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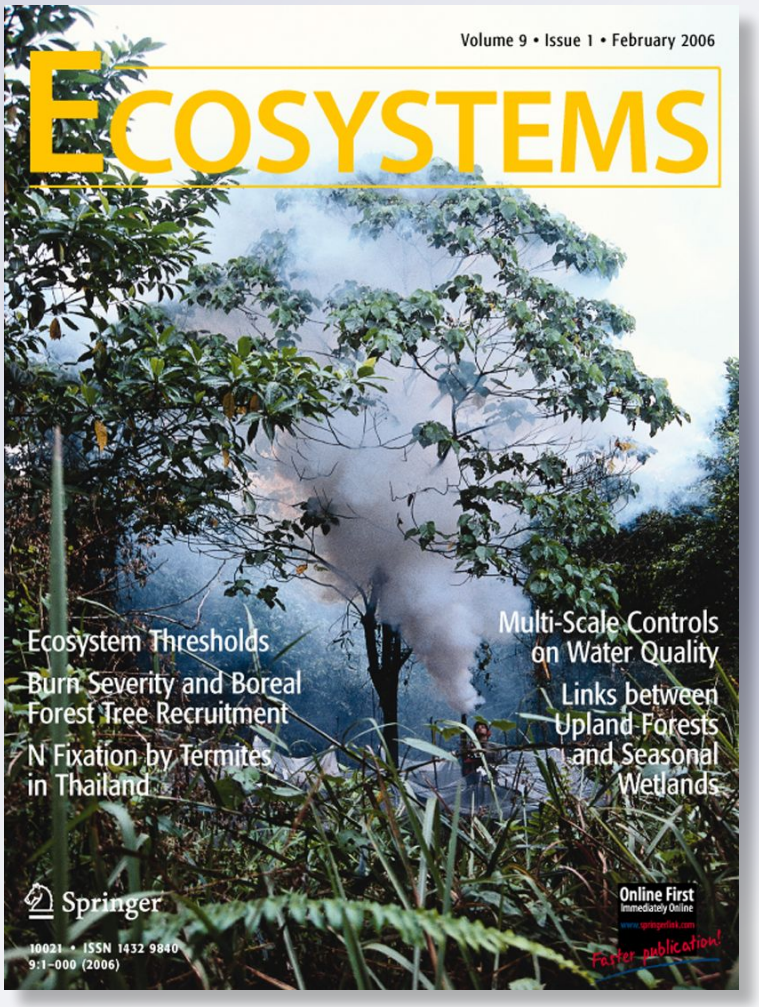

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Soil Coverage Reduces Photodegradation and Promotes the Development of Soil-Microbial Films on Dryland Leaf Litter

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Abstract

Litter decomposition is a central focus of ecosystem science because of its importance to biogeochemical pools and cycling, but predicting dryland decomposition dynamics is problematic. Some studies indicate photodegradation by ultraviolet (UV) radiation can be a significant driver of dryland decomposition, whereas others suggest soil–litter mixing controls decomposition. To test the influence of soil coverage on UV photodegradation of litter, we conducted a controlled environment experiment with shrub (*Prosopis velutina*) leaf litter experiencing two UV levels and three levels of coverage with dry sterile soil. Under these conditions, decomposition over 224 days was enhanced by UV, but increasing soil coverage strongly and linearly diminished these effects. In a complementary study, we placed *P. glandulosa* leaf litter in different habitats in the field and quantified litter surface coverage by soil films. After 180 days, nearly half of the surface area of litter placed under shrub canopies was covered by a tightly adhering film composed of soil particles and fungal hyphae; coverage was less in grassy zones between shrubs. We propose a conceptual model for the shifting importance of photodegradation and microbial decomposition over time, and conclude that (1) soil deposition can ameliorate the direct effects of UV photodegradation in drylands and (2) predictions of C losses based solely on UV effects will overestimate the importance of this process in the C cycle. An improved understanding of how development of the soil–litter matrix mediates the shift from abiotic (photodegradation) to biotic (microbial) drivers is necessary to predict how ongoing changes in land cover and climate will influence biogeochemistry in globally extensive drylands.

Key words: carbon cycle; decomposition; dryland; mesquite; *Prosopis*; photodegradation; soil erosion; soil–litter mixing; ultraviolet radiation.

Introduction

Decomposition of organic material is a crucial component of global biogeochemical cycles that influences soil fertility, the fate, and residence times of carbon and nutrients in organic matter

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pools, and ultimately plant community composition and production (Hobbie 1992; Wardle and others 1998). The prevailing drivers of litter decomposition are traditionally viewed as a combination of abiotic (for example, temperature, moisture) and biotic (for example, litter quality) factors that interact to mediate the community composition and metabolic activity of decomposers (fungi, bacteria, and invertebrates). This traditional view has proven successful in broadly explaining decomposition rates in mesic ecosystems, wherein regional/global patterns are predicted by simple models based on climate parameters, such as actual evapotranspiration (Meentemeyer 1978; Couteaux and others 1995; Aerts 1997) and local dynamics are predicted by litter quality (Hobbie 1992). However, climate and litter quality models (Whitford and others 1981; Aerts 1997; Moorhead and others 1999; Parton and others 2007) typically under-predict decomposition rates in arid and semi-arid systems (hereafter ''drylands''). This disconnect suggests that controls for decomposition in drylands differ fundamentally from those for wetter systems and that unique drivers may be operating in drylands (Austin and others 2009; Throop and Archer 2009).

Recent studies have shown that sunlight and specifically solar ultraviolet radiation (UV; 280–400 nm) can be a significant driver of leaf litter decomposition in dryland ecosystems via the process of photodegradation, although the magnitudes and proposed mechanisms of this process are variable (Austin and Vivanco 2006; Gallo and others 2006; Brandt and others 2010). Photodegradation occurs via photochemical mineralization of photo-reactive compounds, such as lignin (Rozema and others 1997; Day and others 2007)—a major constituent of plant tissue—and/or the transformation of compounds that leads to enhanced solubility and leaching of dissolved organic matter (Anesio and others 1999; Gallo and others 2006). The latter process is thought to be particularly important in wetlands and aquatic ecosystems, whereas the former is viewed as the dominant mechanism of photodegradation in drylands (Zepp and others 2007; Brandt and others 2009). In a semi-arid Patagonian steppe, Austin and Vivanco (2006) found that modifying the solar radiation environment affected decomposition much more strongly than 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 ultraviolet-B radiation (UV-B; 280–320 nm). Similarly, a field litterbag experiment in the Sonoran Desert estimated that solar UV-B was responsible for 14–22% of leaf mass loss (Day and others 2007). Furthermore, an incubation study assessing drivers of CO_2 efflux from litter exposed to solar radiation suggested that UV-driven photodegradation in drylands could account for the liberation of 1–4 g C m^{-2} y^{-1} (Brandt and others 2009). However, not all investigators have found a significant effect of solar UV-B photodegradation on dryland litter decomposition (for example, Kirschbaum and others 2011) and there is evidence that UV-driven photodegradation may vary with litter quality (Uselman and others 2011).

Although, the climate and low and sparse vegetation cover of drylands can create an environment of high solar UV irradiances near ground level, these conditions also favor considerable soil movement via wind and water transport (Breshears and others 2003; Okin and others 2009), which can partially cover and eventually bury plant litter (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 adheres to leaf surfaces to form a film of soil and microbial products (Throop and Archer 2007, 2009). It has been well established that decomposition rates of buried litter exceed those of litter on the surface; however, the nature and dynamics of the soil–litter matrix soil film development and their combined influence on decomposition are largely unknown. In a semi-desert Arizona shrub savanna, the solar radiation environment was poorly correlated with decomposition of surface litter over a 2-year period; instead, decomposition was strongly correlated with levels of soil accumulation and hence the development of the soil–litter matrix (Throop and Archer 2007). The mechanisms driving this response have yet to be elucidated.

Soil coverage of litter could potentially influence decomposition by several mechanisms, with the net effect varying between positive and negative depending on conditions and the extent of coverage. It is likely that soil would serve as a vector for microbial colonization of litter and that it may buffer litter and resident microbes from high temperatures or desiccation that are common in drylands (Moorhead and Reynolds 1991). These effects could enhance decomposition by extending windows of opportunity for microbial activity following rainfall events (for example, Cable and others 2008). Coarse soil particles may also promote surface abrasion of litter and enhance the surface area available to microbial colonization, leaching, or fragmentation (Throop and Archer 2009; Uselman and others 2011). Many decomposer organisms

(bacteria and fungi) are negatively affected by UV (Moody and others 1999; Pancotto and others 2003) and soil coverage could shield these sensitive microbes from solar UV exposure. Finally, it is also likely that soil coverage of litter, either as an adhering soil film or as loose soil in the soil–litter matrix, could partially, and eventually fully shield litter from UV radiation and negate photodegradation effects. If this is the case, current estimates (Brandt and others 2009; Foereid and others 2011) may exaggerate the role of UV photodegradation on decomposition of detached litter. Thus, how solar UV radiation and soil coverage interact to influence decomposition in drylands is a potentially critical, but unexplored issue.

This study probes several facets of UV–soil interactions. Specifically, we conducted a laboratory experiment to isolate photodegradation from microbial decomposition and thereby explicitly test the hypothesis that soil coverage would negate photodegradation. In this experiment, we exposed shrub (velvet mesquite, *Prosopis velutina*) leaf litter from a semi-desert savanna in Arizona, USA to different levels of UV exposure and coverage by dry, sterile soil in a controlled environment. In a separate field experiment, we quantified the rates by which litter is covered by soil and characterized the soil film developing on exposed litter. For these studies, we deployed leaflets of honey mesquite (*P. glandulosa*) shrubs in a desert grassland in New Mexico, USA, and used microscopy to quantify changes in the nature and extent of soil–litter films over a 180-day period. Results from these complementary experiments and previous studies were then combined to develop a generalized conceptual model proposing how the relative importance of photodegradation and soil mixing-microbial effects on litter decomposition might change through time in dryland ecosystems.

Methods

Controlled Environment Study: Soil Cover Influence on Photodegradation

Soil and leaf litter were obtained from the Santa Rita Experimental Range (SRER), a 21,510-ha semi-desert savanna in SE Arizona, USA (31°47′36″N, 110°53′4″W; elevation ca. 800–1,400 m; mean annual temperature and precipitation = 18.9°C and 370 mm, respectively). The SRER includes a series of gently sloping alluvial fans with soils composed of Aridisols, Entisols, and Mollisols. Velvet mesquite (*P. velutina*) is the dominant woody species within the 990- to 1,200-m elevation range and a major contributor to the SRER litter pool. For this study, mesquite litter (initial C:N = 17; N = 2.7%) was collected during late autumn leaf drop by stripping senesced leaflets from trees and oven drying at 30°C (wet weights). Subsamples (n = 12) of this litter were subsequently oven dried at 60°C (dry weights) to construct fresh-dry mass conversions (r^2 = 0.99 for linear regression relating fresh weight to dry weight). Twelve leaflets (ca. 0.05 g) were placed in replicate open-top, shallow (14-mm depth), circular (64-mm diameter) stainless steel containers and arranged so that no overlap of leaflets occurred. Space limitations in the growth chamber where litter incubations took place necessitated the use of small litter containers and therefore relatively small quantities of litter per container.

Surface soils (0- to 2-cm depth) collected at the SRER from inter-shrub locations where organic content is low were hand mixed and passed through a 0.9-mm sieve to remove large soil particles, organic debris and further homogenize the soil. This soil was then oven dried (80°C) and autoclaved (24 h) before application on leaf litter. Litter was covered with a thin layer of soil by hand to achieve intermediate (51.1 ± 1.7%; hereafter ''moderate soil'') and near complete (94.4 ± 0.4%; hereafter ''high soil'') areal coverage of leaflets [quantified by image analysis (ImageJ v.1.37, National Institutes of Health, USA) of digital photographs of representative samples; n = 15–21/treatment]. A ''no soil'' treatment served as the control. To insure as uniform soil coverage as possible and to keep leaflets flat (that is, perpendicular to the light sources), no soil was placed beneath the litter in any of the treatments. The litter–soil mixtures were kept dry, as we sought to quantify photodegradation effects on decomposition under conditions of minimal microbial influences (Smith and others 2010).

Individual leaf litter–soil sample containers were randomly assigned to one of two UV treatments: UV-transparent film (clear cellulose diacetate, JCS Industries, La Mirada, California, USA; cutoff near 290 nm) or UV-absorbing film (UV-B + UV-A absorbing; clear Llumar film, CPFilms, Fieldale, Virginia, USA; cutoff near 390 nm). The films were suspended approximately 15 cm above litter–soil sample containers in a temperature-controlled (30/20°C day/night; RH = 36%) growth chamber (EGC Model M12, Chagrin Falls, Ohio, USA) equipped with HID [400-W metal halide; photosynthetic photon flux density (400–700 nm) = 2,000 μmol m^{-2} s^{-1}] and UV lamps [40-W UVB-313 fluorescent bulbs, Q-Panel, Cleveland, Ohio, USA; unweighted UV-B (280–320 nm) and UV-A

(320–390 nm) irradiances = 756 and 694 mW m^{-2}, respectively]. Spectral irradiance was measured with a double-monochromator UV/Vis spectroradiometer (Model 754, Optronic Laboratories, Orlando, Florida, USA) calibrated for wavelength accuracy (4-W fluorescent lamp at wavelengths 312.9 and 546.1 nm) and absolute responsiveness (200-W tungsten-halogen lamp traceable to a NIST standard), and weighted according to a generalized plant action spectrum (Caldwell 1971) to obtain a measure of biologically effective UV irradiance (UV-B_{BE} = 260 mW m^{-2}). The HID and UV lamps were on for 10.5 h day^{-1} and plastic film was replaced weekly to maintain average daily PAR, UV-A, and UV-B_{BE} doses of 76 mol m^{-2} d^{-1}, 27 kJ m^{-2} d^{-1}, and 8.5 kJ m^{-2} d^{-1}, respectively. The light environment in the chamber provided typical summer clear-sky daily UV-B doses observed at the SRER, approximately 13% higher daily PAR, but only 2% of ambient daily UV-A [P. Barnes and R. Scott, unpublished data from on-site measurements made with a quantum sensor (LI-190, LI-COR, Inc., Lincoln, Nebraska, USA) and broad-band UV sensors (UV-B1 and UV-A1, YES, Inc., Turners Falls, Massachusetts, USA)]. To account for any potential location effects within the chamber, samples and the corresponding treatment films were moved to alternate sides of the chamber when the film was replaced (weekly).

We assessed decomposition by harvesting a subset of the sample containers over time (8, 14, 28, 56, 112, and 224 days) and quantifying litter mass, C, and N content. Oven dry weights (60°C) were determined on litter following careful, light brushing of leaflets to remove soil. Subsamples of leaf material were ashed in a muffle furnace (550°C). Foliar ash content was statistically comparable among the three soil treatments, indicating near complete soil removal from leaf litter before weighing. Dried litter samples were ground to a fine powder (Model 8100 SPEX Mixer/Mill; Metuchen, New Jersey, USA) and C and N was determined for two replicates of each sample on an elemental analyzer (ECS 4010, Costech Analytical; Valencia, California, USA).

The experiment ran for 224 days and consisted of 216 sample containers [2 UV levels (+UV, −UV) × 3 soil coverage levels (none, moderate, and high) × 6 harvest dates × 6 reps/treatment]. Final harvest data were statistically analyzed using ANOVA for a factorial treatment arrangement in a completely randomized design (SAS JMP 8.0, Cary, North Carolina, USA). Pre-planned mean comparisons were made using protected LSD tests of arcsin-transformed data to improve data normality and homoscedasticity. Decomposition decay constants (k, y^{-1}) were estimated using linear regressions of ln-transformed mass loss data and compared statistically with Student's t tests using individual and pooled regression error terms.

Field Study: Soil Film Development

Soil film development was studied following the litterbag methods of Throop and Archer (2007). Naturally senescing honey mesquite (*Prosopis glandulosa*) leaflets were collected on Nov 18–20, 2009 in Las Cruces, New Mexico (initial C:N = 14; N = 3.3%). Damaged or discolored leaflets were discarded. Fiberglass mesh litterbags (10 × 10-cm bags of 16 × 18 size mesh; ~0.9 mm openings; New York Wire Co., Mount Wolf, Pennsylvania, USA) were filled with 2 g of air-dried (30°C for 5 days) leaflets. As the primary purpose of this experiment was to document soil film development resulting from soil deposition, litterbags were deployed on April 19, 2010, in the midst of the windy season, a time of significant soil movement and deposition (Wainwright 2006). Studies were conducted in a desert grassland site at the Jornada Experimental Range (JER), located approximately 25 km NE of Las Cruces, NM (32°33′N, 106°45′W; elevation ca. 1190 m; mean annual temperature and precipitation = 14.7°C and 245 mm, respectively). Vegetation at the site (JER Pasture 11) was a matrix of C_4 grasses (*Bouteloua eriopoda*, *Sporobolous* spp., and *Aristida* spp.) interspersed with small shrubs (*Prosopis glandulosa*, *Ephedra torreyana*, and *Yucca elata*). Soil orders are a mix of Aridisols and Entisols. Litterbags were arrayed in three experimental blocks, with each block comprised of 1 × 1-m plots that were representative of the three dominant land-cover classes (hereafter ''litterbag placements''): grass, shrub (*P. glandulosa*), and bare ground (n = 3 replicate plots/litterbag placement/block). One litterbag was collected from each plot (n = 27 plots) after 0, 30, and 180 days in the field (n = 81 litterbags). Following collection, litter was hand separated from soil that had accumulated in bags. Each leaflet was lightly hand dusted with a small brush to remove any soil not tightly affixed to the surface (that is, material not comprising the soil films).

Soil film development was assessed using stereo and scanning electron microscopy (SEM) on leaflets from a subset of litterbags. Soil film areal coverage of leaflets (27 per vegetation type) was quantified from micrographs obtained on a fluorescent stereo microscope system with 16.5:1 zoom optics and dynamic magnification (0.63× lens with 2.5× zoom on Leica M165 FC, with Leica DFC 310 FX camera,

Leica Microsystems, Wetzlar, Germany). Leaflet area in micrographs was visually classified as bare or covered by soil; and percent cover by soil was quantified using ImageJ v1.44 (National Institutes of Health, Washington, District of Columbia, USA). At each time period, micrographs were obtained for three haphazardly selected leaflets obtained from a litterbag from one set of placements for each of the three blocks (n = 27 leaflets from n = 9 litterbags). Soil film cover and composition on SEM micrographs (Hitachi S-3400N Type II, Hitachi High Technologies, Pleasanton, California, USA) were assessed qualitatively. Visually representative leaflets from each of the three collection times and vegetation placements were mounted onto aluminum stages and sputter coated with a thin layer of gold for 120 s (Desk IV, Denton Vacuum LLC., Moorestown, New Jersey, USA) to improve their electrical conductivity and emission of secondary electrons during SEM microanalysis.

Soil coverage on leaflets (%) at the 180 day collection was analyzed using the generalized linear model (GLM) procedure in SAS version 9.2 (SAS Institute, Cary, North Carolina, USA) with vegetation placement as a class and predictor variable. Post hoc means separation testing was conducted using Fisher's LSD.

Results

Controlled Environment Study: Soil Cover Influence on Photodegradation

Rates of decomposition in the controlled environment study (assessed by decay constants, k; determined from exponential decay models; r^2 = 0.49–0.82) were significantly higher in litter exposed to UV than in litter not exposed to UV, but only for leaves in the no soil and moderate soil coverage treatments (Figure 1; $P < 0.05$ for no and moderate soil; $P > 0.05$ for high soil cover; Student's t test of k values). After 224 days of UV exposure, leaf dry mass loss was greater in the +UV than in the −UV treatments when averaged over soil treatments ($F_{1,28} = 54.16$; $P < 0.0001$), but there was a significant UV × soil cover interaction ($F_{2,28} = 5.54$; $P < 0.01$). Specifically, there were significant differences in mass loss between +UV and −UV treatments in no soil and moderate soil cover treatments, but UV radiation had no effect on mass loss in the high soil cover treatment (Figure 2A). The general pattern of leaf C loss response to UV and soil coverage treatments was similar to that of mass loss (Figure 2B), whereas N loss response showed no consistent patterns or

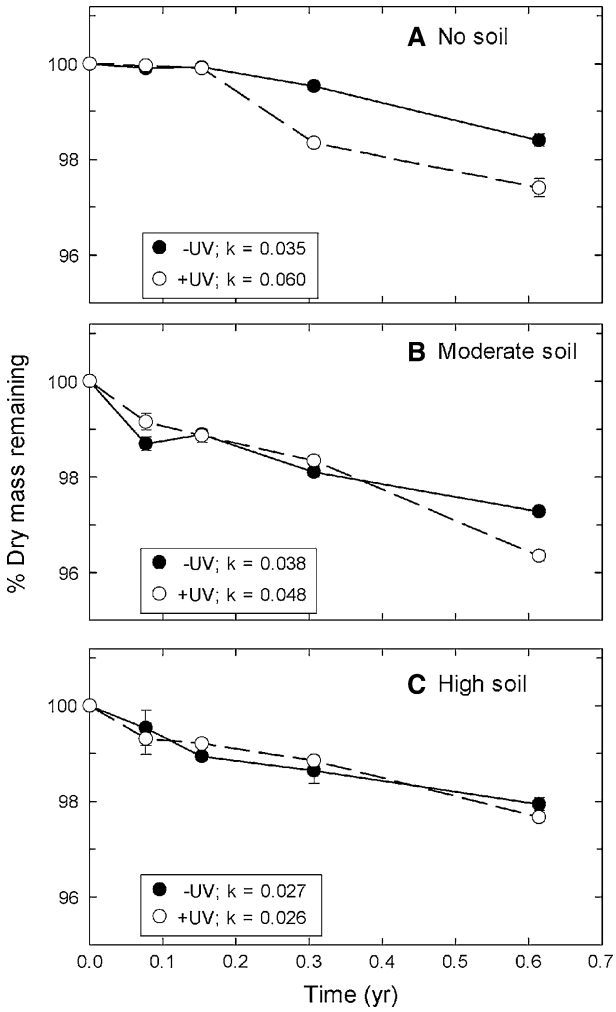

Figure 1. Effect of UV radiation and soil coverage on mass loss in velvet mesquite (*P. velutina*) leaf litter over 224 days in a temperature-controlled growth chamber. **A** Leaf litter with no soil coverage; **B** leaf litter with moderate (ca. 50%) soil coverage; **C** leaf litter with high (ca. 95%) soil coverage and exposed to UV (*open symbols* +UV) and no UV radiation (*closed symbols* −UV). UV exposures simulated daily effective UV-B (280–320 nm) doses for southeastern Arizona, USA, under clear-sky, summer conditions. Constants of decomposition (k, y^{-1}) were derived from regression models of ln(mass remaining) versus time, where k is the slope of this linear model. Data are mean ± SE (n = 5–6); error bars not visible are smaller than the size of the symbol. For clarity, data from 7 and 14-day time periods are not shown as mass losses and treatment differences were not detectable at these early harvest dates.

trends among treatments (data not shown). After 224 days, there were significant, negative linear relationships between percentage of leaf area covered by soil and the relative loss of both mass and C loss, with the relative effects of UV radiation being greater for C loss than mass loss (Figure 2C).

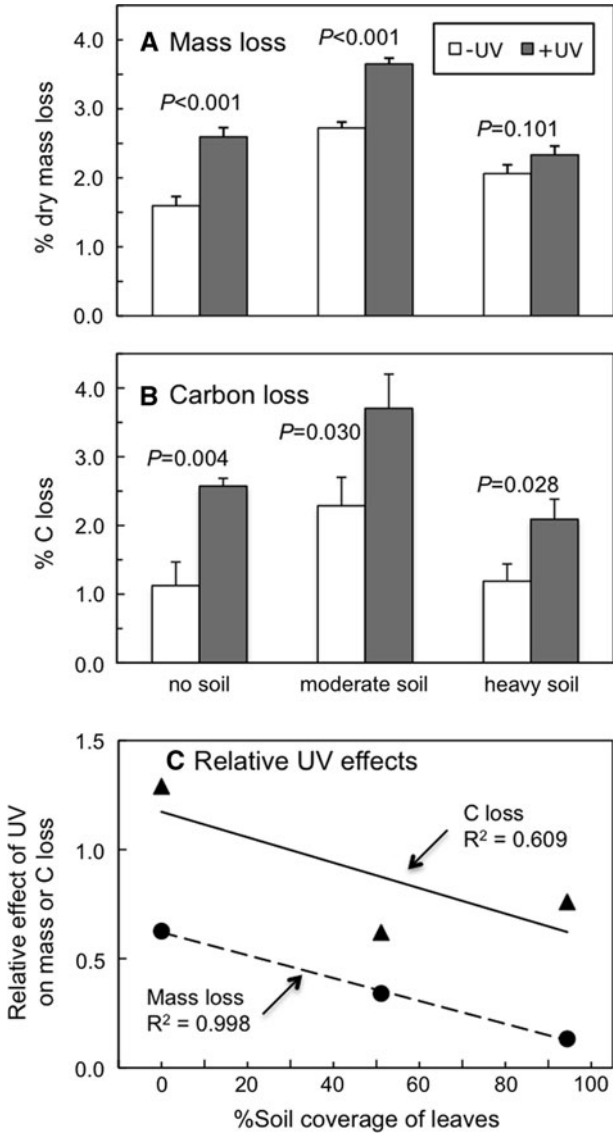

Figure 2. Effect of UV radiation and soil coverage on mass and carbon loss of velvet mesquite (*P. velutina*) leaf litter after 224 days in a temperature-controlled growth chamber with no soil, moderate soil, and high soil coverage. **A** Percent dry mass and **B** percent carbon loss under light regimes with (*solid bars* ''+UV'') and without (*open bars* ''−UV'') UV radiation. Data are mean ± SE (n = 5–6) with P values for mean comparisons of +UV/−UV from protected LSD tests. **C** Relative effect of UV radiation (treatment − control/control) on dry mass (*circles*) and carbon (C) (*triangles*) loss in relation to soil coverage. Estimated equations for linear regressions of mass and C loss versus soil coverage are: $Y_{mass} = -0.0052X + 0.6203$; $Y_C = -0.0058X + 1.1731$, where X = % leaf area covered by soil.

Field Study: Soil Film Development

No adhering soil films were observed on litter surfaces at the 0- and 30-day collections. However, areal coverage of litter at the 180-day collection was 47.3 ± 3.3% (mean ± SE across all vegetation placements) (Figure 3). There was greater soil film coverage on leaflets from bare and shrub plots than on those from grass plots (Figure 4; $F_{2,24} = 4.65$, $P < 0.05$). Visual analysis of SEM micrographs indicated that by day 180 soil films on leaflet surfaces consisted of large, contiguous patches that were several soil particles thick and contained fungal hyphae (Figure 3C, F, I).

Discussion

Photodegradation, the light-driven loss of organic matter via photochemical mineralization, has recently emerged as an overlooked driver that may help explain why models typically under-predict decomposition rates in drylands (Throop and Archer 2009; Austin 2011). The potential importance of photodegradation in biogeochemical cycling is underscored by recent data that suggest a measurable influence of UV radiation on landscape-level CO_2 flux rates (Rutledge and others 2010; but see also Foereid and others 2011). Our results support the idea that photodegradation can be a pathway for C and mass loss from leaf litter. However, this study is, to the best of our knowledge, the first to explicitly document the role of soil cover in mediating photodegradation, and suggests that studies conducted in isolation of soil–litter mixing may overestimate the importance of photodegradation as a driver of dryland decomposition and CO_2 efflux.

Rates and Mechanisms of Photodegradation

Although we detected a statistically significant effect of our UV treatment on mass loss, the overall rates of litter decomposition in this controlled environment study (k = 0.026–0.060 y^{-1}) were much lower than those typically reported in dryland field studies (for example, k = 0.55–0.73 y^{-1} for *P. velutina* in the Sonoran Desert; Throop and Archer 2007). It is likely that these low rates of mass loss were due, in large measure, to the particular environmental conditions of this laboratory experiment. Because we were primarily interested in exploring the physical shielding effects of soil on litter, we used sterilized soil and kept litter samples dry throughout the study. These conditions would have minimized microbial effects on decomposition and also eliminated any interactive effects of photodegradation with moisture that may further hasten mass loss (Gallo and others 2006). Under

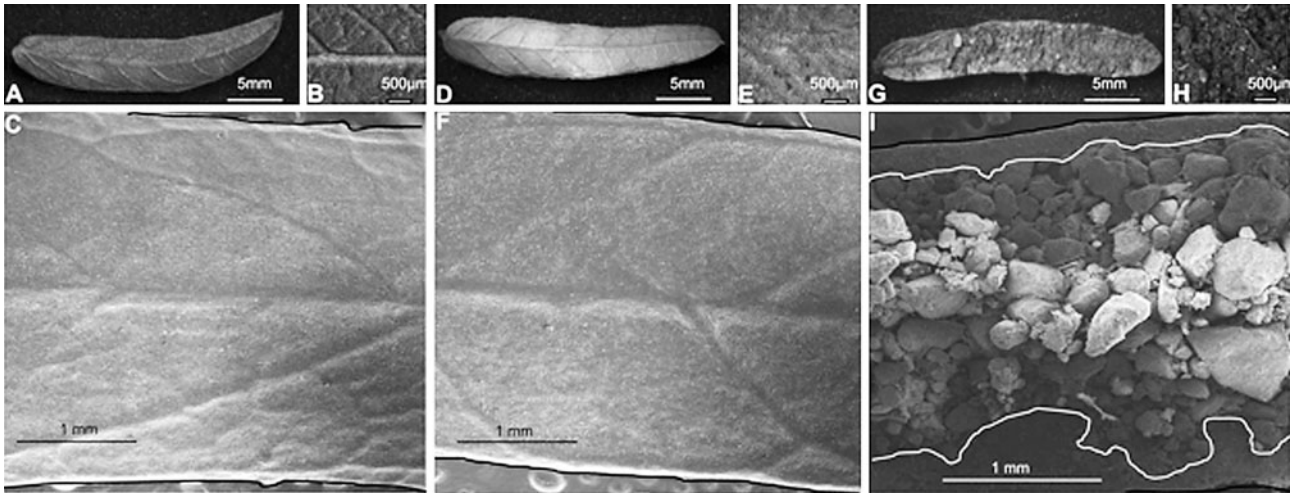

Figure 3. Development of soils films on litter over time (0, 30, and 180 days in **A–C**, **D–F**, and **G–I**, respectively) illustrated by low magnification (×1.6) stereo micrographs showing entire leaflets (**A**, **D**, **G**), high magnification (×3.2) stereo micrographs (**B**, **E**, **H**), and 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.

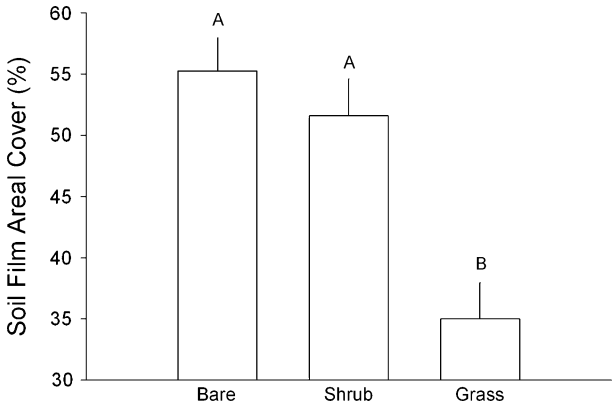

Figure 4. Mean percent areal coverage of leaflets by soil film after 180 days field exposure in different vegetation placements. *Error bars* are SE and *different letters* above *bars* indicate significant differences (Fisher's LSD; $\alpha = 0.05$; $N = 27$ per vegetation type).

moister conditions and in the presence of microbial activity, UV radiation may accelerate decomposition by partially breaking down compounds and facilitating subsequent biotic activity (that is, photo-priming effects; Foereid and others 2010). Photo-priming could further speed up decomposition if exposure to UV radiation makes litter more brittle and susceptible to fragmentation (for example, via raindrop impact). None of these photo-priming effects would have occurred in our controlled environment study. Also, whereas daily PAR and UV-B levels in the chamber were comparable with field conditions, UV-A was largely absent from these light sources and this could have reduced the overall effect of UV on photodegradation. Little is known of the precise spectral sensitivity (that is, action spectrum) of litter or lignin photodegradation (Andrady 1997), but both UV and visible radiation appear to drive this process; however, the shorter UV wavelengths (that is, UV-B; 280–320 nm) appear especially efficient under the natural solar spectrum (Austin and Vivanco 2006; Day and others 2007; Austin and Ballaré 2010). It is possible that the spectral differences between our filtered UV-B lamps and the sun may have contributed to unknown errors in UV dosimetry and thus lower UV exposure levels than would occur under field conditions (Flint and others 2003). It is worth noting, however, that Kirschbaum and others (2011) detected no UV effect on photodegradation in a similar lamp study even though their bulbs were unfiltered and thus their UV treatment included significant short wavelength, highly actinic UV-C radiation (<280 nm). Apart from these photodegradation effects, some mass loss due to C efflux from temperature-dependent decomposition may have also occurred, although the mechanism for this process is not yet known (Lee and others 2012). Decomposition rates from this thermal decomposition would have been lower in our study (day/night temperatures = 30/20°C) than in many dryland field situations where surface soil temperatures can routinely exceed 50°C.

Under field conditions, the overall net effect of UV will reflect a balance between positive (for example, photodegradation) and negative (for example, microbial inhibition) effects such that

decomposition may be increased, decreased, or unaffected by UV exposure depending on prevailing environmental conditions and litter chemistry (for example, Rozema and others 1997; Moody and others 2001; Pancotto and others 2005; Uselman and others 2011). Although some field studies have used methods to minimize the impact of biological processes (for example, biocide application, Austin and Vivanco 2006; bags elevated above the soil, Day and others 2007) or physical processes (for example, litter enclosed in glass jars or litterboxes; Austin and Vivanco 2006; Brandt and others 2009), these processes cannot be realistically isolated under field settings. Hence, laboratory experiments like ours can provide important, albeit limited, mechanistic insights into UV effects on decomposition. How solar UV and soil coverage will independently and interactively influence decomposition under field conditions is unknown, but is under investigation.

Although there remains some uncertainty about the precise mechanisms of photodegradation, available evidence suggests that many losses from photodegradation are gaseous, including CH_4 (McLeod and others 2008; Bloom and others 2010), CO and H_2 (Lee and others 2012), and N_2O (Foereid and others 2010). Along these lines, UV-driven photodegradation of litter has been identified as a potentially significant avenue of CO_2 emissions in dryland ecosystems (for example, Brandt and others 2009). Results from our experiment showed the relative effects of UV radiation to be much stronger for C loss than for mass loss with increasing soil coverage (Figure 2C), supporting the notion that photo-induced gaseous losses of carbon may drive early stages of foliar organic matter decomposition.

Soil Coverage Impacts on Photodegradation

The study here is the first to experimentally demonstrate that soil coverage can protect leaf litter from UV photodegradation, and our field results indicate that the soil coverage treatments used in the controlled environment study reflect realistic levels of soil coverage that occur for litter under natural field conditions. Soil had covered and mixed with leaves in field litterbags within 90 days (DBH, personal observation), but this loose soil in the soil–litter matrix was easily dislodged during litterbag collection and soil films were not yet evident on leaf surfaces (Figure 3D–F). This loose soil would be a rough analog to the loose soil applied in our controlled environment study with respect to physical shielding effects. The shielding effects of soil would presumably be magnified with the development of soil films (here defined as the mixture of soil particles with microbes and their exudates that adhere to the litter surface), which were well developed and clearly evident after 180 days in the field (Figure 3G–I). Unlike the loose soil, these adhering soil films would be more resistant to removal by rainfall and wind, and therefore constitute a relatively permanent UV barrier for litter. The differences in soil film coverage observed among the vegetation placements likely reflects local-scale differences in soil transport that are in turn affected by plant structure (Okin and Gillette 2001; Okin 2008). Although an analysis of the composition of these films was beyond the scope of this study, ocular assessment indicated that they were composed of inorganic and biological constituents. Fungal hyphae were clearly visible on SEM images, and microbial exudates presumably played a role in binding mineral particles to each other and to the leaf surface. The coverage of leaf material by fungi containing UV-absorbing pigments (melanins) could further function to attenuate UV penetration to the litter surface (Butler and Day 1998).

Based on the data presented here, together with observations from previous field studies (Throop and Archer 2007), we propose a generalized conceptual model for photodegradation-soil mixing effects in dryland decomposition. Over a continuum of soil coverage of litter from none (for example, standing dead) to partial (for example, recently detached) to full burial, the mechanisms driving decomposition are predicted to shift from strongly abiotic (photodegradation of standing dead) to strongly biotic (microbial degradation of buried litter), with intermediate conditions consisting of a combination of these processes depending on the extent of development of the soil–litter matrix, its biogeochemical constituency (for example, litter quality, soil mineral composition, and organic matter content of soil), and the prevailing moisture/temperature conditions (Figure 5). As the relative importance of photodegradation and microbial decomposition shift in contrast with each other 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.

All studies to date that have explored the effects of UV on decomposition in drylands have done so without explicitly considering soil–litter mixing. Although such studies may reasonably ascertain

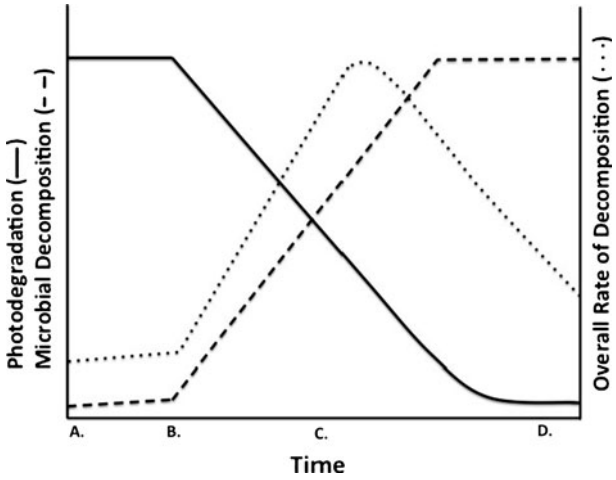

Figure 5. Conceptual model of dryland decomposition dynamics following leaf senescence, illustrating the shifting relative importance of photodegradation and microbial processes through time and consequent changes in the overall rate of decomposition. Additional processes that may be important in decomposition, such as leaching, fragmentation, or detrimental effects of UV on decomposer organisms, are not illustrated. Recently senesced plant material is initially subjected to high rates of photodegradation while it is standing dead (*A*). Limited microbial decomposition may occur on leaf surfaces at this time. Although, 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, 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. 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 composed of compounds highly recalcitrant to decomposition.

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. Soil movement and translocation are common in moisture-limited environments with low vegetation cover, and litter on the ground is frequently covered to varying degrees with soil and eventually buried. Our results suggest soil deposition on litter attenuates UV photodegradation effects, the extent varying with the degree of soil coverage. Studies extrapolating the importance of photodegradation from measurements obtained in soil-free environments, such as litter boxes or glass jars would therefore overestimate its importance. This study may aid, at least in part, in resolving the apparent contradictory findings reported in UV photodegradation and soil deposition studies. For example, in the Sonoran Desert, soil accumulation rather than radiant energy environment was the most significant positive driver of litter decomposition across a broad range of plant canopy covers, and hence solar radiation and temperature regimes (Throop and Archer 2007). Thus, although photodegradation might have been important in the early stages of decomposition, its effects were negated by soil cover of litter over the 1-year course of the study.

Conclusions

Additional studies conducted under realistic field conditions are needed to fully explore how UV radiation and soil coverage interact to influence litter decomposition in dryland ecosystems characterized by soil movement and deposition. In the meantime, this study demonstrates that soil coverage can ameliorate UV photodegradation of litter and suggests caution in estimating and extrapolating the effects of UV radiation on dryland decomposition, CO_2 efflux, and carbon storage in isolation of this mediating factor. Ongoing shifts in dryland life-form composition (for example, from grass to shrub domination), driven by changes in land use and climate, will likely increase soil movement in these environments (Okin and others 2009). The role of soil deposition on litter decomposition in globally extensive dryland ecosystems may thus be magnified under future conditions.

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