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UVB exposure does not accelerate rates of litter decomposition in a semi-arid riparian ecosystem

Shauna M. Uselman*, Keirith A. Snyder, Robert R. Blank, Timothy J. Jones

USDA-Agricultural Research Service, Exotic and Invasive Weeds Research Unit, 920 Valley Road, Reno, NV 89512, USA

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A B S T R A C T

Aboveground litter decomposition is controlled mainly by substrate quality and climate factors across terrestrial ecosystems, but photodegradation from exposure to high-intensity ultraviolet-B (UVB) radiation may also be important in arid and semi-arid environments. We investigated the interactive effects of UVB exposure and litter quality on decomposition in a *Tamarix*-invaded riparian ecosystem during the establishment of an insect biological control agent in northern Nevada. Feeding by the northern tamarisk beetle (*Diorhabda carinulata*) on *Tamarix* spp. trees leads to altered leaf litter quality and increased exposure to solar UVB radiation from canopy opening. In addition, we examined the dynamics of litter decomposition of the invasive exotic *Lepidium latifolium*, because it is well-situated to invade beetle-infested *Tamarix* sites. Three leaf litter types (natural *Tamarix*, beetle-affected *Tamarix*, and *L. latifolium*) differing in substrate quality were decomposed in litterbags for one year in the field. Litterbags were subjected to one of three treatments: (1) Ambient UVB or (2) Reduced UVB (where UVB was manipulated by using clear plastic films that transmit or block UVB), and (3) No Cover (a control used to test for the effect of using the plastic films, i.e. a cover effect). Results showed a large cover effect on rates of decomposition and nutrient release, and our findings suggested that frequent cycles of freeze–thaw, and possibly rainfall intensity, influenced decomposition at this site. Contrary to our expectations, greater UVB exposure did not result in faster rates of decomposition. Greater UVB exposure resulted in decreased rates of decomposition and P release for the lower quality litter and no change in rates of decomposition and nutrient release for the two higher quality litter types, possibly due to a negative effect of UVB on soil microbes. Among litter types, rates of decomposition and net release of N and P followed this ranking: *L. latifolium* > beetle-affected *Tamarix* > natural *Tamarix*. Altered nutrient dynamics with beetle introduction as well as the rapid decomposition rates exhibited by *L. latifolium* are consistent with vulnerability to secondary invasion. In this desert ecosystem, decomposition and nutrient release were strongly affected by litter type and much less so by UVB exposure.

1. Introduction

The process of litter decomposition is controlled mainly by litter quality (e.g. substrate chemistry) and climate factors (e.g. temperature and moisture) (Berg and McClaugherty, 2003; Swift et al., 1979), with climate potentially playing a more important role on a global or regional scale and substrate quality more important on a local scale (Gholz et al., 2000; Meentemeyer, 1978; Parton et al., 2007). By interacting with litter quality, soil community composition may also play a role (Ayres et al., 2009). Despite environmental limitations of extreme temperatures and low soil moisture in arid and semi-arid ecosystems, some studies have observed rates of decomposition in deserts that exceed those predicted by the model of Meentemeyer (1978) that combines climate (actual evapotranspiration) and litter quality (lignin concentration) variables (Schaefer et al., 1985; Whitford et al., 1981). Because of this discrepancy, it has been hypothesized that high levels of solar radiation common to these environments may be an important additional driver of decomposition (Austin and Vivanco, 2006; Moorhead and Callaghan, 1994). Research in aquatic ecosystems has shown that high-energy short-wave ultraviolet-B (UVB) radiation (280–320 nm) aids in the breakdown of dissolved organic matter (DOM) via photochemical reactions, either by reducing humic DOM into more labile DOM or directly mineralizing C (Qualls and Richardson, 2003; Zepp et al., 2003). However, the process of photodegradation of organic matter has not been as extensively studied in terrestrial ecosystems in comparison to freshwater aquatic and marine systems.

* Corresponding author. Tel.: +1 775 784 6057x237; fax: +1 775 784 1712.
E-mail addresses: Shauna.Uselman@ars.usda.gov, s.uselman@sbcglobal.net (S.M. Uselman), Keirith.Snyder@ars.usda.gov (K.A. Snyder), Bob.Blank@ars.usda.gov (R.R. Blank), Timothy.Jones@ars.usda.gov (T.J. Jones).

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Interest in photodegradation in terrestrial environments was initially spurred by concern over increasing exposure to UVB radiation from global ozone depletion (Zepp et al., 2003). Generally, studies that investigated the direct effects of UVB exposure on litter during decomposition have found a wide variety of responses, including faster rates of decomposition (Austin and Vivanco, 2006; Brandt et al., 2007; Day et al., 2007; Rozema et al., 1997), no significant change in rates of decomposition (Gallo et al., 2006; Gehrke et al., 1995; Moody et al., 2001; Newsham et al., 1997; Pancotto et al., 2005; Verhoef et al., 2000), or decreased rates of decomposition (Duguay and Klironomos, 2000; Moody et al., 2001; Pancotto et al., 2003). Only two of the above cited studies, however, examined the interactive effects of litter quality with UVB exposure during decomposition in a field setting with freshly senesced litter (Brandt et al., 2007; Pancotto et al., 2005). As a result, differences in methodologies, litter quality, and site conditions make it difficult to generalize the results of these studies (Flint et al., 2003; Zepp et al., 2007). Incorporating UVB radiation into models of litter decomposition in terrestrial ecosystems is important because of uncertainty in predictions of incident UVB radiation due to factors related to climate change, including changes in cloudiness and atmospheric aerosols and pollutants that interact with UVB radiation (Bais et al., 2007).

Throop and Archer (2009) highlighted the need for studies that use a manipulative approach to test the effect of UVB exposure on decomposition in arid and semi-arid ("dryland") ecosystems. They counted only three such studies in low- to mid-latitude (i.e. $<50^{\circ}$N or S) drylands (i.e. Austin and Vivanco, 2006; Brandt et al., 2007; Day et al., 2007). Of these, only Brandt et al. (2007) examined interactions with litter quality at a semi-arid shortgrass steppe site in the Great Plains, finding that UVB exposure interacted with litter quality. Given that differences in climate can have a large effect on decomposition processes, we were interested in testing whether patterns observed by Brandt et al. (2007) would also be manifested at a site in the Great Basin Desert, which is considerably more arid and experiences a different pattern of precipitation compared to the Great Plains.

In this study, we investigate the interactive effects of litter quality and UVB exposure on decomposition in a *Tamarix*-invaded riparian ecosystem during the establishment of an insect biological control agent in northern Nevada, USA. Originating from central Asia (DeLoach et al., 2003), some species of the genus *Tamarix* L. (*Tamarix ramosissima* Ledeb., *Tamarix chinensis* Lour., and their hybrids (Gaskin and Schaal, 2002); hereafter referred to as *Tamarix*) have successfully invaded riparian areas across several western states (Di Tomaso, 1998; Morisette et al., 2006). To reduce the extent of this invasive tree, an insect biological control agent, the northern tamarisk beetle (*Diorhabda carinulata* Desbrochers, previously classified as *Diorhabda elongata deserticola* Chen (Tracy and Robbins, 2009)), was approved by the USDA-APHIS in 2001 and was subsequently released into *Tamarix*-invaded ecosystems in several western states, including Nevada (DeLoach et al., 2003). Insect herbivory can have several effects on decomposition and nutrient dynamics in ecosystems, including direct effects (e.g. via input of excrement) and indirect effects (e.g. alterations to plant litter chemistry) (Hunter, 2001; Lovett et al., 2002). Indirect effects, such as changes in plant litter quality and/or changes to soil environmental conditions, are less-well studied than direct effects (Hunter, 2001). Successful establishment of the northern tamarisk beetle has largely resulted in severe and large-scale defoliation of *Tamarix*, and these changes have the potential to indirectly affect litter decomposition.

Feeding by the northern tamarisk beetle on *Tamarix* is quickly followed by discoloration and desiccation of the leaf tissue. Irreversible desiccation resulting from herbivory-induced leaf wounding reduces the plant's ability to regulate water loss, and results in rapid and premature leaf drop (Snyder et al., 2010). *Tamarix* trees are less efficient at conserving leaf nutrients via retranslocation when affected by beetle herbivory, which results in leaf litter of higher quality (Uselman et al., 2011). Severe defoliation results in a more open canopy (Dennison et al., 2009), which can alter the understory and soil conditions (Hunter, 2001). Therefore, decomposition and other soil processes may be affected by greater exposure to solar radiation, which is generally high in this Great Basin Desert ecosystem. Increased light availability may also have consequences for understory species composition. In many sites where *Tamarix* has become the dominant overstory species, invasive herbaceous species are also present in the understory, and may be poised to invade this habitat with increased light availability (Hultine et al., 2010). In Nevada, tall whitetop (*Lepidium latifolium* L.) is an invasive herbaceous perennial that is often present in the *Tamarix* understory.

In this study, our first objective was to investigate the interactive effects of UVB exposure and litter quality, in a *Tamarix*-invaded dryland ecosystem in the Great Basin Desert. We hypothesized that there would be a positive effect of UVB exposure on litter decomposition, but that this effect would differ depending on litter quality. Our second objective was to understand indirect effects of insect herbivory on decomposition and nutrient dynamics of *Tamarix* versus *L. latifolium* in this ecosystem. Based on litter quality characteristics, we hypothesized that *L. latifolium* and beetle-affected *Tamarix* litter would exhibit higher rates of decomposition than natural *Tamarix* litter.

2. Methods

2.1. Site description, litter collection, and experimental design

The study site is located along the lower Truckee River near Pyramid Lake, approximately 50 km NE of Reno, Nevada, USA within the Great Basin Desert (39°51′N, 119°23′W; Elevation 1175 m). Average annual precipitation at the site is 173 mm, average maximum temperature is 33.6 °C in July, and average minimum temperature is −6.6 °C in January (based on 48 years of record at Nixon, NV, 4 km away) (Western Regional Climate Center, Desert Research Institute). The riparian area of the terminal end of the river has largely been invaded by *Tamarix*, which is currently the dominant tree, although remnant populations of Fremont cottonwood (*Populus fremontii* S. Watson) and Coyote willow (*Salix exigua* Nutt.) continue to persist. In the lower floodplain, soils are gravelly sands, classified as beaches (Soil Survey Staff, 2009). In the summer of 2007, the northern tamarisk beetle, *D. carinulata*, spread into this lower portion of the river, but the pattern of their dispersal left some areas of *Tamarix* trees unaffected by herbivory.

Freshly senesced *Tamarix* litter was collected in littertraps from plots located within both a beetle-affected area (i.e. trees with beetles) and a control area (i.e. trees with no beetles) of *Tamarix*. Five plots (5 × 5 m) were randomly located within each of these areas, for a total of 10 plots. Plots were located within a single floodplain terrace with the same soil type to control for site conditions, and all plots were within approximately 500 m of each other. Collections in the control area represent naturally senesced litter produced from the beginning of October to the end of December ("control litter"), and collections in the beetle-affected area represent premature freshly senesced litter produced after the first infestation of northern tamarisk beetles in the summer of 2007 ("beetle-affected litter"). Litter was collected frequently, at intervals of a few days to at most two weeks, to avoid leaching of nutrients from rainfall events.

Freshly senesced *L. latifolium* litter was collected approximately 1.4 km downstream of the *Tamarix* litter. Individual fully-senesced whole leaf litter (i.e. leaf with petiole) was obtained in