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Leaf litter age, chemical quality, and photodegradation control the fate of leachate dissolved organic matter in a dryland river

J.B. Fellman[a,*], K.C. Petrone[b], P.F. Grierson[a]

[a] Ecosystems Research Group, School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[b] CSIRO Land and Water, Private Bag 5, Wembley, WA 6913, Australia

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ABSTRACT

We used biodegradable dissolved organic carbon (BDOC) incubations, specific ultraviolet absorbance ($SUVA_{254,}$ indicator of aromatic carbon content) and laboratory experiments to determine the bioavailability and chemical composition of dissolved organic matter (DOM) leached from fresh leaves and litter aged on a seasonally dry floodplain for 2, 4, and 6 months. Our objective was to elucidate how litter age and solar radiation affect the bacterial utilization of DOM released from floodplain leaf litter when inundated. Leachate percent BDOC ranged from 22 to 47% for three different leaf species and significantly decreased ($p < 0.05$) with increasing litter age. However, total BDOC (mg C L^{-1}) was unrelated to litter age. Bacterial utilization of DOM leachate collected from litter aged on the floodplain for four and six months significantly increased following 48 h of irradiation for all species but there was no difference for leachate from fresh and two month old litter. The photo-mediated increase in percent BDOC was concomitant with a decrease in aromatic carbon content, as $SUVA_{254}$ values decreased on average $9 \pm 6\%$ for light exposure experiments. Our findings demonstrate that sunlight moderates the degradation of plant litter in the terrestrial environment through the photo-mediated shift in DOM composition and its bioavailability in streams.

1. Introduction

The input of allochthonous organic matter to streams is widely recognized as a key component of ecosystem energy budgets (Minshall, 1967; Wallace et al., 1997). In forested, headwater streams, as much as 99% of the annual energy input is allochthonous and leaf litter accounts for 29% of this energy input (Fisher and Likens, 1973). After submersion, leaves can be colonized by bacteria, fungi and invertebrates, thereby providing both a physical substrate and food source (Sanpera-Calbet et al., 2009). A large fraction of initial leaf mass can also be leached (up to 40%) as dissolved organic matter (DOM) within the first few days after submersion (Boulton, 1991; McDowell and Fisher, 1976), and its lability is an important control of stream metabolism. Consequently, there is a rich history of studies evaluating stream uptake of DOM leached from leaf litter (Bernhardt and McDowell, 2008; Kaplan and Bott, 1983; Lock and Hynes, 1976).

The uptake of DOM by stream ecosystems depends on a number of factors including its chemical composition (e.g., elemental ratio, molecular weight) and inorganic nutrient status, both of which can be altered by photolytic processes (Moran et al., 2000). For instance, photochemical release of NH_4 from DOM can alleviate N limitation and increase bacterial metabolism of humic DOM (Bushaw et al., 1996). Photolytic processes may also degrade recalcitrant DOM into a range of lower molecular weight compounds (e.g., acetate) and amino acids (e.g., glycine and alanine) that are more readily available for bacterial uptake (Buffam and McGlathery, 2003; Moran and Zepp, 1997). In contrast, irradiation of bioavailable, algal-derived DOM may form more biorefractory photoproducts, such as carbon gases (e.g., carbon monoxide) and radicals (e.g., hydrogen peroxide), which reduce bacterial growth (Obernosterer et al., 1999; Tranvik and Kokalj, 1998). These studies have all converged on the hypothesis that initial DOM quality influences the bacterial growth response following irradiation, where light transforms allochthonous DOM mainly into more labile compounds but algal-derived DOM into compounds of decreased bacterial substrate quality (Moran and Covert, 2003; Obernosterer et al., 1999; Tranvik and Bertilsson, 2001). However, little is known about how solar radiation affects bacterial utilization of allochthonous DOM of varying lability.

Rivers draining dryland landscapes are prime examples of aquatic environments where DOM cycling could be strongly

* Corresponding author.
E-mail address: jbfellman@uas.alaska.edu (J.B. Fellman).

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influenced by photolytic processes because they typically have low riparian forest coverage and receive extensive solar radiation. Dryland rivers have variable and unpredictable flow regimes, especially in Australia where river discharge is nearly three times as variable as the world average (Davies et al., 1994). Many Australian rivers also have extensive periods when surface water is limited to a series of temporary pools or waterholes (Bunn et al., 2003). During dry periods, leaf litter can fall directly into pools. However, large amounts of detritus (e.g., of *Eucalyptus* or *Melaleuca* spp. that generally dominate these systems) also accumulate on the floodplain and dry stream channel (Briggs and Maher, 1983), where both biotic (Melillo et al., 1982) and photolytic processes (Austin and Vivanco, 2006; Pancotto et al., 2005) can degrade plant litter and modify its chemical composition. Therefore, DOM leached from aged and partially degraded plant litter during an ensuing flood could be largely biorefractory but more susceptible to photo-mediated increases in bacterial availability. To date, the interaction of litter age and photo-alteration on DOM lability has not been directly addressed.

In this study, we use specific ultraviolet absorbance ($SUVA_{254}$, indicator of aromatic carbon content), laboratory light exposure experiments and DOM bioavailability incubations to determine the chemical composition and bioavailability of DOM leached from fresh leaves (time = 0 months) and litter aged on a seasonally dry floodplain for 2, 4, and 6 months. Our objective was to elucidate how litter age and light exposure affect the bacterial utilization of DOM released from floodplain leaf litter when inundated. Although the bioavailability of leachate DOM may decrease with increasing litter degradation (Baldwin, 1999), we assess whether solar radiation may enhance DOM bioavailability depending on its initial lability and chemical composition.

2. Methods

2.1. Site description

Leaf litter was collected from the Marillana Creek catchment in the Pilbara region of northern Western Australia (22° 46′ S, 119° 10′ E). Marillana Creek is an intermittent stream characterized by highly variable surface water flow. The creek is typical of other dryland river systems in the Pilbara where surface water is largely constrained to pools along drainage lines and those with groundwater inputs to surface water. The Pilbara has a semi-arid to subtropical climate with mild winters averaging 11–26 °C and hot summers averaging 24–40 °C. Solar radiation is high and generally in excess of 30 Megajoules m^{-2} for much of the year (Australian Bureau of Meteorology, 2011). Rainfall in the region averages 350 mm yr^{-1} and varies greatly both within and among years, but the majority falls during the summer cyclone season from December to March. Droughts of more than three years duration are common and the inter-annual variability in precipitation (coefficient of variation) is more than 100%. Rainfall for the study period was <50 mm and there was no surface flow in Marillana Creek. The geology of the Pilbara is complex and includes some of the oldest exposed rock on the earth's surface. As a result, floodplain soils and sediments have low organic matter and nutrient pools (<1% for total C, <0.1% for total N, and <0.05% for total P; McIntyre et al., 2009).

Riparian environments of Marillana Creek are typical of the Pilbara region in that they often have dense stands of trees adjacent to the main channel, in stark contrast to the open grasslands and shrublands of the surrounding floodplains. These riparian woodlands are generally dominated by *Eucalyptus camaldulensis subsp. refulgens* and *E. victrix*. Other common trees are the legumes, *Acacia coriacea* and *Acacia citrinoviridis*, which often form a patchy scrub mixed with *Eucalyptus* spp. especially on secondary channels or along broad reaches of rivers. *Melaleuca* spp. are also common in the region, particularly *Melaleuca argentea*, which can often be the dominant tree around waterholes or where there is permanent water 1–2 m within the soil surface. Leaf fall in Marillana Creek is greatest during the Austral winter months of June through September and *Eucalyptus* spp. typically account for >70% of total leaf fall (Fellman, unpubl.).

2.2. Field procedures

We collected foliage during May of 2009 from then dominant trees, *E. camaldulensis subsp. refulgens*, *A. coriacea*, and *M. argentea*. While extractable DOM and nutrients may be greater from live foliage compared to naturally senescent litter (e.g., Cleveland et al., 2004), we used live foliage in this study: 1) to ensure all leaf material was similar in age at the start of field incubations, and 2) windfall of branches and live foliage is quite common in the Pilbara such that non-senescent leaves can contribute significantly to litter fall. Foliar samples were randomly collected from trees located along a 50 m transect extending parallel to the creek channel by clipping leaves from trees at a height of 1.5 m. Foliage was removed from large stems prior to placement in the litter bags.

Approximately 50 g of leaf material for each species was returned to the laboratory for initial extractions, while the remaining leaves were placed in mesh litter bags for field incubations. Approximately 15 g of leaf litter for each species was placed into each litter bag (40 cm × 70 cm, mesh size = 1 mm), and litter was evenly spread throughout each litter bag. In total, 27 litter bags (three tree species × three time intervals and three replicates) were placed at different locations along the riparian transect and adjacent to foliage collection sites. After 2, 4, and 6 months, three replicate litter bags for each tree species were collected from different locations along the riparian transect, composited into one litter bag for each species, and returned to the laboratory for analysis.

2.3. Chemical analysis of leaf litter and litter leachate

Leaf litter extractions of DOM were performed on fresh leaves (time = 0 months) and litter aged on the dry floodplain for 2, 4, and 6 months following a similar procedure outlined in Cleveland et al. (2004). All litter was lightly brushed to remove any soil or particulates collected during field incubations. Four replicate extractions were performed for each tree species by cutting approximately 10 g of air-dried litter into small pieces (<2 cm^2). Cut litter was placed into 1000 mL glass beakers and extracted in 500 mL of Milli-Q water for 2 h at room temperature (~20–25 °C). All extractions were gently stirred on a shaker table. Litter leachates were immediately filtered through a pre-combusted, Whatman GF/F filter (nominal pore size 0.7 μm) and stored in acid-washed, HDPE bottles for initial chemical analyses or laboratory experiments (see below).

Dissolved organic carbon (DOC) and total dissolved N (TDN) concentrations were measured by high temperature catalytic oxidation on a Shimadzu TOC/TN-V analyzer. All DOC and TDN data were reported as the mean of three to five replicate injections, for which the coefficient of variance was always <2%. Nitrate–nitrogen (NO_3–N) and ammonium–nitrogen (NH_4–N) were measured using a colorimetric detection method on a Technicon auto-analyzer (Technicon, 1977). Dissolved organic N (DON) was calculated as the difference between TDN and dissolved inorganic N (DIN = NH_4–N + NO_3–N). Soluble reactive phosphorus (SRP) was measured using the ascorbic acid method with a 1 cm quartz cell (Murphy and Riley, 1962).

We used specific ultraviolet absorbance ($SUVA_{254}$) of DOM, which is an indicator of aromatic carbon content (Weishaar et al.,