Soil Biology & Biochemistry 78 (2014) 160–169

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Non-additive effects of mixing different sources of dissolved organic matter on its biodegradation

Junqiang Zheng [a, b], Zhihong Xu [b, *], Yuzhe Wang [b, c], Haibo Dong [b], Chengrong Chen [b], Shijie Han [a, *]

[a] State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China
[b] Environmental Futures Research Institute and School of Biomolecular and Physical Sciences, Griffith University, Nathan 4111, Australia
[c] Key Laboratory of Pollution Processes and Environmental Criteria, College of Environmental Science and Engineering, Nankai University, Tianjin 300071, China

ARTICLE INFO

Article history:
Received 17 February 2014
Received in revised form
17 July 2014
Accepted 25 July 2014
Available online 13 August 2014

Keywords:
Non-additive effect
Biodegradation
Litters
Dissolved organic carbon
NMR

ABSTRACT

To examine the potential impact of plant species richness on ecosystems, we studied non-additive effects of different plant litters on the biodegradation rate of dissolved organic matter (DOM) when mixing plant leaf-derived DOM derived from different plant species. A full factorial biodegradation experiment (31 possible singular and multiple combinations of five litter type-derived DOM sources) was conducted using plant litters from the five most abundant plant species in a subtropical watershed ecosystem, from which dissolved organic carbon (DOC) disappearance was measured. Loss of DOC over time was considered biodegradable DOC. We tested whether DOM diversity, measured as source species richness and composition, would affect biodegradation rates. Overall, we found significant non-additive (synergistic) effects of DOM diversity on biodegradation rates of DOM, which were explained both by plant species richness and composition. Across all treatments, a significantly higher biodegradation rate was correlated with the presence of DOM from higher nitrogen (N) containing plant litters; conversely, the presence of lower N decreased these rates. The N content and chemical characteristic of DOM might influence the magnitude of the synergistic effect. Our results suggest that loss of plant litter species diversity would not affect DOC biodegradation rate, provided that at least two species are conserved. However, the variability in DOC biodegradation rate across the treatments decreased with increased DOM diversity at three incubation time points. Our results also indicate that in an ecosystem with low plant biodiversity, loss of key species such as *Lophostemon confertus* could reduce the synergistic effects on DOC biodegradation rate.

1. Introduction

Leaching of dissolved organic matter (DOM) from plant leaf litters inundated in water is a vital process in the low-lying land and riparian ecosystems. Rainfall events have also been reported to transfer significant amounts of dissolved organic carbon (DOC) from terrestrial to aquatic systems, which is widely recognized as a key component of ecosystem energy budgets (Fisher and Likens, 1973; Bernhardt and McDowell, 2008; Chow et al., 2009). Earlier studies have shown that DOM derived from plant litters decays rapidly and is a readily available carbon (C) and energy source for heterotrophic bacteria (Moran and Hodson, 1900; Cleveland et al., 2004). The microbial biodegradation of DOM drives many biogeochemical, biological and chemical cycles (Marschner and Kalbitz, 2003). Thus, the fate of plant leaf-derived DOM is important for C and nutrient cycling in both terrestrial and aquatic ecosystems. Plant leaf litter-derived DOM may be highly heterogeneous in terms of chemical composition and molecular structure. Properties of DOM determine its biodegradation properties (Marschner and Kalbitz, 2003; Blumfield et al., 2004). For example, some authors have shown that carbohydrates and amino acids are labile DOM components and phenols and polyphenols generally accumulate in incubation experiments (Haider, 1992; Boissier and Fontvieille, 1993; Kalbitz et al., 2003a,b). It seems reasonable to assume that the differences in biodegradation rates of DOM are caused by differences in DOM composition among different plant species. Although the importance of DOM in various ecosystems has been

---

* Corresponding authors. Tel.: +86 024 83970343.
E-mail addresses: zhihong.xu@griffith.edu.au (Z. Xu), zhjq79@yahoo.com (S. Han).

http://dx.doi.org/10.1016/j.soilbio.2014.07.023

emphasized (Chen et al., 2005; Xu et al., 2009), the effect of plant species diversity on DOM biodegradation rate is not well understood.

Widespread change in plant species richness (due to extinction, extirpation or invasion) has prompted research exploring the relationship between biodiversity and ecosystem function (Tilman et al., 1996; Hector and Bagchi, 2007). Previous studies investigated the effects of plant species richness with a focus on aboveground biomass (Tilman et al., 1996, 1997; Fridley, 2001), and recently, some studies examined the effects of plant species diversity on leaf litter decomposition dynamics in both terrestrial and aquatic ecosystems (Lecerf et al., 2007; Keith et al., 2008). Most studies have usually demonstrated both a positive and minor effect of species richness on leaf litter decomposition rate (Gartner and Cardon, 2004; Lecerf et al., 2011). Several experiments have been performed in the laboratory using leached DOM from leaf litters to investigate biodegradation dynamics (Cleveland et al., 2004; Wallace et al., 2008). Most of the experiments have focused on how abiotic and biotic factors control the dynamics of biodegradation (Cleveland et al., 2004; Fellman et al., 2013). In nature, however, DOM from different litter types do not always decompose separately; rather, they frequently decompose together in a mixture. If biodegradation dynamics in plant litter mixtures are the mathematical means of their components, the biodegradation rate of single plant litter derived DOM can be used to predict the biodegradation dynamics when the plant species invades or is extirpated from an ecosystem. Alternately, if biodegradation of DOM mixtures are non-additive, research on biodegradation rates of plant litter mixtures are required for us to understand C and/or other element dynamics in the affected ecosystems. To our knowledge, no attention has been given to the biodegradation of DOM derived from plant leaf litters to determine whether this process in riparian or catchment ecosystems is affected by plant species diversity.

The effect of mixing DOM derived from different plant litters could be either additive or non-additive (Lecerf et al., 2011). A non-additive effect of diversity arises only through interactions among species (richness and/or compositional effect), while an additive effect indicates individual species presence/absence is significant (compositional effect) (Kominoski et al., 2007; Kominoski and Pringle, 2009). Additive substrate effects are assumed to be mainly due to the independent decomposition of organic matter from different sources (Johnson et al., 2006); however, augmentation or repression of the biodegradation process might be happening in a DOM mixture. Certain mixings of different litter-derived DOM are more likely to produce a complementary effect in their patterns of resource use for microbes and can increase the rate of biodegradation of DOM. Moreover, a few studies found that the extract from some plant leaf was able to have inhibitory effects against bacteria (Abeysinghe, 2010; Obeidat et al., 2012). The biodegradation of DOM from other plants would decrease when mixing with the extract with antimicrobial activity, and displaying a negative non-additive effect. There is clear evidence suggesting that observed variance in the aboveground production and litter decomposition experiments may deviate substantially from expected values due to a non-additive effect (Lecerf et al., 2011). It remains unknown whether the leaching of C from plant litters will follow the same pattern.

Our objectives of this study were to 1) determine whether DOC biodegradation rates vary among the treatments involving DOC derived from plant leaves from a single vegetation species or DOC derived from the leaves of multiple species; and 2) upon detection of a diversity effect, assess whether the effect is due to DOC richness and/or the composition of the mixtures. We hypothesized that if non-additive effects would exist, they would arise from plant litter species composition rather than richness; if plant species composition effects would exist, the presence of high quality (or lower C:N) species is likely driving the highest positive non-additive effect. We had predicted that DOM species would have dissimilar effects on biodegradation of DOM and that DOM from litter species with differing chemical properties would produce significant positive non-additive effects. We also expected that the effects of diversity on DOC biodegradation rates would be reduced if the mixing occurred after an initial DOM incubation period.

2. Materials and methods

2.1. Site description

We collected fresh plant leaf litter materials of 5 species from the riparian area within a dam-watershed ecosystem (27° 56′ S, 152° 51′ E), Wyaralong Dam, located in the Queensland, Australia. This site is situated on sandy loam soil and was recently inundated due to the construction of the dam. These five species were chosen to represent the most common plant functional types present in the ecosystem. Soil at the riparian site is a brown kurosols and the site slope position is .5–2%. The annual rainfall is about 900 mm at Wyaralong dam region. The mean minimum temperature was 13.1 °C and mean maximum temperature was 26.5 °C (since 2007).

2.2. Vegetation, sampling and processing

We collected fresh plant leaf litters of five species. These included a dominant tree species (*Lophostemon confertus* (Br.) Wilson & Waterh), a low grass species with high N content (*Cynodon dactylon* (L.) Pers.), a high grass species with low N (*Heteropogon contortus* (L.) Beauv. ex Roem. & Schult.), a legume species (*Chamaecrista rotundifolia* (Pers.) Greene), and a sagebrush species (*Chrysocephalum apiculatum* (Labill.) Steetz) (Table 1). Soil for inoculation was sampled in the ecosystem. Ten soil cores of (0–10 cm depth) were taken randomly using a corer (5 cm in diameter). The abscised leaf litters and soil samples were transported on ice and stored at 4 °C until analyses. Soil was sieved (<2 mm) to mix and remove plant materials prior to making the inocula.

2.3. DOC biodegradability

2.3.1. Experiment I

We conducted two DOC biodegradation experiments using a method adapted from Don and Kalbitz (2005). In the first experiment (Exp I), we focused mainly on the DOM released from a short-term water immersion. Within 2 h of arrival in the laboratory, whole plant leaf litters equivalent to 5 g dry weight were soaked in 500 mL of ultra-pure cold water in beakers for 24 h at 4 °C to minimize microbial activity during the extraction process. The solution extracted from the litters was filtered through pre-washed

Table 1
Summary of initial plant litter and DOM properties.

	Abbr.	Litter C%	Litter N%	Litter lignin%	C/N (DOM^{1})	C/N (DOM^{2})
Lophostemon confertus	L	49.19	1.02	27.00	57.13	248.11
Chamaecrista rotundifolia	R	46.79	2.51	12.89	12.10	5.56
Cynodon dactylon	D	41.29	1.23	7.69	11.51	38.46
Chrysocephalum apiculatum	A	45.37	1.01	13.05	69.10	110.57
Heteropogon contortus	H	42.83	.29	11.16	166.63	126.39

Note: DOM^{1} from the first experiment ($n = 4$); DOM^{2} from the second experiment ($n = 4$).