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The functional quality of decomposing litter outputs from an Arctic plant community is affected by long-term exposure to enhanced UV-B

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ABSTRACT

Plant exposure to enhanced UV-B radiation typically induces changes in leaf secondary metabolite profiles which will be inherited in litter, affecting litter breakdown and the carbon (C) dynamics of sensitive plant communities. A key enzyme in the decomposition process is phenol oxidase which is influenced by litter quality and, hence, a decomposition bioindicator. Here we investigated dwarf shrub litter decomposition following experimental community exposure to enhanced UV-B over two decades in the Swedish sub-Arctic. We examined the hypothesis that foliar UV-B exposure would alter litter quality to elevate phenol oxidase activity. This was tested in the field by measuring phenol oxidase activity in freshly collected mixed-community litter from under our experimental vegetation. A laboratory mesocosm was next used in a decomposition assay to investigate individual species responses over eight weeks, with an emphasis on the quality of leachate outputs from decomposing litter (from *Empetrum hermaphroditum*, *Vaccinium vitis-idaea*, *Vaccinium uliginosum*). In the assay bi-weekly collections of leachate were analysed for phenol oxidase activity, together with total phenolics and dissolved organic C (DOC). At the end of the assay litter mass loss and respired C were also determined. The initial assessment on field mixed-community litter found no enhanced UV-B treatment (henceforth: 'UV-B treatment') effect on phenol oxidase activity. However, in the controlled laboratory mesocosm assay, significant species-specific effects of the UV-B treatment were evident, with increased phenol oxidase activity in *V. vitis-idaea* leachate ($P < 0.001$) and a significant reduction ($P = 0.05$) in respired C. Leachate DOC release from the UV-B treatment was greater in both *Vaccinium* species and the effect on *V. uliginosum* was significant ($P < 0.05$). The UV-B treatment had no effect on the total phenolic concentration of litter or leachates for any species, but there were significant differences in leachate total phenolics, both over time and between species. Also the initial phenolic concentration in leachates from the decomposing litter of *E. hermaphroditum* was greater than both *Vaccinum* species. Results suggest a species specific role for UV-B in influencing enzyme function and decomposition, dependent on individual traits. This has implications for decomposition dynamics in this system and more widely. Our study highlights the value of using a laboratory assay to gain a mechanistic understanding the species level impacts of a global change factor (UV-B) on decomposition, which are otherwise obscured by community-level responses and difficult to determine under field conditions.

1. Introduction

Global environmental change research often focuses on climatic drivers, despite the ecological effects of UV-B remaining poorly-understood (Paul et al., 2012). There exists a high likelihood that elevated UV-B will interact with other global environmental change factors until at least 2050 (Bodeker et al., 2007), including warming (Zepp et al., 2011) and elevated CO_2. Collectively, these environmental cues can alter the secondary metabolite phenolic profile of plant tissue (Semerdjieva et al., 2003; Hansen et al., 2006; Zvereva and Kozlov, 2006), with largely unknown consequences for decomposition dynamics and carbon (C) storage at the planetary scale. The implications of such changes have been under-investigated, but are likely to involve impacts appropriate to species-level functional traits, that scale up across entire plant communities and biomes.

In the Arctic-boreal biome dwarf shrub heath habitats are a key component of this environmentally sensitive region (Tybirk et al., 2000; Nilsson and Wardle, 2005). They have an important role

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in modulating material flows of C within this region, contributing to the 1600 Pg C stored in Arctic soils over the last ca. 6000 years, which is over half the total C stored in soil globally (Tarnocai et al., 2009). Dwarf shrubs have conservative nutrient cycling traits appropriate to an acidic and nutrient limiting soil environment, including phenolic litter that restricts nutrient turnover rate (Aerts, 1999). The high concentrations of lignin and other polyphenols bound in dwarf shrub litter are mobilised by a suite of extracellular phenol oxidase enzymes excreted from plant roots and decomposer microbial communities (Sinsabaugh, 2010). Phenol oxidase activity is a recognised bioindicator of decomposition activity (Sinsabaugh, 2010), especially in the organic-rich soils common to northern latitude shrub communities (Freeman et al., 2001, 2004). Few studies have considered whether a range of environmental drivers potentially altering litter phenolic quality may also influence processes governing the breakdown and transfer of plant C to soil.

The phenolic UV-B screening compounds found in plant tissues (Teramura and Sullivan, 1994; Searles et al., 2002; Semerdjieva et al., 2003) and tissue lignin (Van de Staaij et al., 2002) are induced by UV-B exposure have been shown previously to affect litter decomposition rates in the Arctic (Gehrke et al., 1995). Semerdjieva et al. (2003) determined that UV-B further increased levels of both cell wall-bound and intra-cellular phenolics in three *Vaccinium* species. Similarly in birch foliar phenolic compounds (flavonoids) can be induced via UV-B exposure (Tegelberg et al., 2001; De La Rosa et al., 2001), but not all studies have shown these results (e.g. Anttila et al., 2010; Kotilainen et al., 2008; Kostina et al., 2001). In Gehrke et al. (1995) the phenolic-tannin composition of litter from the Arctic shrub *Vaccinium uliginosum* was assessed following foliar exposure to enhanced UV-B. Significantly greater levels of litter total phenolic compounds were also found to reduce litter decomposition rates. UV-B has also been shown to induce lignin production in leaves and resulting litter in species specific manner that typically reduces decomposition rates in temperate ecosystems (Rozema et al., 1997; Cybulski et al., 2000; Austin and Ballaré, 2010), although increased decomposition has been shown in oak (Newsham et al., 1999, 2001). Collectively the studies outlined suggest ways in which UV-B induced changes can influence the recalcitrance of organic material via changes to the chemical signature of litter. Such impacts could alter future C storage in systems where exposure to UV-B radiation is changing.

Previous studies have shown that phenol oxidase activity is a sensitive indicator of substrate nitrogen content and phenolic composition, and may be strongly affected by pH and moisture content (Sinsabaugh et al., 2008, 2010). Higher molecular weight phenolic compounds, including condensed tannins can reduce phenol oxidase activity (Allison, 2006), but little is known about how phenol oxidase responds to compounds released to litter, following leaf exposure to enhanced UV-B. Such UV-B induced changes may include enhanced levels of foliar secondary metabolite phenylpropanoid UV-B 'screening' compounds (Lavola, 1998). Phenol oxidase activity has been assessed in a UV-B litter decomposition study by Gallo et al. (2006). However, their study evaluated only the direct effect of UV-B on litter photodegradation and not decomposition impacts from pre-exposure of foliage during growth. In the current study we investigated how enhanced UV-B exposure during foliar growth affected subsequent litter decomposition. During our initial field study we examined UV-B impacts on mixed community litter under field conditions by assessing differences in phenol oxidase activity. We then used a laboratory incubation as a recognised tool (Luo et al., 2011) to investigate the effects of UV-B on decomposition output products and decomposition rates, building on earlier an litter decomposition study by Gehrke et al. (1995) using litter from two Arctic *Vaccinium* shrub species collected at a site similar to the present study. Our laboratory mesocosm assay allowed us to assess in more detail differences in the composition and function of decomposition products from three shrub species (*Empetrum hermaphroditum*, *Vaccinium vitis-idaea* and *V. uliginosum*) over time, allowing potential mechanisms of UV-B influences on decomposition dynamics to be determined. By working at the species-level we were able to overcome an acknowledged influence of plant traits on decomposition processes (Cornwell et al., 2008) and determine individual species responses to UV-B. Deciduous Arctic shrubs, for example, typically have lower levels of lignified phenolic-tissue than evergreen species (Hobbie, 1996) and decompose faster (Cornwell et al., 2008). These functional traits suggest that, proportionally, intra-cellular UV-B induced secondary metabolite phenolics may have a greater influence on litter decomposition processes in deciduous leaves.

In this work we hypothesised that enhanced foliar UV-B exposure during growth (henceforth: 'UV-B treatment') would increase litter phenol oxidase activity in the field and under controlled laboratory conditions. In the laboratory mesocosm assay, UV-B induced changes in litter decomposition were hypothesised to drive elevated rates of phenol oxidase activity, and increase the quantities of dissolved organic C (DOC) (Gehrke et al., 1995) and phenolics lost in leachate outputs. Higher dissolved outputs from leachate would increase litter mass loss and were expected to be associated with higher rates of respiration, therefore increasing respired C mass loss.

2. Methods

2.1. Site descriptions and litter collection

Dwarf shrub leaf litter samples were collected at peak growing season (July 2010 and 2011) beneath the closed shaded canopy of ericaceous dwarf shrub vegetation in an enhanced UV-B experiment in sub-Arctic birch heath, Abisko Scientific Research Station in northern Sweden (68.35°N, 18.82°E). Experimental plots had been exposed to long term enhanced UV-B ($n = 4$) over 20 growing seasons (1991–2010). The vegetation, sub-arctic *Empetrum-Vaccinium myrtillus* dwarf shrub heath described by Sonesson and Lundberg (1974), had three litter forming shrub species in our experimental area. Their order of abundance by cover was (with the relative percentage contribution of each to total litter mass in parentheses): *E. hermaphroditum* L. (49.0%) > *V. vitis-idaea* L. (24.5%) > *V. uliginosum* L. (26.5%). Each species contributes to litter mass according to its relative abundance and growth habit (deciduous or evergreen), the less-abundant deciduous shrub, *V. uliginosum*, contributes a greater proportion of litter mass than evergreen *V. vitis-idaea*. The soils in the area comprise a 2–20 cm deep layer of highly organic material ('O-horizon'), overlying glacial till interspersed by occasional erratics. Soil organic matter content at the experimental site is 94.8 (±0.9) % (Jones et al., 2014).

The UV-B treatments ($n = 4$) were provided by irradiation from fluorescent lamps (Q-PANEL UVB-313, Cleveland, OH, USA) suspended from frames and seasonally controlled by timers to provide the equivalent to 15% ozone depletion under cloudless skies during the growing season (see Johanson et al., 1995a). Treatments started in early May of each year (depending on time of snow melt) and terminated in early September (at leaf fall). The control (ambient UV-B) plots ($n = 4$) used window glass to filter UV-B radiation whilst the UV-B treatment involved the use of UV-B transparent plexiglass with a cellulose acetate filters (for further experimental details see Johanson et al., 1995a, 1995b and Gwynn-Jones et al., 2012). The experimental treatments have been maintained in this way throughout the period (1991–2011) and although this square wave approach has been superseded by more modern approaches the value of this site and research is in its longevity. Litter samples were collected from areas centrally located within plots under