Sunlight and Soil–Litter Mixing: Drivers of Litter Decomposition in Drylands

Paul W. Barnes, Heather L. Throop, Steven R. Archer, David D. Breshears, Rebecca L. McCulley, and Mark A. Tobler

Contents

P.W. Barnes (✉) • M.A. Tobler
Department of Biological Sciences, Loyola University New Orleans, New Orleans, LA 70118, USA
e-mail: pwbarnes@loyno.edu; tobler@loyno.edu

H.L. Throop
Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA
e-mail: throop@nmsu.edu

S.R. Archer • D.D. Breshears
School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA
e-mail: sarcher@ag.arizona.edu; daveb@email.arizona.edu

R.L. McCulley
Department of Plant and Soil Science, University of Kentucky, Lexington, KY 40546, USA
e-mail: rebecca.mcculley@uky.edu

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U. Lüttge, W. Beyschlag (eds.), *Progress in Botany*, Progress in Botany 76,
DOI 10.1007/978-3-319-08807-5_11

Abstract Decomposition of leaf litter is a key component of biogeochemical cycles but the mechanisms driving it in arid and semiarid ecosystems (drylands) remain unresolved. Here, we review recent findings that demonstrate dual roles of solar radiation (ultraviolet and photosynthetically active radiation) and soil–litter mixing as drivers of decomposition in drylands. We focus on the known and potential mechanisms by which these factors influence leaf litter decomposition, explore how the importance of these two drivers may shift over time, and propose possible avenues by which these factors may interact. Special attention is given to UV in sunlight, as this radiation is known to have multiple roles in influencing decomposition and has received considerable recent research attention. We also identify important uncertainties and challenges and offer a generalized conceptual model to guide future research aimed at enhancing our mechanistic understanding and quantitative modeling of the processes by which soil deposition and solar radiation together influence leaf litter decomposition rates in globally extensive dryland ecosystems.

1 Introduction

Decomposition of organic material strongly controls patterns of nutrient and carbon (C) retention and release in ecosystems. Although C and nutrients in the litter pool account for only a small portion of system-wide totals, the relatively rapid turnover of this pool makes leaf litter decomposition a key component of biogeochemical cycles (Aerts 1997; Berg and Laskowski 2005). Traditionally, the prevailing drivers of litter decomposition in terrestrial ecosystems have been viewed as a combination of abiotic (e.g., temperature, moisture) and biotic (e.g., litter quality) factors interacting to mediate decomposer community composition and metabolic activity, and considerable progress has been made in developing a mechanistic understanding of the controls over decomposition at local, regional, and global scales (Meentemeyer 1978; Couteaux et al. 1995; Aerts 1997; Hibbard et al. 2005; Cable et al. 2011). However, predicting decomposition dynamics in globally extensive arid and semi-arid systems (hereafter "drylands") has proven to be problematic, with models typically underestimating its rates (Whitford et al. 1981; Moorhead and Reynolds 1991; Kemp et al. 2003; Parton et al. 2007; Adair et al. 2008).

The disconnect between decomposition models and measurements suggests controls over decomposition in drylands differ fundamentally from those in wetter environments and that unique drivers may be operating in drylands (reviewed in Throop and Archer 2009; Austin 2011; King et al. 2012). Recently, several studies have shown that ultraviolet (UV; 280–400 nm) and photosynthetic active radiation (PAR; 400–700 nm) in ambient sunlight can accelerate litter mass loss in drylands via the process of photodegradation (Austin and Vivanco 2006; Brandt et al. 2007; Day et al. 2007; Brandt et al. 2010). Although the magnitudes and proposed mechanisms of photodegradation are variable and poorly understood (King et al. 2012; Song et al. 2013a), it may be an important, historically overlooked driver that could potentially explain, at least in part, why traditional models typically underpredict decomposition rates in drylands (Throop and Archer 2009; Austin 2011). Photodegradation results in the direct loss of a number of gases, including CO_2 (Brandt et al. 2009; Lee et al. 2012), CH_4 (McLeod et al. 2008; Bloom et al. 2010), CO (Schade and Crutzen 1999; Lee et al. 2012), and N_2O (Foereid et al. 2010), and recent analyses suggest that photodegradation of surface litter could have a measurable influence on landscape-level CO_2 flux rates, and ultimately C storage (Brandt et al. 2009; Rutledge et al. 2010).

While the climate and low and sparse vegetation cover of drylands create conditions of high solar radiation flux near ground level, these environments also favor considerable soil movement via wind and water transport (Breshears et al. 2003; Okin et al. 2009b), which can partially cover and eventually bury plant litter on the soil surface (Throop and Archer 2007). This combination of litter and the soil that covers it (the “soil–litter matrix”) includes both loose soil mixed with litter and soil that, over time, adheres to leaf surfaces to form a complex aggregate of soil and microbial products (Throop and Archer 2009; Barnes et al. 2012; Hewins et al. 2013). Although the nature and development of this soil–litter matrix remains poorly understood, available evidence indicates that decomposition in drylands can be strongly correlated with levels of soil accumulation onto litter and hence the development of this soil–litter matrix (Throop and Archer 2007). The mechanisms underlying this response have yet to be fully elucidated; however, the mixing of soil and litter and the resultant soil–litter matrix appears to enhance microbial activity (Hewins et al. 2013) while simultaneously shielding litter from photodegradation (Barnes et al. 2012). Soil coverage may also shield sensitive microbes from potential detrimental effects of solar UV (Moody et al. 1999; Johnson 2003; Cockell et al. 2008). An increased understanding of the factors that influence soil deposition onto litter, the processes governing soil–litter matrix development, and the mechanisms by which solar radiation and soil–litter mixing interact to influence decomposition appears critical to understanding litter decomposition in drylands and resolving seemingly conflicting views on this process.

Here we examine the dual roles of sunlight and soil–litter mixing as drivers of litter decomposition in dryland ecosystems. Specifically, we focus on the known and potential mechanisms by which these factors influence leaf litter degradation, explore how the importance of these two drivers may shift over time, and propose possible avenues by which these factors may interact to influence decomposition. We give special attention to UV in sunlight, as this radiation is known to have multiple roles in influencing decomposition and has received considerable recent research attention. We also identify important uncertainties and challenges and offer a generalized conceptual model to guide future research aimed at enhancing our mechanistic understanding and quantitative modeling of the processes by which soil deposition and solar radiation together influence leaf litter decomposition rates in globally extensive dryland ecosystems.

2 Overview

Solar radiation (UV and PAR) and soil–litter mixing can influence decomposition of leaf litter in dryland ecosystems by multiple mechanisms, and interactions between these and other environmental factors can further modify these effects (Fig. 1; see Table 1 for definition of terms). The total radiation exposure of litter (Fig. 1B) will be influenced by a combination of climatic, landscape/vegetation, and species-specific factors (Fig. 1A) that determine the timing and duration of exposure. The effects of solar radiation (primarily UV) on biotic processes generally reduce rates of decomposition (−) though there is the potential for some beneficial effects (Fig. 1D). The effects of sunlight on abiotic processes (primarily photodegradation) tend to enhance (+) decomposition (Fig. 1E). Both of these processes exhibit distinct spectral sensitivities (i.e., action spectra) depending on the underlying chromophores and mechanisms involved (Fig. 1C). Solar radiation can also influence decomposition via its effects on leaf chemistry and structure

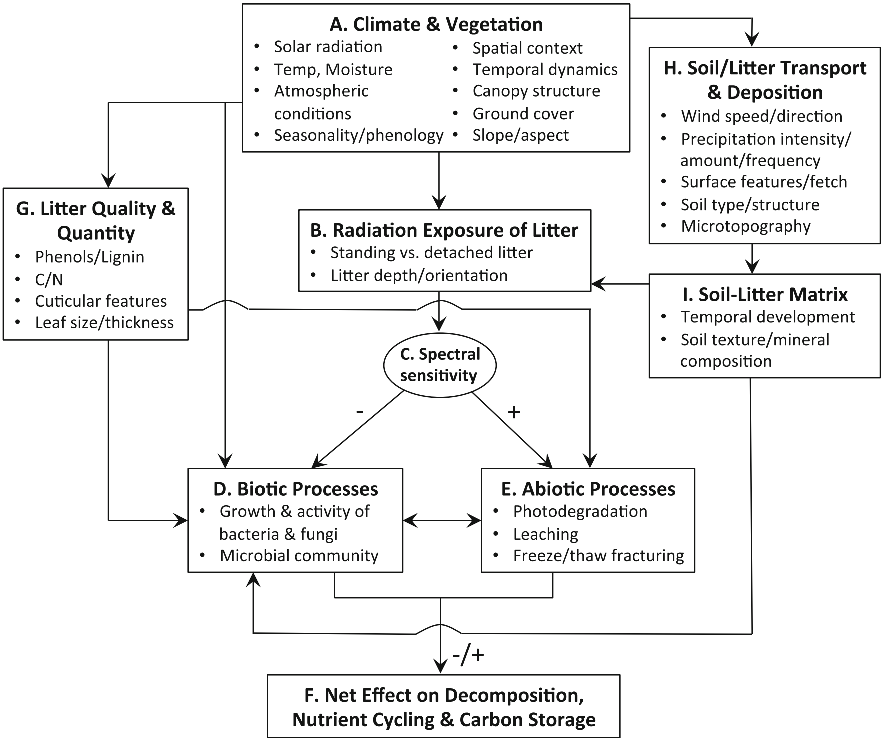


Fig. 1 Potential effects of solar radiation (UV and PAR) and soil–litter mixing on leaf litter decomposition in drylands, including interactions with other environmental factors. See Table 1 for definition of terms

Table 1 Terminology used to describe the various mechanisms by which solar radiation influences terrestrial litter decomposition. Although "photodegradation" is sometimes used broadly to include all radiation effects on mass loss, including microbial effects, we use it in a strict sense to refer only to abiotic effects on mass loss

Name	Mediation	Process	Material intercepting radiation	Outcome for plant litter decomposition	Examples
Primary photodegradation (Fig. 1E; aka photolysis; photooxidation[a])	Abiotic	Solar radiation breaks chemical bonds in litter via the direct absorption of radiation by photoreactive compounds	Litter	Efflux of gaseous compounds and mass loss	Austin and Vivanco (2006); Brandt et al. (2009); Lee et al. (2012)
Secondary photodegradation (Fig. 1E)	Abiotic	Breakdown of litter via reactive intermediates formed by primary photodegradation	Litter	Fragmentation and mass loss; increased potential for leaching, increased surface area for microbial attack	Austin and Vivanco (2006); Brandt et al. (2009); Lee et al. (2012)[b]
Thermal degradation	Abiotic	Low temperature (<100 °C) breakdown of chemical bonds in litter; may occur in absence of solar radiation; enhances photodegradation	Litter	Efflux of gaseous compounds and mass loss	Lee et al. (2012)
Photopriming (Fig. 1E→1D)	Abiotic/ biotic	Primary and/or secondary photodegradation that affects subsequent microbial decomposition	Litter	Often, but not always, enhanced microbial activity promoting mass loss	Foereid et al. (2010)
Microbially enhanced photodegradation (Fig. 1D→1E)	Biotic	Microbes modify litter which then influences photodegradation	Microbes	Increased mass loss	Ma et al. (2012)
Microbial photoinhibition (Fig. 1D)	Biotic	Solar radiation stress on microbial physiology/communities, affecting microbial decomposition	Microbes	Usually, but not always, decreased microbial activity and reduced mass loss	Duguay and Klironomos (2000); Verhoef et al. (2000); Newsham et al. (1997)

(continued)

Table 1 (continued)

Name	Mediation	Process	Material intercepting radiation	Outcome for plant litter decomposition	Examples
Plant photochemistry (Fig. 1G)	Abiotic/ biotic	Solar radiation-induced changes in plant tissue structure and/or chemical composition that affect later microbial decomposition and/or photodegradation	Live plants including leaves and stems	Attenuated microbial activity leading to reduced mass loss; effects on photodegradation unknown at present	Gehrke et al. (1995); Rozema et al. (1997); Pancotto et al. (2003)

[a] Lee et al. (2012) found that O_2 was not required for this process; thus photo-oxidation is apparently one of several pathways for photodegradation of compounds in litter

[b] Field and laboratory methods to date do not differentiate between abiotic decomposition from primary or secondary photodegradation

(Fig. 1G), which subsequently influences both biotic and abiotic degradation processes when foliage dies (Fig. 1D, E).

Soil accumulation onto litter will be influenced by meteorological, vegetation, landscape, and edaphic factors (Fig. 1A) that influence the rate, magnitude, and direction of soil and litter transport and soil deposition (Fig. 1H). Over time, and depending on soil mineralogy and particle size composition, a complex mixture of soil, plant material, and microbial products can develop to form an adhesive soil–litter matrix (Fig. 1I) that can shield litter from solar radiation (Fig. 1B), reduce photodegradation (Fig. 1E), and enhance microbial processes (Fig. 1D).

Ultimately, the net effect of solar radiation and soil deposition on the rates of decomposition, nutrient cycling, and carbon storage (Fig. 1F) will depend on the weighted contribution of biotic and abiotic processes and may be positive, negative, or neutral depending on the relative strength of the individual effects. Subsequent sections review our current understanding of the factors itemized in Fig. 1, examine how interactions among them might play out under field conditions, and address some of the knowledge gaps and challenges associated with quantifying them.

3 Sunlight, UV Radiation and Decomposition

3.1 Brief History and Overview of Experimental Approaches

The solar spectrum at the Earth's surface consists of a mixture of UV, PAR, and near-infrared (IR) radiation, with the majority of the energy and photon flux coming from the latter two wavebands. Although the UV component of the spectrum comprises a small (<5 %) portion of the total surface solar irradiance, its influence on terrestrial plants and ecosystems can be significant (Day and Neale 2002; Ballaré et al. 2011; Paul et al. 2012; Wargent and Jordan 2013). Historically, research examining UV effects on decomposition was undertaken to evaluate potential ecological impacts of the changing solar ultraviolet-B (UV-B; 280–320 nm) regime associated with stratospheric ozone depletion, and field studies were therefore often conducted in high-latitude ecosystems where ozone loss was acute (Gehrke et al. 1995; Pancotto et al. 2003; Zaller et al. 2009). These studies typically employed plastic films to reduce ambient solar UV-B (i.e., UV-exclusion experiments) or filtered UV-emitting lamps to simulate elevated solar UV-B conditions (i.e., UV-B-enhancement experiments) associated with ozone depletion. More recently, efforts have shifted to explore the mechanisms and fundamental roles of UV-B, UV-A (320–400 nm), and PAR in influencing terrestrial decomposition and biogeochemistry using a combination of field radiation-attenuation experiments and controlled laboratory experiments with artificial light sources. Although the technical issues and uncertainties associated with the different experimental approaches to UV experiments are beyond the scope of this review (but see Caldwell et al. 1983a; Flint et al. 2003; Aphalo et al. 2013), it is worth noting that the detection of UV effects on decomposition appears to be influenced by the nature and type of experiments conducted (i.e., field UV-exclusion vs. lamp studies and field vs. laboratory studies, King et al. 2012; Song et al. 2013a). These findings suggest that experimental techniques used to manipulate UV exposure and the maintenance of proper spectral balances (i.e., UV-B:UV-A:PAR ratios) are important in interpreting both the quantitative and qualitative effects of UV radiation on decomposition (Fig. 1D, E), as has been well documented for UV studies on higher plants (e.g., Caldwell and Flint 1989; Flint et al. 2003; Krizek 2004).

3.2 Mechanisms for Solar Radiation Influence on Decomposition

Findings to date indicate that UV (and PAR), either at ambient or enhanced levels, can influence litter decomposition in terrestrial ecosystems via multiple mechanisms including effects on microbes (Fig. 1D) and abiotic photochemistry (Fig. 1E) as well as effects mediated through alterations in leaf chemistry (Fig. 1G and recent meta-analyses of King et al. 2012; Song et al. 2013a). These processes also interact with one another [e.g., abiotic processes such as photodegradation may enhance or retard biotic (microbial) process; Fig. 1E→D] and multiple pathways can occur within a given process (e.g., different pathways of photodegradation as described below). The terminology surrounding these processes and the mechanism underlying them is somewhat ambiguous in the literature, and interpretations are further complicated with respect to what constitutes “primary” vs. “secondary” and “direct” vs. “indirect” effects. Table 1 summarizes the definitions and interpretations used in this paper.

Photodegradation (Fig. 1E) is an abiotic process that occurs via photochemical mineralization of photo-reactive compounds (King et al. 2012), such as lignin (i.e., primary photodegradation; Table 1), and/or the transformation of compounds as a result of solar radiation-induced formation of reactive oxygen species and other intermediates (i.e., secondary photodegradation; Rozema et al. 1997; Anesio et al. 1999; Gallo et al. 2006; Day et al. 2007; Austin and Ballaré 2010; King et al. 2012). Photodegradation is enhanced in the presence of oxygen but also occurs under anoxic conditions, suggesting there are multiple chemical pathways involved (Lee et al. 2012). While photodegradation has long been viewed as an important mechanism influencing decomposition in aquatic ecosystems (e.g., Zepp et al. 1995), only recently has it been shown to be an important driver of decomposition in terrestrial ecosystems (Henry et al. 2008; Brandt et al. 2010; Song et al. 2012). In a semi-arid Patagonian steppe, Austin and Vivanco (2006) found that reducing solar radiation affected decomposition much more strongly than reducing microbial decomposition with a biocide treatment, and they attributed about 60 % of the observed litter mass loss to shortwave radiation. About half of this mass loss was due to UV-B. Similarly, 14–22 % of leaf mass loss was attributed to solar UV-B in a field litterbag experiment in the Sonoran Desert (Day et al. 2007). However, not all investigators have found significant photodegradation effects (e.g., Kirschbaum et al. 2011) and there is evidence that the degree of photodegradation may vary with litter chemical composition (Uselman et al. 2011; Lee et al. 2012) and moisture (Schade and Crutzen 1999; Andrady et al. 2003; Gallo et al. 2006). Photodegradation rates increase with increasing ambient temperature (Lee et al. 2012). Furthermore, thermal degradation, the thermal decay of litter compounds at relatively low temperatures (<100 °C; well below the ignition point), can account for a substantial component of measured trace gas fluxes in photodegradation experiments (Lee et al. 2012). Increases in temperature from solar radiation may therefore influence litter decay both through enhancing photodegradation and from thermal degradation alone.

The effects of UV radiation on bacteria and fungi (Fig. 1D) tend to be negative, with growth, survival, and the production and germination of spores generally inhibited, especially by UV-B (Table 1, Caldwell et al. 2007). These "microbial photoinhibition" effects of sunlight are generally thought to be manifestations of detrimental impacts on DNA and repair processes (Hughes et al. 2003; Johnson 2003; Jacobs et al. 2005; Gunasekera and Sundin 2006). However, species vary in their UV sensitivity (Moody et al. 1999; Braga et al. 2001; Ulevičius et al. 2004), resulting in shifts in microbial community composition when material is exposed to sunlight (Kadivar and Stapleton 2003; Rangel et al. 2004). The UV tolerance of microbes may be related to the solar UV environment of origin, with microbes from sites with low UV exposures being more sensitive to UV insult than those from sites experiencing higher UV fluxes (Gunasekera et al. 1997; Zucconi et al. 2002). Microbes isolated from deserts, where natural UV exposure is high (e.g., the Atacama, Gobi, and Negev Deserts), can be relatively tolerant to wide ranges of UV irradiation (including UV-C; <280 nm) (Paulino-Lima et al. 2013), especially when present as desiccated spores and associated with soil particles (Cockell et al. 2008; Osman et al. 2008).

Not all effects of UV on microbes are negative, however. UV (together with blue light) can stimulate spore production and hyphal development in some fungi (Gressel and Rau 1983; Nagahashi and Douds 2003) and benefit microbial growth. Also, the effects of UV on microbes will depend on prevailing environmental conditions (i.e., temperature, moisture, and substrate availability) that influence microbial activity (Rangel et al. 2004; Gunasekera and Paul 2007; Belnap et al. 2008). Consequently, the overall effect of solar UV (UV-B + UV-A) on the community composition and function of microbial decomposers may be complex (Denward et al. 2001; Johnson 2003; Kadivar and Stapleton 2003). In relatively wet ecosystems (e.g., forests, marshes, and bogs), solar UV-B has been shown to retard litter mass loss and microbial activity and change microbial community composition, but effects are often subtle and variable over time (Newsham et al. 1997; Moody et al. 2001; Pancotto et al. 2003; M. Tobler and P. Barnes, unpubl data). The effect of UV on microbial-driven decomposition is little understood in drylands. It is conceivable that UV effects would be less important and more temporally variable in drylands as compared to moist environments due to the more extreme temperatures and the sparse, intermittent nature of precipitation in drylands that govern microbial activity, and therefore potential sensitivity to UV (see for example Belnap et al. 2008). Alternatively, the often intense UV in drylands may be sufficient to exceed the UV tolerances of microbial decomposers, at least under certain conditions.

Solar radiation also influences decomposition by altering the chemistry and structure of live plant tissue ("plant photochemistry" effects; Table 1; Fig. 1G). Exposure to ambient or enhanced UV-B typically elevates levels of phenylpropanoid compounds (flavonoids and related phenolics) that serve as UV-absorbing compounds and free radical scavengers (Caldwell et al. 1983b; Day 1993; Searles et al. 2001; Agati and Tattini 2010). Changes in UV-B during plant growth has also been linked with changes in leaf C, N, P, K, and lignin concentrations (Song et al. 2013b). How these UV-induced changes in live leaf chemistry might influence subsequent litter photodegradation is unknown. It does appear that UV-absorbing compounds can persist for some time even in dried leaf tissue (Ryel et al. 2010) and this may protect inner mesophyll cells in litter from photodegradation effects. Nonetheless, the potential for these plant photochemistry effects on decomposition suggests that differences in decomposition rates may exist between sun- and shade leaves of the same plant as there can be significant variation in phenolics and other chemical constituents in leaves within plant canopies depending upon the light environment experienced during development (Barnes et al. 2013). Also, both UV and PAR can alter leaf structure (e.g., leaf size or area, thickness, and area/mass ratios (Fig. 1G) (Boardman 1977; Barnes et al. 2005), which may then influence subsequent photodegradation (e.g., Anesio et al. 1999).

Changes in leaf chemistry induced by UV exposure (Fig. 1G) can, in turn, influence decomposer organisms (Fig. 1D). For example, Gehrke et al. 1995) found significantly lower rates of microbial decomposition in *Vaccinium uliginosum* litter collected from plants growing in an arctic heathland exposed to enhanced UV-B and attributed the differences to increased polyphenol and reduced cellulose contents in the litter. Similar UV-induced increases in phenolics and changes in other chemical constituents have been linked to decreases in mass loss and/or microbial activity in decomposing leaves of *Calamagrostis epigeios* (Rozema et al. 1997), *Hordeum vulgare* (Pancotto et al. 2005), and *Alnus incana* (Kotilainen et al. 2009), but not all plant species exhibit these responses (Newsham et al. 2001; Kotilainen et al. 2009; Song et al. 2013b).

In addition to modifying microbial decomposition through changing live leaf chemistry, solar radiation may affect decomposition through photodegradation that then modifies subsequent microbial decomposition (Fig. 1E→D). The "photopriming" of litter (Table 1) may break down or partially degrade compounds, leaving litter with a higher proportion of constituents more susceptible to microbial decomposition. Thus, even when primary and secondary photodegradation may have little effect on litter mass loss, respiration rates in subsequent incubations with moisture and soil can be positively correlated with length of prior radiation exposure (Foereid et al. 2010). Photopriming may be of particular importance in the "conditioning" of standing litter prior to its detachment and incorporation into the soil (Fig. 1B). However, photopriming can also enhance C mineralization from surface soil organic matter (Mayer et al. 2012). Although some laboratory studies have not observed photopriming (Brandt et al. 2009; Kirschbaum et al. 2011), these may have been of insufficient time, radiation intensity, or incorrect wavelengths to produce measureable change. It is also likely that there will be considerable variation in plant species susceptibility to photopriming, with species most susceptible to mass loss through primary photodegradation also being the most affected by photopriming. Future photopriming experiments with multiple species in field situations are needed to assess whether this is a frequent or important facet of the photodegradation processes.

3.3 Evaluating the Role of Sunlight on Decomposition in Natural Settings

It is clear from field and laboratory studies to date that UV and PAR *can* play substantive roles in decomposition under experimental conditions, but it is likely that their effect will be attenuated by other factors under field conditions. The overall net effect of UV on litter decomposition under field conditions will reflect a balance between positive (e.g., photodegradation, photopriming, microbially enhanced photodegradation) and negative (e.g., microbial photoinhibition, plant photochemistry) effects (Table 1) such that decomposition may be increased, decreased, or unaffected by UV exposure depending on prevailing environmental conditions and litter chemistry (Fig. 1F; e.g., Rozema et al. 1997; Moody et al. 2001; Pancotto et al. 2005; Brandt et al. 2007; Smith et al. 2010; Uselman et al. 2011). This balance will also be influenced by the amount, wavebands, and timing of solar UV radiation received by litter (Fig. 1B, Song et al. 2013a). Understanding radiation loads that litter typically experiences under field conditions and assessing the impact of these exposures on decomposition is a crucial next step for advancing our understanding of the role of sunlight in influencing abiotic and biotic processes in natural systems.

Little is known of the precise nature of the dose–response relationships for the various mechanisms of UV-driven decomposition and whether there are differences in dose responses for abiotic and biotic mechanisms. Certainly, the UV exposure of standing and ground litter will vary over short (e.g., diurnal) and long (e.g., seasonal) time scales, and these patterns can be modified by cloud cover (Fig. 2a, b). Indeed, during the summer monsoon period in the North American Sonoran Desert (July–August), clouds can reduce daily UV-B levels by 50 % relative to seasonal maximum clear sky conditions (Fig. 2a). Due to the strong seasonality of solar UV, the timing of litter production is also important in influencing litter UV exposure, and differences in UV doses would be expected between dryland plant growth forms

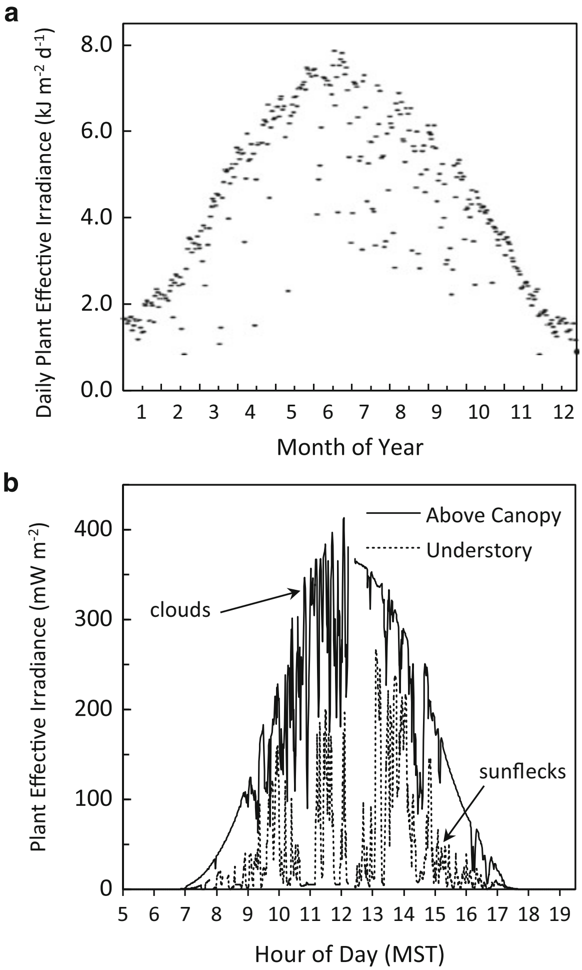


Fig. 2 The surface solar UV radiation environment in a semi-desert savanna [Sonoran Desert, Santa Rita Experimental Range (SRER), southeastern Arizona, USA; 31° 47′ 36″ N, 110° 53′ 4″ W; elevation ca. 1,000 m]. (**a**) Integrated daily UV-B irradiance [weighted according to the generalized plant action spectrum of Caldwell (1971) and normalized to unity at 300 nm] over 2012. UV measurements were made with a broadband UV sensor (UVB-1 pyranometer; Yankee Environmental Systems, Inc.; Turners Falls, MA, USA) calibrated against a double monochromator scanning UV spectroradiometer (OL 756; Gooch & Housego, Orlando, FL, USA). (**b**) Representative diurnal course of plant effective UV-B irradiance above and below the canopy of an isolated, mature *Prosopis velutina* shrub (Fig. 4) on 22 May 2013. Measurements were made with calibrated broadband UV-B sensors (SKU 430; Skye Instruments, Ltd., Powys, UK)

which differ in leaf chemistry (Sect. 3.2, Fig. 1G) and also in leaf phenology and leaf area duration (e.g. C_3 and C_4 grasses, grasses and shrubs, evergreen and deciduous shrubs; Figs. 1A and 4a). High photodegradation potential is likely in settings where the primary growing season occurs during wet, warm spring months, leaving large amounts of standing dead and surface litter exposed to solar radiation during dry, hot summer months when cloud cover is low. Photodegradation accounted for a substantial portion of the dry season ecosystem CO_2 flux in a California annual grassland (Rutledge et al. 2010)—ostensibly a consequence of the Mediterranean climate. Unfortunately, many of the field UV-exclusion decomposition studies conducted to date do not report UV or PAR irradiances, which makes it difficult to both interpret and compare results from studies conducted at different locations and times of year. At a minimum, total daily PAR and appropriate effective UV irradiances (UV-B and UV-A; see below) should be reported over the time period when decomposition data are collected.

The effectiveness of incident radiation in driving litter decomposition will be determined, in part, by the spectral sensitivity of the underlying decomposition processes (Fig. 1C). Action spectra represent the relative effectiveness of different wavelengths of radiation in causing biophysical responses and are typically developed under very controlled laboratory conditions (Holmes 1997). While few action spectra specific to decomposition have been developed, representative action spectra of related processes may yield insights. Potentially important action spectra for biotic and abiotic processes involved in litter decomposition are shown in Fig. 3, along with action spectra commonly used in UV photobiology studies. These indicate that UV effects on both biotic and abiotic processes are strongly wavelength-dependent, with shorter wavelengths showing greater quantum effectiveness than longer wavelengths (Fig. 3a). However, the slopes of these curves can vary considerably. For example, within the UV-B range (280–320 nm), the effectiveness of UV in damaging DNA can increase five orders of magnitude with decreasing wavelength. By comparison, UV-induced CO emission increases less than one order of magnitude over this same waveband. The relatively flat action spectrum for this aspect of photodegradation is consistent with experiments demonstrating that photodegradation can be caused by UV-A and visible (PAR) in addition to UV-B (Anesio et al. 1999; Austin and Ballaré 2010).

Action spectra are used to identify potential chromophores mediating photobiological responses and, in UV studies, as weighting functions to derive measures of biologically effective UV irradiance. In the case of weighting functions, measured raw spectral irradiances (Fig. 3b) are multiplied by relative effectiveness derived from the action spectrum, and then summed over the appropriate wavelength range, to give the *biologically effective radiation* (Fig. 3b, Caldwell and Flint 1997). Thus, the selection of the action spectrum can significantly influence the calculated biologically effective radiation. Steep action spectra (e.g., microbial DNA damage) amplify the importance of the shorter wavelengths (i.e., UV) to a greater degree than flatter action spectra (e.g., CO emissions; Fig. 3a). Because of this, differences in the spectral sensitivities of biotic and abiotic decomposition processes (Fig. 1C) would have important implications for experimental procedures and for interpreting the consequences of stratospheric ozone depletion and latitudinal UV gradients on decomposition. For example, using a relatively steep action spectrum, such as that

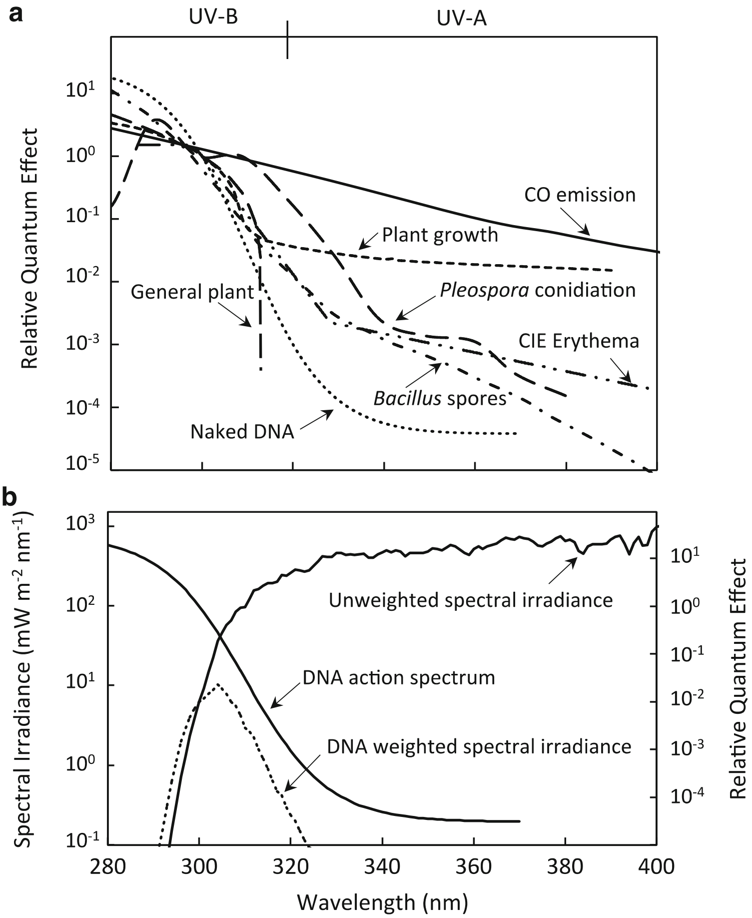


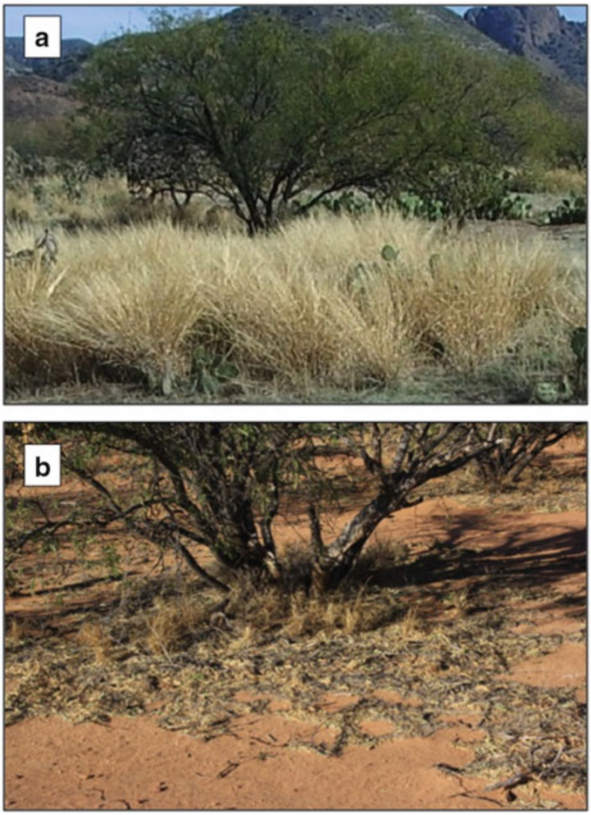
Fig. 3 Representative action spectra and biological weighting functions used in UV photobiology (note log scale on *y*-axes). (**a**) Relevant action spectra for biotic and abiotic processes associated with decomposition and common action spectra used as biological weighting functions in UV photobiology. All action spectra are normalized to unity at 300 nm and have been converted to quantum units if originally reported in energy units. The general plant action spectrum is from Caldwell (1971). The DNA action spectrum is for UV-induced damage to "naked" microbial DNA (Setlow 1974). The *Bacillus* action spectrum is based on the inactivation of spores as reported by Cockell et al. (2003). The *Pleospora* action spectrum is for UV-induced conidiation (asexual spore production) in the fungus *P. herbarum* originally described by Leach and Trione (1966) as reported by Ensminger (1993). CIE is the human erythemal action spectrum (McKinlay and Diffey 1987a, b), a widely used weighting function to report UV irradiances and the basis for the UV Index. The plant growth action spectrum describes the influence of UV on shoot elongation (Flint and Caldwell 2003). The CO emission action spectrum is for savanna grass (*Trachypogon* sp.) leaf litter (Schade et al. 1999). This action spectrum extends into the visible (>600 nm), but only the UV portion is shown here. (**b**) UV spectral irradiance at midday under clear skies on 7 June 2011 at the SRER as measured with a UV scanning spectroradiometer (see Fig. 1), the DNA damage action spectrum from panel **a**, and the calculated biologically effective UV irradiance weighted according to the DNA action spectrum. For this spectrum, the unweighted UV-B and UV-A irradiances are 2.5 and 43.1 W m^{-2}, respectively, and the DNA weighted UV irradiance is 0.10 W m^{-2}

for DNA, to report effective UV radiation may be inappropriate for photodegradation studies and could result in large errors if UV doses were applied using lamps that differ in spectral composition relative to natural sunlight (i.e., UV fluorescent bulbs, Flint and Caldwell 1996). Furthermore, the shift in the UV spectrum in favor of the shorter wavelengths as a result of ozone depletion becomes significant only if a relatively steep action spectrum exists (Caldwell et al. 1986). Finally, because of latitudinal variation in stratospheric ozone thickness and prevailing solar angles, there is a potential natural latitudinal gradient in ambient solar UV-B (Caldwell et al. 1980; Barnes et al. 1987). However, this latitudinal UV gradient would be trivial for responses exhibiting a relatively flat action spectrum, such as that for CO emissions. If other photodegradation processes exhibit a similarly flat action spectrum, this may explain, in part, why Brandt et al. (2010) found no strong differences in UV-driven photodegradation across a latitudinal gradient of grassland sites in North America. Because of the fundamental importance of action spectra in UV photobiology, additional studies are needed to develop and test appropriate action spectra/weighting functions for processes involved in litter decomposition.

The UV environment of litter in drylands also exhibits substantial spatial variability as a result of the pronounced discontinuous nature of vegetative cover in these ecosystems (i.e., herbaceous patches in a matrix of bare soil or tree/shrub patches in a matrix of bare soil and herbaceous plants, Noy-Meir 1979/80; West 1983; Evenari et al. 1985). In systems with discontinuous cover of woody plants, litter often accumulates in the understories of woody plants (Fig. 4b) and thus receives considerably less UV (and PAR) than that in the intercanopy zones (Fig. 2b). The UV exposure of litter will also depend on the depth of litter layer (Henry et al. 2008) and vertical position within the litter layer (Lin and King 2013) (Fig 1B). The angle at which litter is oriented would also have strong influences over its exposure to solar radiation, with vertically oriented standing dead (e.g., grasses; Fig. 4a) potentially intercepting less radiation than would detached litter resting horizontally on the soil surface. Orientation effects would, however, be less for UV than PAR because of the pronounced diffuse (isotropic) nature of solar UV radiation.

Once the litter falls to the soil surface, it may become covered with loose soil and tightly bound soil–litter films that can block solar radiation from hitting the litter and consequently negate photodegradation (Fig. 1I→B, Barnes et al. 2012). Because of these complexities, quantifying the actual UV exposure of litter in field environments is challenging. The use of inexpensive biological or synthetic UV dosimeters (e.g., Rahn and Lee 1998; Turner et al. 2009) deployed in a variety of habitats and conditions over varying time periods would aid in quantifying the patterns of UV exposure at spatial and temporal scales relevant to litter decomposition.

Fig. 4 Temporal and spatial aspects of litter production and distribution in a semi-desert savanna (Sonoran Desert, SRER; see Fig. 2 for location details). (**a**) End-of growing season standing litter of the C_4 grass *Heteropogon contortus* with the winter-deciduous shrub, *Prosopis velutina*, before leaf drop. Note the spatial heterogeneity in herbaceous cover. (**b**) Spatial variation in bare ground, surface litter accumulation, and light conditions under and near a *P. velutina* canopy after leaf drop and prior to the onset of the growing season (photos: S. Archer)



4 Soil–Litter Mixing and Decomposition

4.1 Soil Redistribution in Drylands

Dryland ecosystems are, by definition, water-limited, and this water limitation usually results in a mosaic of vegetation cover that is sparse and incomplete, with herbaceous patches in a matrix of bare soil or tree/shrub patches in a matrix of bare soil and herbaceous plants. As a consequence of sparse and patchy ground cover, soil erosion and associated processes of transport and deposition can be particularly pronounced (Fig. 1H, Kirkby 1980; Heathcote 1983; Fryrear 1985; Toy et al. 2002). Wind- and water-driven transport of soils is widely recognized as having a substantial influence on nutrient and vegetation distribution (e.g., Ludwig et al. 1997; Okin et al. 2006; Peters et al. 2006). Even so, the mechanisms by which plant community structure and ecosystem processes are influenced by wind and water transport of soils are poorly understood. Different physical forces promote movement of soil via wind and water, but these processes share three critical phases: detachment of soil particles from the soil surface, transport as overland flow or

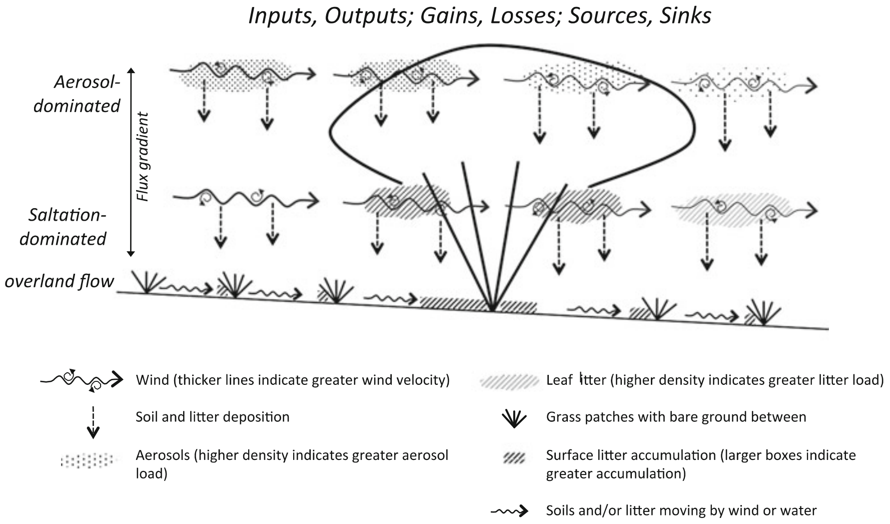


Fig. 5 Schematic representation of wind and water redistribution of soil and plant litter leading to the development of a soil–litter matrix (Fig. 1H, I) in drylands characterized by herbaceous patches in a matrix of bare soil or tree/shrub patches in a matrix of bare soil and herbaceous plants. In this figure a single shrub (large plant) is surrounded by grasses (small plants) and bare ground. Aerosols, saltating soil particles, and overland flow transfer soils and litter from areas of low vegetation cover to areas of higher vegetation cover. Net exchanges and source–sink relationships are mediated by the area, density, spacing, and stature of vegetated patches, the size and connectivity of bare gaps, topography, and disturbances such as fire and grazing

aerosols, or via saltation, and deposition at a location (Toy et al. 2002). These processes are interrelated and produce a net flux that can result in either an accumulation or erosional loss of soil at a given location (Fig. 5). Within sites, winderosion (net vertical dust flux) appears to be correlated with wind-driven transport (horizontal dust flux; Whicker et al. 2006). Evaluating the role of erosion on fine-scale processes such as decomposition requires coupled estimates of transport and deposition (Fig. 1H). Numerous studies have documented broad-scale or long-term manifestations of wind and water erosion, but few have focused on erosion and associated transport and especially redistribution at the finer spatial scales (cm–m) and the shorter time frames (weeks to a few years) relevant to litter decomposition (e.g., Whicker et al. 2002; Ludwig et al. 2005). Rates of wind erosion are poorly documented relative to those of water erosion, even though a recent evaluation that included major dryland ecosystem types (grassland, shrubland, woodland) found that annual rates of wind-driven soil transport could exceed those of water-driven transport by an order of magnitude or more (Breshears et al. 2003).

Soil transport by both wind and water is highly dependent on and sensitive to changes in woody plant cover (Fig. 1A→H, Bagnold 1941; Fryrear 1985; Reid et al. 1999; Wilcox et al. 2003; Warner 2004; Breshears et al. 2009). Notably, there has been a strong, directional increase in woody plant cover in drylands over the past century (Archer et al. 1995). This global-scale change has altered the quality and quantity of litter inputs (e.g. Hibbard et al. 2003) and the spatial and temporal patterns of erosion processes (Schlesinger et al. 1990; Okin et al. 2009a; Ravi et al. 2009a, 2010). These shifts in grass-woody plant ratios may potentially affect decomposition rates by mediating soil transport processes that determine rates of soil deposition into litter (Figs. 1H→I and 5). Recent research highlights two complementary aspects of horizontal dust flux: increased production with reduction in grass cover (Li et al. 2007) and capture by shrubs and grasses (Field et al. 2009). The later work highlights an important mechanism by which horizontal sediment flux and associated nutrients are likely to be deposited onto litter beneath plant canopies.

4.2 Litter Redistribution in Drylands

Wind and water promote the detachment and redistribution of plant litter, increasing spatial heterogeneity of litter and its nutrient constituents (Fig. 5). Although often observed and clearly evident (Fig. 6) the magnitude, patterns of litter redistribution, and the dynamics and ecological significance of litter mass and nutrient transfer have seldom been quantified in drylands. Surface water flows can redistribute detached litter and soil particles and concentrate them in ostensibly predictable locations related to microtopography and obstructions posed by rocks, animal disturbances, and other plants. In dryland plant communities with woody vegetation, coarse woody debris on the soil surface can trap and retain leaf and twig litter and soil. These accumulations presumably hasten the localized

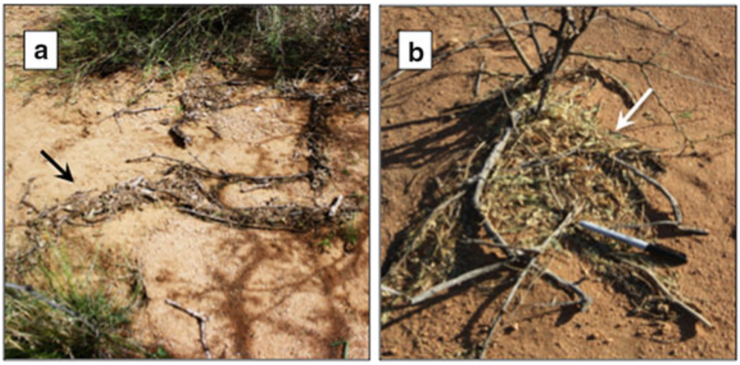


Fig. 6 Localized accumulation of surface litter (*arrows*) in a semi-desert savanna (Sonoran Desert, SRER; see Fig. 2 for location details). (**a**) Litter accumulation in a bare patch as a result of microtopography. (**b**) Litter accumulation at the base of a small woody plant with coarse woody debris on soil surface. Note marking pen for scale (photos: S. Archer)

formation of soil–litter matrices. The self-facilitated burial of coarse woody debris would also accelerate its breakdown.

Redistribution of surface litter by overland flow of water is supplemented by wind-mediated transfers. Nutrient inputs can be substantially augmented by litter transferred from upwind to downwind communities (Shen et al. 2011). Redistribution of litter by wind from ridge tops to leeward locations in the Arctic can lead to increases in C and N inputs and subsequent increases in soil respiration in depositional locations (Fahnestock et al. 2000). As with water, litter transported by wind accumulates in predictable locations that likely vary depending on the size, shape, density, and mass of the litter and vegetation and landscape features that cause turbulence and alter wind speed and direction (Fig. 1H).

Assessing the biogeochemical consequences of litter redistribution and its subsequent decomposition at a given site requires quantifying inputs (gains) and outputs (losses). Most of the litter generated by a plant falls on the ground near the plant subsequent to detachment (input), but some litter is transported away from the plant by wind or overland flow (output) (Fig. 5). Litter deposited near a plant's canopy may be supplemented by litter transferred from other plant patches on the landscape (input). However, quantifying these litter inputs and outputs is challenging. Litter deposition has typically been quantified using litter traps, but the design of such traps is generally strongly biased toward the collection of gravity-deposited litter, and it is difficult to know what fraction of the litter in a trap, if any, is derived from external sources. Quantifying litter ground cover and its change through time offers alternative perspectives on the net outcomes of local litter gains and losses, but here too, it is difficult to know the amount of litter arriving from external sources. Furthermore, local surface litter cover reflects a hard-to-quantify combination of reductions (owing to burial by soil, comminution by arthropods and weathering) and increases (associated with inputs of new litter from local or external sources). Litter arriving from outside sources may also differ in quality relative to that of the locally produced litter and such differences may be pronounced in drylands consisting of heterogeneous patches of annuals, perennial grasses, and shrubs.

In locales where litter accumulates, the soil surfaces may be stabilized by formation of the soil–litter matrix, likely reducing ground surface temperatures and PAR and UV radiation levels. These changes could also promote the establishment of plants whose wind- and water-dispersed seeds would be likely to accumulate in the litter deposition zones. Locations where the soil–litter matrix forms via the processes outlined in Sect. 4.1 may therefore represent nutrient cycling "hot spots," a nascent phase in the formation of vegetated patches and a feedback mechanism reinforcing the persistence and expansion of vegetated patches. At the landscape scale, the dynamics of soil–litter patches will depend on the degree of bare gap connectivity (Okin et al. 2009b), and source–sink relationships governed by interactions among disturbance (e.g., grazing, fire), topography, and prevailing winds (e.g., Ravi et al. 2009b; Bestelmeyer et al. 2013). Multiple drivers interacting across scales probably combine with positive feedbacks to govern litter–soil distribution and redistribution (e.g., D'Odorico et al. 2012).

4.3 Soil–Litter Mixing and Decomposition

Once litter is on the ground it is inevitably covered with varying degrees of soil or other litter and, in some cases, fully buried (Fig. 6). Initially, litter is covered with loose soil that can be easily dislodged. Over time, soil films consisting of soil particles, microbes, and microbial exudates develop and adhere to the litter surface (Fig. 7; Barnes et al. 2012; Hewins et al. 2013). Unlike loose soil, these adhering soil films are more resistant to removal by rainfall and wind. At time scales of weeks to months, however, soil films are dynamic and may develop or degrade in response to temperature and moisture conditions (D. Hewins and H. Throop, unpublished). These soil films appear to be composed of inorganic and biological constituents with fungal hyphae and microbial exudates binding mineral particles to each other and to the leaf surface (Fig. 7). The specific nature of the abiotic and biotic components of these soil films and the degree and timing of soil film coverage will likely be influenced by site-specific edaphic and vegetation factors that influence local-scale differences in soil transport (Okin and Gillette 2001; Okin 2008).

While positive correlations have been found between rates of litter decomposition and the degree of soil–litter mixing (e.g., Throop and Archer 2007), the underlying mechanisms of this response have yet to be elucidated. Soil coverage of litter could potentially influence decomposition by several mechanisms, with the net effect ranging from positive to negative depending on conditions and the extent of coverage (Fig. 1I→B, I→D). Soil may serve as a vector for microbial colonization of litter. In a laboratory incubation study, soil–litter mixing led to differences in the quantity and composition of phospholipid fatty acids extracted from the soil–litter matrix following the first week of the incubation, suggesting that colonization

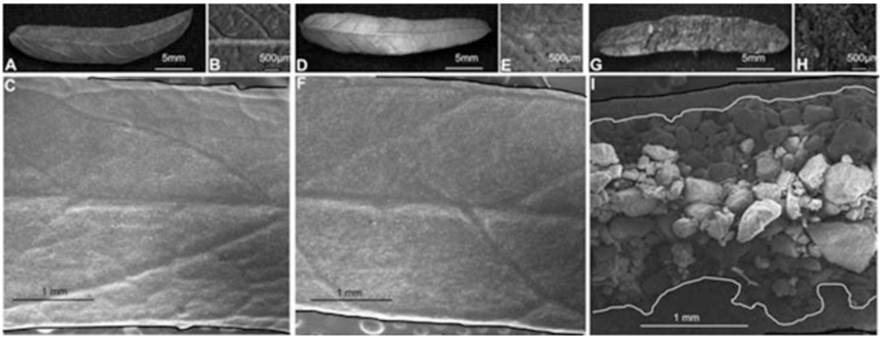


Fig. 7 Development of soil films on *Prosopis glandulosa* leaf litter over time (0, 30, and 180 days in **a**–**c**, **d**–**f**, and **g**–**i**, respectively) in a Chihuahuan Desert shrubland (Jornada Experimental Range, New Mexico, USA; 32°33′ N, 106°45′ W; elevation ca. 1,190 m) illustrated by low magnification (×1.6) stereo micrographs showing entire leaflets (**a**, **d**, **g**), high magnification (×3.2) stereo micrographs (**b**, **e**, **h**), and SEM micrographs (×25, ×31, and ×35 for **c**, **f**, and **i**, respectively). In the SEM micrographs, *black lines* denote leaflet margins and *white lines* denote the edge of the soil film (from Barnes et al. 2012)

may be influenced by soil–litter mixing (Lee et al. 2014). Soil–litter mixing may also buffer litter and resident microbes from the high temperatures and desiccation that commonly occur in drylands (Moorhead and Reynolds 1991). These effects could enhance decomposition by extending windows of opportunity for microbial activity following rainfall events (e.g., Cable et al. 2011). Indeed, soil–litter mixing strongly enhanced C mineralization in a laboratory experiment when the soil–litter matrix was subjected to wetting–drying cycles (Lee et al. 2014). The arrival of soil at the litter surface via saltating soil particles or the translocation of litter via overland flow may also promote surface abrasion and increase the surface area available to microbial colonization, leaching, or fragmentation (Throop and Archer 2009; Uselman et al. 2011). Enhanced microbial colonization of recently detached litter may be offset by the negative effects of solar UV on microbes (Sect. 3.2), but subsequent soil coverage, either as an adhering soil film or as loose soil, could partially and eventually fully shield litter from UV radiation and therefore ameliorate its adverse effects (Cockell et al. 2003; Barnes et al. 2012). Soil cover may therefore mediate photodegradation and other abiotic forces (Fig. 1D, E).

5 Integrated Conceptual Model of UV and Soil Mixing Effects on Dryland Decomposition

Based on findings from field and laboratory studies, we have proposed a generalized conceptual model for UV-soil mixing effects in dryland decomposition (Fig. 8, Barnes et al. 2012). Over a continuum of soil coverage of litter from none (e.g., standing dead) to partial (e.g., recently detached) to full burial, the mechanisms driving decomposition are predicted to shift from strongly abiotic (photodegradation of standing dead driven by UV together with PAR) to strongly biotic (microbial degradation of buried litter). Intermediate conditions consist of a combination of these processes whose influence varies depending on the extent of development of the soil–litter matrix, its biogeochemical constituency (e.g., litter quality, soil mineral composition, and organic matter content of soil [Fig. 1G, I]), the microbial community composition and activity (Fig. 1D), and the prevailing moisture/temperature conditions (Fig 1A). As the relative importance of photodegradation and microbial decomposition change through time, the overall rate of decomposition may approximate a unimodal curve that reflects the outcome of interactions between the speed of the concurrent drivers of decomposition and the recalcitrance of the chemical constituents present in the litter.

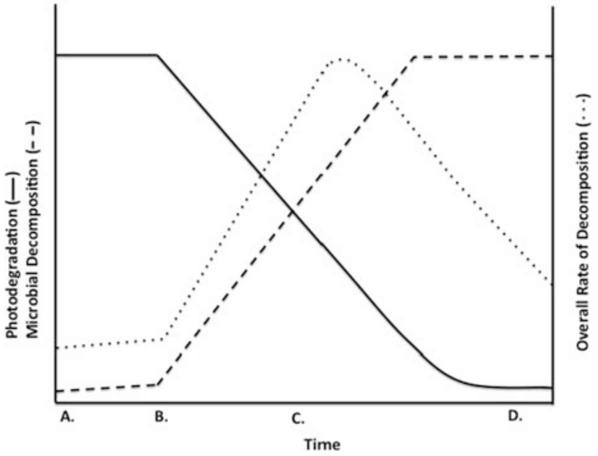


Fig. 8 Conceptual model of dryland decomposition following leaf senescence, illustrating the shifting relative importance of abiotic (photodegradation, Table 1) and biotic (microbial) processes through time and consequent changes in the overall rate of decomposition (Fig. 1F). Additional processes that may be important in decomposition, such as UV effects on microbes (Fig. 1D), leaching, fragmentation (Fig. 1E), or effects of UV on leaf chemistry/structure (Fig. 1G) are not illustrated. Recently senesced plant material is initially subject to high rates of photodegradation while it is standing dead (A). Limited microbial decomposition may occur on leaf surfaces at this time. While the majority of decomposition that occurs at this time is from photodegradation, the overall rates of decomposition remain low. When standing dead plant material falls to the soil surface (B), the soil–litter matrix develops (Figs. 1I and 6), gradually covering the litter (C). During this time the relative importance of photodegradation declines while microbial decomposition increases due to colonization opportunities, favorable microclimate, or abrasion afforded by the litter–soil matrix. Decomposition rates increase with microbial colonization, and overall rates of decomposition peak due to rapid losses of easily decomposable chemical constituents in the litter. Negative effects of UV on microbes are small and transient initially but increase over time in association with increased microbial biomass and activity until soil coverage negates these negative effects. Eventually nearly all the litter surface is cover by soil (D) and photodegradation accounts for a trivial portion of decomposition while microbial degradation prevails. The overall rate of decomposition is low as remaining litter is highly recalcitrant. From Barnes et al. (2012)

6 Summary and Conclusions

Over the past several decades, significant progress has been made in understanding the nature and importance of solar radiation in influencing litter decomposition in terrestrial ecosystems. Although a number of uncertainties remain, the information available indicates that solar UV (UV-B and UV-A) and PAR can have positive, negative, or minimal effects on decomposition depending on the balance of abiotic (photodegradation) and biotic (microbial) processes (Fig. 1D, E). In moisture-limited ecosystems (i.e., grasslands, savannas, and deserts), the net effects of sunlight/UV on decomposition are generally positive and photodegradation is now being considered as an important driver of decomposition that may account for the discrepancies between measurements and model predictions of decomposition rates. However, the majority of studies to date that have explored the effects of UV and PAR on decomposition in drylands have done so without explicitly considering soil–litter mixing. While such studies may reasonably ascertain decomposition of standing plant litter, their extrapolation to decomposition of detached plant litter on soil surfaces fails to take into account the formation of soil–litter complexes (Fig. 1I) that can strongly mediate or even negate these abiotic effects. Soil and litter movement and translocation are common in moisture-limited environments with low and patchy vegetation cover, and litter on the ground is frequently covered to varying degrees with soil and eventually buried. This mixing of soil and litter is associated with increased rates of decomposition. Although the mechanisms underlying these soil-mixing effects remain to be fully explored, it is likely that the formation of soil–litter–microbial complexes enhance microbial activity while simultaneously shielding litter from photodegradation. Thus, extrapolating the importance of photodegradation from measurements obtained in environments with either no soil or soil with restricted movement (e.g., litter boxes or glass jars) would overestimate the importance of photodegradation. Additional studies conducted under realistic field conditions are needed to fully explore how solar radiation and soil coverage interact through time to influence litter decomposition in dryland ecosystems characterized by soil movement and deposition. A greater understanding of the interactive effects of soil deposition and sunlight may aid, at least in part, in resolving the seemingly contradictory findings reported in photodegradation and soil deposition studies. Ongoing shifts in dryland life-form composition (e.g., from grass to shrub domination), driven by changes in land use and climate, will likely increase soil movement in these environments (Okin et al. 2009b). The role of soil deposition on litter decomposition in globally extensive dryland ecosystems may thus be magnified under future conditions.

Acknowledgments Financial support was provided by the US National Science Foundation (DEB 0815897 [Loyola University], DEB 0815808 [New Mexico State University], DEB 0816162 [University of Arizona], DEB 0814461 [University of Kentucky]), the Loyola University J.H. Mullahy Endowment for Environmental Biology, and the Jornada Basin LTER (DEB 0618210). Additional support was provided by the Arizona and Kentucky Agricultural Experiment Stations, and the University of Arizona – Universidad Nacional Autonoma de Mexico Drylands Research Consortium (#15), and US National Science Foundation (EAR 0724958 and 1331408 [University of Arizona]). We thank Jason P. Field, Daniel B. Hewins, Dean Keller, Darin J. Law, Hanna Lee, Eva Levi, Cianna Logie, Rachel Power, Katie Predick, Theresa Melhem, and Lee Chedister for related research and discussions.

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