

ESSAY REVIEW

Pulse dynamics and microbial processes in aridland ecosystems

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Summary

1. Aridland ecosystems cover about one-third of terrestrial environments globally, yet the extent to which models of carbon (C) and nitrogen (N) cycling, developed largely from studies of mesic ecosystems, apply to aridland systems remains unclear.
2. Within aridland ecosystems, C and N dynamics are often described by a pulse-reserve model in which episodic precipitation events stimulate biological activity that generate reserves of biomass, propagules and organic matter that prime the ecosystem to respond rapidly to subsequent precipitation events.
3. The role of microbial C and N processing within the pulse-reserve paradigm has not received much study. We present evidence suggesting that fungi play a critical and underappreciated role in aridland soils, including efficient decomposition of recalcitrant C compounds, N-transformations such as nitrification, and nutrient storage and translocation of C and N between plants and biotic soil crusts. While fungi may perform some of these functions in other ecosystems, this ‘fungal loop’ assumes particular importance in the N cycle in aridlands because water availability imposes even greater restrictions on bacterial activity and physicochemical processes limit accumulation of soil organic matter (SOM).
4. We incorporate these findings into a Threshold-Delay Nutrient Dynamics (TDND) model for aridland ecosystems in which plant responses to pulsed precipitation events are mediated by a fungal loop that links C and N cycling, net primary production (NPP) and decomposition in aridland soils.
5. *Synthesis.* Arid ecosystems are highly sensitive to global environmental change including N deposition and altered precipitation patterns; yet, models from mesic ecosystems do not adequately apply to aridland environments. Our ‘fungal loop’ N cycle model integrates spatial structure with pulse dynamics and extends the pulse-reserve paradigm to include the key role of microbial processes in aridland ecosystem dynamics.

Key-words: aridland ecosystems, decomposition, decoupled systems, fungal loop, net primary production, pulse-dynamics, soil carbon, soil nitrogen

Introduction

Much is known about the carbon (C) and nitrogen (N) cycles of mesic environments (Schlesinger 1997; Bardgett 2005). In general, the hydrologic cycle integrates C and N dynamics by transporting nutrients, sustaining biotic activity, and controlling the magnitude and spatial distribution of anaerobic processes, thereby linking the production, decomposition and storage of organic matter, and controlling the rates of reactions that drive the C and N cycles. In mesic environments organic nutrient

pools often accumulate over long time periods and most of the N required for primary production is supplied by the mineralization of stored organic matter rather than external inputs. Where moisture is predictable and sufficient, the C and N cycles are more or less closed and tightly coupled through the production and decomposition of organic matter (Asner *et al.* 1997).

How well does this basic model apply to the arid and semi-arid ecosystems that cover nearly one-third of continental land area (UNESCO 1977), and are expanding as the result of climate change and population pressures? Like mesic environments, water controls biological processes in arid

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ecosystems, but high temperatures and erratic moisture inputs impose a pulsed pattern on biological activities (Noy-Meir 1973; Belnap *et al.* 2004, 2005b; Loik *et al.* 2004). Because most rainfall events are small (< 2 mm) water availability is spatially heterogeneous as well as sporadic, so nutrients tend to accumulate during extended dry periods when plant and microbial growth are restricted (White *et al.* 2004; Welter *et al.* 2005). Depending on magnitude and season, the rainfall events that punctuate these dry periods selectively trigger temperature-dependent biological activities, including plant and microbial nutrient uptake, respiration and growth, as well as biogeochemical processes such as decomposition and denitrification. Large rare events can lead to nutrient translocation through percolation and runoff as a function of landscape position, topography and soil texture (Schlesinger *et al.* 1999; Walvoord *et al.* 2003; Ludwig *et al.* 2005; Welter *et al.* 2005). This pattern not only restricts biotic activities to episodic pulses, but also leaves net primary production (NPP) and decomposition processes uncoupled much of the time.

The production and decomposition of organic matter are not only decoupled in time via pulsed precipitation, but they are also spatially heterogeneous (Schlesinger *et al.* 1996; Kieft *et al.* 1998; Ravi *et al.* 2007). Unlike mesic ecosystems where canopy cover is typically continuous, plant communities in aridland environments are often spatially discontinuous with patches of vegetation (Schlesinger *et al.* 1990; Kéfi *et al.* 2007; Scanlon *et al.* 2007) interspersed with patches of soil that are often colonized by biological crusts (Belnap *et al.* 2005a,b). Biocrust soils, variously dominated by lichens, mosses and cyanobacteria, are widely distributed in arid regions (Belnap & Lange 2003) and serve as the interface for exchanges between the soil and atmosphere (Belnap *et al.* 2003). They have been described as a mantle of fertility because they fix varying amounts of both C and N (Garcia-Pichel *et al.* 2003), depending on the relative abundance of lichens, mosses and cyanobacteria (Belnap 2002). Historically, processes within vegetated patches and crust soils were assumed to be relatively independent (Schlesinger *et al.* 1990), yet evidence is now accumulating to suggest that these patches may be interconnected by networks of fungal hyphae.

In mesic systems, decomposition processes are overwhelmingly biological. The bulk of NPP is metabolized as detritus through soil-based decomposer food webs, and the rates of these processes relative to NPP affect soil formation, C storage and N dynamics. Under these conditions, measures of climate (evapotranspiration) or litter chemistry (lignin, C : N) can be used as surrogates for biotic activity in decomposition models (Meentemeyer 1978; Sinsabaugh & Moorhead 1996; Moorhead & Sinsabaugh 2006). These empirical relationships generally do not extend to arid systems (Whitford *et al.* 1982, 1986, 1988; Schaefer *et al.* 1985; Parton *et al.* 2007; Vanderbilt *et al.* 2007) because physicochemical processes contribute to organic matter breakdown even when microbial activity is constrained. On the surface, solar radiation and wind degrade, fragment, and redistribute litter (Pauli 1964; Moorhead & Reynolds 1989; Gallo *et al.* 2006; Austin & Vivanco 2006). These conditions, combined with limited

activities of soil fauna (Belnap *et al.* 2005a), reduce the incorporation of foliar litter into soil, thereby slowing the accumulation of soil organic C and N, and accentuating the relative contributions of rhizodeposition and biological crust production to soil C and N pools.

Physicochemical decomposition may also be important below-ground. Most aridland soils have alkaline pH, which supports high oxidative enzyme potentials (Stursova *et al.* 2006). These conditions favour the breakdown of recalcitrant organic compounds, which may further limit soil organic matter (SOM) accumulation (Stursova & Sinsabaugh 2008), even as microbes compete for labile C inputs (Sponseller 2007).

Recently, a number of authors have called for a greater understanding of microbial processes in below-ground ecosystems (Bardgett *et al.* 2005; Fitter 2005; Harrison *et al.* 2007; Jackson *et al.* 2007). Here we argue that the C and N cycles in aridland soils differ substantially from those in mesic systems. First, while precipitation patterns constrain both NPP and decomposition in aridland ecosystems (Noy-Meir 1973), decomposition potential may exceed annual NPP because of contributions from abiotic processes (Austin & Vivanco 2006). Consequently, breakdown of organic matter may be less water limited than NPP, and less related to ecological constraints such as litter quality (C : N ratio, lignin content; Austin & Vivanco 2006; Parton *et al.* 2007; Vanderbilt *et al.* 2007). To the extent that decomposition potentials exceed NPP, arid ecosystems may be functionally analogous to wet tropical forests in that nutrient cycling is more directly linked to primary production than to the mineralization of stored SOM. Because aridland soils are chronically dry and contain little organic matter, fungi rather than bacteria may dominate decomposition and N transformation processes through symbiotic associations with primary producers (States & Christensen 2001; States *et al.* 2003; Allen 2007; Porrás-Alfaro *et al.* 2007). Our hypothesis is that fungal networks link plants and biological soil crusts. Supported by biotrophic carbon, these networks control nutrient transformation and translocation, and functionally integrate plant and biocrust metabolism (Fig. 1).

Below, we review recent research from the Sevilleta LTER site in central New Mexico, USA, and elsewhere, that supports the existence of a 'fungal loop' that dominates soil N transformation and dynamically links the metabolism of plants and biological soil crusts. We then present a conceptual model, the Threshold-Delay Nutrient Dynamics (TDND) model (Fig. 2) that builds upon an earlier formulation (Reynolds *et al.* 2004) in which we explicitly incorporate microbial functional types, soil resources and the fungal loop into the traditional pulse-reserve paradigm.

A case study in the northern Chihuahuan Desert: evidence for a fungal loop

STUDY SITE

The Sevilleta LTER site in central New Mexico, USA, contains extensive areas of semi-arid grassland dominated by

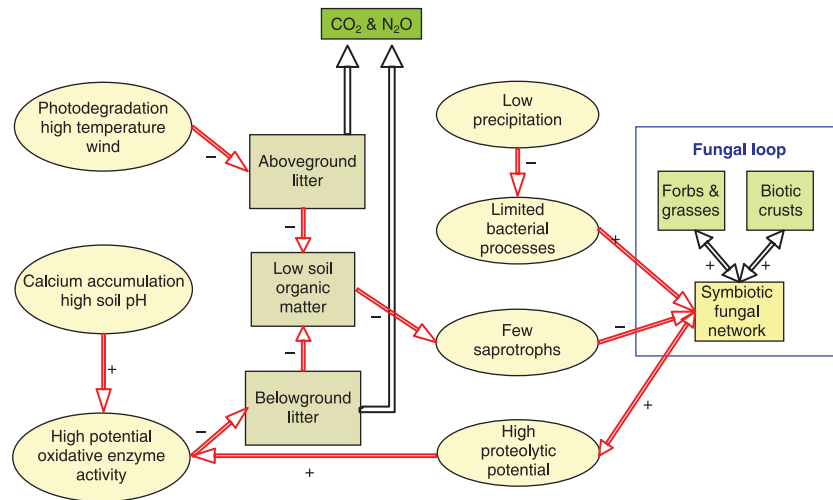


Fig. 1. Environmental conditions that favour a 'fungal loop' in aridland ecosystems. In aridland ecosystems, soil temperatures are often high while soil organic matter (SOM), C and N are generally quite low, and soil moisture frequently occurs in pulses of short duration. Low nutrient and SOM content results from an interaction between abiotic and biotic drivers. Decomposition of above-ground litter is driven primarily by abiotic factors including UV radiation, high temperatures and wind. Rates of below-ground decomposition are high because of the high rates of oxidative enzyme activity, which breaks down recalcitrant C compounds and limits SOM formation. High soil temperatures and low precipitation favour fungi over bacteria. As a consequence, fungi drive below-ground decomposition and form a complex hyphal network, or loop, that integrates biotic crusts on soil surfaces with patches of vegetation. C and N move bidirectionally in this loop depending on the nutrient demands of the fungi. Positive (+) and negative (–) effects are indicated.

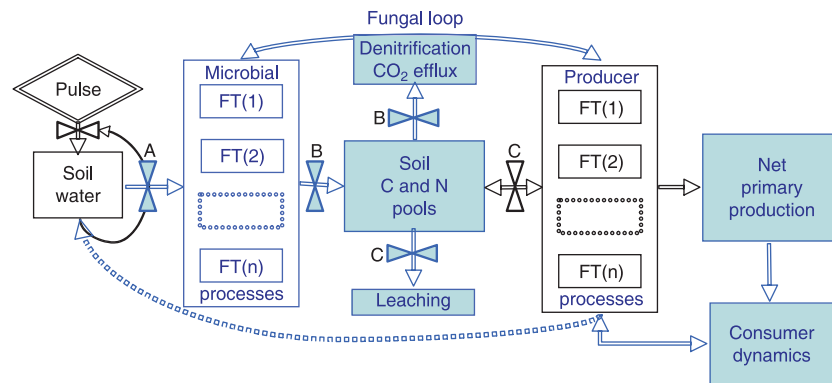


Fig. 2. The threshold-delay nutrient dynamics (TDND) model for aridland ecosystems (modified from Ogle & Reynolds 2004 and Reynolds *et al.* 2004). The TDND model retains the key features from the original model (in black), including the role of pulse precipitation events, antecedent soil moisture, time lags and primary producer functional types (e.g. annuals, C_4 grasses, shrubs, succulents, along with crust components, such as lichens and mosses). Our revised model (in blue) adds microbial functional types (e.g. AM fungi, saprophytes, dark septate endophytes, prokaryotic N fixers, cyanobacteria) to highlight the key role that microbial composition and processes play, particularly through the fungal loop, in mediating the C and N cycles, net primary production and potential feedbacks by consumers. At (A) the effect of the moisture pulse is regulated by the size of the precipitation event plus antecedent soil moisture. At (B), the moisture pulse is sufficient to drive microbial processes (decomposition, C-fixation by cyanobacteria, denitrification) but it is not plant sufficient for uptake by higher plants. At (C), moisture is sufficient for plant growth, and potentially soil leaching. Both (A) and (B) occur with small rain events but (C) may only occur following a large rain event or multiple small events. FT, functional type.

long-lived C_4 species, *Bouteloua eriopoda* and *B. gracilis*. Annual precipitation is *c.* 250 mm of which 60% falls in episodic monsoon events from July through September (Gosz *et al.* 1995; Pennington & Collins 2007). The average annual temperature is 13.2 °C (average low 1.6 °C in January, average high 33.4 °C in July). Soils are classified as Typic Haplargids with a lithology of piedmont alluvium, and are < 2 million-

years-old (Buxbaum & Vanderbilt 2007). From 1999–2004, above-ground net primary productivity in *B. eriopoda*-dominated grassland (ANPP) averaged 51.0 g m⁻² (Muldavin *et al.* 2008). Atmospheric N deposition is 0.2 g m⁻² year⁻¹ (Báez *et al.* 2007). The site was moderately grazed from the late 1800s until 1973 when the site became part of the US National Wildlife Refuge System.

EXTRACELLULAR ENZYME ACTIVITY (EEA) AND DECOMPOSITION IN ARID ECOSYSTEMS

The low rates of organic matter accumulation in aridland soils are likely a result of multiple factors, including microclimate, low NPP, microbial and abiotic degradation, and possibly invertebrates (Whitford 2002). Another contributing factor may be the presence of a stabilized pool of soil enzymes, particularly oxidative enzymes, whose activity is less restricted by moisture than that of the decomposers themselves.

The extracellular enzymes expressed by bacteria and fungi are the proximate agents of organic matter decomposition (Sinsabaugh *et al.* 2002). EEA, in turn, reflects the effort by microbes to acquire limiting nutrients including C, N and P. The distribution of EEA within the alkaline soils of aridlands is distinct from that of mesic soils, which are generally acidic (Stursova *et al.* 2006; Zeglin *et al.* 2007). Potentials for enzymes that decompose proteins (e.g. aminopeptidase) and recalcitrant C compounds such as lignin and humic substances (e.g. peroxidase) exceed those of mesic soils by more than an order of magnitude in both absolute terms and in relation to the activities of enzymes that break down cellulose, which generally dominate the EEA of mesic soils (Stursova *et al.* 2006; Zeglin *et al.* 2007; Stursova & Sinsabaugh 2008).

The EEA distribution in aridland soils is partly a direct result of soil pH, which has been shown to be a controlling variable for microbial diversity and function (Fierer & Jackson 2006; Schimel *et al.* 2007). In the Southwestern United States, soil pH often ranges from 7.5 to 8.5 partly in response to high rates of atmospheric calcium deposition (Chadwick *et al.* 1994; Monger 2006). The pH optima of glycosidases (e.g. cellulase, chitinase) generally range from 4 to 6 while those of proteolytic and oxidative enzymes generally range from 7 to 9 (Sinsabaugh *et al.* 2002). In addition, it is also likely that soil pH affects EEA indirectly by altering microbial community composition and selecting for microbial populations that can acquire nutrients from an alkaline environment.

Soil N availability interacts with soil pH to affect microbial community structure and EEA in Sevilleta soils (Corkidi *et al.* 2002; Johnson *et al.* 2003; Stursova *et al.* 2006; Zeglin *et al.* 2007). In a long-term N-amendment experiment at the Sevilleta, potential glycosidase activity in rhizosphere soils was twice that of control plots while in biocrust soils, aminopeptidase activity was lower by half. The magnitude of the EEA responses is directly related to inorganic N concentrations (Stursova *et al.* 2006). Thus, under ambient conditions soil C and N are limiting and enzymatic degradation of proteins may be a major source for microbial C and N.

In their response to N deposition, arid grassland soils at the Sevilleta are similar to temperate forest soils in that cellulolytic and other glycosidase activities, as well as phosphatase, increase. Arid grasslands are conspicuously different from mesic systems in that oxidative activities show no response to N fertilization (Stursova *et al.* 2006; Zeglin *et al.* 2007), whereas these activities generally decline with N addition in mesic systems, resulting in lower rates of lignin and humus

degradation and accumulation of SOM (Sinsabaugh *et al.* 2002; Frey *et al.* 2004; Gallo *et al.* 2004; Waldrop *et al.* 2006). This difference implies that the controls on expression of oxidative enzymes differ between the two systems, potentially because of differences in community composition (e.g. Ascomycetes vs. Basidiomycetes dominance). Thus, as found in many plant communities (e.g. Suding *et al.* 2005), microbial communities in mesic and arid environments vary in their responses to N addition.

THE ROLE OF FUNGI IN THE N CYCLE

Both bacteria and fungi have pathways for transforming N. In mesic systems, the bacterial processes of dissimilatory denitrification and autotrophic nitrification dominate redox reactions, while fungi are generally considered to dominate N mineralization and translocation within the litter and upper mineral soil horizon. Emerging evidence from the Sevilleta and elsewhere suggests, however, that fungi may control all these processes in some aridland soils (McLain & Martens 2005, 2006; Crenshaw *et al.* 2008) principally because they can metabolize at higher temperatures and lower water potentials than either plants or bacteria (Griffin 1972; Allen 2007). Consequently, the N cycle of arid ecosystems may be distinct from that of wetter systems in that prokaryotic processes make a more modest contribution to annual N fluxes than do fungi.

In arid ecosystems, as in other ecosystems, primary producers (grasses, biological soil crusts) have extensive symbioses with fungi (States 1978; Barrow 2003; Johnson *et al.* 2006). These symbioses may enhance desiccation resistance during dry periods and act as networks for water and nutrient transport during pulses of water availability (Allen 2007). At the Sevilleta, as in other arid areas, the fungal components of this symbiotic network include arbuscular mycorrhizal fungi (Glomeromycota), dark-septate endophytes, and a variety of saprotrophic and parasitic fungi (Barrow & Osuna 2002; Corkidi *et al.* 2002; Porras-Alfaro *et al.* 2007, 2008), all of which are supported to varying degrees by carbon obtained through close association with primary producers. In the desert grassland at Sevilleta, for example, the relative abundance of arbuscular mycorrhizae has declined as aridity has increased. The dominant fungal group in foliage, roots, bulk soil and biocrusts are members of the Pleosporales (dark septate ascomycetes), many of which form endophytic associations with plants that may function similarly to mycorrhizae (Porras-Alfaro *et al.* 2007). Conspicuously rare are filamentous Basidiomycetes that are prominent in mesic soils and considered to be the most efficient degraders of lignocellulose.

Within this fungal network, assimilatory denitrification and heterotrophic nitrification are supported by biotrophic carbon flow from plants and cyanobacteria (Green & Sinsabaugh 2008) and saprotrophic mineralization of protein (Stursova *et al.* 2006). When water is available, rates of N₂O production from Sevilleta grassland soils are comparable to those of mesic ecosystems (Crenshaw *et al.* 2008). When amended with cycloheximide, a fungal biocide, N₂O production

declined by 80–95%. Inhibition of nitrous oxide reductase with acetylene had only marginal effects, presumably because most fungi lack this enzyme, making N_2O the principal product of heterotrophic denitrification.

The Sevilleta findings are consistent with those reported for Sonoran Desert soils. Using microcosms to manipulate labelled C and N sources in combination with water potential and antibiotics, McLain & Martens (2005, 2006) concluded that denitrification and nitrification in Sonoran Desert soils were predominantly fungal processes, and that most N_2O was generated by fungal nitrification pathways that are supported by the mineralization of protein. Indeed, EEA results (described above) confirm that both Chihuahuan and Sonoran desert soils have high proteolysis potentials. The dominant contribution of fungi, in general, and heterotrophic nitrification, in particular, to N_2O generation is consistent with the hypothesis that fungi in close association with primary producers are the locus for N cycling in arid ecosystems.

Growing evidence from fungal community and biogeochemical studies supports the hypothesis that the patch mosaic of cyanobacterial crusts and grass tussocks in semi-arid grasslands are functionally integrated by a fungal network. At Sevilleta, tracer studies using ^{15}N - NO_3^- - and ^{13}C , ^{15}N -labelled glutamate showed that ^{15}N can be translocated from both biocrusts and foliage of a dominant perennial C_4 grass, blue grama (*B. gracilis*), at rates up to 40 cm day^{-1} , a distance equivalent to two–four patch lengths, in quantities comparable to rates of N deposition and denitrification (Green & Sinsabaugh 2008). In contrast, ^{13}C from glutamate moved from foliage to crust, and between crust patches, but was not transferred from plant to plant, suggesting that glutamate was not necessarily translocated intact and that plant photosynthate may support biocrust metabolism during periods of active growth. This pattern is consistent with nutrient translocation by arbuscular mycorrhizal fungi, but molecular and microscopic analyses of the fungal communities indicate that dark septate fungi dominate root-fungal symbioses (Porrás-Alfaro *et al.* 2008). At the Sevilleta, grass roots generally do not extend into the open soil patches where cyanobacteria-dominated crusts occur (Bhark & Small 2003), which provides circumstantial evidence that a fungal network may spatially integrate resource availability.

Our case for the importance of a biotrophic fungal network at the Sevilleta is based on the convergence of several environmental characteristics that collectively limit accumulation of SOM, sustain high phenol oxidative, and proteolytic enzyme potentials and encourage development of drought tolerant symbioses between primary producers and fungi (Fig. 1). At present, evidence for the fungal loop is fragmentary and its relative importance to ecosystem function is likely to vary in relation to plant community composition, climate and edaphic variables, such as soil texture and pH. However, our studies at Sevilleta suggest that soil enzymes, fungi and cyanobacteria may be considered functional reserves in the context of the traditional pulse-reserve model for arid ecosystem function. These reserves have activation thresholds in relation to water availability that are lower than those of

plants, creating nonlinear and, at times, decoupled interactions among ecosystem components in relation to precipitation patterns.

The TDND model

The marked differences in moisture availability and temperature between mesic and arid environments alter the relative importance of various biogeochemical processes to the extent that many models of C and N cycling developed for mesic systems cannot be readily applied to arid environments. The growing season in many aridland ecosystems is characterized by low, variable and unpredictable precipitation regimes (Noy-Meir 1973; Rodríguez-Iturbe *et al.* 1999; Whitford 2002; Pennington & Collins 2007). The pulse-reserve paradigm, the key organizing principle in aridland ecosystems (Noy-Meir 1973), was developed to describe ecosystem responses to individual precipitation pulses. Specifically, biologically significant rainfall events trigger a pulse of growth that yields reserves (e.g. seeds, NPP) that accumulate until moisture from a rainfall event is depleted. Reynolds *et al.* (2004) and Ogle & Reynolds (2004) criticized the original pulse-reserve model because it does not effectively incorporate time lags (e.g. Huxman *et al.* 2004), thresholds (e.g. Ogle & Reynolds 2004) and prior state conditions, nor does it account for interactions among multiple precipitation events (e.g. Schwinning & Sala 2004). Indeed, water pulses occur at a variety of spatial and temporal scales in aridland ecosystems (Knapp *et al.* 2002; Porporato *et al.* 2003; Loik *et al.* 2004; Swemmer *et al.* 2007; Muldavin *et al.* 2008) confounding the link between individual rainfall events and system response. Thus, in aridland ecosystems, the response to seasonal, annual and interannual rainfall patterns is complex and nonlinear (Brown & Ernest 2002).

Reynolds *et al.* (2004) modified the original pulse-reserve model to account for its deficiencies. In their revised model (Fig. 2, in black), pulses of precipitation generate and/or add to existing soil moisture leading to production responses that may vary among plant functional types depending on species abundances, antecedent conditions (recent rain events) and seasonality (e.g. cool or warm season). The direct linkage between antecedent soil moisture and plant functional types also allows for variable production responses to occur as a consequence of variation in rainfall event sizes and intervals (Schwinning *et al.* 2003; Muldavin *et al.* 2008).

The Reynolds *et al.* (2004) model is a significant improvement over the original version, but we believe it is still insufficient because of its focus only on soil water content and its lack of attention to other limiting soil resources, such as C and N. Nor does their model, developed to describe plant community dynamics, explicitly include microbial processes, particularly those from biotic crusts, which fix both C and N. As noted above, both abiotic and microbial processes influence C and N cycles in aridland ecosystems. Moreover, N fertilization experiments suggest that aridland ecosystems are likely to be co-limited by water, C and N (Austin *et al.* 2004; Welter *et al.* 2005; Báez *et al.* 2007; Sponseller 2007). Thus, a more complete

pulse-reserve model for aridland ecosystems must include C and N dynamics, along with microbial functional types, processes and interactions.

Here we modify the Reynolds *et al.* (2004) model (Fig. 1, in blue) to include linkages between rainfall pulses, microbial functional types and processes, soil nutrient dynamics, plant production and consumers (including feedbacks), as well as important temporal discontinuities in nutrient availability and uptake kinetics. For example, small rainfall events (e.g. 50% of precipitation events are < 2 mm at Sevilleta, 90% are < 10 mm) do not initiate plant growth responses but they do initiate enzymatic and microbial processes (C and N fixation and mineralization) on soil surfaces, particularly biocrusts, leading to large CO₂ effluxes (Kurc & Small 2007) and increases in plant available N (Kieft *et al.* 1998; White *et al.* 2004; Belnap *et al.* 2005b; Stursova *et al.* 2006). Thus, during small rainfall events microbial processes are decoupled from plant production. Infiltration following larger rainfall events or a series of smaller events extends the zone for enzymatic and microbial activity and, depending on season, temporarily couples microbial and plant metabolism, including uptake, translocation and transformation. After rainfall, soil moisture is not depleted uniformly across the soil profile. Biocrust surfaces will dry rapidly, shutting down microbial C and N fixation, while subsurface soil moisture sustains nutrient mineralization, translocation and plant growth. Eventually soil moisture will fall below thresholds for plant metabolism while fungi may continue to translocate nutrients and produce biomass.

Variation in the frequency and intensity of precipitation will control the spatiotemporal extent of plant, crust, fungal and bacterial activities. Nutrient cycling and production of biotic reserves are maximized when sources and sinks of carbon and nutrients are effectively coupled by moisture availability. Conversely, loss of moisture coupling spatiotemporally isolates biogeochemical processes, creating nonlinearities in precipitation–response relationships.

Considerable observational and experimental work is needed to refine many aspects of the TDND model, and evaluate its utility for describing processes in aridland ecosystems, especially in an era of rapid environmental change. The products of such research will likely be a better understanding of the effects of precipitation variability and N deposition on soil N and C dynamics and storage in the context of plant and biocrust responses in aridland ecosystems worldwide. Like other regions, the arid Southwestern United States is experiencing climatic change (Cook *et al.* 2004; Leung *et al.* 2004; Meehl & Tibaldi 2004; Seager *et al.* 2007) and increasing rates of atmospheric N deposition (Fenn *et al.* 2003; Báez *et al.* 2007). The consequences of increased N loading, more intense droughts, and greater climatic extremes for primary production, decomposition and biogeochemical cycles in arid ecosystems are poorly known. Our hypothesis – that the N and C cycles in semi-arid environments are frequently decoupled and dominated by a fungal loop linked to symbiotic carbon flow from both plants and biological soil crusts – is an attempt to spatially and temporally integrate the principal structural and functional elements of arid ecosystems. Indeed, temporally

decoupled processes may occur in other extreme environments, such as alpine tundra (Schmidt *et al.* 2007), thus this model may have implications beyond aridland ecosystems. Nevertheless, a better mechanistic link between pulse dynamics, microbial composition and function, and below-ground ecosystem dynamics is vital to understand how aridland ecosystems will respond to interactions among multiple global change phenomena.

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References

- Allen, M.F. (2007) Mycorrhizal fungi: highways for water and nutrients in arid soils. *Vadose Zone Journal*, **6**, 291–297.
- Asner, G.P., Seastedt, T.R. & Townsend, A.R. (1997) The decoupling of terrestrial carbon and nitrogen cycles. *BioScience*, **47**, 226–234.
- Austin, A.T. & Vivanco, L. (2006) Plant litter decomposition in a semiarid ecosystem controlled by photodegradation. *Nature*, **442**, 555–558.
- Austin, A.T., Yahjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A. & Schaeffer, S.M. (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, **142**, 221–235.
- Báez, S., Fargione, J., Moore, D.I., Collins, S.L. & Gosz, J.R. (2007) Atmospheric nitrogen deposition in the northern Chihuahuan desert: temporal trends and potential consequences. *Journal of Arid Environments*, **68**, 640–651.
- Bardgett, R.D. (2005) *The Biology of Soil: A Community and Ecosystem Approach*. Oxford University Press, Oxford, UK.
- Bardgett, R.D., Bowman, W.D., Kaufmann, R. & Schmidt, S.K. (2005) Linking aboveground and belowground communities: a temporal approach. *Trends in Ecology and Evolution*, **20**, 634–640.
- Barrow, J.R. (2003) Atypical morphology of dark septate fungal root endophytes of *Bouteloua* in southwestern USA rangelands. *Mycorrhiza*, **13**, 239–247.
- Barrow, J.R. & Osuna, P. (2002) Phosphorus solubilization and uptake by dark septate fungi in fourwing saltbush, *Atriplex canescens* (Pursh) Nutt. *Journal of Arid Environments*, **51**, 449–459.
- Belnap, J. (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils*, **35**, 128–135.
- Belnap, J. & Lange, O. (2003) *Biological Soil Crusts: Structure, Function, and Management*, 2nd edn. Springer-Verlag, New York.
- Belnap, J., Hawkes, C.V. & Firestone, M.K. (2003) Boundaries in miniature: two examples from soil. *BioScience*, **53**, 739–749.
- Belnap, J., Phillips, S.L. & Miller, M.E. (2004) Response of desert biological soil crusts to alterations in precipitation frequency. *Oecologia*, **141**, 306–316.
- Belnap, J., Phillips, S.L., Sherrod, S. & Moldenke, A. (2005a) Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology*, **86**, 3007–3017.
- Belnap, J., Welter, J.R., Grimm, N.B., Barger, N. & Ludwig, J. (2005b) Linkages between microbial and hydrologic processes in arid and semi-arid watersheds. *Ecology*, **86**, 298–307.
- Bhark, E.W. & Small, E.E. (2003) The relationship between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems*, **6**, 185–196.
- Brown, J.H. & Ernest, S.K.M. (2002) Rain and rodents: complex dynamics of desert consumers. *BioScience*, **52**, 979–987.
- Buxbaum, C.A.Z. & Vanderbilt, K. (2007) Soil heterogeneity and the distribution of desert and steppe plant species across a desert–grassland ecotone. *Journal of Arid Environments*, **69**, 617–63
- Chadwick, O.A., Kelly, E.F., Merritts, D.M. & Amundson, R.G. (1994) Carbon dioxide consumption during soil development. *Biogeochemistry*, **24**, 115–127.
- Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M. & Stahle, D.W. (2004) Long term aridity changes in the western United States. *Science*, **306**, 1015–1018.

- Corkidi, L., Rowland, D.L., Johnson, N.C. & Allen, E.B. (2002) Nitrogen fertilization alters the functioning of arbuscular mycorrhizae at two semiarid grasslands. *Plant and Soil*, **240**, 299–310.
- Crenshaw, C., Lauber, C.L., Sinsabaugh, R.L. & Staveland, L.K. (2008) Fungal dominance of nitrogen transformations in semiarid grassland. *Biogeochemistry*, **87**, 17–27.
- Fenn, M.E., Baron, J.S., Allen, E.B., Reuth, H.M., Nydick, N.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W. & Neitlich, P. (2003) Ecological effects of nitrogen deposition in the western United States. *BioScience*, **53**, 404–420.
- Fierer, N. & Jackson, R.B. (2006) The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 626–631.
- Fitter, A.H. (2005) Darkness visible: reflections on underground ecology. *Journal of Ecology*, **93**, 231–243.
- Frey, S.D., Knorr, M., Parrent, P.L. & Simpson, R.T. (2004) Chronic enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests. *Forest Ecology and Management*, **196**, 159–171.
- Gallo, M.E., Amonette, R., Lauber, C.L., Sinsabaugh, R.L. & Zak, D. (2004) Short-term changes in oxidative enzyme activity and microbial community structure in nitrogen-amended north temperate forest soils. *Microbial Ecology*, **48**, 218–229.
- Gallo, M.E., Sinsabaugh, R.L. & Cabaniss, S.E. (2006) The role of ultraviolet radiation in litter decomposition in arid ecosystems. *Applied Soil Ecology*, **34**, 82–91.
- García-Pichel, F., Johnson, S.L., Youngkin, D. & Belnap, J. (2003) Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microbial Ecology*, **46**, 312–321.
- Gosz, J.R., Moore, D.I., Shore, G.A., Grover, H.D., Rison, W. & Rison, C. (1995) Lightning estimates of precipitation location and quantity on the Sevilleta LTER, New Mexico. *Ecological Applications*, **5**, 1141–1150.
- Green, L.E. & Sinsabaugh, R.L. (2008) Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. *Journal of Ecology*, in press.
- Griffin, D.M. (1972) *Ecology of Soil Fungi*. Syracuse University Press, Syracuse, New York.
- Harrison, K.A., Bol, R. & Bardgett, R.D. (2007) Preferences for different nitrogen forms by coexisting plant species and soil microbes. *Ecology*, **88**, 989–999.
- Huxman, T.E., Tissue, D., Snyder, K., Leffler, J., Ogle, K., Pockman, W.T., Sandquist, D.R. & Williams, D.G. (2004) Precipitation pulses and carbon fluxes in semi-arid and arid ecosystems. *Oecologia*, **141**, 254–268.
- Jackson, R.B., Fierer, N. & Schimel, J.P. (2007) New directions in microbial ecology. *Ecology*, **88**, 1343–1344.
- Johnson, N.C., Hoeksema, J.D., Bever, J.D., Chaudhary, V.B., Gehring, C., Klironomos, J. *et al.* (2006) From Lilliput to Brobdingnag: extending models of mycorrhizal function across scales. *BioScience*, **56**, 889–900.
- Johnson, N.C., Rowland, D.L., Corkidi, L., Egerton-Warburton, L.M. & Allen, E.B. (2003) Nitrogen enrichment alters mycorrhizal allocation at five mesic to semi-arid grasslands. *Ecology*, **84**, 1895–1908.
- Kéfi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A. & de Ruiter, P.C. (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, **449**, 213–217.
- Kieft, T.L., White, C.S., Loftin, S.R., Aguilar, R., Craig, J.A. & Skaar, D.A. (1998) Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. *Ecology*, **79**, 671–683.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. & McCarron, J.K. (2002) Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science*, **298**, 2202–2205.
- Kurc, S.A. & Small, E.E. (2007) Soil moisture variations and ecosystem scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research*, **43**, doi: 10.1029/2006WR005011.
- Leung, L.R., Qian, Y., Bian, X.D., Washington, W.M., Han, J.G. & Roads, J.O. (2004) Mid-century ensemble regional climate change scenarios for the western United States. *Climatic Change*, **62**, 75–113.
- Loik, M.E., Breshears, D.D., Lauenroth, W.K. & Belnap, J. (2004) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia*, **141**, 269–281.
- Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J. & Iameson, A.C. (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology*, **86**, 288–297.
- McLain, J.E.T. & Martens, D.A. (2005) Nitrous oxide flux from amino acid mineralization. *Soil Biology and Biochemistry*, **37**, 289–299.
- McLain, J.E.T. & Martens, D.A. (2006) N₂O production by heterotrophic N transformations in a semiarid soil. *Applied Soil Ecology*, **32**, 253–263.
- Meehl, G.A. & Tibaldi, C. (2004) More intense, more frequent, and longer lasting heat waves in the 21st Century. *Science*, **305**, 994–997.
- Meentemeyer, V. (1978) Macroclimate and lignin control litter decomposition rates. *Ecology*, **59**, 465–472.
- Monger, C.H. (2006) Soil development in the Jornada Basin. *Structure and Function of a Chihuahuan Desert Ecosystem* (eds K.M. Havstad, L.F. Huenneke & W.H. Schlesinger), pp. 81–106. Oxford University Press, Oxford, UK.
- Moorhead, D.L. & Reynolds, R.F. (1989) Mechanisms of surface litter mass loss in the northern Chihuahuan Desert: a reinterpretation. *Journal of Arid Environments*, **16**, 157–163.
- Moorhead, D.L. & Sinsabaugh, R.L. (2006) A theoretical model of litter decay and microbial interaction. *Ecological Monographs*, **76**, 151–174.
- Muldavin, E.H., Moore, D.I., Collins, S.L., Wetherill, K. & Lightfoot, D. (2008) Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*, **155**, 123–132.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Ogle, K. & Reynolds, J.F. (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia*, **141**, 282–294.
- Parton, W.J., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C. & Fasth, B. (2007) Global scale similarities in nitrogen release patterns during long-term decomposition. *Science*, **315**, 361–364.
- Pauli, F. (1964) Soil fertility problem in arid and semi-arid lands. *Nature*, **204**, 1286–1288.
- Pennington, D. & Collins, S.L. (2007) Remotely-sensed response of an aridland ecosystem to pervasive drought. *Landscape Ecology*, **22**, 897–910.
- Porporato, A., D'Odorico, P., Laio, F. & Rodriguez-Iturbe, I. (2003) Hydrologic controls on soil carbon and nitrogen cycles. I. Modeling scheme. *Advances in Water Research*, **26**, 45–58.
- Porrás-Alfaro, A., Herrera, J., Sinsabaugh, R.L. & Natvig, D. (2007) Effect of long-term nitrogen fertilization on mycorrhizal fungi associated with a dominant grass in a semiarid grassland. *Plant and Soil*, **296**, 65–75.
- Porrás-Alfaro, A., Herrera, J., Sinsabaugh, R.L., Odenbach, K., Lowrey, T. & Natvig, D. (2008) A novel root fungal consortium associated with a dominant desert grass. *Applied Environmental Microbiology*, in press.
- Ravi, S., D'Odorico, P., Zobeck, T.M., Over, T.M. & Collins, S.L. (2007) Feedbacks between fires and wind erosion in heterogeneous arid lands. *Journal of Geophysical Research*, **112**, G04007, doi: 10.1029/2007JG000474
- Reynolds, J.F., Kemp, P.R., Ogle, K. & Fernández, R.J. (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, **141**, 194–210.
- Rodriguez-Iturbe, I., Porporato, A., Ridolfi, L., Isham, V. & Cox, D. (1999) Probabilistic modeling of water balance at a point: the role of climate, soil and vegetation. *Proceedings of the Royal Society, London*, **455**, 3789–3805.
- Scanlon, T.M., Caylor, K.K., Levin, S.A. & Rodriguez-Iturbe, I. (2007) Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature*, **449**, 209–213.
- Schaefer, D., Steinberger, Y. & Whitford, W.G. (1985) The failure of nitrogen and lignin control of decomposition in a North American desert. *Oecologia*, **65**, 382–386.
- Schimel, J.P., Balsler, T.C. & Wallenstein, M. (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, **88**, 1386–1394.
- Schlesinger, W.H. (1997) *Biogeochemistry: An Analysis of Global Change*, 2nd edn. Academic Press, New York.
- Schlesinger, W.H., Abrahams, A.D., Parsons, A.J. & Wainwright, J. (1999) Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: I. rainfall simulation experiments. *Biogeochemistry*, **45**, 21–34.
- Schlesinger, W.H., Reikes, J.A., Hartley, A.E. & Cross, A.F. (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, **77**, 364–374.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, **247**, 1043–1048.
- Schmidt, S.K., Costello, E.K., Nemergut, D.R., Cleveland, C.C., Reed, S.C., Weintraub, M.N., Meyer, A.F. & Martin, A.M. (2007) Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. *Ecology*, **88**, 1379–1385.
- Schwinning, S. & Sala, O.E. (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*, **141**, 211–220.
- Schwinning, S., Starr, B.I. & Ehleringer, J.R. (2003) Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia*, **136**, 252–260.

- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., et al. (2007) Model projections of an imminent transition to a more arid climate in south-western North America. *Science*, **316**, 1181–1184.
- Sinsabaugh, R.L. & Moorhead, D.L. (1996) Synthesis of litter quality and enzyme approaches to decomposition modeling. *Driven by Nature: Plant Litter Quality and Decomposition* (eds G. Cadisch & K. Ciller), pp. 363–375. CAB International, London, UK.
- Sinsabaugh, R.L., Carreiro, M.M. & Alvarez, S. (2002) Enzyme and microbial dynamics during litter decomposition. *Enzymes in the Environment* (ed. R. Burns), pp. 249–266. Marcel Dekker, Oxford, UK.
- Sponseller, R.A. (2007) Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Global Change Biology*, **13**, 426–436.
- States, J.S. (1978) Effect of atmospheric pollutants on the microbial decomposition process of an arid ecosystem. *Proceedings, 4th Joint Conference on Sensing of Environmental Pollutants*, pp. 54–56. American Chemical Society, Washington, DC.
- States, J.S. & Christensen, M. (2001) Fungi associated with biological soil crusts in desert grasslands of Utah and Wyoming. *Mycologia*, **93**, 432–439.
- States, J.S., Christensen, M. & Kinter, C.L. (2003) Soil fungi as components of biological soil crusts. *Biological Soil Crusts: Structure, Function, and Management*, 2nd edn (eds J. Belnap & O.L. Lange), pp. 155–166. Springer-Verlag, New York.
- Stursova, M. & Sinsabaugh, R.L. (2008) Stabilization of oxidative enzymes in desert soil may limit organic matter accumulation. *Soil Biology and Biochemistry*, **40**, 550–553.
- Stursova, M., Crenshaw, C. & Sinsabaugh, R.L. (2006) Microbial responses to long term N deposition in a semi-arid grassland. *Microbial Ecology*, **51**, 90–98.
- Suding, K.N., Collins, S.L., Gough, L., Clark, C.M., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S.C. (2005) Functional and abundance based mechanisms explain diversity loss due to nitrogen fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 4387–4392.
- Swemmer, A.M., Knapp, A.K. & Snyman, H.A. (2007) Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *Journal of Ecology*, **95**, 780–788.
- UNESCO (1977) *World Map of Arid Regions*. United Nations Educational, Scientific and Cultural Organization, Paris, France.
- Vanderbilt, K.L., White, C.S., Hopkins, O. & Craig, J.A. (2007) Aboveground decomposition in arid environments: results of a long-term study in central New Mexico. *Journal of Arid Environments*, doi: 10.1016/j.jaridenv.2007.10.010.
- Waldrop, M.P., Zak, D.R., Blackwood, C.B., Curtis, C.D. & Tilman, D. (2006) Resource availability controls fungal diversity across a plant diversity gradient. *Ecology Letters*, **9**, 1127–1135.
- Walvoord, M.A., Phillips, F.M., Stonestrom, D.A., Evans, R.D., Hartsough, P.C., Newman, B.D. & Striegl, R.G. (2003) A reservoir of nitrate beneath desert soils. *Science*, **302**, 1021–1024.
- Welter, J.R., Fisher, S.G. & Grimm, N.B. (2005) Nitrogen transport and retention in an aridland watershed: influence of storm characteristics on terrestrial–aquatic linkages. *Biogeochemistry*, **76**, 421–440.
- White, C.S., Moore, D.I. & Craig, J.A. (2004) Regional-scale drought increases potential soil fertility in semiarid grasslands. *Biology and Fertility of Soils*, **40**, 73–78.
- Whitford, W.G. (2002) *Ecology of Desert Systems*. Academic Press, New York.
- Whitford, W.G., Repass, R., Parker, L.W. & Elkins, N.Z. (1982) Effects of initial litter accumulation and climate on litter disappearance in a desert ecosystem. *American Midland Naturalist*, **108**, 105–110.
- Whitford, W.G., Steinberger, Y., Mackay, W., Parker, L.W., Freckman, D., Wallwork, J.A. & Weems, D. (1986) Rainfall and decomposition in the Chihuahuan Desert. *Oecologia*, **68**, 512–515.
- Whitford, W.G., Stinnett, K. & Anderson, J. (1988) Decomposition of roots in a Chihuahuan Desert ecosystem. *Oecologia*, **75**, 8–11.
- Zeglin, L.H., Stursova, M., Sinsabaugh, R.L. & Collins, S.L. (2007) Microbial responses to nitrogen addition in three contrasting grassland ecosystems. *Oecologia*, **154**, 349–359.

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