Do Changes in Connectivity Explain Desertification?

GREGORY S. OKIN, ANTHONY J. PARSONS, JOHN WAINWRIGHT, JEFFREY E. HERRICK, BRANDON T. BESTELMEYER, DEBRA C. PETERS, AND ED L. FREDRICKSON

Arid and semiarid regions cover more than 40% of Earth's land surface. Desertification, or broadscale land degradation in drylands, is a major environmental hazard facing inhabitants of the world's deserts as well as an important component of global change. There is no unifying framework that simply and effectively explains different forms of desertification. In this article, we argue for the unifying concept that diverse forms of desertification, and its remediation, are driven by changes in the length of connected pathways for the movement of fire, water, and soil resources. Biophysical feedbacks increase the length of connected pathways, explaining the persistence of desertified landscapes around the globe. Management of connectivity in the context of environmental and socioeconomic change is essential to understanding, and potentially reversing, the harmful effects of desertification.

Keywords: desertification, connectivity, erosion, fire, vegetation dynamics

Broadscale land degradation in arid and semiarid regions of the globe—desertification—directly affects about 250 million people in the developing world through the loss of soil nutrients and reduction in the land's productivity, and could potentially affect the 2.5 billion people who live in drylands worldwide (Reynolds et al. 2007). In addition to imposing the direct impacts of land degradation on people living in drylands, desertification is increasingly recognized as an important element of global change. For instance, changes in vegetation structure and albedo as a result of desertification can significantly affect regional climate, with feedbacks to ecosystem dynamics (Taylor et al. 2002). Desertification has been shown to affect animal biodiversity (Bestelmeyer 2005). Atmospheric dust, with its myriad effects (Okin et al. 2004, Kaufman et al. 2005, Kellogg and Griffin 2006), is produced by erosional processes in deserts worldwide and increases with desertification (Moulin and Chiapello 2006). A recent report by Seager and colleagues (2007) suggests that increasingly arid conditions are expected in the next decades in the southwestern United States, southern Europe, the Mediterranean, and the Middle East. This "aridification" will contribute to desertification, with significant impacts on human populations and important feedbacks within the global environment.

Understanding the causes and consequences of desertification requires an integrated analysis of the dynamics and interactions of key biophysical and socioeconomic variables across multiple spatial and temporal scales (Reynolds et al. 2007). The objective of this article is to describe the unifying concept that the length of connected pathways (LOCOP) in landscapes explains four major types of desertification in terms of both the patterns and the processes that occur. The LOCOP concept can also serve as a framework for anticipating future landscape dynamics and for guiding management and remediation efforts.

The term "desertification" has been used to refer to many disparate land degradation phenomena, but, in part because of the flexibility of the term, an integrated biophysical understanding of the processes of desertification has been lacking. Any general biophysical model of desertification and the feedbacks that propagate it must encompass at least four dominant forms of desertification, as reflected in changes in vegetation cover, composition, and spatial distribution (figure 1): form 1, vegetation loss due to agriculture (Puigdefabregas 1998, Okin et al. 2001); form 2, vegetation loss due to changes in climate or land use (Khalaf and Al-Ajmi 1993, Gonzalez 2001); form 3, invasion of woody vegetation into perennial grasslands (Van Auken 2000, Cabral et al. 2003); and form 4, invasion of exotic grasses into desert shrublands, resulting in replacement of woody vegetation (D'Antonio and Vitousek 1992). Each of these forms of desertification is associated with a complex suite of changes in dynamic soil properties, micrometeorology, and animal communities. Each is also sustained by an important set of feedbacks (figure 2).

BioScience 59: 237–244. ISSN 0006-3568, electronic ISSN 1525-3244. doi:10.1525/bio.2009.59.3.8

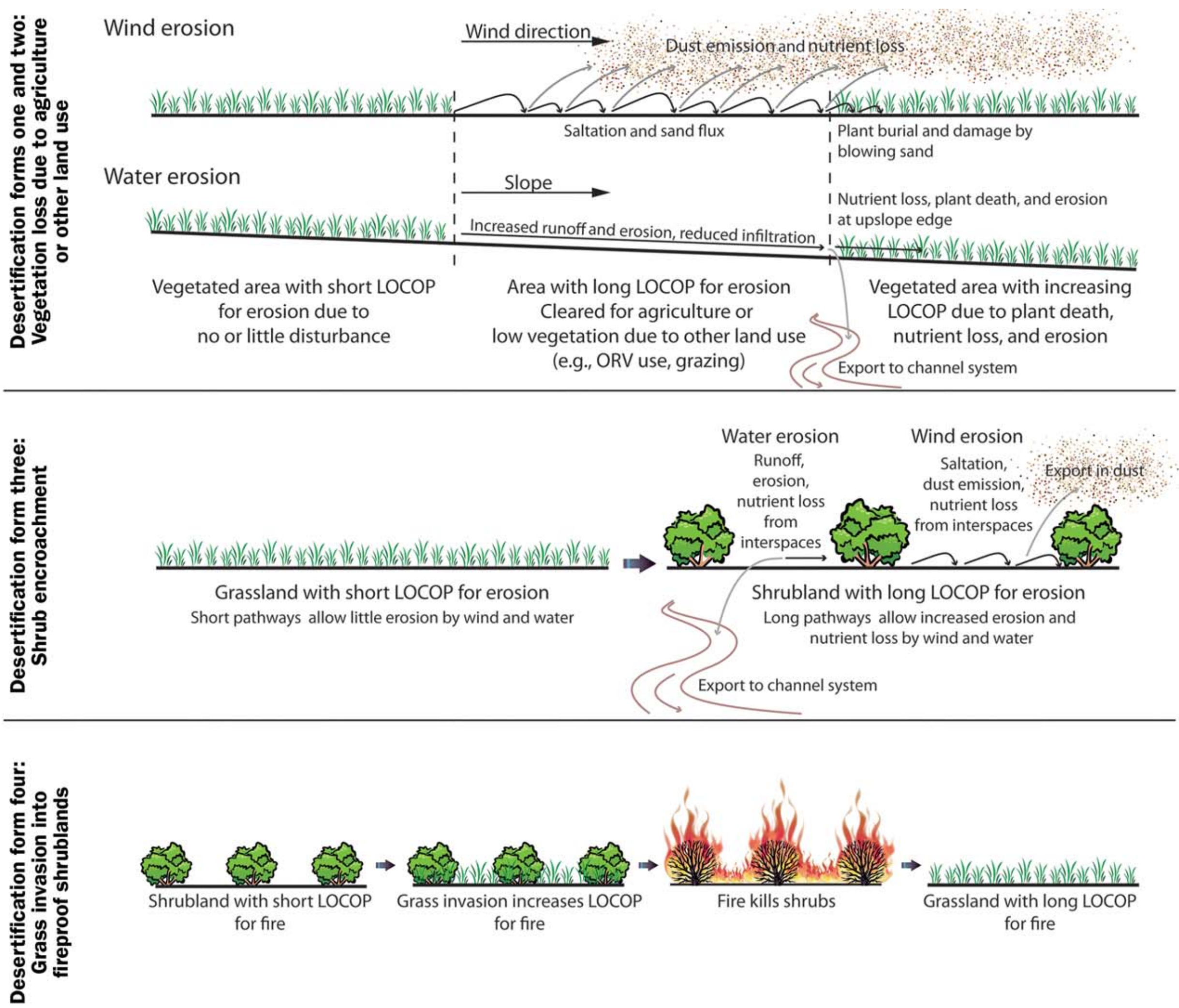

Figure 1. Schematic representation of the four forms of desertification and feedback processes that can be explained by changes in connectivity. Abbreviation: LOCOP, length of the connected pathway; ORV, off-road vehicle.

Here we argue that these four dominant forms of desertification have key commonalities that serve as the basis of a mechanistic understanding of the biophysical aspects of desertification. The biological feedbacks model proposed by Schlesinger and colleagues (1990) and widely used by others in environments around the world, though relevant to many systems, explains only one aspect of desertification (shrub encroachment) at only one scale (the plant interspace). Furthermore, it fails to fully define the fundamental processes that make desertification so difficult to reverse in many regions. The cross-scale interactions framework of Peters and colleagues (2004) describes one class of desertification events that propagate through time and space and are driven by a change in dominant processes. However, this model does not account for broadscale changes in vegetation that occur nearly simultaneously, such as vegetation loss with agriculture. The more recent interacting-elements framework of Peters and colleagues (2006) provides an overall structure for understanding the dynamics of complex landscapes in arid and semiarid regions. However, this framework does not provide details on how transport vectors interact with vegetation. The structural and functional connectivity framework of Turnbull and colleagues (2008) discusses the interrelation between landscape structure and abiotic connectivity, but only in the context of water relations. To date, the biophysical commonality between different forms of desertification has not been adequately explained in terms of a unifying principle. Here we propose that the underlying principle is changing connectivity in landscapes undergoing desertification.

Landscape connectivity

Connected pathways serve as conduits for the movement of fire, water, or soil resources borne by water or wind. We argue that the four main forms of desertification are related by changes in connectivity, which is defined specifically as the length of connected pathways, or LOCOP (figure 2). This definition of connectivity confers more specificity to the recent connectivity framework developed to explain how processes at local to regional scales can influence continental-scale dynamics (Peters et al. 2008).

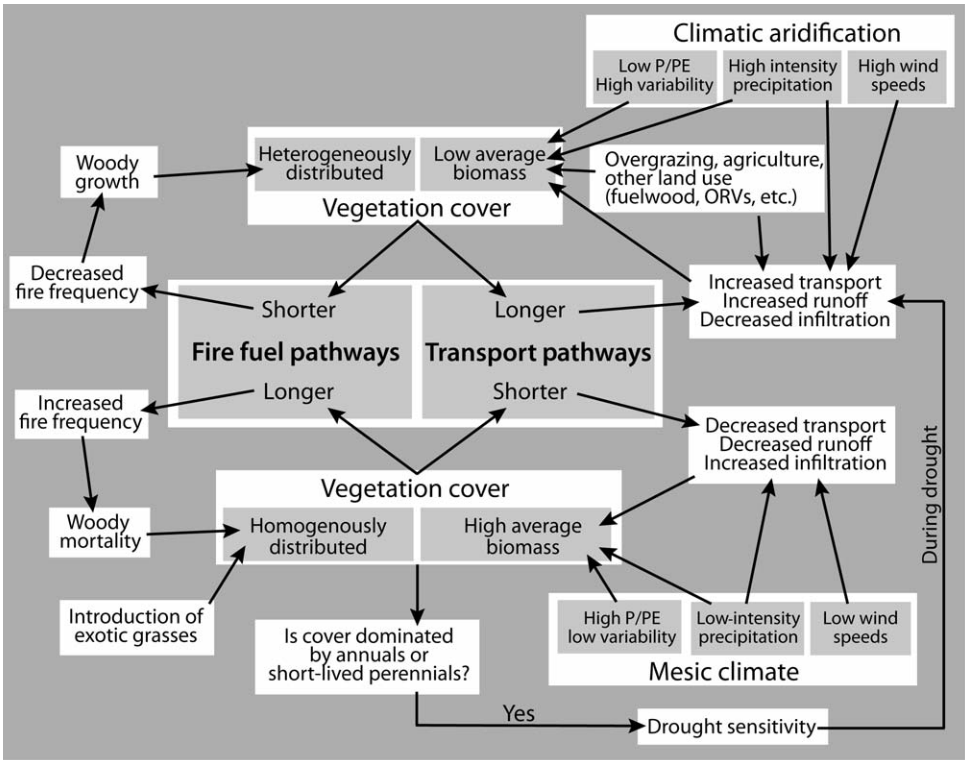

Figure 2. A model of desertification linking the length of the connected pathway, or LOCOP, to climate change, land use, and vegetation cover. Abbreviations: ORVs, off-road vehicles; P/PE, precipitation/potential evapotranspiration.

Removal of vegetation to create arable fields (form 1) allows the cleared area to act as a connected pathway for runoff, water erosion, and wind erosion, thus reducing infiltration and increasing the removal of soil, nutrients, and other resources (Okin et al. 2001, Avni 2005). The connectivity of agricultural fields during the drought of the 1930s has been implicated in the Dust Bowl in the United States (Peters et al. 2007). Vegetation loss due to other land use, such as grazing or off-road vehicle use (form 2), similarly opens gaps that act as connected pathways for wind and water (Webb 1982, Khalaf and Al-Ajmi 1993). Although these gaps usually appear (at least initially) as small, open patches at intensively used sites (e.g., near water sources, along trails or roads), they can expand because of the resulting reductions in soil moisture and other soil resources. In the case of shrub encroachment into perennial grasslands (form 3), where the transport of soil resources by wind and water reinforces fertile islands (Schlesinger et al. 1990), bare transport pathways between shrubs provide the requisite connectivity (Bartley et al. 2006, Peters et al. 2006, Mueller et al. 2007a, Okin 2008). When shrublands are replaced by a continuous cover of exotic grasslands (form 4), senescent grass during the dry season provides connectivity for fire; fires of sufficient intensity and duration to kill woody plants cannot occur without a nearly continuous or connected stratum of fuel.

Other authors have noted the importance of connectivity in deserts. Much of the previous work on connectivity has focused on the importance of hydrologic connectivity in controlling runoff and sediment movement (Cammeraat 2002, 2004, Imeson and Prinsen 2004, Bracken and Croke 2007, Mueller et al. 2007a, Reaney et al. 2007). Okin and Gillette (2001) and McGlynn and Okin (2006) used geostatistical arguments based on connectivity to explain patterns in vegetation caused by wind erosion. Appreciation for the role of connectivity in the feedbacks between transport processes and plant processes that control ecosystem structure in deserts has also emerged in the last several years. Dunkerley and Brown (1999) invoked flow of water and sediment in unvegetated patches to explain banded vegetation in Australia. Sandercock and colleagues (2007) studied the importance of vegetation in controlling connectivity and geomorphic change in arid river channels in mediterranean Europe. Ludwig and colleagues (2007) developed an index of "leakiness" that relates resource flow from patchy arid and semiarid landscapes to the health of these landscapes for Australia (table 1). Peters and colleagues (2006) discussed the role of connectivity in determining resource flow and explaining patterns across scales in complex landscapes. Ares and collegues (2003a, 2003b) investigated the relationship between vegetation distribution and transport processes in Argentina. Li XR and colleagues (2006) investigated the use of straw checkerboards designed to reduce

Table 1. The average size of unvegetated linear transport pathways.

Site	Average size of linear transport pathways (meters)	Directional leakiness index
75 meters from water (most degraded)	27.7	0.9
1400 meters from water (intermediate)	1.9	0.14
Cattle exclosure (least degraded)	0.5	0.014

Note: Calculations were made using the method of McGlynn and Okin (2006) for data from Ludwig and colleagues (2002) for three Australian grazed savanna sites. The directional leakiness index (DLI) is an index of the resource loss potential of a system. A fully functioning (i.e., conserving) system has DLI = 0.0. A system that is completely unable to conserve its resources (i.e., a completely leaky system) has DLI = 1.0.

connectivity for arid land remediation in China. Discussions of forms of desertification other than those explicitly addressed here, such as the reduction of cover that accompanies the building of earthworks that disrupt overland flow (Schlesinger and Jones 1984), implicitly recognize the importance of connectivity in the lateral distribution of resources. Clearly, there is growing recognition of the importance of connectivity in desert landscapes.

But instead of seeing connectivity as simply an emergent phenomenon, our view is that the connectivity of landscape pathways serves as the underlying and unifying concept for understanding desertification. Landscape-change processes and feedbacks depend on connectivity because connected pathways provide the conduits for processes (fire propagation and wind or water movement) that are directly responsible for changing the spatial distribution of resources and vegetation (figure 2). Thus, changes in connectivity provide not only a way to understand desertification but also a framework to evaluate strategies for desertification mitigation. Successful strategies will be those that manage connectivity in effective ways. For example, many traditional soil conservation measures such a shelterbelts, no-till agriculture, mulching, and terracing essentially reduce the connectivity of the landscape with respect to wind and water erosion.

A review by Van Auken (2000) of the likely controls on shrub encroachment (form 3) has supported the role of cattle grazing in reducing grass biomass, thus reducing fire frequency in an environment where fires are necessary for the control of woody seedlings (D'Odorico et al. 2006). In this view, shrub encroachment is promoted by a reduction in grass (i.e., fuel) connectivity. This analysis would seem to contradict our assertion that greater connectivity is the key factor controlling desertification. However, one must consider the dominant processes in a landscape that drive desertification. In the case of shrub encroachment, the dominant processes in desertification are wind and water erosion (Schlesinger et al. 1990). Though a reduction in grass biomass resulting from grazing shortens fuel and fire pathways, it simultaneously lengthens the abiotic transport pathways of wind and water erosion. Fire limits the establishment of shrub seedlings, but it cannot drive the landscape entirely to the desertified and stable shrubland state. When desertification manifests as fire-induced conversion of woody shrublands to exotic grasslands (form 4), the situation is the opposite, but the analysis remains the same. Invasion of exotic grasses lengthens the fire-fuel pathways while simultaneously shortening abiotic transport pathways. Here, fire is responsible for the death of woody species and is the dominant process that controls the conversion of fireproof woodlands to exotic grasslands.

Scale and connectivity

The key concept in the connectivity model of desertification is the connected pathway. Connected pathways are conduits on the land surface that allow relatively free movement of fire, water, and materials borne by both water and wind. The size of connected pathways is measurable, and therefore our model is scale explicit. The overall connectivity of a landscape is a function of the size distribution of its connected pathways. A landscape with many short pathways will have a low degree of connectivity, whereas a landscape composed mostly of long pathways will have a high degree of connectivity.

Because connected pathways are of varying sizes, our model serves to integrate multiple hierarchies of scale. For instance, the fertile islands model explains desertification at the plant-interspace scale because it pertains to the movement of soil resources from plant interspaces to adjacent areas beneath plant canopies (Schlesinger et al. 1990). The connectivity model includes the plant-interspace scale because plants are naturally connected to their adjacent interspaces, but it supersedes that model because connected pathways also explain how the plant-interspace scale connects with larger scales. Long connected pathways account for the loss of soil resources at a larger scale and the transport of that material over longer distances. Thus, on a slope with short connected pathways, small amounts of sediment are eroded from one area but deposited nearby, whereas on a slope with long connected pathways, a much larger area contributes sediment and erosional areas are further separated from depositional areas (Bartley et al. 2006). If connected pathways are long enough, transport can feed into a river network or ephemeral lake in a closed basin, effectively removing the water and waterborne resources from the landscape entirely. In the case of wind, short pathways may result in the redistribution of coarse material and litter from interspaces to under-canopy areas (Okin et al. 2006a). Longer pathways will result in significant wind erosion (figure 3; Li J et al. 2007, Okin 2008) and the loss of nutrient-rich dust that can be transported thousands of kilometers with significant impacts on downwind ecosystems (Okin et al. 2004).

At a regional scale, climatic variables influence the size of connected pathways and thus exert an influence on processes at finer scales. For instance, the area that contributes runoff to a point increases with greater rainfall intensity (Wainwright et al. 2002), and the proportion of the landscape undergoing wind erosion increases with wind speed (Okin 2005, 2008). Thus, greater rain intensity or wind strength results in increasingly connected landscapes. Furthermore, because new recruits can occur in locations that interrupt transport pathways and the death of individuals can extend existing pathways, climatic conditions controlling establishment (Neilson 1986) and mortality (Schultz and Ostler 1993) can further influence pathway length and landscape connectivity. Likewise, fire connectivity is controlled by wind speed during the fire as well as by the amount of senescent biomass available, a result of climatic conditions during the previous growing season.

The length of connected pathways

The existence of a connected spatial corridor does not by itself ensure that a process can act along a pathway. Energy to

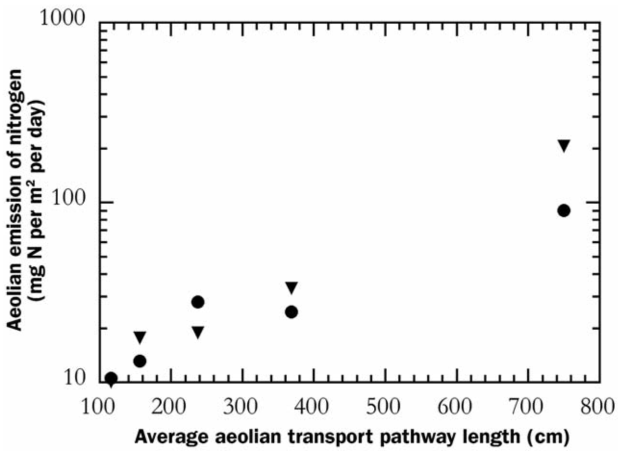

Figure 3. The emission of nitrogen (in milligrams of nitrogen per square meter per day) on dust from experimental plots in the Jornada Experimental Range, New Mexico, versus the length of the average aeolian transport pathway, in centimeters. Source: Based on data from Li FR and colleagues (2005) for spring (triangles) and summer (circles) of 2005.

move material or to propagate fire is also required. Thus, there is not any single value that can be used to differentiate short pathways, which do not contribute significantly to biophysical transport or fire propagation, from long pathways, which do. The effectiveness of a pathway for biophysical transport or fire propagation is an increasing, nonlinear function of the length of the transport pathway and the energy available for transport (e.g., volume of runoff and slope in the case of water erosion or wind speed in the case of soil erosion and fire). Thus, for any landscape, what constitutes a short or long transport pathway depends on the forcing conditions at a particular place and time. Nonetheless, a consideration of the literature suggests that short pathways generally are less than 0.5 to 1 meters (m) in size, whereas long pathways are more than 2 to 5 m in size.

For instance: (a) Under prevailing conditions in south-central New Mexico, unvegetated gaps smaller than 1 to 2 m do not appear to contribute appreciably to aeolian flux (Okin et al. 2006a), and gaps larger than 5 to 10 times the height of the upwind vegetation are unaffected by the presence of vegetation (Okin et al. 2006b). (b) A rainfall experiment in southern Arizona showed two to eight times more erosion from a shrubland with plant spacing of 2 to 5 m compared with a grassland on similar soils with plant spacing of 0.2 to 0.5 m (Parsons et al. 1996). The shrubland sites also experienced equilibrium runoff conditions more often than did the grassland sites. The vegetation cover on the grassland site was 33%, whereas the shrubland site had 44% cover. Thus, although the shrubland site had greater vegetation cover, the longer connected pathways led to higher rates of erosion and more frequent runoff production at the site. (c) Wildland fire requires a nearly continuous stratum of fuel. The invasion of nonnative grasses into shrublands of the southwestern United States has provided this continuous fuel bed during and after wet years (e.g., Brooks and Matchett 2006). Plant spacings in Mojave Desert shrublands are more than 4 to 5 m (figure 4; Wallace et al. 2000). Thus, unvegetated gap sizes greater than 4 to 5 m do not appear consistent with propagation of fire in these environments. Areas with unvegetated gaps of more than 4 to 5 m must necessarily have short fire-fuel pathways.

Connected pathways exist in every landscape, though there may be a threshold length required to initiate cascading landscape changes. Indeed, for short pathways, local resource redistribution is a beneficial effect of connectivity: (a) water deposited at the base of a plant at the end of a short pathway contributes to the growth of that plant, and (b) nutrient-rich litter and fine soil particles that are deposited at the end of a short wind or water pathway contribute to the fertility of the soils at that site. When bare, erodible patches coalesce to create interconnected transport pathways, however, wind and water erosion can remove or significantly redistribute soil resources. Changes in grazing, land use, climate, or other factors are required to change connectivity so that short connected pathways coalesce to form long pathways, which are then further elongated by feedback processes. Extreme events such as drought, intense grazing, or other human activities may trigger pathway coalescence. Once pathways have become very long, further lengthening is limited by landscape characteristics, such as topography and soil parent material, that can change only on very slow timescales.

Feedbacks to connectivity

When transported material reaches the end of a pathway, it behaves in ways that tend to lengthen the pathway. For example, sand transported by wind can bury, abrade, or strip leaves from plants that interrupt the flow, increasing mortality

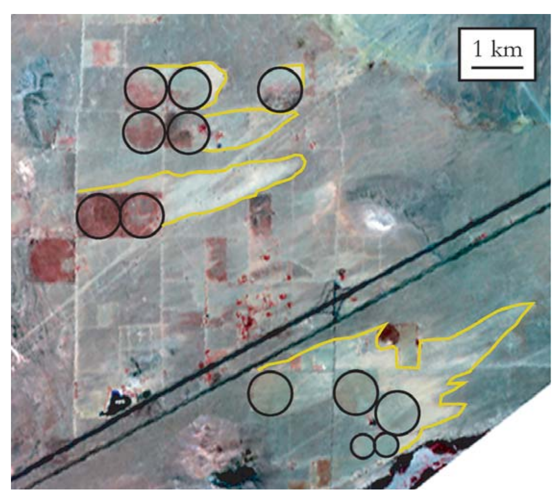

Figure 4. AVIRIS (Airborne Visible/Infrared Imaging Spectrometer) image (NIR:Green:Blue::R:G:B) of abandoned central-pivot agricultural fields in the Mojave Desert (black circles). Areas of wind-blown sand leading to expanding desertification are outlined in yellow. Source: Adapted from Okin and colleagues (2001).

and effectively lengthening the connected pathway (figure 4; Okin and Gillette 2001). Likewise, through gully erosion, runoff generated over a large area and funneled into a channel can cut through microtopographic barriers that would otherwise have interrupted the flow. In the absence of gully erosion, runoff flowing from a high-connectivity shrub patch (i.e., an area with long connected pathways) to a low-connectivity grass patch (i.e., an area with short connected pathways) does not immediately infiltrate upon reaching the boundary (figure 5). Instead, the runoff travels beyond the patch boundary, resulting in an effective increase in the connectivity of the landscape. The vegetation at the boundary, in turn, has experienced removal of accumulated soil nutrients in the runoff and relatively little infiltration of the runoff water, with negative consequences for later growth (Mueller et al. 2007b).

Feedbacks also exist in fire-driven desertification. A landscape dominated by short pathways for the spread of fire can resist the influence of fire because, in the absence of a connected fuel load, the consequence of an ignition event is minor. A landscape dominated by long connected pathways for the spread of fire is prone to the effects of fire because the fire can easily spread (Brown and Minnich 1986, Brooks and Matchett 2006). Ignition of a grassy patch can kill or damage woody plants within and at the downwind edges of a fire. The resulting reduction in woody cover opens further areas for invasion of grasses.

Thus, positive feedbacks increase the length of connected pathways in arid lands (figure 2) and small disturbances can cause short pathways to coalesce, resulting in long pathways with landscape- and regional-scale consequences (Peters et al. 2004). The presence of these feedbacks further explains why the major forms of desertification have proven so difficult to mitigate despite many decades of effort (Whitford et al. 1995).

Significant changes in climate may be able to short-circuit positive feedback loops by interrupting long pathways through increased recruitment, reduced wind speed, or lower rainfall intensity. However, the persistence of desertified ecosystems suggests that the ability of other factors to overcome positive feedback processes may be limited.

Managing connectivity

Aridification of arid and semiarid areas has already begun and is expected to continue for the next 50 years in the southwestern United States (Seager et al. 2007). The ensuing droughts can be expected to reduce establishment and increase mortality of desert plants, leading to decreased cover and greater length of connected pathways for transport processes. Wind speed and rainfall intensity may also increase in the coming decades (IPCC 2007), leading to greater effective connectivity of arid landscapes. Invasion of native grasslands and shrublands by exotic grasses will continue, particularly with the introduction of new varieties (e.g., the US Department of Agriculture's cold-resistant "Frio" variety of buffelgrass), resulting in connectivity of fuel. Each of these changes clearly presents new management challenges, particularly because they are associated with positive feedbacks that make them difficult to reverse (Peters et al. 2004). They may also present new opportunities for management.

For instance, an understanding of the degree of connectivity in a landscape can aid in triage of remediation efforts. Areas that are dominated by long connected pathways will not respond to small-scale manipulations because those pathways present inertia that a small-scale manipulation cannot overcome. Remediation resources should be directed to cases where they can do the most good, namely, to cases where the scale of the potential remediation matches the scale of landscape connectivity.

Managing increasingly dynamic arid landscapes will require significant changes in the ways in which we assess, monitor, and respond to changes in connectivity within these landscapes. Assessment and monitoring protocols must be sensitive to changes in connectivity at the management-unit scale to provide the information required to rapidly adapt management. A protocol that reflects the size distribution of intercanopy gaps (Herrick et al. 2005) has already been adopted by the National Resource Conservation Service's National Resource Inventory and applied at more than 10,000 points in the United States, but most monitoring programs continue to document only vegetation cover and composition. This same indicator can also be applied at the management-unit scale to minimize the proportion of the soil surface exposed in gaps that are susceptible to wind erosion (Okin et

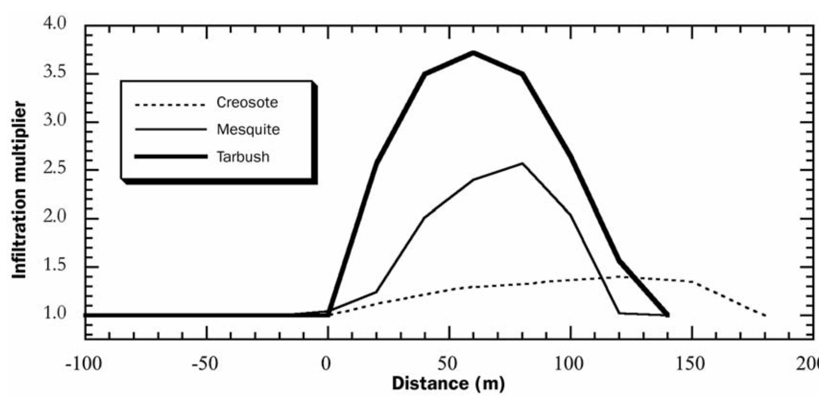

Figure 5. Relative infiltration of water flowing downslope from three shrublands (negative distances) into grasslands (positive distances), with the grass-shrub boundary at distance = 0 meters. The infiltration multiplier at a point is the infiltration rate at that point divided by the infiltration in the high-connectivity shrubland. Water infiltrates preferentially (e.g., infiltration multiplier > 1) in low-connectivity grasslands downslope of high-connectivity shrublands, which contribute runoff (e.g., infiltration multiplier is approximately 1). Source: Adapted from data in Mueller and colleagues (2007b).

al. 2006a). This indicator can be used by ranchers to decide when to move livestock, and by federal land managers to control off-highway vehicular traffic to reduce the risk of crossing wind or water erosion thresholds.

In addition to providing managers early warning data on potential degradation associated with changes in connectivity, these data could be used to identify potential opportunities for remediation. For example, greater hydrologic and sediment connectivity upslope, or sediment connectivity upwind, may offer opportunities for increased production or restoration in downslope or downwind locations. For millennia, humans managed connectivity by (a) selecting highly connected parts of the landscape to enhance water availability for crop production (Homburg et al. 2005), (b) designing production systems and soil and water conservation practices that reduce connectivity among patches of bare soil (Bennet 1939), and (c) creating terraces to capture and exploit sediment associated with upslope connectivity. Nevertheless, connectivity in the management of noncultivated dryland ecosystems is rarely explicitly considered in the development of new strategies, particularly at the multiple scales at which it is relevant. By considering linkages at the landscape scale, managers can often take advantage of greater upslope connectivity to promote reduced connectivity in downslope positions (e.g., by constructing barriers; Herrick et al. 2006). In essence, changes in connectivity result in a constantly shifting mosaic of resource availability. Better understanding of this mosaic and the processes that control it can help managers to identify opportunities for promoting recovery while limiting efforts in areas where they are likely to have little effect.

Changes in the degree of connectivity in drylands—defined by the length and number of connected pathways for the movement of fire, water, or soil resources by wind and water—are a key indicator of desertification worldwide. Feedbacks that increase connectivity in drylands help explain the persistence of desertified ecosystems, even where the drivers have been reduced or eliminated (Herrick et al. 2005). Research into practical ways to manage landscape connectivity by interrupting connected pathways is needed if effective means for the control, and perhaps reversal, of desertification are to be found. This research must be integrated with an understanding of key socioeconomic variables to ensure that the practices proposed are realistic (Liu et al. 2007). To the extent possible, the biophysical and socioeconomic components of desertification research should be integrated (Reynolds et al. 2007).

Acknowledgments

This research was supported by NSF-DEB grants 0720218 and 0717448 from the National Science Foundation (NSF) Division of Environmental Biology and grant DEB-0618210 from the NSF Long Term Ecological Research program. We also thank the reviewers for their valuable comments.

References cited

Ares JO, Del Valle H, Bisigato A. 2003a. Detection of process-related changes in plant patterns at extended spatial scales during early dryland desertification. Global Change Biology 9: 1643–1659.

Ares JO, Bertiller MB, Bisigato A. 2003b. Estimates of dryland degradation in Argentina with Fourier signatures from low-altitude monochromatic images with high spatial resolution. Landscape Ecology 18: 51–63.

Avni Y. 2005. Gully incision as a key factor in desertification in an arid environment, the Negev highlands, Israel. Catena 63: 185–220.

Bartley R, Roth CH, Ludwig JA, McJannet D, Liedloff AC, Corfield J, Hawdon A, Abbot B. 2006. Runoff and erosion from Australia's tropical semi-arid rangelands: Influences of ground cover for differing space and time scales. Hydrological Processes 20: 3317–3333.

Bennet HH. 1939. Soil Conservation. New York: McGraw-Hill.

Bestelmeyer BT. 2005. Does desertification diminish biodiversity? Enhancement to ant diversity by shrub invasion in southwestern USA. Diversity and Distributions 11: 45–55.

Bracken LJ, Croke J. 2007. The concept of hydrological connectivity and its contribution to understanding runoff-dominated geomorphic systems. Hydrological Processes 21: 1749–1763.

Brooks ML, Matchett JR. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. Journal of Arid Environments 67: 148–164.

Brown DE, Minnich RA. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist 116: 411–422.

Cabral AC, De Miguel JM, Rescia AJ, Schmitz MF, Pineda FD. 2003. Shrub encroachment in Argentinean savannas. Journal of Vegetation Science 14: 145–152.

Cammeraat ELH. 2002. A review of two strongly contrasting geomorphological systems within the context of scale. Earth Surface Processes and Landforms 27: 1201–1222.

———. 2004. Scale dependent thresholds in hydrological and erosion response of a semi-arid catchment in southeast Spain. Agriculture, Ecosystems and Environment 104: 317–332.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Reviews of Ecological Systems 23: 63–87.

D'Odorico P, Laio F, Ridolfi L. 2006. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. American Naturalist 167: E79–E87.

Dunkerley DL, Brown KJ. 1999. Banded vegetation near Broken Hill, Australia: Significance of surface roughness and soil physical properties. Catena 37: 75–88.

Gonzalez P. 2001. Desertification and a shift of forest species in the West African Sahel. Climate Research 17: 217–228.

Herrick JE, van Zee JW, Havstad KM, Burkett LM, Whitford WG. 2005. Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems. Tucson: University of Arizona Press. (21 January 2009; *http://usda-ars.nmsu.edu/Monit_Assess/monitoring.htm*)

Herrick JE, Havstad KM, Rango A. 2006. Remediation research at the Jornada: Past and future. Pages 278–304 in Havstad KM, Huenneke L, Schlesinger WH, eds. Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin LTER. Oxford (United Kingdom): Oxford University Press.

Homburg JA, Sandor JA, Norton JB. 2005. Anthropogenic influences on Zuni agricultural soils. Geoarchaeology: An International Journal 20: 661–693.

Imeson AC, Prinsen HAM. 2004. Vegetation patterns as biological indicators for identifying runoff and sediment source and sink areas for semi-arid landscapes in Spain. Agriculture, Ecosystems and Environment 104: 333–342.

[IPCC] Intergovernmental Panel on Climate Change. 2007. Climate Change 2007: The Physical Science Basis. Cambridge (United Kingdom): Cambridge University Press. (21 January 2009; *www.ipcc.ch/ipccreports/ar4-wg1.htm*)

Kaufman YJ, Koren I, Remer LA, Rosenfeld D, Rudich Y. 2005. The effect of smoke, dust, and pollution aerosol on shallow cloud development over the Atlantic Ocean. Proceedings of the National Academy of Sciences 102: 11207–11212.

Kellogg CA, Griffin DW. 2006. Aerobiology and the global transport of desert dust. Trends in Ecology and Evolution 21: 638–644.

Khalaf FI, Al-Ajmi D. 1993. Aeolian processes and sand encroachment problems in Kuwait. Geomorphology 9: 111–134.

Li FR, Kang LF, Zhang H, Zhao LY, Shirato Y, Taniyama I. 2005. Changes in intensity of wind erosion at different stages of degradation development in grasslands of Inner Mongolia, China. Journal of Arid Environments 62: 567–585.

Li J, Okin GS, Hartman LJ, Epstein HE. 2007. Quantitative assessment of wind erosion and soil nutrient loss in desert grasslands of southern New Mexico, USA. Biogeochemistry 85: 317–332.

Li XR, Xiao HL, He MZ, Zhang JG. 2006. Sand barriers of straw checkerboards for habitat restoration in extremely arid desert regions. Ecological Engineering 28: 149–157.

Liu JG, et al. 2007. Complexity of coupled human and natural systems. Science 317: 1513–1516.

Ludwig JA, Eager RW, Bastin GN, Chewings VH, Liedloff AC. 2002. A leakiness index for assessing landscape function using remote sensing. Landscape Ecology 17: 157–171.

Ludwig JA, Bastin GN, Chewings VH, Eager RW, Liedloff AC. 2007. Leakiness: A new index for monitoring the health of arid and semiarid landscapes using remotely sensed vegetation cover and elevation data. Ecological Indicators 7: 442–454.

McGlynn IO, Okin GS. 2006. Characterization of shrub distribution using high spatial resolution remote sensing: Ecosystem implication for a former Chihuahuan Desert grassland. Remote Sensing of Environment 101: 554–566.

Moulin C, Chiapello I. 2006. Impact of human-induced desertification on the intensification of Sahel dust emission and export over the last decades. Geophysical Research Letters 33: L18808. doi:10.1029/2006GL025923

Mueller EN, Wainwright J, Parsons AJ. 2007a. Impact of connectivity on the modeling of overland flow within semiarid shrubland environments. Water Resources Research 43. doi:10.1029/2006WR005006

———. 2007b. The stability of vegetation boundaries and the propagation of desertification in the American Southwest: A modelling approach. Ecological Modelling 208: 91–101.

Neilson RP. 1986. High-resolution climatic analysis and Southwest biogeography. Science 232: 27–34.

Okin GS. 2005. Dependence of wind erosion and dust emission on surface heterogeneity: Stochastic modeling. Journal of Geophysical Research 110: D11208. doi:10.1029/2004JD005288

———. 2008. A new model for wind erosion in the presence of vegetation. Journal of Geophysical Research: Earth Surface 113: F02S10. doi:10.1029/2007JF000758

Okin GS, Gillette DA. 2001. Distribution of vegetation in wind-dominated landscapes: Implications for wind erosion modeling and landscape processes. Journal of Geophysical Research 106: 9673–9683.

Okin GS, Murray B, Schlesinger WH. 2001. Degradation of sandy arid shrubland environments: Observations, process modelling, and management implications. Journal of Arid Environments 47: 123–144.

Okin GS, Mahowald N, Chadwick OA, Artaxo P. 2004. The impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. Global Biogeochemical Cycles 18: GB2005. doi:10.1029/2003GB002145

Okin GS, Herrick JE, Gillette DA. 2006a. Multiscale controls on and consequences of aeolian processes in landscape change in arid and semiarid environments. Journal of Arid Environments 65: 253–275.

Okin GS, McGlynn IO, Gillette DA. 2006b. A new model for representation of non-erodible elements in wind erosion studies. Page 18 in Nickling WG, Turner S, Gillies JA, Puddister M, eds. Program and Abstracts: Sixth International Conference on Aeolian Research. Guelph (Canada): University of Guelph.

Parsons AJ, Abrahams AD, Wainwright J. 1996. Responses of interrill runoff and erosion rates to vegetation change in southern Arizona. Geomorphology 14: 311–317.

Peters DPC, Pielke RA, Bestelmeyer BT, Allen CD, Munson-McGee S, Havstad KM. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. Proceedings of the National Academy of Sciences 101: 15130–15135.

Peters DPC, Bestelmeyer BT, Herrick JE, Monger HC, Fredrickson E, Havstad KM. 2006. Disentangling complex landscapes: New insights to forecasting arid and semiarid system dynamics. BioScience 56: 491–501.

Peters DPC, Sala OE, Allen CD, Covich A, Brunson M. 2007. Cascading events in linked ecological and socioeconomic systems: Predicting change in an uncertain world. Frontiers in Ecology and the Environment 5: 221–224.

Peters DPC, Groffman PM, Nadelhoffer KJ, Grimm NB, Collins SL, Michener WK, Huston MA. 2008. Living in an increasingly connected world: A framework for continental-scale environmental science. Frontiers in Ecology and the Environment 5: 229–237. doi:10.1890/070098

Puigdefabregas J. 1998. Ecological impacts of global change on drylands and their implications for desertification. Land Degradation and Development 9: 393–406.

Reaney SM, Bracken LJ, Kirkby MJ. 2007. Use of the Connectivity of Runoff Model (CRUM) to investigate the influence of storm characteristics on runoff generation and connectivity in semi-arid areas. Hydrological Processes 21: 894–906.

Reynolds JF, et al. 2007. Global desertification: Building a science for dryland development. Science 316: 847–851.

Sandercock PJ, Hooke JM, Mant JM. 2007. Vegetation in dryland river channels and its interaction with fluvial processes. Progress in Physical Geography 31: 107–129.

Schlesinger WH, Jones CS. 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Botanical Gazette 145: 116–124.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. Science 247: 1043–1048.

Schultz BW, Ostler WK. 1993. Effects of prolonged drought on vegetation association in the northern Mojave Desert, Las Vegas, Nevada. Pages 228–235 in Roundy BA, McArthur ED, Haley JS, Mann DK, eds. Proceedings: Wildland Shrub and Arid Land Restoration Symposium; 1993 October 19–21. Las Vegas (NV): US Department of Agriculture, Forest Service, Intermountain Research Station. General Technical Report INT-GTR-315.

Seager R, et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 16: 1181–1184.

Taylor CM, Lambin EF, Stephenne N, Harding RJ, Essery RLH. 2002. The influence of land use change on climate in the Sahel. Journal of Climate 15: 3615–3629.

Turnbull L, Wainwright J, Brazier RE. 2008. A conceptual framework for understanding semi-arid land degradation: Ecohydrological interactions across multiple-space and time scales. Ecohydrology 1: 23–34.

Van Auken OW. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31: 197–215.

Wainwright J, Parsons AJ, Schlesinger WH, Abrahams AD. 2002. Hydrology-vegetation interactions in areas of discontinuous flow on a semi-arid bajada, southern New Mexico. Journal of Arid Environments 51: 319–338.

Wallace CSA, Watts JM, Yool SR. 2000. Characterizing the spatial structure of vegetation communities in the Mojave Desert using geostatistical techniques. Computers and Geosciences 26: 397–410.

Webb RH. 1982. Off-road motorcycle effects on a desert soil. Environmental Conservation 9: 197–208.

Whitford WG, Martinez-Turanzas G, Martinez-Meza E. 1995. Persistence of desertified ecosystems: Explanations and implications. Environmental Monitoring and Assessment 37: 319–322.

Gregory S. Okin (e-mail: okin@ucla.edu) is with the Department of Geography at the University of California, Los Angeles. Anthony J. Parsons and John Wainwright are with the Department of Geography at the University of Sheffield, United Kingdom. Jeffrey E. Herrick is a research soil scientist, Brandon T. Bestelmeyer is a research ecologist, Debra C. Peters is an ecologist, and Ed L. Fredrickson is a rangeland management specialist, all with the US Department of Agriculture's Agricultural Research Service, Range Management Research, in Las Cruces, New Mexico.