Journal of Arid Environments 160 (2019) 1–10

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Nutrient dynamics during photodegradation of plant litter in the Sonoran Desert

Becky A. Ball[a,*,1], Maximilian P. Christman[b,1], Sharon J. Hall[c]

[a] School of Mathematical and Natural Sciences, Arizona State University at the West Campus, Glendale, AZ, USA
[b] School of Sustainability, Arizona State University, Tempe, AZ, USA
[c] School of Life Sciences, Arizona State University, Tempe, AZ, USA

ARTICLE INFO

Keywords:
Photodegradation
Decomposition
N deposition
Sonoran desert
Nutrient dynamics
Ambrosia deltoidea

ABSTRACT

Arid and semi-arid ecosystems are experiencing increased rates of atmospheric nitrogen (N) deposition, but the ecological fates of excess nutrients in aridlands are unclear given the few studies conducted in deserts compared to mesic ecosystems. Altered decomposition resulting from increased N availability may not be important in arid ecosystems with significant photodegradation, which may be less influenced by nutrient content than biologically-mediated decomposition. Additionally, nutrient dynamics during decomposition have been studied almost exclusively in mesic ecosystems. To understand the potential impacts of N deposition on mass loss and chemical dynamics during aridland decomposition, we assessed N and phosphorus (P) dynamics of decomposing litter in a long-term N + P enrichment experiment in both urban (+N deposition) and outlying areas (-N deposition) of the Sonoran Desert. Litter was decomposed with and without UV radiation for 9 months, measuring mass loss, litter chemistry, and bacterial biomass. UV radiation significantly accelerated mass loss and altered N and P dynamics, and there was an impact of the urban environment and experimental fertilization on nutrient dynamics. Overall, these patterns suggest that the aridland urban environment, where rates of N deposition are elevated, alters nutrient dynamics during decomposition but not the fraction of litter lost to photodegradation.

1. Introduction

Arid and semi-arid ecosystems are among the fastest urbanizing areas globally (UNDP, 2007). Like in other ecosystems, atmospheric N deposition to drylands is increasing due to anthropogenic combustion and agricultural sources, more than doubling natural background N inputs with 5–30 kg N ha^{-1} yr^{-1} arriving to some areas of the southwestern U.S. (Fenn et al., 2003; Dentener et al., 2006; Sobota et al., 2013). In the Sonoran Desert, the Phoenix metropolitan area is home to 4.6 million people and is one of the largest and fastest-growing metropolitan areas in the U.S (Koebler, 2011; U.S. Census Bureau, 2015). As such, N deposition is ~20% higher within the city core (7.2 kg ha^{-1} yr^{-1}) than outside of the city (Lohse et al., 2008; Cook, 2014), and within the high end of the N critical load for arid ecosystems (3–8 kg ha^{-1} yr^{-1})(Allen and Gelser, 2011).

The excess N from deposition can influence plant uptake, and therefore growth and litter chemistry. In mesic systems, N deposition increases both foliar N content and plant growth rates (e.g., Aber et al., 1995; Magill et al., 2004), but in forests, high soil N can cause a reduction in growth if it displaces other critical nutrients via cation leaching (Driscoll et al., 2001; Adams, 2003) or causes a shift in the arbuscular mycorrhizal community associated with plant roots (Egerton-Warburton and Allen, 2000; Van Diepen et al., 2007). Furthermore, as biotic N uptake becomes 'N saturated', excess N inputs can decrease plant diversity and increase N losses as gases or through soil water (Pardo et al., 2011). In contrast, arid and semi-arid ecosystems are water limited during many times of the year and thus may not respond to N enrichment in the same way as mesic forests and grasslands (Chapin, 1980; Hall et al., 2011; Sinsabaugh et al., 2015). Although only a handful of studies have explored long-term impacts of N enrichment in deserts (Allen and Gelser, 2011; Hall et al., 2011; Ladwig et al., 2012), these and other experiments show that nutrient enrichment increases foliar nutrient content but not production in perennial shrubs and increases production of herbaceous plants (annual grasses and forbs) only during wet seasons when water is less limiting (e.g., Padgett and Allen, 1999; Vourlitis et al., 2009; Hall et al., 2011).

* Corresponding author. School of Mathematical and Natural Sciences, Arizona State University at the West Campus, 1407 W. Thunderbird Rd., Glendale, AZ, 85306, USA.
E-mail address: becky.ball@asu.edu (B.A. Ball).
[1] This manuscript is co-led by undergraduate student M. Christman and faculty mentor B. Ball.

https://doi.org/10.1016/j.jaridenv.2018.09.004
Received 5 January 2018; Received in revised form 25 May 2018; Accepted 11 September 2018
Available online 22 September 2018
0140-1963/

To date, no studies have explored the impacts of long-term nutrient enrichment on litter nutrient dynamics during decomposition in arid ecosystems. Nutrient dynamics during decay include the initial immobilization of nutrients by microorganisms and eventual release from plant litter as it is decomposed (Blair et al., 1992; Mooshammer et al., 2012). Their biological activity may be limited by water, N, and occasionally phosphorus (P) availability in the litter and surrounding soil (Ostertag and Hobbie, 1999; Hobbie and Vitousek, 2000; Bi et al., 2012), suggesting excess nutrient availability would stimulate nutrient dynamics. However, water availability can limit biologically-driven decomposition in aridlands (Yahdjian et al., 2006; Brandt et al., 2007). Additionally, abiotic decomposition by ultraviolet (UV) radiation (photodegradation) is a significant pathway of organic matter turnover in aridlands, accounting for 33–60% of litter mass loss and up to 14% of total NPP in arid areas (Austin and Vivanco, 2006; Brandt et al., 2007; Foereid et al., 2011; King et al., 2012), at least when soil coverage does not block UV (Barnes et al., 2012). Recent work explores carbon (C) mineralization during this abiotic process (e.g., Brandt et al., 2009; Lee et al., 2012), but less is known about the rate or form of nutrient release during photodegradation. Research from wetter ecosystems suggests that N release varies with UV exposure, depending upon the stage of decomposition and possibly decomposer organisms' sensitivity to heat and UV (Henry et al., 2008; Smith et al., 2010; Song et al., 2014). Only a couple of photodegradation studies in steppe ecosystems have tracked N through time, showing either no effect of UV on N dynamics or a decrease in N immobilization with UV radiation with no change in mineralization (Brandt et al., 2007; Wang et al., 2015). Rates of photodegradation may not be limited by litter nutrient content as could be the case during biotic decomposition (Berg and Matzner, 1997; Hobbie and Vitousek, 2000; Bi et al., 2012), suggesting that this abiotic pathway may be resistant to excess N. Furthermore, biologically recalcitrant compounds such as lignin significantly limit litter degradation in mesic ecosystems (e.g., Melillo et al., 1982; McClaugherty and Berg, 1987; Taylor et al., 1989), but lignin absorbs and is broken down by UV radiation (Day et al., 2007; Austin and Ballare, 2010). The breakdown of lignin during photodegradation into less complex C compounds may further stimulate biological degradation (Wang et al., 2015; Austin et al., 2016).

To understand the potential impacts of nutrient enrichment on decomposition in aridlands, we assessed N and P dynamics of decomposing litter from native shrubs in a long-term nutrient enrichment experiment in both urban and outlying areas of the northern Sonoran Desert. Given that existing knowledge attributes photodegradation mass loss primarily to C gas emissions, we hypothesized that mass loss and lignin degradation would increase with the presence of UV radiation, but litter N and P dynamics will not be impacted by UV radiation. Instead, we expected that nutrient dynamics would follow patterns consistent with biologically-driven decomposition in other ecosystems, where nutrient-enriched litter (from fertilized plots and desert remnants within the city) will contain higher nutrient content and faster rates of litter N loss during decomposition, with lower levels of immobilization early in decay (e.g., Aber et al., 1990; Ball et al., 2009a) than non-enriched litter (from control plots and outlying desert). Further, we hypothesized that nutrient-enriched litter will degrade faster, with greater mass loss and lignin loss, than non-enriched litter because growth of decomposer organisms will be faster when they are released from nutrient limitation on litter with lower nutrient ratios (e.g., Melillo et al., 1982; McClaugherty and Berg, 1987).

2. Materials and methods

2.1. Study site and experimental design

We measured decomposition in 10 native Sonoran Desert sites in central Arizona, located within the 6400 km^2 boundaries of the Central Arizona-Phoenix Long-Term Ecological Research (CAP-LTER) project (Fig. 1). Soils at these sites are Aridisols, with Typic Haplargids characterizing the city core and Typic Haplargids and Typic Calciargids to the east of the city. Mean daily maximum and minimum temperatures in this region are 30 °C and 15 °C, respectively. Annual average rainfall is 193 mm, distributed bimodally through the year, with 35% as convective monsoon storms from June to September and 65% from Pacific frontal storms between November and March. Since 2005, the CAP LTER has monitored N deposition at these sites, showing levels of 8.2 kg N ha^{-1} yr^{-1} inside the city core, 22% higher than the 6.7 kg N ha^{-1} yr^{-1} to the east of the city (Cook, 2014). Concurrent with these measurements, CAP LTER has assessed ecosystem responses to long-term N and P enrichment at these sites in a manipulative field fertilization experiment (60 kg N ha^{-1} yr^{-1} as solid NH_4NO_3 and 120 kg P ha^{-1} yr^{-1} as triple superphosphate added alone and in combination to 20 m × 20 m plots in each site)(see Hall et al., 2011 for full details).

During the autumn of 2012, we collected litter from individuals of triangle-leaf bursage (*Ambrosia deltoidea*), a dominant, drought-deciduous herbaceous shrub that has been shown to accumulate excess N and P in these plots (Hall et al., 2011). *Ambrosia deltoidea* litter was collected from twenty or more individuals at each of the 5 urban sites inside the city (totaling 100 + shrubs), from both the N + P fertilization plots and unfertilized ('control') areas, and pooled by treatment to create one homogenized bag of each treatment. Similarly, litter was collected and homogenized within each of the N + P fertilized and control treatments in the 5 non-urban, outlying desert sites. Initial chemical properties of the four treatments are reported in Table 1. Collected litter from each region (inside [urban] and outside of city [outlying], as defined by their position relative to the city) was dried, weighed, and placed in litterbags (see below) and then set out on the soil surface in one location within the region from which the litter originated: inside the city (SME; Fig. 1) and outside the city (SRR). In other words, we decomposed plant litter in the region in which it was grown (inside or outside the city), allowing us to understand the influence of the urban location on both litter production and decomposition environment while avoiding artifacts that may result from decomposer communities working on non-native litter. The field sites SME and SRR were selected because they have comparable 10-year average annual rainfall (Hall et al., 2011), though rainfall during 2013 when the experiment was conducted differed between the two locations (SME received 130 mm while SRR received 185 mm).

2.2. Laboratory and field methods

We decomposed *A. deltoidea* litter in litterbags composed of UV transparent plastic film (ACLAR 33C Film) and UV opaque plastic film (CON-TROL-CURE UV Blocking Films, UV Process Supply Inc.) in each of the two desert locations (inside and outside the city). These plastics are similar to those used by Day et al. (2007) and Austin and Vivanco (2006) for the same purpose. Following (Day et al., 2007), the plastic film was shaped into 10 cm × 10 cm pouches, sealed with UV-transparent tape on all sides, and ~2 mm holes were drilled through the film on both sides, in a grid pattern with approx. 1 cm between holes, to allow water movement. Three grams of *A. deltoidea* litter from both the N + P and control treatments were placed into 16 replicate UV-transparent and UV-opaque litterbags (2 locations x 2 fertilization treatments x 2 bag types = 8 treatments x 16 replicate bags each = 128 litterbags). All litterbags were placed in the field in late December 2012 in non-fertilized areas on level ground, in direct sunlight away from plants. Fertilized litter was not decomposed in fertilized plots to avoid impacting biogeochemical pools and fluxes in the long-term experimental plots, and the fertilized and control litter were decomposed in the same soil environment within its originating part of the city. Litterbags were arranged in four replicate blocks, with bags laid out randomly in grids with approximately 30 cm of spacing in between them to avoid cross-contamination. Table 1 presents initial litter chemistry for each treatment. Four replicates of each of the 8 treatments were

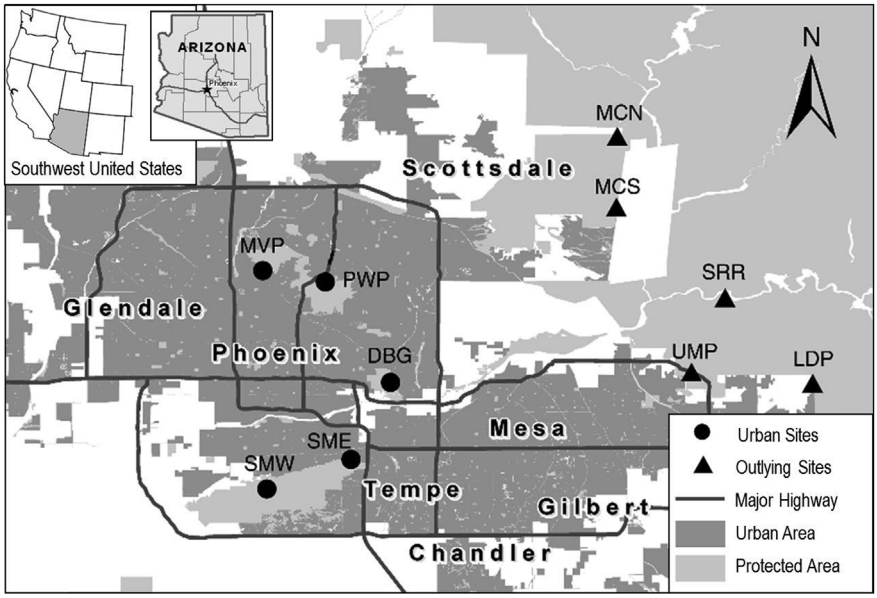


Fig. 1. Map of study sites within the Phoenix metropolitan area (central AZ; 'Urban') and surrounding the city ('Outlying'). Urban sites: Mountain View Park (MVP); Piestewa Peak (PWP); Desert Botanical Garden (DBG); South Mountain Park, east side (SME); South Mountain Park, west side (SMW). Outlying desert sites: McDowell Mountain Regional Park, north side (MCN); McDowell Mountain Park, south side (MCS); Salt River Recreation Area (SRR); Usery Mountain Regional Park (UMP); Lost Dutchman State Park (LDP).

Table 1
Initial chemical properties for *Ambrosia deltoidea* litter collected from control and N + P fertilized plots, both inside and outside the Phoenix city core.

Location	%N	%P	C:N:P	%Lignin	% Cellulose	% Hemicellulose
Inside city						
Control	2.80	0.10	1:17:473	5.07	7.08	5.00
Fertilized	2.75	0.12	1:17:387	8.76	7.95	5.91
Outside city						
Control	2.36	0.07	1:21:689	8.28	11.19	6.90
Fertilized	2.46	0.11	1:25:436	8.54	8.69	7.88

retrieved after 10 weeks in early February, 20 weeks in late April, 30 weeks in early July, and 40 weeks in late September 2013.

2.3. Sample analyses

Immediately following litter bag collection from the field, approximately five leaves from each litter sample were put into 10 ml of a 4% formalin solution to preserve the bacteria present on the leaves. The remaining litter samples were air-dried for at least a week. Once dry, accumulated sediment was scraped off of the litter, and the sediment and litter (now mostly sediment-free) were weighed separately. Five leaves were weighed to estimate the mass of leaves preserved in formalin, then the entire litter sample was ground using a ball mill (Spex-Certiprep 8000D, Metuchen, New Jersey, USA). Ash-free dry mass (AFDM) was determined by incinerating a subsample of the ground litter at 600 °C in a muffle oven for 3 h, and mass loss calculated as proportion of initial AFDM remaining. The difference in mass loss between the UV opaque and transparent bags for any given Location × Fertilization treatment is assumed to be the result of photodegradation, which can be used to calculate what proportion of total mass loss in the UV-transparent bags is attributed to photodegradation.

Litter %C and %N were measured from a 3 mg subsample of ground litter on a CHN elemental analyzer (Perkin Elmer PE2400, Waltham, Massachusetts, USA). Litter %P was measured using nitric acid digestion. Briefly, 100 mg of ground sample was inserted into a combustion safe tube with 10 ml of 70% nitric acid. Samples sat in the acid for 15 min followed by microwaving at 175 °C for 20 min using a microwave digestion system (MARS 5 Microwave Reaction System, Matthews, North Carolina, USA). Once digested, the sample tubes were slowly opened in the fume hood, then poured into containment vials and analyzed for P content on an Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES, Thermo iCAP6300, Hudson, New Hampshire, USA). Nutrient ratios (C:N, C:P, N:P) were calculated using these data. Litter lignin was measured using the sequential acid digestion method (Van Soest, 1994). Briefly, 0.5 g of ground sample was placed into fiber filter bags and then digested in a fiber analyzer (ANKOM A200 Fiber Analyzer, Macedon, New York, USA) using neutral detergent, followed by acid detergent, then 72% sulfuric acid to identify cellulose, hemicellulose, and lignin, respectively. Filter bags were then ashed at 500 °C for 5.5 h to correct the lignin content for non-organic recalcitrant compounds.

Following Ball et al. (2009b) and Ball and Virigina (2014), litter bacterial cell counts were conducted by sonicating the formalin-preserved leaves for 30 min in an ice water bath. After sonication, 2 ml of the formalin solution was added to an ethanol-rinsed filtration manifold, stained with 500 µl 25 × SYBR Green for 15 min, then vacuum filtered through a 0.2 µm black polycarbonate filter (supported by a 0.45 µm backing filter). The column was rinsed with 1 ml sterilized deionized H_2O, again vacuum filtered, then the filter slide mounted and stored in the refrigerator in the dark until counted. Cells were enumerated using epifluorescent microscopy (1000 ×) by counting ten random fields and categorizing cells into shape (coccoid or rod) and size class (small and large). Cell biovolumes were calculated using equations for the geometric shape size classes (Wetzel and Likens, 2000) based on diameter measurements using a stage micrometer and expressed as biovolume per g AFDM. Size and shape are necessary to calculate biovolume, and are then summed into a total biovolume for each sample. Since previous conversion factors from biovolume to biomass have not been established for this site, data are presented as biovolume.

2.4. Data analyses

An Analysis of Covariance (ANCOVA) was used to determine how litter mass loss and chemical properties differed with treatment over the course of 40 weeks, with time as a continuous factor (following e.g., Ball et al., 2009c; Ball et al., 2018). Essentially, Time was treated as a continuous, numerical explanatory variable in the statistical model with the three categorical main effects: location (inside or outside the city), nutrient fertilization (N + P or control), and presence of UV radiation (UV-opaque or transparent litterbags). All possible interactions of Location, Fertilization, UV, and Time were also included in the model. Statistical analyses were conducted in R 2.15.1 (The R Foundation).

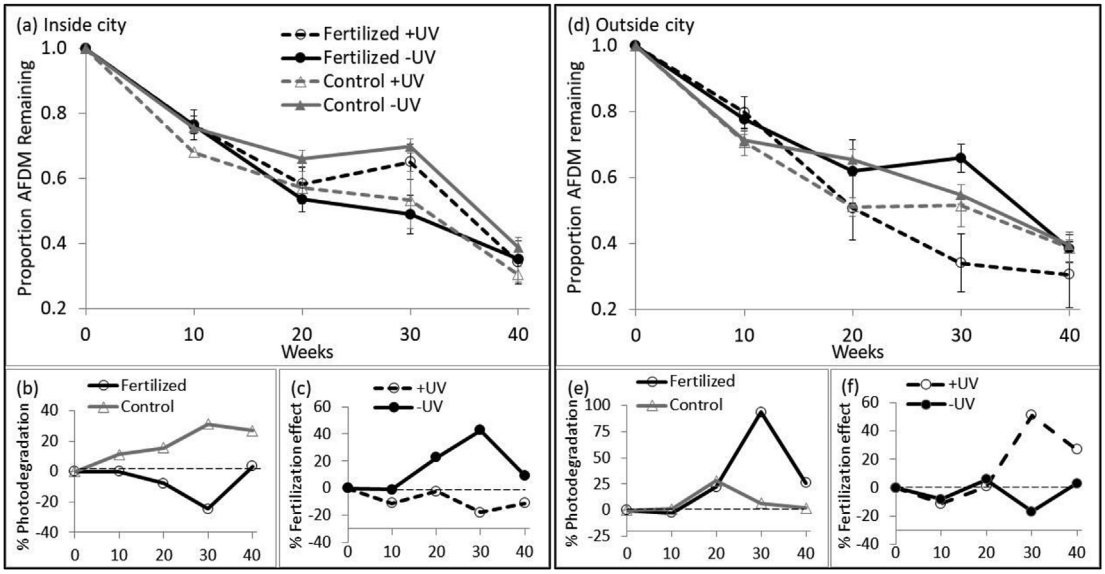


Fig. 2. Litter properties during decomposition of N + P fertilized or control *A. deltoidea* litter over the course of 40 weeks of degradation (December through September) in either -UV or +UV litterbags, both inside the city (left column) and outside (right column). Top panels (a,d) depict proportion of ash-free dry mass (AFDM) remaining. Data points are average (n = 4) ± SE. Bottom panels revisualize the same data to highlight (b,e) the percent of decomposition that is the result of photodegradation, calculated as the percent difference in mass loss between the average from the +UV and average from the –UV litterbags in both control and fertilized litter; and (c,f) the fertilization effect size on decomposition, calculated as the percent difference in mass loss between the average fertilized and average control litter from both the +UV and –UV litterbags. Positive values reflect increased mass loss with photodegradation or fertilization.

3. Results

Litter mass loss during decomposition in the Sonoran Desert was affected by nutrient enrichment, location relative to the city, and UV radiation in complex ways (Fig. 2a,d; significant Location × UV*Fertilization interaction for AFDM remaining in Table 2). As expected, UV radiation significantly affected litter mass loss, but the effect of UV was moderated by location (urban vs. outlying) and fertilization (N + P fertilized vs. control). UV radiation increased mass loss in control litter more strongly inside than outside the city, but UV radiation increased mass loss in nutrient-fertilized litter only outside of the city (Fig. 2b,e). At the end of the 40-week study, photodegradation accounted for ~2%–27% of total mass loss across the treatments, though it ranges throughout the study from −25% to 93%, depending upon treatment and stage of decay (Fig. 2b,e). Contrary to our hypotheses, nutrient enrichment (both in terms of urban location or fertilization) did not result in an ecologically significant increase the rate of decomposition overall at the end of the 9 month period, except perhaps for + UV litter outside the city (Fig. 2c,f).

Contrary to our prediction, litter N and P dynamics were influenced by UV radiation, but this effect, too, was moderated by location in the city, with P dynamics further influenced by fertilization (Fig. 3; significant Location × UV interaction for N content and Location × UV*Fertilization for P content in Table 2). Initially (at time 0), fertilized and city core litter contained higher levels of %P than control or outlying litter, respectively (Table 1). In the outlying location, P was immobilized over the first 10–20 weeks, whereas inside the city, where initial %P was higher, P immobilization is minimal and only in the control -UV treatment (Fig. 3a and b). In both the urban and outlying areas, fertilization reduced immobilization compared to control litter of the same location and UV treatment. UV radiation also reduced immobilization from the litterbags, at least temporarily, compared to the -UV litter. %N was initially higher in litter from inside the city than outside (Table 1). Inside the city, litter N decreased over time with very

Table 2
Significance results (p-values) of the Analysis of Covariance investigating the effects of Location (two levels: inside or outside the city), UV presence (two levels: +UV in UV-transparent litterbags or –UV in UV-opaque litterbags), Fertilization (two levels: N + P fertilized or control), and sampling Time (0–40 weeks, continuous factor) on litter properties during decomposition. Significant p-values (α = 0.05) indicated in bold. AFDM = Ash-free dry mass. Because bacterial biovolume was only measured at the end, Time was not included in the model. Associated F-values and degrees of freedom (df) are listed in Appendix B.

	AFDM remaining	P	N	Lignin	Bacterial biovolume
Location	0.294	**< 0.001**	**< 0.001**	**< 0.001**	**0.002**
UV	**0.003**	**< 0.001**	**0.002**	**0.019**	0.436
Fertilization	0.580	**0.003**	**0.042**	**< 0.001**	0.641
Time	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	–
Location × UV	0.087	0.221	**0.011**	0.990	0.451
Location × Fertilization	0.639	0.231	0.100	**< 0.001**	**0.006**
UV × Fertilization	0.574	0.377	0.545	0.165	0.309
Location × Time	0.990	0.285	0.882	0.559	–
UV × Time	0.573	0.966	0.345	0.651	–
Fertilization × Time	0.206	0.526	0.392	0.591	–
Location × UV × Fert	**0.009**	**0.013**	0.059	**0.004**	**0.013**
Location × UV × Time	0.502	0.618	0.744	0.598	–
Location × Fert × Time	0.510	0.903	0.773	0.173	–
UV × Fert × Time	0.559	0.817	0.978	0.895	–
Location × UV × Fert × Time	0.349	0.177	0.151	0.890	–

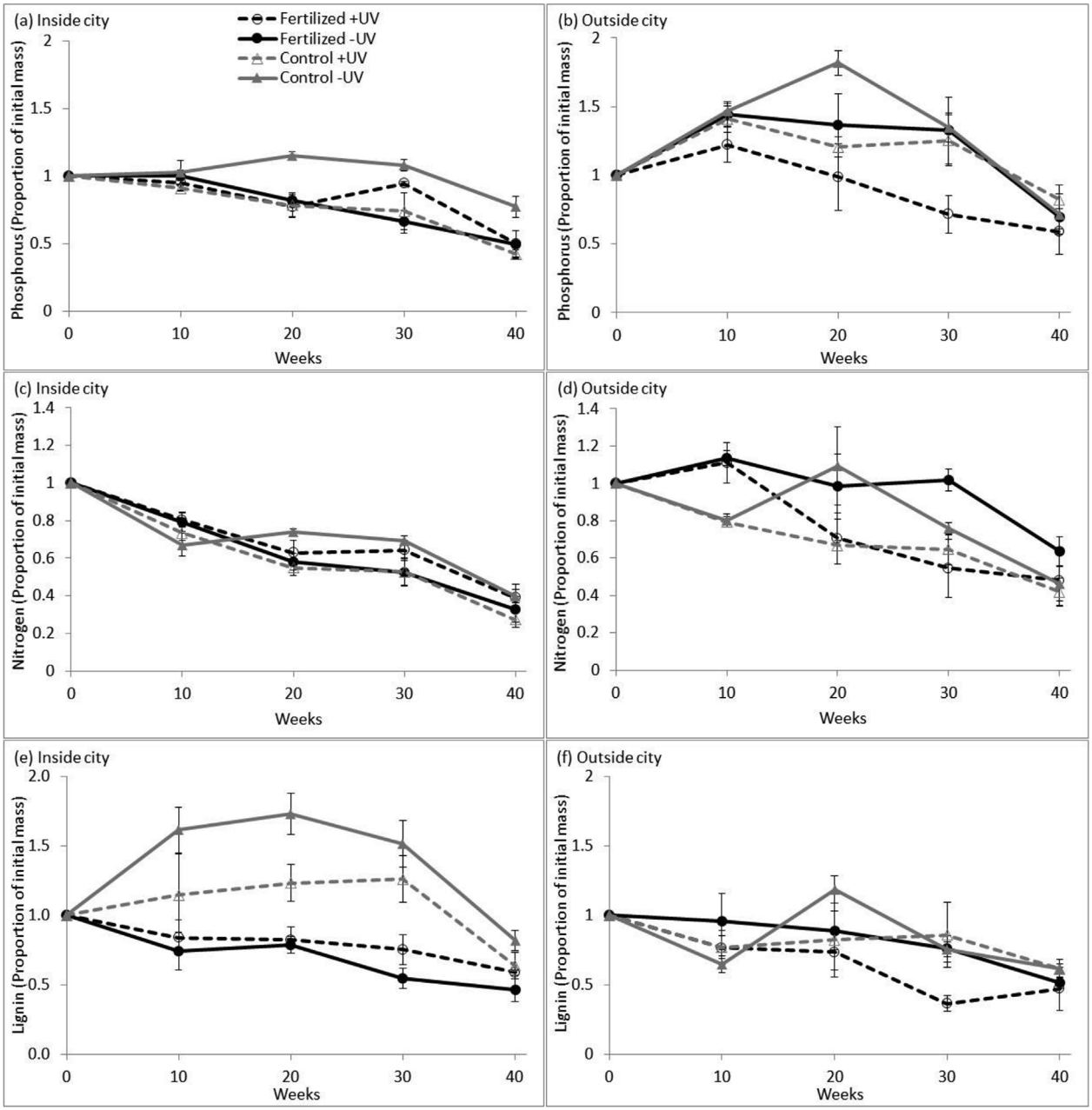


Fig. 3. Litter chemical content during decomposition of N + P fertilized or control *A. deltoidea* litter over the course of 40 weeks of degradation (December through September) in either -UV or + UV litterbags, both inside the city (left column) and outside (right column). Panels depict litter proportion of initial amounts remaining of: (c,d) P; (e,f) N; and (g,h) lignin in dry mass. Data points are average (n = 4) ± SE.

little evidence for immobilization, whereas outside the city N was immobilized (Fig. 3c and d) with a lower net loss of N content than the urban treatments, dropping from an initial 2.8% N to 1.3–1.6% N inside the city at 40 weeks, compared to an initial 2.4% N dropping to 1.8–2.3% N outside the city. Fertilization only marginally influenced litter N content (Table 2). UV radiation also tended to increase the rate of N loss compared to -UV treatments of the same location and fertilization, though this was more noticeable outside the city than inside (significant Location × UV interaction, Table 2). In addition to influencing N and P content, UV radiation interacted with location to influence nutrient ratios. Litter N:P and C:P ratios were higher in the presence of UV radiation when decomposed inside the city, but not outside the city (significant Location × UV interaction, Appendix A).

Lignin content in fertilized litter decreased in mass over time, but increased initially in control litter, particularly inside the city (Fig. 3e and f, Table 2). The presence of UV radiation decreased the amount of lignin in litter for each treatment except fertilized litter inside the city where we also see lower mass loss. Cellulose and hemicellulose were unaffected by treatments (data not shown).

Bacterial biovolume at the end of the field incubation differed between locations, interacting with fertilization and UV (Table 2), though not in the manner predicted. Without UV radiation, biovolume was greater inside the city than outside, and was not affected by fertilization treatment (Fig. 4). However, when UV radiation was allowed, bacterial biovolume inside the city was lower with fertilization, while the opposite is true outside the city where biovolume was greater on fertilized litter. Therefore, our hypothesis that bacterial biomass would be greater on the nutrient enriched litter and correlated with mass loss was only partially supported.

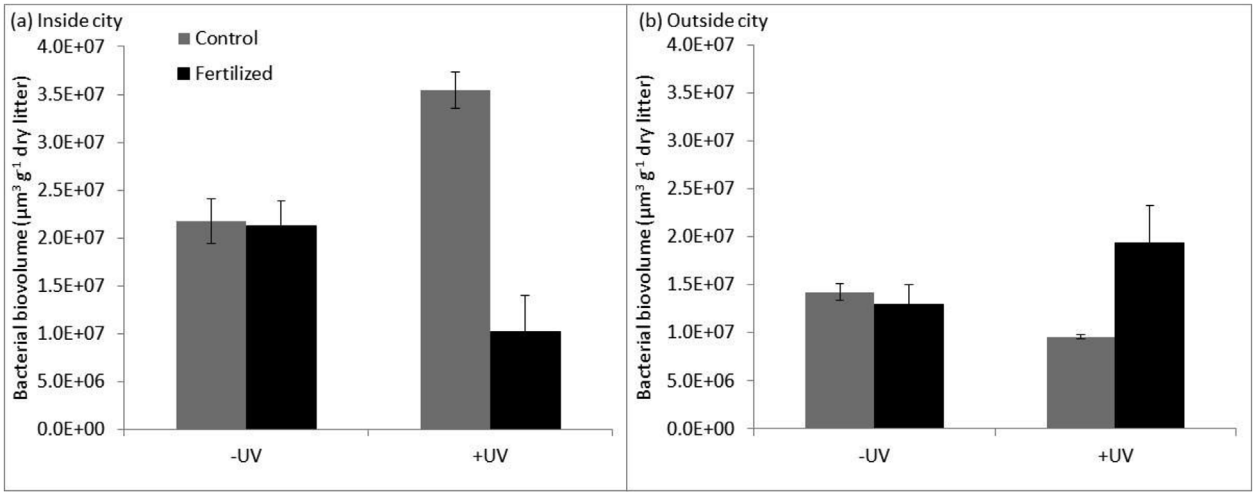


Fig. 4. Bacterial biovolume growing on N + P fertilized or control *A. deltoidea* litter after 40 weeks of degradation (December through September) in either -UV or + UV litterbags at a location (a) in the city core or (b) outside the city.

4. Discussion

4.1. Mass loss and nutrient dynamics during photodegradation

As expected, we found that photodegradation is a significant pathway of litter decomposition in aridlands, given the statistically significant effect of UV radiation on the decomposition of *A. deltoidea* litter in unshaded environments over an initial 9 months, though photodegradation ranged from either minimal to only a quarter of the total mass loss at the end of the 40 weeks. This fraction is lower than other studies which show a 30% or greater contribution of photodegradation when monitoring decomposition for a year or more (Austin and Vivanco, 2006; King et al., 2012). Notably, we measured more mass loss during 9 mo, ending with only 40% mass remaining, than other dryland studies of photodegradation (e.g., 80% mass remaining at 9 mo in Austin and Vivanco (2006)). The comparatively greater biological decomposition we measure might explain the respectively smaller contribution of photodegradation to overall mass loss. It is possible that photodegradation could account for a larger proportion of mass loss during later stages of decomposition when the biologically labile compounds have been mineralized and the relative proportion of biological decomposition declines. Indeed, we see the greatest contribution of photodegradation to mass loss in our litter at 30 weeks, during the Sonoran Desert's dry season when biological decomposition is limited and overall mass loss is slow, compared to the rainy seasons when mass loss, and presumably decomposer activity, was greater (Appendix C).

UV radiation also did not consistently decrease litter lignin content. A study in a subtropical ecosystem also found that lignin loss did not respond to UV radiation in early stages of decay (Song et al., 2014), and it is possible that increased lignin degradation in the +UV bags would account for greater mass loss after the 9 mo period sampled here. Lignin degradation also does not appear to be related to precipitation, given that the rainy periods did not have a consistent effect in comparison to the dry period. Determining the reason for the unexpected lignin dynamics requires further study. The lack of significant effect of UV on cellulose and hemicellulose degradation is also in line with previous work demonstrating that photodegradation does not correlate with the spectral absorbance of cellulose (Austin and Ballare, 2010).

Photodegradation reduced overall litter mass, and moderately altered N and P dynamics. N dynamics during photodegradation have been reported elsewhere (where N dynamics differed in litter from arid sites, Parton et al., 2007; and photodegradation had no impact on N dynamics, Wang et al., 2015), but we are not aware of any other reports of P dynamics during photodegradation. Photodegradation tended to increase mass loss and nutrient release in all treatments except fertilized litter inside the city. The fertilized litter inside the city is a unique case in all of our metrics, which we discuss below. Overall, the rates of microbial nutrient immobilization and mobilization during decomposition, which differ with and without photodegradation in our results, will influence nutrient availability in soils for plants and soil communities. Because N and P dynamics are influenced by UV radiation, it is possible that what is already known in the literature about N and P uptake and mineralization during decomposition would not necessarily apply to arid ecosystems, and might underestimate soil nutrient availability.

4.2. Impact of urbanization and fertilization on nutrient dynamics

N and P dynamics responded to differences in nutrient availability due to experimental fertilization and urbanization. Initial litter N was not greater in fertilized litter, reflecting previous results showing that plants are not always able to take up the excess N except during wet years, leading to only a marginal impact of fertilization on litter N during decomposition. However, initial litter N concentration is higher inside the city than outside of the city, possibly resulting from higher rates of anthropogenic N deposition. Though initial %N is higher, over time the litter from the urban core loses more N to end with a lower N content than litter from outside the city after 40 weeks of decomposition. Increased N availability in the city core litter potentially removed any N limitation of the decomposer microbes, allowing them to release existing litter N throughout the decomposition process, whereas more litter N was retained outside the city to maintain stoichiometric requirements of the litter microbes. This suggests that N deposition can alter N dynamics during decomposition even in arid ecosystems. Of course, multiple environmental factors covary with location beyond just atmospheric N deposition, such as other forms of pollution (e.g., carbon; Lohse et al., 2008; Hamilton and Hartnett, 2013) and precipitation (Appendix C) that could impact litter nutrient dynamics, so differences we measure between the urban and outlying locations are the result of a combination of intertwined environmental conditions. These combined differences appear to result in immediate N release from litter, with decreased N immobilization, at least in the first year of decomposition.

Nitrogen immobilization was minimal in our litter, with only very modest amounts of immobilization outside the city, even in the earliest stages of the experiment, indicating that microbes did not have to take up excess N from the soil to go about their metabolic processes during decomposition (e.g., Moore et al., 2006). The steady release of N with

little or no immobilization support the results of a cross-site study by Parton et al. (2007), who found a similar pattern in arid grasslands that they presumed to be the result of photodegradation. We find this pattern in litter with and without photodegradation, though nutrient loss is enhanced in the presence of UV radiation. C:N ratios in the litter were consistently below the values reported in the literature below which net mineralization occurs (Paul and Clark, 1989; Parton et al., 2007). This pattern supports the conclusion that aridland decomposer microbes are not N limited (e.g., Sponseller and Fisher, 2008), though herbaceous plants grow in response to N additions when precipitation provides available water (Hall et al., 2011). In contrast, decomposing litter immobilized P in the first few months outside the city, leading to an initial rise in P followed by a decrease over time, similar to other ecosystems (Qualls and Richardson, 2000). This pattern suggests that decomposer microbes in this desert ecosystem (whether inside or outside the city) are more limited by P, though also likely co-limited by accessible C substrate, given that fertilization alone did not enhance decomposition rate (Ostertag and Hobbie, 1999). Litter fertilization increased overall P content to reduce C:P, more so outside the city, suggesting that the excess N deposition does not lead to greater P-limitation inside the city compared to outside the city.

4.3. Combined effect of urbanization, fertilization, and photodegradation

Overall, the impact of urbanization and fertilization on mass loss and photodegradation is complex. UV radiation inhibited mass loss of fertilized litter inside the city but accelerated mass loss outside the city. The same pattern is reflected in bacterial biomass on the litter at 40 weeks, with +UV bags hosting a smaller bacterial biomass on fertilized litter inside the city. In other words, inside the city, UV radiation decreases bacterial biomass on fertilized litter, which then slows decomposition and nutrient release. These results suggest that nitrophilic bacteria (i.e., bacteria growing in N-rich environments, sensu e.g. Lilleskov et al., 2002; Koyama et al., 2014) on nutrient-rich litter in the city may be sensitive to UV such that solar radiation inhibits biological decomposition in this environment. While it is known that bacterial taxa differ in UV sensitivity (e.g., Gascón et al., 1995; Joux et al., 1999) and soil microbial communities can be significantly altered by UV radiation (Wang et al., 2015), we are not aware of evidence concerning the UV sensitivity specifically of copiotrophic bacteria in arid soils. Further, bacterial biomass is not the sole determinant of mass loss, because biomass was greater inside the city while rates of mass loss were roughly equivalent to outside the city. The mechanism causing this complex interaction between fertilization and UV to reverse its impact inside versus outside the city will therefore require further exploration. This relationship could be influenced by many factors that differ with Location in this study, encompassing both initial litter chemical composition as well as the decomposition environment. One possibility is the slightly higher precipitation (by 35 mm) outside the city during the study (Appendix C), which may have stimulated bacterial activity to match that inside the city, despite the lower biomass. Even beyond precipitation, urban and outlying areas will differ in their heat and energy dynamics to influence soil moisture, which could interact with nutrient fertilization to impact decomposition. Future research should investigate this role of moisture on the dynamics of photodegradation. Additionally, it is possible that soil properties differing between the two locations influence their response to UV and fertilization. For example, the higher soil N inside the city may have altered the microbial community functioning to respond differently to UV radiation and fertilization than outside the city (Hall et al., 2009; Hall et al., 2011; Ball and Alvarez Guevara, 2015). The combination of fertilization and UV radiation decreased mass loss and increased N loss in the first year of decomposition in subtropical China (Song et al., 2014), as we saw inside the city. Song et al. (2014) suggest that this interaction is the result of N combining with lignin and phenolic compounds to produce new compounds that are difficult to decompose, which could be explored as one possible reason for the difference between litter from inside versus outside the city.

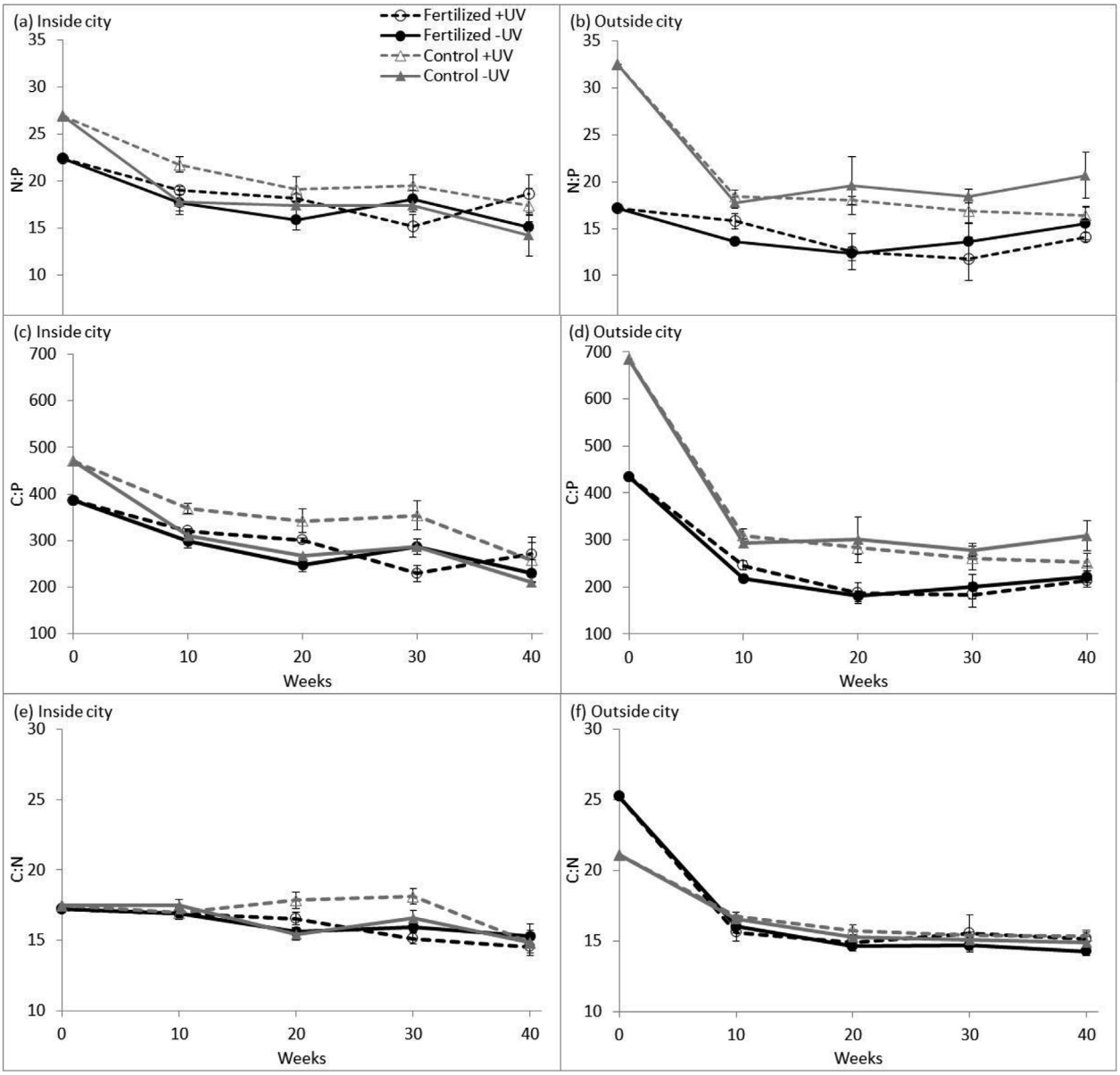
4.4. Conclusion

In conclusion, we found that photodegradation increases mass loss and alters nutrient dynamics in both urban and outlying environments. Mass loss and nutrient dynamics are also impacted by the urban activity, including N deposition, inside the city and experimental fertilization. These aridland decomposers appear to be more P limited than N limited, and the excess N available inside the city increased the rate of N release from litter in comparison to outside the city. Notably, fertilized litter inside the city is the only situation where UV radiation slowed decay rather than stimulated it, suggesting the nitrophilic bacteria on this litter may be sensitive to UV.

Acknowledgements

At Arizona State University, Jessica Alvarez Guevara and Jack Ramsey were instrumental in helping with the initial processing of samples. At the Goldwater Environmental Lab, Sara Avery ran all tests on the elemental analyzer and Roy Erickson ran the ICP-OES. The New College of Interdisciplinary Arts and Sciences and Barrett, the Honors College at ASU provided funding for the litter degradation field and laboratory analyses. The thoughtful comments from three reviewers improved this manuscript. This material is based upon work supported by the National Science Foundation under grant number DEB-1026865 for the Central Arizona-Phoenix Long-Term Ecological Research (CAP LTER).

Appendix A. Nutrient ratios of litter during decomposition of N + P fertilized or control *A. deltoidea* litter over the course of 40 weeks of degradation (December through September) in either -UV or + UV litterbags, both inside the city (left column) or outside (right column). Panels depict (a,b) N:P ratio, for which the ANCOVA shows significant Location × Fertilization ($P = 0.004$), Location × UV ($P = 0.011$) and Location × Time ($P = 0.005$) interactions.; (c,d) C:P ratio, for which the ANCOVA shows significant Location × UV ($P = 0.033$) and Location × Fertilization*Time ($P = 0.037$) interactions; (e,f) C:N ratio, for which the ANCOVA shows significant effects of Location ($P = 0.001$), Fertilization ($P = 0.001$) and Time ($P < 0.001$)

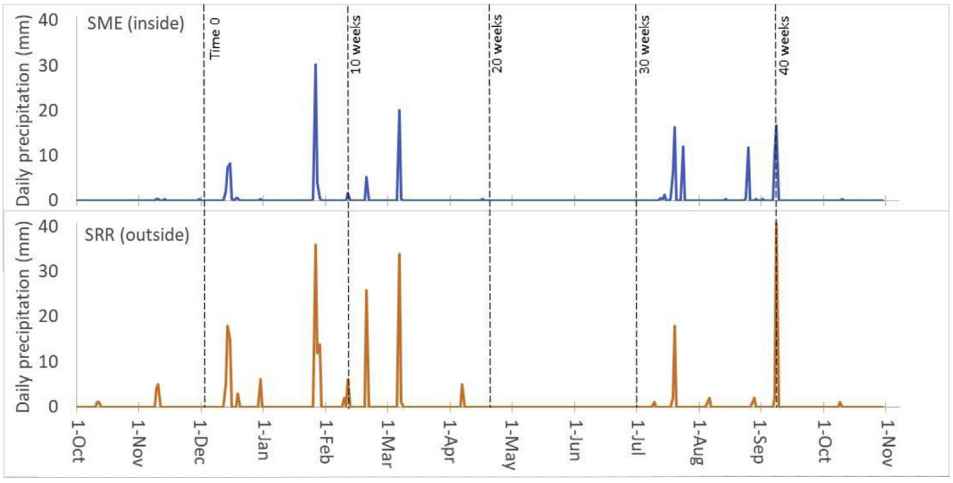


Appendix B. F-values and associated degrees of freedom (factor, residuals) to accompany the p-values in Table 2 from the Analysis of Covariance investigating the effects of Location (two levels: inside or outside the city), UV presence (two levels: +UV in UV-transparent litterbags or –UV in UV-opaque litterbags), Fertilization (two levels: N + P fertilized or control), and sampling Time (0–40 weeks, continuous factor) on litter properties during decomposition

	AFDM remaining	N	P	Lignin	Bacterial biovolume
Location	$1.11_{1,98}$	$32.78_{1,120}$	$45.01_{1,120}$	$19.53_{1,117}$	$12.36_{1,20}$
UV	$9.40_{1,98}$	$10.55_{1,120}$	$13.87_{1,120}$	$5.64_{1,117}$	$0.63_{1,20}$
Fertilization	$0.31_{1,98}$	$4.21_{1,120}$	$9.33_{1,120}$	$36.37_{1,117}$	$0.22_{1,20}$
Time	$144.35_{1,98}$	$118.45_{1,120}$	$52.57_{1,120}$	$24.56_{1,117}$	–

Location × UV	$2.99_{1,98}$	$6.60_{1,120}$	$1.52_{1,120}$	$< 0.01_{1,117}$	$0.59_{1,20}$
Location × Fertilization	$0.22_{1,98}$	$2.76_{1,120}$	$1.45_{1,120}$	$16.46_{1,117}$	$9.32_{1,20}$
UV × Fertilization	$0.32_{1,98}$	$0.37_{1,120}$	$0.79_{1,120}$	$1.95_{1,117}$	$1.09_{1,20}$
Location × Time	$< 0.01_{1,98}$	$0.02_{1,120}$	$1.16_{1,120}$	$0.34_{1,117}$	–
UV × Time	$0.32_{1,98}$	$0.90_{1,120}$	$< 0.01_{1,120}$	$0.21_{1,117}$	–
Fertilization × Time	$1.62_{1,98}$	$0.74_{1,120}$	$0.40_{1,120}$	$0.29_{1,117}$	–
Location × UV × Fert	$7.05_{1,98}$	$3.65_{1,120}$	$6.37_{1,120}$	$8.50_{1,117}$	$7.45_{1,20}$
Location × UV × Time	$0.45_{1,98}$	$0.11_{1,120}$	$0.25_{1,120}$	$0.28_{1,117}$	–
Location × Fert × Time	$0.44_{1,98}$	$0.08_{1,120}$	$0.01_{1,120}$	$1.88_{1,117}$	–
UV × Fert × Time	$0.34_{1,98}$	$< 0.01_{1,120}$	$0.05_{1,120}$	$0.02_{1,117}$	–
Location × UV × Fert × Time	$0.89_{1,98}$	$2.09_{1,120}$	$1.84_{1,120}$	$0.02_{1,117}$	–

Appendix C. Daily precipitation for the year encompassing the litterbag study at the two sites where litterbags were decomposed: South Mountain East (SME) inside the city and Salt River Recreation Area (SRR) outside the city. Dashed vertical lines represent the initial date of placement in December 2012, and each of the 10-week sampling dates



References

Aber, J., Magill, A., McNulty, S., Boone, R., Nadelhoffer, K., Downs, M., Hallett, R., 1995. Forest biogeochemistry and primary production altered by nitrogen saturation. Water Air Soil Pollut. 85, 1665–1670.

Aber, J.D., Melillo, J.M., McClaugherty, C.A., 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. 68, 2201–2208.

Adams, M.B., 2003. Ecological issues related to N deposition to natural ecosystems: research needs. Environ. Int. 29, 189–199.

Allen, E.B., Gelser, L.H., 2011. North American deserts. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T. (Eds.), Assessment of Nitrogen Deposition Effects and Empirical Critical Loads of Nitrogen for Ecoregions of the United States. U.S. Forest Service, Newtown Square, PA, USA, pp. 133–142.

Austin, A.T., Ballare, C.L., 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. Proc. Natl. Acad. Sci. U.S.A. 107, 4618–4622.

Austin, A.T., Méndez, M.S., Ballaré, C.L., 2016. Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. Proc. Natl. Acad. Sci. Unit. States Am. 113, 4392–4397.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555–558.

Ball, B., Bradford, M., Hunter, M., 2009a. Nitrogen and phosphorus release from mixed litter layers is lower than predicted from single species decay. Ecosystems 12, 87–100.

Ball, B.A., Adams, B.J., Barrett, J.E., Wall, D.H., Virginia, R.A., 2018. Soil biological responses to C, N and P fertilization in a polar desert of Antarctica. Soil Biol. Biochem. 122, 7–18.

Ball, B.A., Alvarez Guevara, J., 2015. The nutrient plasticity of moss-dominated crust in the urbanized Sonoran Desert. Plant Soil 389, 225–235.

Ball, B.A., Bradford, M.A., Coleman, D.C., Hunter, M.D., 2009b. Linkages between below and aboveground communities: decomposer responses to simulated tree species loss are largely additive. Soil Biol. Biochem. 41, 1155–1163.

Ball, B.A., Virginia, R.A., 2014. Microbial biomass and respiration responses to nitrogen fertilization in a polar desert. Polar Biol. 37, 573–585.

Ball, B.A., Virginia, R.A., Barrett, J.E., Parsons, A.N., Wall, D.H., 2009c. Interactions between physical and biotic factors influence CO_2 flux in Antarctic dry valley soils. Soil Biol. Biochem. 41, 1510–1517.

Barnes, P.W., Throop, H.L., Hewins, D.B., Abbene, M.L., Archer, S.R., 2012. Soil coverage reduces photodegradation and promotes the development of soil-microbial films on dryland leaf litter. Ecosystems 15, 311–321.

Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ. Rev. 5, 1–25.

Bi, J., Zhang, N., Liang, Y., Yang, H., Ma, K., 2012. Interactive effects of water and nitrogen addition on soil microbial communities in a semiarid steppe. J. Plant Ecol. 5, 320–329.

Blair, J.M., Crossley, D.A., Callaham, L.C., 1992. Effects of litter quality and microarthropods on N-dynamics and retention of exogenous ^{15}N in decomposing litter. Biol. Fertil. Soils 12, 241–252.

Brandt, L.A., Bohnet, C., King, J.Y., 2009. Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. Journal of Geophysical Research-Biogeosciences 114.

Brandt, L.A., King, J.Y., Milchunas, D.G., 2007. Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. Global Change Biol. 13, 2193–2205.

Chapin, F.S., 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Systemat. 11, 233–260.

Cook, E., 2014. Atmospheric nitrogen deposition in a large semi-arid city is lower than expected: findings from a methods comparison. Dissertation In: Direct and Indirect Ecological Consequences of Human Activities in Urban and Native Ecosystems. Arizona State University.

Day, T.A., Zhang, E.T., Ruhland, C.T., 2007. Exposure to solar UV-B radiation accelerates mass and lignin loss of *Larrea tridentata* litter in the Sonoran Desert. Plant Ecol. 193, 185–194.

Dentener, F., Drevet, J., Lamarque, J.F., Bey, I., Eickhout, B., Fiore, A.M., Hauglustaine, D., Horowitz, L.W., Krol, M., Kulshrestha, U.C., Lawrence, M., Galy-Lacaux, C., Rast, S., Shindell, D., Stevenson, D., Van Noije, T., Atherton, C., Bell, N., Bergman, D., Butler, T., Cofala, J., Collins, B., Doherty, R., Ellingsen, K., Galloway, J., Gauss, M., Montanaro, V., Muller, J.F., Pitari, G., Rodriguez, J., Sanderson, M., Solmon, F., Strahan, S., Schultz, M., Sudo, K., Szopa, S., Wild, O., 2006. Nitrogen and sulfur deposition on regional and global scales: a multimodel evaluation. Global Biogeochem. Cycles 20, 21.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2001. Acid Rain Revisited: Advances in Scientific Understanding since the Passage of the 1970 and 1990 Clean Air Act Amendments, vol. 1 Hubbard Brook Research Foundation. Science Links Publication no. 1.
Egerton-Warburton, L.M., Allen, E.B., 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecol. Appl. 10, 484–496.
Fenn, M.E., Haeuber, R., Tonnesen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Jaffe, D.A., Copeland, S., Geiser, L., Rueth, H.M., Sickman, J.O., 2003. Nitrogen emissions, deposition, and monitoring in the western United States. Bioscience 53, 391–403.
Foereid, B., Rivero, M.J., Primo, O., Ortiz, I., 2011. Modelling photodegradation in the global carbon cycle. Soil Biol. Biochem. 43, 1383–1386.
Gascón, J., Oubiña, A., Pérez-Lezaun, A., Urmeneta, J., 1995. Sensitivity of selected bacterial species to UV radiation. Curr. Microbiol. 30, 177–182.
Hall, S.J., Ahmed, B., Ortiz, P., Davies, R., Sponseller, R.A., Grimm, N.B., 2009. Urbanization alters soil microbial functioning in the Sonoran Desert. Ecosystems 12, 654–671.
Hall, S.J., Sponseller, R.A., Grimm, N.B., Huber, D., Kaye, J.P., Clark, C., Collins, S.L., 2011. Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. Ecol. Appl. 21, 640–660.
Hamilton, G.A., Hartnett, H.E., 2013. Soot black carbon concentration and isotopic composition in soils from an arid urban ecosystem. Org. Geochem. 59, 87–94.
Henry, H.A.L., Brizgys, K., Field, C.B., 2008. Litter decomposition in a California annual grassland: interactions between photodegradation and litter layer thickness. Ecosystems 11, 545–554.
Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. Ecology 81, 1867–1877.
Joux, F., Jeffrey, W.H., Lebaron, P., Mitchell, D.L., 1999. Marine bacterial isolates display diverse responses to UV-B radiation. Appl. Environ. Microbiol. 65, 3820–3827.
King, J.Y., Brandt, L.A., Adair, E.C., 2012. Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. Biogeochemistry 111, 57–81.
Koebler, J., 2011. 10 Metro Areas with the Largest Population Growth. (U.S. News & World Report).
Koyama, A., Wallenstein, M.D., Simpson, R.T., Moore, J.C., 2014. Soil bacterial community composition altered by increased nutrient availability in Arctic tundra soils. Front. Microbiol. 5.
Ladwig, L.M., Collins, S.L., Swann, A.L., Xia, Y., Allen, M.F., Allen, E.B., 2012. Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. Oecologia 169, 177–185.
Lee, H., Rahn, T., Throop, H., 2012. An accounting of C-based trace gas release during abiotic plant litter degradation. Global Change Biol. 18, 1185–1195.
Lilleskov, E.A., Fahey, T.J., Horton, T.R., Lovett, G.M., 2002. Belowground ectomychorrhizal fungal community change over a nitrogen deposition gradient in Alaksa. Ecology 83, 104–115.
Lohse, K.A., Hope, D., Sponseller, R., Allen, J.O., Grimm, N.B., 2008. Atmospheric deposition of carbon and nutrients across an arid metropolitan area. Sci. Total Environ. 402, 95–105.
Magill, A.H., Aber, J.D., Currie, W.S., Nadelhoffer, K.J., Martin, M.E., McDowell, W.H., Melillo, J.M., Steudler, P., 2004. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. For. Ecol. Manag. 196, 7–28.
McClaugherty, C., Berg, B., 1987. Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. Pedobiologia 30, 101–112.
Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.
Moore, T.R., Trofymow, J.A., Prescott, C.E., Fyles, J., Titus, B.D., 2006. Patterns of carbon, nitrogen and phosphorus dynamics in decomposing foliar litter in Canadian forests. Ecosystems 9, 46–62.
Mooshammer, M., Wanek, W., Schnecker, J., Wild, B., Leitner, S., Hofhansl, F., Blöchl, A., Hämmerle, I., Frank, A.H., Fuchslueger, L., Keiblinger, K.M., Zechmeister-Boltenstern, S., Richter, A., 2012. Stoichiometric controls of nitrogen and phosphorus cycling in decomposing beech leaf litter. Ecology 93, 770–782.
Ostertag, R., Hobbie, S.E., 1999. Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. Oecologia 121, 564–573.
Padgett, P., Allen, E., 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to mediterranean coastal sage scrub of California. Plant Ecol. 144, 93–101.
Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., Baron, J.S., Bobbink, R., Bowman, W.D., Clark, C.M., Emmett, B., Gilliam, F.S., Greaver, T.L., Hall, S.J., Lilleskov, E.A., Liu, L., Lynch, J.A., Nadelhoffer, K.J., Perakis, S.S., Robin-Abbott, M.J., Stoddard, J.L., Weathers, K.C., Dennis, R.L., 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. 21, 3049–3082.
Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C., Fasth, B., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315, 361–364.
Paul, E., Clark, F., 1989. Soil Microbiology and Biochemistry. Academic Press, San Diego, CA.
Qualls, R.G., Richardson, C.J., 2000. Phosphorus enrichment affects litter decomposition, immobilization, and soil microbial phosphorus in wetland mesocosms. Soil Sci. Soc. Am. J. 64, 799–808.
Sinsabaugh, R.L., Belnap, J., Rudgers, J., Kuske, C.R., Martinez, N., Sandquist, D., 2015. Soil microbial responses to nitrogen addition in arid ecosystems. Front. Microbiol. 6.
Smith, W.K., Gao, W.E.I., Steltzer, H., Wallenstein, M.D., Tree, R., 2010. Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. Global Change Biol. 16, 484–495.
Sobota, D.J., Compton, J.E., Harrison, J.A., 2013. Reactive nitrogen inputs to US lands and waterways: how certain are we about sources and fluxes? Front. Ecol. Environ. 11, 82–90.
Song, X., Zhang, H., Jiang, H., Peng, C., 2014. Combination of nitrogen deposition and ultraviolet-B radiation decreased litter decomposition in subtropical China. Plant Soil 380, 349–359.
Sponseller, R.A., Fisher, S.G., 2008. The influence of drainage networks on patterns of soil respiration in a desert catchment. Ecology 89, 1089–1100.
Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70, 97–104.
U.S. Census Bureau, 2015. 2015 Census Data.
UNDP, 2007. World Urbanization Prospects: the 2007 Revision Population Database. United Nations Population Division, Dept. of Economics and Social Affairs.
Van Diepen, L.T.A., Lilleskov, E.A., Pregitzer, K.S., Miller, R.M., 2007. Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions. New Phytol. 176, 175–183.
Van Soest, J., 1994. Nutritional Ecology of the Ruminant, second ed. Cornell University Press, Ithaca, NY.
Vourlitis, G.L., Pasquini, S.C., Mustard, R., 2009. Effects of dry-season N input on the productivity and N storage of Mediterranean-type shrublands. Ecosystems 12, 473–488.
Wang, J., Liu, L., Wang, X., Chen, Y., 2015. The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. Global Change Biol. 21, 2095–2104.
Wetzel, R.G., Likens, G.E., 2000. Limnological Analyses, third ed. Springer, New York.
Yahdjian, L., Sala, O.E., Austin, A.T., 2006. Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian steppe. Ecosystems 9, 128–141.