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Animal generation of green leaf litter in an arid shrubland enhances decomposition by altering litter quality and location

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ABSTRACT

Soil carbon (C) and nutrients are derived largely from decomposition of plant biomass. Animals that generate greenfall, or green leaf litter, influence C and nutrient cycling dynamics by altering the phenological condition, and therefore nutrient quality, of plant litter entering the soil, and transporting litter among microsites. Microsite effects on decomposition rates are particularly pronounced in arid and semi-arid ecosystems where vegetation cover is often patchy. We investigated differences in decomposition of greenfall and senesced litter of three common Chihuahuan Desert plants from which animals frequently generate greenfall. A litterbag study was used to quantify differences in mass, C, and nitrogen (N) losses between green and senesced leaves in shrub intercanopy and subcanopy microsites in desert shrublands. We found significant differences in nutrient concentration of green and senesced leaves, and that both litter condition (green or senesced) and microsite affected decomposition rate. For two of the three litter species, greenfall decomposed more rapidly than senesced litter; for all three species, litter decomposed more rapidly in intercanopy than subcanopy microsites. These results support the idea that creation and translocation of greenfall by animals are important mechanisms regulating decomposition speed and C and nutrient transfer from plant biomass into the soil.

1. Introduction

Animals modify ecosystems through numerous mechanisms. One of the most prominent mechanisms is herbivory, which affects growth and productivity at the individual-plant level, as well as net primary productivity (NPP) and plant composition at the community level. By altering the quantity and quality of plant biomass that enters the litter pool, animals also influence carbon (C) and nutrient cycling. Many animals create greenfall, green leaf litter that is a byproduct of herbivory (Kerley et al., 1997; Risley and Crossley, 1988, 1993; Steinberger and Whitford, 1983), reproductive strategy (Whitford and Steinberger, 2010), or habitat modification (Davidson et al., 1988; Weltzin et al., 1997). In doing so, these animals not only alter litter quality, but may also alter the litter location within the landscape, which may induce changes in decomposition dynamics.

Greenfall typically constitutes a higher quality litter substrate than senesced leaves of the same species because green leaves have not yet undergone nutrient resorption in preparation for leaf senescence and abscission (Risley and Crossley, 1993). Because decomposition processes like nitrogen (N) mineralization and the overall rate of organic matter breakdown are often limited by nutrient availability, even a small amount of greenfall in the litter pool can have a disproportionately large influence on decomposition dynamics (Blood et al., 1991; Constantinides and Fownes, 1994; Cornelissen et al., 2000; Fonte and Schowalter, 2004; Lodge and McDowell, 1991; Risley and Crossley, 1988, 1993).

Animals that create greenfall may also alter decomposition by moving green leaves to a microsite in the landscape different from where litter would typically accumulate (Kerley et al., 1997; Steinberger and Whitford, 1983). Abiotic conditions that influence decomposition (e.g. sunlight exposure, temperature, moisture) may be quite different among microsites (He et al., 2013), particularly in drylands (arid and semiarid ecosystems), which are often characterized by a heterogeneous landscape of patchy vegetation cover and resource distribution (Okin et al., 2015; Smith et al., 2012). Heterogeneity in vegetation appears to be a major factor causing soil-litter mixing and photodegradation, with both processes being of unique importance to decomposition in drylands (reviewed in Barnes et al., 2015; King et al., 2012). Soil-litter mixing (SLM), or contact between soil particles and plant litter, serves as a vector for microbial colonization of litter and the

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formation of a soil film on the litter surface that protects the litter and decomposers from UV radiation and buffers litter microclimate, extending the temporal window of possible microbial activity (Barnes et al., 2012; Joly et al., 2017; Lee et al., 2014). SLM occurs to the greatest extent in the bare or sparsely vegetated microsites that persist between shrub canopies or other patches of vegetation, where soil and organic matter are most vulnerable to wind and water (Breshears et al., 2003; Li et al., 2007). Photodegradation, the direct or indirect breakdown of litter by solar radiation, is also more prominent in unvegetated microsites where there is no vegetation canopy or accumulation of organic material to provide protection from sunlight exposure (King et al., 2012). Photodegradation may be particularly important where plant biomass persists as standing dead litter for months or years following senescence (Campbell and Keller, 1932), potentially undergoing extensive photodegradation before reaching the soil (Barnes et al., 2015).

We asked how the quality and decomposition of greenfall differ from senesced litter in drylands, and how greenfall in the litter pool might affect C and nutrient cycling at the landscape level. We used three common Chihuahuan Desert plant species in our study: *Larrea tridentata* (creosotebush), *Sporobolus flexuosus* (mesa dropseed), and *Yucca elata* (soaptree yucca). Jackrabbits and small rodents frequently generate greenfall from these plant species. *We hypothesized that decomposition would be more rapid in 1) greenfall than naturally senesced litter, because of the higher nutrient concentration in green than senesced leaves, and 2) intercanopy than subcanopy microsites, because of increased exposure to decomposition drivers like soil-litter mixing and photodegradation in the less vegetated open area between shrub canopies.* We used a litterbag study to quantify differences in litter mass, C, and N losses between green and senesced leaves placed in shrub intercanopy and subcanopy microsites, and then used these results to estimate the landscape-level impact of greenfall on decomposition rate.

2. Materials and methods

2.1. Study site

Research was conducted in the northern Chihuahuan Desert at the Jornada Basin Long Term Ecological Research (LTER) site in Dona Ana County, New Mexico, USA. The climate at the Jornada is arid with mean annual precipitation of 245 mm and mean annual temperature of 14.7° C (Havstad and Schlesinger, 2006). The Jornada Basin is characterized by a patchy matrix of grass- and shrub-dominated plant communities typical of the Chihuahuan Desert. The Jornada Basin was historically grassland, but due to a combination of factors including livestock grazing and drought, it is now a matrix of shrubs (*Prosopis glandulosa, Larrea tridentata, Flourensia cernua*), annual grasses, perennial bunch grasses, and bare ground (Gibbens et al., 2005; Schlesinger et al., 1996).

We measured quality and decomposition of greenfall and senesced litter from the shrub, *Larrea tridentata*, perennial bunch grass, *Sporobolus flexuosus*, and yucca, *Yucca elata* (hereafter, *Larrea*, *Sporobolus* and *Yucca*). All three species are common in the Chihuahuan Desert. Greenfall from *Larrea* is frequently generated by jackrabbits (*Lepus californicus*) browsing on new woody stem growth as a source of water during the dry winter and spring months (Currie and Goodwin, 1966; Hayden, 1966; Steinberger and Whitford, 1983; Westoby, 1980). Jackrabbits consume the stem cambium and then discard uneaten stem wood and attached green leaves near the base of the shrub or in the shrub intercanopy (Steinberger and Whitford, 1983). *Larrea* has a particularly high leaf resorption efficiency for both N (42–61%) and phosphorous (72–86%; Lajtha, 1987), making the nutrient content of greenfall substantially greater than that of senesced litter. In the Chihuahuan Desert, creosotebush greenfall contributes approximately 66 kg ha^{-1} of stem and 35 kg ha^{-1} of green leaf biomass to the litter pool annually, approximately one fifth of naturally senesced shrub litter inputs (Steinberger and Whitford, 1983).

Kangaroo rats (*Dipodomys merriami*, *D. ordii,* and *D. spectabilis*) create greenfall from tall, tussock-forming grasses like mesa dropseed (*Sporobolus*), black grama (*Bouteloua eriopoda*), and threeawns (*Aristida* spp.), by pruning grass tillers in the summer and fall, possibly as a water source (Sipos et al., 2002; Soholt, 1977). Kangaroo rats eat only a small portion at the bottom of the tiller, rarely caching any of the cuttings and leaving the majority of the tiller on the ground (Kerley and Whitford, 2009; Kerley et al., 1997; Sipos et al., 2002). Green grass tillers have N levels roughly 3–7 g N kg^{-1} greater than recently senesced grass tillers and litter from many grasses persists as standing dead litter for one of more years following senescence (Kerley et al., 1997), further enhancing the relatively high nutrient status of greenfall. Greenfall from *Sporobolus* and other tall tussock grasses averages 2 kg ha^{-1} in areas where kangaroo rats are active, with as much as 10 kg ha^{-1} in some grasslands (Kerley et al., 1997).

Yucca greenfall is created by woodrats (*Neotoma* spp.) that prune green leaves, possibly as a source of water during the dry winter and spring months (Lee, 1963), or as structural material for midden construction (per. obs.). Woodrats may remove hundreds of leaves from a single *Yucca* rosette, occasionally leaving plants almost entirely defoliated (pers. obs.). Greenfall is taken back to the woodrats' middens, as evidenced by the green leaves often visible sticking out of a midden entrance, or incorporated into the outer architecture of a midden (per. obs.).

We used a litterbag study to measure decomposition of greenfall and naturally-senesced litter from *Larrea*, *Sporobolus* and *Yucca*. All plants occur on the Jornada Basin LTER but are not found immediately adjacent to each other. To address this spatial distribution, we established a separate study site for each species. All three sites were in livestock exclosures to prevent damage to litterbags. The *Larrea* study site was on the fan piedmont slope of Mt. Summerford (106°47′24″ W, 32°30′37″ N), where the soil is a loamy-skeletal, mixed, thermic Typic Haplocalcid (Nickel-Upton association; Soil Survey Staff 1999, 2003). *Larrea* is the dominant vegetation at this site with prickly pear cactus (*Opuntia imbricata*), several native perennial grasses (*Muhlenbergia porteri*, *Dasyochloa pulchella*, *Bouteloua eriopoda*), and a variety of forbs also present, although vegetation cover is sparse between creosotebush shrub canopies (Huenneke et al., 2002; Peters and Gibbens, 2006). The *Sporobolus* and *Yucca* study sites were adjacent to each other on the Jornada basin floor (106°49′56″ W, 32°35′58″ N), where the soil is a coarse-loamy, mixed, thermic Typic Haplargid (Onite-Pajarito association; Soil Survey Staff 1999, 2003). Honey mesquite (*Prosopis glandulosa*) is the dominant shrub, with *Yucca*, broom snakeweed (*Gutierrezia sarothrae*), native perennial grasses (*Sporobolus, S. contractus*, *Aristida* spp., *B. eriopoda*), and a variety of forbs also present (Huenneke et al., 2002; Peters and Gibbens, 2006).

2.2. Experimental design

At each of the three study sites, eighteen microsites were designated for litterbag placement: nine replicates in shrub intercanopy microsites and nine in shrub subcanopy microsites. Intercanopy microsites were designated in unvegetated patches of bare soil, at least one shrub canopy width from the nearest shrub and in an area large enough that litterbags could be placed at least 15 cm apart from each other and the nearest herbaceous vegetation. Subcanopy microsites were located beneath *Larrea* shrubs at the *Larrea* study site and beneath *Prosopis glandulosa* shrubs at the *Yucca* and *Sporobolus* study sites (*Larrea* canopy diameter = 207 ± 7.4 cm, height = 125 ± 7.1 cm; mesquite canopy diameter = 189 ± 5.7 cm, height = 85 ± 1.8 cm). Shrubs used for microsites were at least one canopy diameter away from any neighboring shrubs.