

Resolving the Dryland Decomposition Conundrum: Some New Perspectives on Potential Drivers

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Abstract Decomposition of organic matter is a crucial component of biogeochemical cycles that strongly controls nutrient availability, productivity, and community composition. The factors controlling decomposition of litter in arid and semi-arid systems remain poorly understood, with an unresolved disconnect between measured and modeled decay rates. In contrast, decay rates in mesic systems are generally quite successfully predicted by models driven by climatic variables. Here, we explore the reasons for this disconnect by reviewing literature on the biotic and abiotic controls over dryland decomposition. Recent research on decomposition in drylands suggests that several key drivers of dryland decomposition have been historically overlooked and not included in models. In particular, UV photodegradation and soil transport processes, both a function of vegetation structure, may strongly influence dryland decomposition dynamics. We propose an expanded framework for studying dryland decay that explicitly addresses vegetation structure and its influence on decomposition. Spatial heterogeneity of vegetation in dryland systems necessitates considering how the spatial and temporal context of vegetation influences soil transport patterns and UV photodegradation, both of which may in turn affect abiotic and biotic decomposition processes.

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1 Introduction

The concentration and distribution of nutrients in the soil fundamentally affect plant community composition and productivity. In most circumstances, the proximate source of nutrients for plant growth is the decomposition of organic matter. Via influences on soil fertility, decomposition rates may affect plant community composition and production, which in turn, feed back to affect the timing, quality and quantity of litter inputs (Aerts 1997b; Hobbie 1992). The litter and soil organic matter pools account for a large portion of C in terrestrial ecosystems (Schimel 1995; Schlesinger 1997), and the relatively rapid turnover of the leaf litter pool makes leaf litter decomposition one of the most dynamic components of biogeochemical cycles (Aerts 1997a). As such, understanding patterns and controls over decomposition rates are crucial to understanding C and nutrient balance.

The controls and dynamics of litter decomposition in arid and semi-arid ecosystems (hereafter “drylands”), are considerably less well understood than in mesic systems. This discrepancy may reflect the paucity of research in drylands relative to mesic systems and/or failure to include or appropriately represent key drivers. The fact that decomposition rates in mesic systems are reasonably well predicted by climatic variables, while measured decomposition rates in drylands are typically much greater than would be predicted based on climatic variables (Meentemeyer 1978; Whitford et al. 1981; Parton et al. 2007), suggests the latter. The mechanisms responsible for this disconnect are unclear. Here, we (1) review literature on controls over dryland decomposition, (2) discuss mechanisms related to UV photodegradation and soil transport processes that may account for discrepancies between predicted and measured decomposition rates in drylands, and (3) propose an expanded framework for studying decomposition in dryland systems.

2 Patterns of Dryland Decomposition

Decomposition rates are typically determined by quantifying differences in mass loss from mesh litterbags deployed in the field for varying lengths of time. As such, measured litter decay embodies a set of ecological processes spanning from comminution and fragmentation to mineralization. Decay rates can be expressed either in terms of percent mass loss or with the decay constant, K , which is the exponent of a single exponential decay model and thus represents mass loss over time (Olson 1963). Dryland decomposition is generally slower and more variable than that in mesic systems, reflecting variability in both litter composition and environmental conditions Whitford (2002).

Our mechanistic understanding of controls over decomposition has progressed (Meentemeyer 1978; Couteaux et al. 1995; Aerts 1997a), but predicting decomposition dynamics in dryland systems remains problematic (Kemp et al. 2003; Parton et al. 2007). Direct abiotic forces broadly predict decomposition rates, with regional/global patterns predicted by climate variables such as actual evapotranspiration (Aerts 1997a; Meentemeyer 1978). Decay rates over 5- and 10-year periods in the Long-term Intersite Decomposition Experiment Team (LIDET) study, in which common

litter was tracked across sites in North and Central America, were best predicted with synthetic indices of climate variables (Gholz et al. 2000; Parton et al. 2007). Models based on climatic drivers consistently underestimate decay rates in drylands, suggesting decomposition controls differ from those in mesic systems (Parton et al. 2007). At local scales, decomposition is sensitive to initial litter chemistry (e.g., C:N ratios and lignin content; Hobbie 1992) and to indirect influences of vegetation (e.g., plant structural influences on microclimate; Mack and D’Antonio 2003). It is not yet clear how to resolve these broad- and fine-scale perspectives.

Recent research has advanced our understanding of the driving forces in organic matter decay in drylands. It appears that mechanisms driving decomposition in drylands may fundamentally differ from those operating in mesic systems. As such, different approaches may be needed to quantify cause–effect relationships and to develop robust generalizations.

3 Drivers of Decomposition

Local drivers of decomposition are either biotic (e.g., litter quality and decomposer organisms) or abiotic (e.g., temperature, moisture, UV radiation). These interact and may affect decomposition either directly or indirectly (e.g., soil moisture may affect decomposition via mediating decomposer community composition; Fig. 1). Although the prevailing dogma has been that the primary drivers in drylands are abiotic and that the importance of biotic drivers is reduced relative to mesic systems (MacKay et al. 1994; Osler et al. 2004), both biotic and abiotic drivers can strongly influence dryland decomposition rates.

3.1 Abiotic Drivers

3.1.1 Temperature

Temperature may affect decomposition via influences on enzyme kinetics or the activities and populations of decomposer organisms. Temperature is an important regulator of decomposition in some temperate and high latitude systems (Aerts

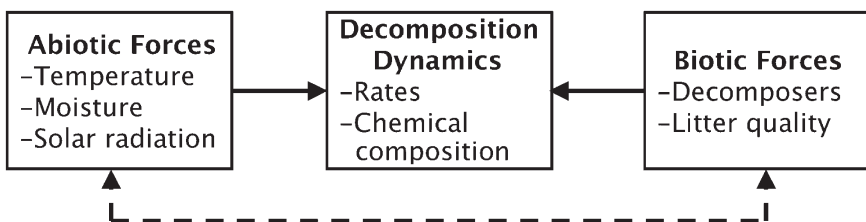


Fig. 1 Direct and indirect drivers of decomposition as traditionally addressed by decomposition studies. Biotic and abiotic facts are assumed to affect decomposition dynamics either directly (solid lines) or indirectly by affecting other processes (dashed lines)

2006; Hobbie 1996; McHale et al. 1998), and strong links between temperature and microbial respiration (Kirschbaum 2000) suggest temperature should strongly affect biologically-driven decomposition when moisture is not limiting. However, because optimal temperatures for microbial activity are often exceeded during the infrequent periods of growing season moisture availability in drylands, temperature-driven responses may be truncated (MacKay et al. 1986). Few studies have directly studied the relationship between temperature and decomposition in drylands. A shade treatment in the Chihuahuan Desert that decreased surface temperatures stimulated microarthropod populations, but this did not translate into subsequent changes in decay rates (MacKay et al. 1986). Temperature could also influence decomposition via its affect on near-surface soil and litter moisture content.

3.1.2 Precipitation/Moisture Availability

Precipitation and soil moisture availability also control decomposition in many systems (Austin and Vitousek 2000; McCulley et al. 2005), with moisture influencing the activities and population dynamics of decomposers. In addition, the moisture-limited nature of drylands may influence macro-decomposers (see Sect. 3.2.2.). Substantial physical decomposition can occur by leaching of water-soluble compounds (Sullivan et al. 1999) and, although seldom quantified, raindrop impact may cause substantial physical fragmentation of litter (Whitford 2002). Low annual precipitation in drylands suggests decomposition from these processes would be lower than in mesic systems, although moisture pulses associated with high-intensity convective storms typical of drylands may cause episodes of high litter fragmentation and leaching. Furthermore, standing dead may persist for long periods in drylands before it is transferred to surface litter pools, allowing considerable opportunities for leaching and fragmentation losses from raindrop impact.

Biological processes affecting dryland decomposition are generally limited by moisture availability. Two types of observational studies have been used to investigate moisture influences: decomposition in response to variation in rainfall patterns within a site and simultaneous litterbag deployments across a precipitation gradient. Studies assessing the role of within-site precipitation variability have observed decay rates in litterbags deployed at different times of the year or across years that differ in precipitation regime. Such studies have universally demonstrated a positive relationship between precipitation and decomposition rate (Ekaya and Kinyamario 2001; Pucheta et al. 2006; Strojan et al. 1987; Weatherly et al. 2003). Although such studies are confounded by intra-annual variability in temperature or decomposer communities, the consistent positive responses suggest local decay rates are limited by precipitation. Similarly, there was a positive correlation between decay rate and soil moisture for buried roots along a moisture gradient on a Chihuahuan Desert bajada (Mun and Whitford 1998). Manipulative studies using rainout shelters to reduce precipitation or sprinklers to increase precipitation have also

demonstrated positive relationships between precipitation and decay rates (Brandt et al. 2007; Whitford et al. 1986; Yahdjian et al. 2006). The influence of precipitation may also depend on the stage of litter decomposition. In the Chihuahuan Desert, decomposition rates did not respond to altered precipitation until after 19 months in a 41-month study (Kemp et al. 2003).

Drylands also differ from mesic systems with respect to rainfall distribution, with rainfall pulses strongly controlling biological activities. Changes in the frequency, distribution, or size of rainfall events more strongly regulate ecological processes in drylands than does mean annual precipitation (Schwinning et al. 2004). The role of rainfall pattern was demonstrated with a Chihuahuan Desert study in which supplementation of 25 mm per month increased decomposition rates when added in 4 weekly aliquots, but not when added as a single monthly aliquot (Whitford et al. 1986). While links between precipitation distribution and decomposition have not been explicitly addressed, precipitation pulses are known to strongly control soil respiration and soil C fluxes (Huxman et al. 2004). We expect that decomposition should respond similarly.

3.2 *Biotic Drivers*

Biotic properties affecting decomposition include litter quality and the decomposer community present. While biotic drivers strongly affect decay rates in many mesic systems, they appear to be relatively less important in drylands (MacKay et al. 1994; Osler et al. 2004). In particular, litter fragmentation is primarily the result of decomposers in mesic systems, whereas abiotic processes appear to be more important in drylands (Whitford 2002). However, decomposer organisms can strongly affect litter breakdown via litter fragmentation and chemical transformations. The organisms present on decomposing material will vary with litter chemistry, microsite, temperature and moisture. Succession in decomposer community composition likely occurs as decomposition progresses from litter fragmentation through mineralization.

3.2.1 *Litter Quality*

Local rates of decomposition may be strongly controlled by the initial chemical composition of litter with N, lignin, and lignin:N being particularly important predictors of decomposition rates (Hobbie 1992). If the importance of biotic processes as decomposition drivers is lower in dryland than mesic systems (Whitford 2002), the importance of litter quality may be similarly reduced. However, there is little evidence in support of this inference. Consistent with studies in mesic systems, dryland studies quantifying litter quality and decomposition rates have also generally found positive influences of N and P and negative influences of lignin on decomposition rates (Table 1).

Table 1 Relationships between litter chemistry and decomposition rates in dryland studies

Litter chemistry variables	Influence on <i>K</i>	Study length	Location	Study species	References
Lignin	None	1 year	Chihuahuan Desert	<i>Yucca elata</i>	Schaefer et al. 1985
Lignin:N	None			<i>Larrea tridentata</i>	
C:N	None			<i>Flouresnia cernua</i>	
				<i>Prosopis glandulosa</i>	
				<i>Chilopsis linearis</i>	
				Mixture of annuals	
Lignin	–	21 months	Argentinean semi-arid grassland	<i>Poa ligularis</i>	Moretto et al. 2001
N	+			<i>Stipa gyneriodes</i>	
P	+			<i>Stipa tenuissima</i>	
C:N	–				
Lignin:N	–				
Lignin:P	–				
Lignin	–	2 years	Argentinean semi-arid grassland	<i>Poa ligularis</i>	Moretto and Distel 2003
N	+			<i>Stipa gyneriodes</i>	
P	+				
C:N	–				
Lignin:N	–				
Lignin:P	–				
Lignin	–	1 year	Sonoran Desert, Mexico	<i>Encelia farinose</i>	Martínez-Yrizar et al. 2007
N	–			<i>Olneya tesota</i>	
Lignin:N	–				
N	+	1 year	Sonoran Desert, Arizona	<i>Prosopis velutina</i>	Throop and Archer 2007
C:N	–			<i>Eragrostis lehmanniana</i>	

For each study, the decay rates (*K*) for at least two species with differing litter chemistry were compared. All studies are for leaf litter exposed on the soil surface in mesh litterbags

3.2.2 Decomposer Organisms

The role of organisms as drivers of decomposition and the identity of the functional groups involved are poorly understood and highly variable among drylands. Different suites of decomposers have very different impacts on litter breakdown, with macrofauna (2–20 mm; e.g., isopods, beetles) and mesofauna (100 µm–2 mm; e.g., mites, collembolans) generally involved with comminution of litter of different particle sizes, and microfauna (<100 µm; e.g., bacteria, fungi, nematodes) involved in chemical transformation of progressively smaller litter particles and molecules. Targeted biocides (Table 2) and litterbags with mesh sizes that discriminate based

Table 2 Summary of dryland studies using biocide treatments to explore decomposer impacts on decay rates

Treatments	Influence on K	Location	Time (months)	References
Biocide	–	Colorado short-grass steppe	9	Vossbrinck et al. 1979
Insecticide	–	Chihuahuan Desert ^a	1	Santos et al. 1981
Fungicide + insecticide	– – ^b			
Fungicide + insecticide + nematocide	– – ^b			
Insecticide	–	Chihuahuan Desert	6	Elkins and Whitford 1982
Biocide	–	Chihuahuan Desert ^a	4	Moorhead and Reynolds 1989
Fungicide	0	Chihuahuan Desert	5	MacKay et al. 1994
Insecticide	0			
Biocide	–			
Fungicide + Bacteriacide	0	Patagonian steppe	18	Austin and Vivanco 2006

Treatment influence on decomposition is expressed as the change in the decay constant, K , for treatments relative to the control. A decrease in K relative to the control is indicated by –; no influence is indicated by 0

^aBuried litter

^b K varied with treatments, control > insecticide > fungicide + insecticide = fungicide + insecticide + nematocide

on the size of decomposers have been used to assess the relative contribution of functional groups on decomposition.

The influence of macrofauna on dryland decomposition is highly variable in space and time. Macrofauna can be more important decomposers in drylands than mesic systems, with subterranean termites consuming >50% of the annual NPP in some dryland ecosystems (Johnson and Whitford 1975; Whitford et al. 1982; Silva et al. 1985) and redistributing large quantities of litter from the soil surface into subsurface galleries. In semi-arid Botswana, mass removal of wood was positively associated with the presence of termites that translocated surface litter to subterranean galleries where it is colonized by fungi (Schuurman 2005). In contrast, mass removal rates were not affected by the presence of non-fungus growing termite species. Similarly, leaf-cutter ants (*Atta* spp. and *Acromyrmex* spp.) may move considerable amounts of litter to subsurface fungus gardens in some dryland systems (Tadey and Farji-Brener 2007; Wetterer et al. 2001). Along with termites, colonization by tenebrionid beetle larvae and Thysanurans occurred on buried filter paper and cotton cloth in the Namib Sand Sea during dry periods (Jacobson and Jacobson 1998). However, macrofauna common in mesic systems (e.g., Annelids) are typically not abundant in drylands.

Mesofauna may also be important decomposers in drylands, although relationships between mesofaunal abundance and decay rates may be quite complex.

Several studies in the Chihuahuan Desert have documented a decrease in decomposition rates with chemical exclusion of microarthropods, particularly mites, although these exclusions may be the result of changing abundance of other decomposer organisms, such as bacteria and nematodes (Elkins and Whitford 1982; Santos et al. 1981). In contrast, other studies have found no microarthropod effects on decomposition (Silva et al. 1985). These discrepancies may simply reflect interannual variation and fluctuations in microarthropod abundance. When present, microarthropods may exert particularly strong indirect control over decomposition by regulating decomposer communities. For example, Santos et al. (1981) attributed the 40% decrease in decay rates for insecticide-treated litterbags to the elimination of predatory mites that allowed populations of bacteria-feeding nematodes to increase.

Experimental tests of the roles of microfauna activity in decomposition using chemical inhibitors have documented neutral to positive impacts of microbes on dryland decomposition rates (Table 2) in contrast to their more consistently positive impact in mesic systems. Strong temporal and spatial heterogeneity in the role of microbes in dryland decomposition are likely, however, given variation in soil moisture. For example, in the hyperarid Namib Sand Sea, decomposition rates of buried material were driven by precipitation-induced fungal colonization (Jacobson and Jacobson 1998).

3.3 Novel Drivers in Drylands

Decomposition studies in drylands have typically focused on controlling variables known to be important in more mesic systems (e.g., temperature, precipitation, soil or litter nutrient status, and microbial community), but robust generalizations for dryland decomposition remain elusive. Several recent studies suggest that mechanisms involved in dryland litter decay may differ substantially from that of mesic systems. A crucial distinction between drylands and mesic systems is the spatial heterogeneity of plant canopies in drylands; this difference in canopy cover may be at least in part responsible for some of these observed differences in driving mechanisms. Studies of canopy structure influence on decomposition in mesic systems have documented positive, negative, and neutral influences (Edmonds 1979; Binkley 1984; Zhang and Zak 1995; Hope et al. 2003). This variation in response may be due to system-specific differences in the nature of canopy influences on microclimate and subsequent microbial activity. In dryland systems, woody plant canopies may alter soil water availability by affecting canopy interception, stem-flow, throughfall, evapotranspiration, and hydraulic redistribution, or decrease the intensity of solar radiation (including UV) and alter soil surface temperatures relative to inter-canopy areas (Breshears et al. 1997; Schlesinger and Pilmanis 1998; Zou et al. 2005) to influence decomposition dynamics. Furthermore, microbial pools are likely to be concentrated in subcanopy area with high organic matter relative to inter-canopy spaces (McCulley et al. 2004; Smith et al. 1994).

3.3.1 UV Photodegradation

Photodegradation by ultraviolet (UV) radiation was proposed over 40 years ago as a mechanism for litter breakdown in environments receiving high inputs of solar radiation (Pauli 1964). UV-B radiation is known to enhance decay of dissolved organic carbon and nitrogen compounds in aquatic systems (Zepp et al. 2007). Research on photodegradation of wood and paper products indicates absorption of radiative energy by lignin, cellulose, and hemicellulose leads to the formation of free and peroxy radicals (reviewed in Moorhead and Callaghan 1994). In addition to UV-B, shorter energy wavelengths (UV-A and visible light) may also drive photodegradation (Schade et al. 1999). While there are clear mechanisms by which photodegradation may occur, its contribution to dryland litter decomposition is currently not well understood.

The possibility of photodegradation in litter decomposition has led many to suggest this as an important driving mechanism in dryland systems with high radiative loads. Failure to explicitly account for photodegradation has been posited as an explanation for the disconnect between measured and modeled decay rates (Moorhead and Callaghan 1994; Parton et al. 2007; Whitford 2002). Photodegradation was also posited as the cause for decay in the absence of biotic activity following biocide application (MacKay et al. 1994) and for an unexpected positive correlation between initial litter lignin concentration and mass loss in a field study with six litter types in the northern Chihuahuan Desert (Schaefer et al. 1985). While the combination of greater solar radiation in most drylands and less total radiative interception by canopies suggest that photodegradation could be relatively more important in drylands than mesic systems, few studies have explicitly quantified UV impacts in drylands.

Three recent studies have offered, to our knowledge, the first manipulative tests of the role of photodegradation in low- to mid-latitude drylands. Each of these studies compared decay rates of leaf litter under UV-absorbing filters with those under UV-transmitting filters (Table 3). In the semi-arid Patagonian Steppe, Austin and Vivanco (2006) assessed decay of mixed grass litter in plastic-sided "litterboxes" covered with differing films to create three UV environments and found strong positive correlations between radiative load and decay rates. Similarly, Day et al. (2007) found greater rates of *Larrea tridentata* leaf mass loss under near ambient than reduced UV-B. Leaves exposed to near ambient UV-B also had greater mass loss of lignin, carbon, fats and lipids from than those in reduced UV-B settings. Finally, in the semi-arid Colorado shortgrass steppe, Brandt et al. (2007) found slower decay rates in litterbags deployed under shelters in which the majority of UV-A and UV-B was blocked. However, mass loss was greater in the near-ambient relative to reduced UV treatment only under dry conditions for litter with an initially high C:N. In this study, UV radiation enhanced loss of holocellulose, but did not affect lignin loss. Taken together, these manipulative studies provide strong support for the notion that UV radiation can accelerate litter breakdown under field conditions.

Photodegradation has also been invoked as a possible mechanism to explain microsite variation in decay rates in drylands, although evidence is not as clear as for the manipulative studies discussed above. Observations of greater decay

Table 3 Low- and mid-latitude dryland field studies using UV filters to manipulate solar energy environment

Radiation manipulation	Location	Mass loss from radiation	Litter chemistry variables measured	Chemical response to radiation	Time (months)	Area:litter mass ratio (cm ² :g)	References
Reduced UV-B	Patagonian steppe	+33% ^a	None		18	200	Austin and Vivanco 2006
Reduced total radiation	Patagonian steppe	+60% ^a	None		18	200	Austin and Vivanco 2006
Reduced UV-A and UV-B	Colorado short-grass steppe	5%	Holocellulose	+	36	33	Brandt et al. 2007
Reduced UV-B	Sonoran Desert, Arizona	+14–22%	Lignin Total organic C	NC NC	4 and 5	56	Day et al. 2007
			Total organic N	NC			
			C:N	NC			
			Lignin loss	+			
			Fats and lipids loss	+			
			Holocellulose loss	-			

Decomposition responses were investigated in terms of mass loss and litter chemistry. NC indicates no change in that response variable

^aChange in the decay constant, *K*

constants on bare soil microsites compared to under shrub canopy microsites in desert scrub in Mexico were attributed to higher solar radiation on bare soil microsites (Arriaga and Maya 2007). However, there were no explicit measurements of radiation or other variables that might differ between the two microsites. Similarly, Martínez-Yrizar et al. (2007) attributed higher decay rates in “plains” sites relative to “hillslope” and “arroyo” sites in the Sonoran Desert to differences in UV photo-degradation and termite colonization. Although the plains site had less aboveground biomass and only widely-spaced canopy cover, evidence for the role of UV was again circumstantial.

The risk of attributing microsite differences in decay rates to solar radiation while other factors co-vary was illustrated by a recent study of decomposition in an Arizona semi-desert grassland (Throop and Archer 2007). In a 1-year litterbag study, decay constants were significantly higher for bags deployed in bare soil microsites compared to under intact mesquite (*Prosopis velutina*) shrub canopies. However, decomposition rates were equally depressed under intact canopies as in sites where canopies were mechanically removed immediately prior to the start of the experiment. Solar radiation alone therefore did not explain differential decay rates in this study, with decay rates for litterbags in high UV environments spanning the range of K values observed in the study (Fig. 2). Definitive evidence for the role

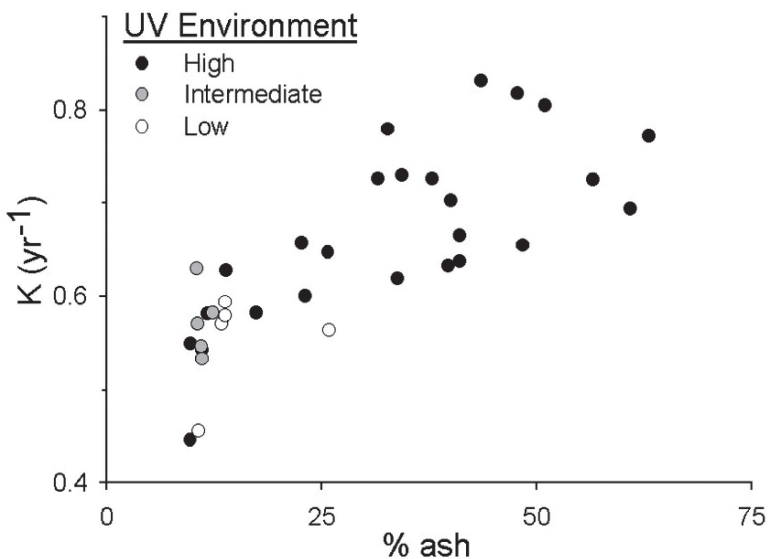


Fig. 2 Decomposition of mesquite leaflets (represented by K , the decay constant) in the Sonoran Desert, USA was strongly and positively correlated with soil deposition into litterbags (as indicated by % ash; Throop and Archer 2007). K varied two-fold, but not necessarily as a simple function of UV environment (high = open areas with no plant canopy cover; low = under shrub canopies where light was attenuated ~55%). High UV environments are those with no woody canopy cover, Intermediate UV environments are under recently girdled mesquite shrubs, and Low are under mesquite shrubs with intact canopies

of photodegradation in dryland litter decay requires explicit manipulative experiments.

An alternative to field reductions of ambient radiative loads is experimentally exposing litter to differing radiative treatments with UV-emitting bulbs. In a 6-month experiment with no radiation or 12 h per day of radiation from UV-A and UV-B emitting bulbs, decay rates did not differ among radiation treatments for either juniper (*Juniperus monosperma*) or piñon pine (*Pinus edulis*) litter (Gallo et al. 2006). Changes in chemical composition appear to have been driven by moisture treatments rather than UV exposure. Several high latitude studies have also used UV-emitting bulbs, and the majority have found no significant UV effects on mass loss (Table 4). While manipulative experiments with artificial radiation sources provide highly controlled experimental conditions, a challenge with using experimental radiation sources is that these systems often do not realistically mimic natural solar radiation. Ratios of wavelengths that affect biological processes and photochemical reactions in natural systems may differ from those present in artificial sources (Caldwell and Flint 1997). Total radiation may differ as well, with Gallo et al. (2006) estimating that microcosm UV treatments provided only a third of the midday UV intensity that would have been experienced at their field site.

Although recent field manipulative studies provide evidence that UV photodegradation *can* play a role in drylands (Austin and Vivanco 2006; Brandt et al. 2007; Day et al. 2007), there is still considerable uncertainty regarding the specific biochemical pathways at play and the relative importance of photodegradation as a driver of dryland decomposition. Field experiments have attributed mass losses due to photodegradation from 5 to 60% (Table 3). Why might the results of these studies be so different? First, the study species varied, with two studies using grass litter and one study using material from an evergreen shrub. It is likely that tissues from different species vary considerably in susceptibility to photodegradation, with greatest rates of photodegradation likely in species that have high concentrations of photo-absorptive compounds such as lignin. Further, species may differ in the degree to which the cuticle provides protection from photodegradation, and the persistence of the cuticle after leaf senescence. The relative importance of photodegradation may also vary with time, depending on the susceptibility of chemical constituents present and the succession and activity of decomposer organisms. The field manipulative studies outlined above ranged from 4 to 36 months of UV exposure.

Another confounding factor in comparing study results is among-study variation in the wavelengths manipulated. By employing a treatment that blocked nearly all solar radiation, Austin and Vivanco (2006) found that although UV-B was responsible for the approximately half of the observed photodegradation, other wavelengths, including photosynthetically active radiation (400–700 nm), also significantly affected mass loss. Thus, the UV-specific filters used by Brandt et al. (2007) and Day et al. (2007) may underestimate total photodegradation effects as they exclude shorter wavelengths. However, blocking all solar radiation may have the complication of attenuating temperature (Austin and Vivanco 2006). Total solar radiation also varied among sites, with the higher latitudes of Colorado (40°49'N) and Patagonia (45°41'S)

Table 4 Growth chamber and high latitude studies investigating the influence of manipulated UV radiation on litter chemistry and mass loss

Radiation manipulation	Location	Litter chemistry variables measured	Chemical response to radiation	Mass loss from radiation	Time (months)	Area:litter mass ratio (cm ² :g)	References
No radiation vs UV-B irradiated	Growth chambers; Sweden	Lignin	-	None	2	Information not provided	Gehrke et al. 1995
		α -cellulose	-				
		Soluble carbohydrates	NC				
		Tannins	NC				
Enhanced UV-A; Enhanced UV-A and UV-B	Outdoor UV exposure bed; United Kingdom	C loss	-	None	16	125 (estimate)	Newsham et al. 1997
		N	NC				
		Lignin	NC				
		Holocellulose	NC				
		Ca	NC				
		Mg	NC				
		K	NC				
		P	NC				
Enhanced UV-B	The Netherlands	Soluble carbohydrates	NC	+8% ^a	2	36	Rozeema et al. 1997
		Starch	NC				
		α -cellulose	NC				
		Tannins	NC				
		C	NC				
		Hemicellulose loss	+				
		Lignin Loss	+				
		N loss	+				
Enhanced UV-A; Enhanced UV-A and UV-B	The Netherlands	Leached nutrients	NC	None	6	44	Verhoef et al. 2000

(continued)

Table 4 (continued)

Radiation manipulation	Location	Litter chemistry variables measured	Chemical response to radiation	Mass loss from radiation	Time (months)	Area:litter mass ratio (cm ² :g)	References
Reduced UV-B	Tierra del Fuego, Argentina	Lignin	NC	-26%	4.6	50	Pancotto et al. 2003
Reduced UV-B	Tierra del Fuego, Argentina	Cellulose Soluble Carbohydrates	NC NC	None	29	19	Pancotto et al. 2005
No radiation vs. UV-A and UV-B irradiated	Growth chambers with UV-emitting bulbs	Cellulose Lignin Lignin:N Dissolved organic C	NC NC NC NC	None	6	Information not provided	Gallo et al. 2006
		Phenols	NC				
		C	NC				
		N ^b	NC				

NC indicates no change in response variable

^aEstimated from figures

^bComparison between "wet-dark" and "wet-UV" treatments

likely experiencing reduced intensity of solar radiation relative to the Arizona (33.5°N) experiment. Finally, methods of containing litter varied widely among studies; these may be responsible for substantial among-study variation. Brandt et al. (2007) suggest that their lower percentage of mass loss ascribed to photodegradation relative to Austin and Vivanco (2006) was, at least in part, the result of interception of solar radiation by the mesh litterbags used to contain material. In contrast, the litterbox design of Austin and Vivanco (2006) and the envelopes made of UV filters by Day et al. (2007) minimized structural interception of radiation.

Methodological variation in the ratio of treatment area to litter mass would similarly affect photodegradation. As a rough index of litter exposure to solar radiation, we calculated the treatment area (cm²)/litter mass (g) ratio for the three dryland experiments which manipulated UV radiation (Table 3). There was a large variation in ratios, ranging from 33 to 200, and a positive relationship between this index and the percentage of decomposition attributed to photodegradation.

We suggest photodegradation may be particularly important in drylands due to the persistence of standing dead in these systems. Synchronous drops of all tree and shrub leaves, or even predictable annual drop of leaf material, occur less frequently in drylands than in temperate mesic ecosystems. Similarly, grass material not consumed by herbivores may persist for several years as standing dead before being incorporated into the surface litter pool. This standing dead material would be subject to decomposition via photodegradation and leaching, while breakdown by decomposer organisms would be minimal.

UV radiation has also been proposed to affect decomposition rates by altering the activities, populations, or community composition of decomposer organisms by direct deleterious effects or indirectly, by changing litter quality (Duguay and Klironomos 2000; Pancotto et al. 2003, 2005; Rozema et al. 1997; Verhoef et al. 2000). Along these lines, accelerated decomposition of litter exposed to attenuated UV-B radiation in Tierra del Fuego was attributed to UV effects on fungal communities (Pancotto et al. 2003). Thin layers of litter or soil are likely to effectively shield decomposers from UV radiation, and thus UV effects on decomposers via modification of tissue quality may ultimately prove more important than deleterious effects on decomposers (Zepp et al. 2007). In another experiment, UV-B indirectly influenced barley decay as barley grown in an attenuated UV environment decomposed more quickly than did litter from plants grown under near-ambient UV-B. Attenuated UV exposure during barley growth led to reduced lignin:N, phosphorous, cellulose, and UV-B absorbing compounds (Pancotto et al. 2005). A meta-analysis of plant responses to artificial UV-B sources found a significant increase in UV-B absorbing compounds in response to elevated UV (Caldwell et al. 2003). The accumulation of such compounds would likely slow microbially-mediated decomposition.

3.3.2 Soil Deposition

The water-limited nature of dryland systems usually results in a patchy mosaic of vegetation and bare ground, with the relative abundance and stature of woody

plants defining the general ecosystem type (e.g., grassland, shrubland, savanna, woodland). In addition to affecting solar radiation inputs to the litter layer, patterns of canopy cover in dryland systems lead to pronounced patterns of erosion and associated processes of soil transport and deposition (Fryrear 1985; Toy et al. 2002). Wind and water transport of soils are widely recognized as having a substantial influence on nutrient and vegetation distribution (Okin et al. 2006; Peters et al. 2006). By redistributing litter across the landscape, transport processes affect the location and microclimate in which litter decays. Importance of these redistribution processes on spatial patterns of decomposition is unknown, as decomposition studies typically use litterbags to constrain litter at a location.

In addition to re-distributing litter, transport processes may influence decomposition by affecting the rate and pattern of soil deposition onto litter (or burial of litter) and the creation of a “litter–soil matrix”. Although a number of studies have explored decay rates of buried litter relative to surface litter in drylands (Moretto et al. 2001; Pucheta et al. 2006), the importance of soil mixing into litter has received little research attention. Indirect evidence that this mechanism may be important in dryland decomposition was recently presented in a study designed to tease apart the direct and indirect influences of plant canopies in a desert grassland invaded by shrubs (Throop and Archer 2007). In that study, litterbags were deployed in different microenvironments: beneath intact shrub canopies, inter-canopy areas, and in areas where shrubs were recently removed. If the direct influences of canopies on microclimate were a prevailing driver, faster decay rates would be expected in inter-canopy areas where solar radiation and temperature were greatest. In contrast, shrub-enhanced soil nutrient availability and decomposer communities would be expected to enhance decomposition under both intact shrub canopies and recently-removed canopies relative to inter-canopy areas if biological factors were a main driver of decay. Surprisingly, decomposition rates were equally depressed in areas of current or recently-removed shrub canopy cover relative to inter-canopy areas, indicating that neither decomposer communities/soil nutrient levels nor indirect canopy influences on microclimate had important influences on decomposition. Litterbag placements included low (under shrub canopies) and high (open areas between shrubs or settings where shrubs had been removed) light environments, with K (the decay constant) varying by a factor of two – but not in relation to the light environment. Instead, there was a strong positive correlation between the amount of soil deposited in litterbags and decomposition, with lowest deposition into litterbags in shrub-influenced sites (Fig. 2). The fact that soil accumulation in litterbags was lowest in shrub-influenced zones suggests that soil movement must be lowest in these areas. In this system, sub-canopy areas typically have higher litter and grass cover than inter-canopy areas (Tiedemann and Klemmedson 2004), and this likely reduces soil transport and increases deposition (Schlesinger and Pilmanis 1998; Tiedemann and Klemmedson 2004). It is interesting to note that the relationship between soil deposition and decomposition found by Throop and Archer (2007) was serendipitous. Without the manipulated canopy cover experiments, photodegradation would have been the most parsimonious explanation for accelerated decay rates in inter-canopy locations relative to subcanopy locations.

Although to our knowledge no other studies have explicitly addressed the role of litter–soil mixing on dryland decomposition, several studies provide circumstantial evidence suggesting that the soil–litter matrix may affect dryland decomposition. Day et al. (2007) suggest that contact with the soil may have sped decay rates of twigs deployed on the soil surface relative to twigs placed on other surfaces. However, this pattern was not observed for other litter type treatments in the same study. Photodegradation was invoked as a possible mechanism for greater decomposition in a “plains” microhabitat relative to “hillside” and “arroyo” sites in the Sonoran Desert (Martínez-Yrizar et al. 2007), but other potential among-site differences were not explored. We suggest that greater bare ground area in the plains may have been associated with enhanced soil transport and hence a higher probability of litter burial and subsequent increases in decay rates.

We hypothesize that soil deposition into the litter–soil matrix affects decomposition through several mechanisms. First, soil deposited onto litter may serve as a vector for microbial colonization of litter. Microbial colonization in litter may be limited in drylands, particularly if bacteria are dominant relative to fungi, and because of the heterogeneous distribution of microbes across the landscape (McCulley et al. 2004). Mechanisms that transport decomposers into litter may therefore be particularly important in drylands. If soils serve as an important microbial transport vector, then soils transported from areas of high microbial biomass, such as underneath shrub canopies (McCulley et al. 2004; Smith et al. 1994), may promote faster microbial litter colonization, and hence faster decomposition compared to soils transported from areas of low microbial biomass, such as inter-canopy areas. Second, soil deposition may effectively buffer litter, and resident decomposer organisms, from high temperatures and low moisture (Elkins and Whitford 1982; Whitford 2002), and prolong windows of environmental conditions suitable for microbial activity. This buffering may be particularly important in drylands because of the infrequency of suitable conditions for microbial activity and pulsed nature of precipitation events. Third, soil transport may cause physical abrasion to leaf litter, enhancing rates of fragmentation and increasing the surface area available for microbial attack. Explicit manipulative experiments are needed to determine which, if any, of these mechanisms play important roles in affecting dryland decomposition.

3.3.3 Combined Influences of Photodegradation and Soil Transport

While photodegradation clearly has the potential to affect decomposition rates, the impact of this driver has been highly variable when documented. We propose that interactions between photodegradation and soil transport may be responsible, at least in part, for the observed among-experiment variation. Soil deposition into the soil–litter matrix may inhibit photodegradation if soil effectively shields litter from UV radiation. In litterbag studies in the Sonoran Desert, we have observed that a thin film of soil frequently develops on litter within several months of exposure. The relationship between soil layer thickness and shielding is unclear; further

research is needed to determine what, if any, shielding is provided by a thin soil film versus a thicker coverage of soil. If this interaction between photodegradation and transport processes occurs, soil deposition may enhance litter decomposition while simultaneously decreasing rates of photodegradation. The net outcome of these offsetting interactions is unknown, but would potentially influence both mass loss and chemical composition. In contrast, if the soil deposition into the litter–soil matrix enhances decay via abrasion and physical fragmentation, it is possible that soil deposition would intensify the effects of photodegradation, as it would expose unprotected new surface area of tissue that may have photo-reactive compounds. However, this enhancement would only occur on any tissue not shielded from UV by soil cover.

The temporal dynamics of photodegradation will be important in affecting the nature of interactions with soil deposition. If photodegradation is most important in catalyzing litter break down early in the decomposition process, there may be little influence with soil deposition as photodegradation will occur while leaf material remains as standing dead or on the soil surface prior to litter–soil matrix development. The rate at which the interaction between photodegradation and soil deposition occurs will also be a function of the rates of soil deposition which, in turn, is a function of vegetation structure.

3.3.4 Expanded Framework

We propose an expanded framework for understanding and predicting patterns and processes of decomposition in drylands (Fig. 3). This framework expands the traditional focus on abiotic and biotic controls over decomposition to explicitly include the litter–soil matrix, and the factors that influence its development. While biotic and abiotic drivers in the traditional framework have been generally successful at predicting decomposition dynamics in mesic systems, spatial heterogeneity of vegetation in dryland systems necessitates considering how the spatial and temporal context of vegetation influences wind and water soil transport patterns, which in turn affect development of the litter–soil matrix. The litter–soil matrix may then indirectly dictate decay by strongly mediating both abiotic and biotic processes.

Experimental tests of this expanded framework will require a reconsideration of traditional litterbag methods. Experimental approaches will need to be expanded to include vegetation structure and measurements of, and ultimately manipulations of, soil transport processes. Adaptations of the litterbag method may be appropriate for initial explorations of the expanded framework. For example, litterbags can be deployed under different patterns of vegetation structure that differ in soil transport processes, and soil accumulation into litterbags can be measured directly or estimated via ash content (Throop and Archer 2007). The contrasting results of Austin and Vivanco (2006) and Throop and Archer (2007) could be largely the result of different methods and associated study foci. Traditional litterbags may enhance soil accumulation, restrict UV transmission to litter, reduce contact between litter and the soil surface, and minimize photodegradation by virtue of the low ratio of treat-

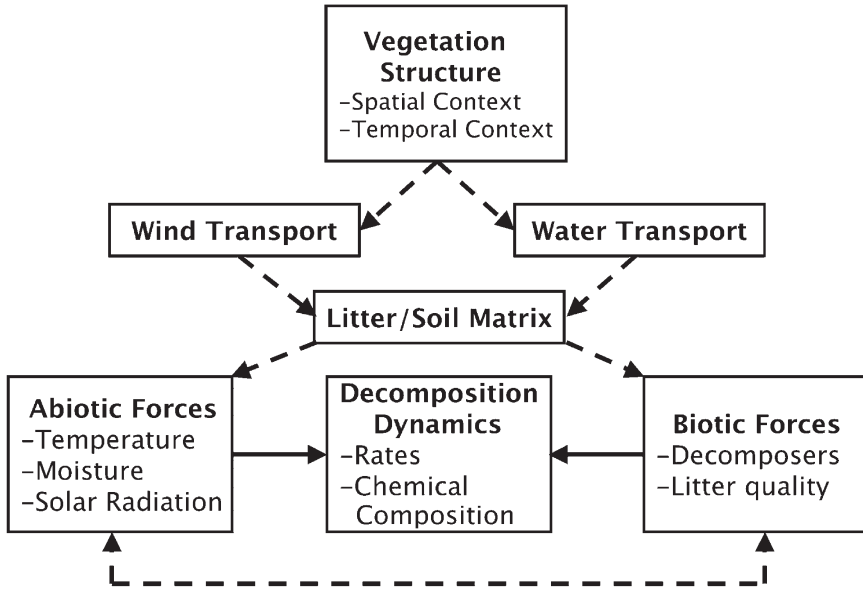


Fig. 3 Expanded framework for addressing decomposition in drylands. This framework includes erosion-based drivers, and proposes that development of the litter/soil matrix is a key but overlooked component of dryland decomposition. We hypothesize this matrix is controlled by wind/water transport of soil which, in turn, is controlled by vegetation structure. We further hypothesize that as the litter–soil matrix develops, biotic and abiotic drivers are strongly mediated

ment area:litter mass. Plastic-framed litterboxes covered with perforated UV filters (Austin and Vivanco 2006) minimize interception of radiation, but also minimize development of the litter–soil matrix by restricting air and water flow. Mesh cages (Torres et al. 2005) circumvent some of the aforementioned artifacts of litterbags and litterboxes, but careful consideration must be given to mesh size. Fine mesh will restrict movement of wind- and water-transported soil, whereas coarser mesh will be more susceptible to losing litter fragments, hence confounding measurement of mass losses from decay with those due to fragmentation and export.

We suggest that understanding decomposition processes in drylands within our expanded framework will be facilitated by standardizing, or at least reporting, the ratio of treatment area to litter mass (see Table 3). This index can be used to facilitate cross-site comparisons, and using a standard ratio may be useful for cross-site comparisons. Depending on study objectives, however, system-specific differences in litterfall rates and standing pools of litter may make it desirable to use the litter layer typically present at the study site(s) as a guide for determining the appropriate area:mass ratio.

Ideally, assessments of decomposition dynamics will include analyses of how both litter and soil move across the landscape and interact at locations where litter accumulates to determine in situ decomposition. Although explicitly measuring both litter transport patterns and decay rates would be extremely challenging,

linking soil and litter transport with decomposition dynamics will ultimately be crucial to understanding controls over dryland decomposition. Models based on a mechanistic understanding derived from key soil deposition–litter decomposition studies may be one method for making these links.

4 Conclusions

Litter decomposition dynamics exert strong controls over biogeochemical processes. These controls may be particularly important in drylands where litter, soil organic matter, and mineral nutrient pools are generally very small but may turn over rapidly. Short-term decomposition dynamics are particularly important in drylands because of the pulsed nature of precipitation drivers and the relatively small size of litter, soil organic matter, and mineral nutrient pools.

Recent studies have identified several processes historically overlooked as drivers in dryland decomposition dynamics. Incorporation of these processes may help explain the persistent disconnect between modeled and measured decomposition rates in drylands. Photodegradation, soil transport processes, and their interaction may be crucial determinants of decomposition. It is likely that photodegradation is more important in dryland than mesic systems due to the combination of greater solar radiative loads and less attenuation of incoming radiation from plant canopies. Transport of soil by wind and water is similarly enhanced in drylands due to low, discontinuous and patchy vegetative cover. We suggest that future research on dryland decomposition consider a framework that extends beyond traditional abiotic and biotic drivers to consider how vegetation structure mediates decomposition via its influence on soil transport.

Acknowledgements We have benefited from discussions about decomposition and drylands with P. Barnes, D. Breshears, and W. Whitford. This work was supported in part by USDA-NRI Managed Ecosystems 2005–35101–15408 to S.A., H.T., and M. McClaran and by the NSF-NMSU Advance Program to H.T.

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