian transport occurs when the erosivity of the wind exceeds the erodibility of the surface (Bagnold 1941). The erosivity of the wind is driven primarily by wind speed and surface roughness (e.g., Kawamura 1951), whereas the erodibility of the surface is controlled mainly by vegetation cover and the threshold wind shear velocity of the soil (i.e., the shear velocity of the wind above which aeolian transport would occur for the bare soil alone). The soil's threshold is dependent on soil texture, soil moisture, organic matter, and crusting (e.g., Gillette et al. 1980).

Because vegetation extracts momentum from the wind and, in doing so, produces leeside wakes where the erosivity of the wind is reduced, plants strongly affect the amount and spatial distribution of aeolian transport (Raupach 1992). Specifically, the amount, distribution, and height of vegetation patches modulate the amount of aeolian transport through controlling the size of bare soil gaps between vegetation elements (Okin 2008). The size of bare gaps, in relation to the height of the upwind vegetation, defines structural connectivity with respect to aeolian transport. Therefore, shrublands experience considerably more horizontal aeolian transport and dust emission than grasslands on the same soils (Gillette and Pitchford 2004, Bergametti and Gillette 2010). For aeolian transport, connectivity (structural and functional) is a function of the size of gaps between plants as well as wind speed. Stronger wind decreases the

size of the protected wake area in the lee of plants, leading to longer interplant areas that are subject to erosion (Okin 2008, Okin et al. 2015).

Dvnamic vegetation controls on connectivity.

Vegetation cover and biomass affect landscape connectivity and the amount of material (e.g., soil particles, organic matter, propagules, and water) that moves horizontally, driven by wind or water. This is partially because different plant functional types have different architectures, modifying the impact that they have on the wind and water flows with respect to the amount of biomass present. Specifically, the ratio between height and width affects the correlation between biomass and cover (Flombaum and Sala 2007). Shrubs are taller and have higher biomass per unit area than grasses. Therefore, compared with a grassland with the same biomass, a shrubland will have higher bare soil cover and typically will have higher connectivity of soil patches.

Dryland dynamics are affected not only by the spatial scale of the features of interest (e.g., storm size relative to watershed area; Goodrich et al. 1997) but also by the temporal scales at which they are relevant. Precipitation, for instance, can vary at fine spatial scales (hundreds of meters), with convective storms providing highly localized rainfall. Precipitation rates vary within a storm period in ways that directly affect the generation and transport of overland and subsurface flow and thus the hydrologic connectivity among the bare soil spaces between plants (e.g., Wainwright et al. 2000). Wind speed and direction also change on fast timescales, with the strongest gusts sometimes associated with rapid changes in weather patterns (e.g., synoptic fronts and thunderstorm outflows), although smaller features, such as

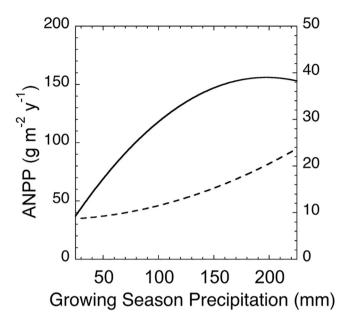


Figure 2. The annual net primary productivity (ANPP) response of grass (solid, left axis) and shrubs (mesquite; dashed, right axis) to growing season precipitation at the JER. Presented are the best-fit curves are from Gherardi and Sala (2015). The different scales of production for grasses and shrubs here result from the experimental design. Peters and colleagues (2012) showed that at broad scales, ANPP in grasslands and mesquite shrublands are similar.

dust devils, can also move sediment across the mosaic of vegetation in a landscape (Bergametti and Gillette 2010).

Vegetation changes occur over slower timescales, ranging from weeks to years, in response to biotic and abiotic drivers that affect individual plants and community composition. With respect to connectivity, the appearance of annuals on the scale of weeks to months (Bergametti and Gillette 2010) can protect the soil from wind and water transport by filling in bare spaces. Broader changes in the vegetation community—that is, transitions from grassland to shrubland—occur at the timescale of years to decades (Peters et al. 2004a, Sala et al. 2012). Depending on the underlying soil and topographic heterogeneity, these slower transitions can occur at both fine and coarse spatial scales across a land-scape. The spatial contagious effect of community change, however, suggests that often, fine-scale community changes merge into broader-scale change (Bestelmeyer et al. 2011).

Changes to topography occur more slowly, in conjunction with the variations in wind, runoff, and vegetation that together determine erosion and deposition. For instance, nebkha dunes (also called coppice dunes) result in significant changes to the topography of shrub-encroached sandy areas (e.g., Rango et al. 2000), with resulting feedbacks on local hydrology (Ravi et al. 2007). Hillslope erosion and deposition occurring due to water transport may take years to centuries, although individual storm events have the capacity for significant geomorphic work that affects

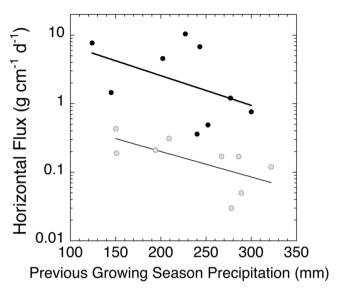


Figure 3. The log-linear relations between horizontal aeolian flux and precipitation in the previous growing season for mesquite shrubland (black) and grassland (gray) at JER from 1999–2008. A greater length of connected pathways for a mesquite shrubland produces nearly an order of magnitude greater transport than a grassland on similar soils (p < .01) with both exhibiting an exponential decrease of aeolian flux with precipitation (both p < .05).

connectivity (e.g., Gutiérrez-Jurado et al. 2007). Similarly, the creation of fertile islands at longer timescales induces localized (but widespread) perturbations on topography that have important effects on wind and water transport (Gibbens et al. 1983, Wainwright et al. 2000).

Within this multiscale context, the annual variability of precipitation at timescales relative to community change has important consequences for the competition between grasses and shrubs, as well as between grasses (Peters et al. 2012), and therefore the connectivity with respect to wind and water that plays such an important role in dryland function. For example, shrubs and grasses in the Chihuahuan desert appear to respond differently to the amount of annual precipitation (figure 2). Grasses have a productivity response that saturates slightly above the mean annual precipitation. As a result, grasses are very sensitive to dry years and relatively insensitive to wet years. Shrubs (here, mesquite), in turn, have the opposite response to precipitation amount, with an exponential increase in growth with precipitation, making them relatively insensitive to drought while still being able to take advantage of above-average precipitation. These results suggest that extremely dry sequences of years would promote a change in the ecosystem from grassland toward a shrub-dominated system with greater structural connectivity.

Interannual precipitation variability among years alters the competitive balance of shrubs and grasses (Peters et al. 2004a,

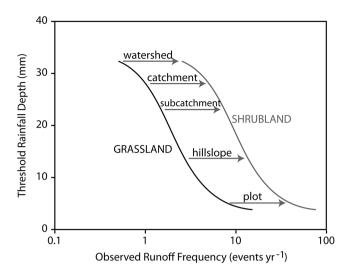


Figure 4. Vegetation-dependent changes in runoff event frequency. Larger rainfall events produce runoff at larger scales, but the greater connectivity of shrublands is expected to make runoff from shrublands at all scales more frequent. Modified from Cammeraat (2004).

Sala et al. 2012, Gherardi and Sala 2015) and influences aeolian transport at two timescales. At the annual timescale, precipitation amount affects plant growth and therefore the structural connectivity that controls aeolian transport. Higher amounts of precipitation that lead to vegetation growth tend to reduce structural connectivity through the growth of annuals or the recruitment of new perennials in bare soil areas and thus reduce aeolian flux for both shrublands and grasslands (figure 3). Changes in community composition at decadal timescales (i.e., grass to shrub transition) can have larger impacts on aeolian transport than interannual changes because of variations in vegetation growth across a full range of precipitation amounts (figure 3).

Wind and water transport in dynamic landscapes under changing vegetation and climate

A key characteristic of both wind and water transport is that the fraction of the landscape affected by these processes changes depending on instantaneous weather and vegetation conditions. For instance, shrubland patches experience more aeolian transport than grassland patches on the same soils (e.g., figure 3; Gillette and Pitchford 2004). This is because a larger area of soil is exposed to erosion in shrublands compared with grasslands—that is, there is generally higher structural connectivity with respect to wind in shrublands, whereas functional connectivity depends on the strength of the wind. Interannual variability in precipitation also contributes to changes in the area affected by wind erosion, but this effect is mostly at the plant-interspace scale. After a relatively wet growing season, for instance, plant interspaces can be filled in by new recruits or annuals. This means that only small exposed areas in the landscape will experience

aeolian transport. After a series of dry growing seasons, on the other hand, larger bare gaps will be more susceptible to aeolian transport because they are less sheltered, and more of the landscape will experience above-threshold winds, resulting in larger amounts of transported sediment during a typical wind event or windy season.

Similar scale-dependent effects occur in runoff generation and water transport (figure 4). Small precipitation events are more frequent than larger events, and overland flow (runoff) therefore occurs more frequently for small events. However, the spatial scale of runoff event frequency is also dependent on the storm areal extent. The smaller and frequent storms tend to produce runoff only at the plot or hillslope scale. Larger-magnitude, less frequent storms that occupy more area produce runoff that integrates over the catchment or watershed scales. Because portions of the landscape dominated by shrubs produce more runoff more quickly than portions of the landscape dominated by grasses (figure 1) due to their higher connectivity with respect to water transport than grasslands, runoff events at all scales occur more frequently in shrublands than in grassland patches. As with wind, wet years that produce timely flushes of annuals and new recruits will have lower hydrologic structural connectivity at the plant-interspace scale, leading to less frequent runoff generation. This analysis makes it clear that there are important interactive effects between precipitation, vegetation productivity, community composition, and topography that affect the amount and spatial extent of wind and water transport and their feedback onto vegetation processes (figure 5).

Even though climate models disagree about trends in precipitation, particularly for drylands in the southwestern United States, there appears to be considerable evidence that precipitation variability, including periods of drought and periods of wet years, will increase in the decades to come (figure 6; Räisänen 2002, Kharin et al. 2007, Wetherald 2010, Fischer et al. 2013). All else being equal, wind and water transport have opposing relationships with respect to precipitation despite the similar effects on connectivity discussed previously. As annual precipitation increases, aeolian transport decreases markedly for both grasslands and shrublands if it leads to increases in vegetation cover during periods of wind. On the other hand, overland flow, and therefore the possibility of water erosion, increases with increasing annual precipitation, in particular if the distribution of rainfall leads to less frequent but more intense events (i.e., more precipitation variability). The increase in runoff, despite the lower structural connectivity of bare interspaces expected under higher precipitation, is due to the fact that hydrologic losses to the subsurface (i.e., infiltration into soils and channel transmission losses) are minimized as a dryland experiences wetter states through well-known links between the runoff response and the antecedent wetness condition. Furthermore, a change in the temporal distribution of rainfall events to a condition of fewer but more intense events will yield higher runoff production (Mckenna and Sala 2018).

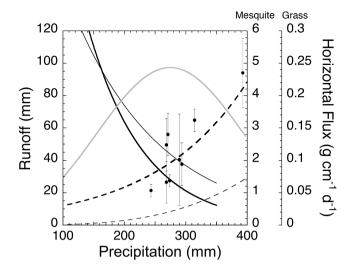


Figure 5. The complex interactions between runoff, aeolian transport, and climate. The thick black line is the best-fit line to horizontal aeolian flux in mesquite areas, and the thin black line is the best-fit horizontal aeolian flux in grassland areas (from figure 3). The symbols represent the mean ± standard deviation of annual runoff from 2 meter × 2 meter experimental plots in shrublands at the Jornada Long Term Ecological Site (New Mexico, USA) from 1983 to 1994. The thick dashed line is the best fit through these data. The thin dashed line is the power law fit through the catchment-scale data presented in figure 1, illustrating increasing hydrologic losses due to lower connectivity at larger scales. The thick gray line is a Gaussian with mean and standard deviation equal to the mean and standard deviation of annual precipitation at the Jornada LTER site from 1926 to 2010: 273 ± 114 millimeters per year.

With increasing variability in the future, the consequence of these opposing relationships for wind and water fluxes with the precipitation amount is that sediment transport by both wind and water is expected to increase. Increasing numbers of dry years should lead to an increasing number of years with high structural connectivity with respect to wind at the plant-interspace scale and therefore large amounts of aeolian transport. Increasing numbers of wet years, on the other hand, should lead to an increasing number of large rainfall events (Trenberth 2011) during those years, resulting in greater transport by water at scales from the plot to the watershed.

Increased aridity, which is anticipated in drylands globally (Seager et al. 2014) and includes anticipated changes in both precipitation and temperature, is also likely to increase both wind and water transport on hillslopes. Increased aridity is associated with higher evaporative demand, thus making individual storms less effective in providing water to vegetation. New recruits or annuals that might fill interspaces and reduce connectivity with respect to both wind and water will be suppressed under more arid conditions (Peters et al. 2012), thereby allowing more frequent and greater transport

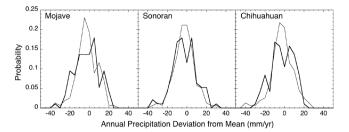


Figure 6. Histograms of anomalies in annual precipitation from historical (1850–2005) and future (2006–2100, RCP8.5) CMIP5 ensemble means for grid cells in the Mojave, Sonoran, and Chihuahuan Deserts. For each period (historical versus future), the average annual precipitation for the period was subtracted from the precipitation in each year, and the results were used to calculate the histogram.

by both wind and water at the plant interspace scale. The increase in water transport would also be influenced by the occurrence of fewer but more intense rainfall events. The community change that is expected to accompany this increased aridity and variability (Peters et al. 2012, Gherardi and Sala 2015) will contribute to increased structural connectivity and transport at the patch scale. Thus, the increased frequency and amount of transport by wind and water that are expected will affect larger fractions of land-scapes, both by increasing the number of interspaces that are experience transport and functional connectivity as well as by contributing to community change toward higher overall structural connectivity.

As with the rest of the globe, the world's drylands will experience an uncertain—but certainly changing—future. These changes will perturb the interactions among plants, wind, and water. Expected changes are anticipated to result in increased transport by wind and water, which are key feedback mechanisms in drylands on community composition and structure (e.g., Mueller et al. 2007a, 2007b, Okin et al. 2009a, Stewart et al. 2014, Yu et al. 2016). These interactive effects are critical when considering how to manage the world's vast drylands (Bestelmeyer et al. 2018). Important choices lie ahead for the management of dryland ecosystems, and understanding the role of wind and water transport processes in shaping them is crucial in determining the ecosystem services they will provide in the coming decades.

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