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Quality of soluble organic C, N, and P produced by different types and species of litter: Root litter versus leaf litter

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ABSTRACT

In forested ecosystems, the quality of dissolved organic matter (DOM) produced by freshly senesced litter may differ by litter type and species, and these differences may influence the amount of DOM that is respired versus that which may either contribute to soil organic matter accumulation or be leached from the ecosystem. In this study, we investigated the effect of litter type (including freshly senesced fine root, leaf, fine woody, and reproductive litter) and species (5 species of leaf litter) on several measures of the quality of DOM produced at a site along a primary successional chronosequence at Mt. Shasta, California. We measured differences in solid litter chemistry (C, N, and P concentration) and differences in the concentration of dissolved organic C, N, and P (DOC, DON, and DOP, respectively), water-soluble monomeric carbohydrates, polyphenols, proteins, fractions of DOC, as well as UV absorbance. For several aspects of DOC quality, DOM from fine roots was less labile than DOM from leaf litter. In contrast to DOC quality, soluble material originating from fine roots was high in labile forms of dissolved N and P in comparison to leaf litter. We also found that leaf litter with greater total %N or %P in solid litter had higher DON or DOP concentration (and higher total soluble P concentration). A very high percentage, on average 72% (up to 89%) of the total P in leaf litter was water-soluble and mostly inorganic P. Concentrations of soluble polyphenols were strongly related to DOC, and concentrations of soluble proteins were significantly related to DON in leaf litter of different species. During primary succession at the Mt. Shasta site, an increasing ratio of root to leaf litter production and shifting species composition has been found to occur, and the results of this study suggest that some aspects of DOC quality reflect a decrease in labile forms of DOC originating from both above and belowground litter. In contrast, dissolved N and P reflect an increase in labile forms with increasing inputs of root litter. In particular, our study has demonstrated important differences in the quality of inputs of DOM from freshly senesced root and leaf litter, and these differences have implications for C and nutrient cycling.

1. Introduction

During initial decomposition, loss of water-soluble substances can account for a substantial portion of total mass loss, in particular for leaf litter (Berg and McClaugherty, 2003). In forested ecosystems, the quality of dissolved organic matter (DOM) produced by freshly senesced litter may differ by litter type and species, and these differences may influence the relative amount of DOM that is: (1) respired (lost from the ecosystem as CO_2), (2) incorporated into microbial biomass, (3) adsorbed to mineral soil (contributing to soil organic matter accumulation), or (4) lost from the ecosystem as dissolved organic C (DOC) through leaching from the soil profile. These fates are not mutually exclusive; for example, DOC may be respired in the litter where it originated or it may percolate into lower soil horizons, adsorb to mineral soil, and then later be respired.

Many studies have examined DOM originating from the bottom of the forest floor (i.e., net fluxes of DOM from the forest floor), and more recently a number of studies have reported on the quality or quantity of DOM produced by freshly senesced litter (Hongve et al., 2000; Cleveland et al., 2004; Don and Kalbitz, 2005; Wieder et al., 2008). However, we know of only two studies that have compared the quality of DOM produced by roots with leaf litter (Yano et al., 2005; Hansson et al., 2010). The quantity of gross DOM produced from freshly senesced leaf and root litter along a primary

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successional chronosequence at the Mt. Shasta Mudflows was presented in a companion study (Uselman et al., 2009). This study presents a detailed evaluation of the quality of the DOM originating from different types and species of litter in the oldest temperate mixed-conifer forest of the chronosequence. By quality, we specifically mean components of DOM that are considered indicative of availability to microbes and/or roots. This study is unique in that we examine DOM originating from freshly senesced root litter and in that we include dissolved organic N (DON) and P (DOP) in our characterization of DOM.

DOM produced by freshly senesced litter may differ by plant species. As noted by Kalbitz et al. (2000) in a review of DOM dynamics in soils, relatively few studies have attempted to relate DOM production to litter quality. In theory, one might expect that differences in the quality of solid leaf litter among species would result in differences in the quality of DOM produced. Indeed, large differences in the amount and quality of DOC leachate from freshly senesced leaf litter of different species have been observed (Qualls et al., 1991; Hongve et al., 2000; Don and Kalbitz, 2005). The effect of differing species may also be seen at the ecosystem level. Indeed, changes in species can influence soil properties and processes, and these changes are thought to be largely mediated through differences in the quantity and/or quality of plant tissue and detritus (Reich et al., 2005). Currie et al. (1996) found different fluxes of DOC in forests of different dominant tree species. However, a review by Michalzik et al. (2001) did not find overall differences between coniferous and deciduous forests on a regional scale.

In addition, variability in the quality of different *types* of solid litter may affect the quality of DOM produced. Yano et al. (2005) found that litter types (needle litter, large woody debris, and fine root) showed large differences in initial quality of the solid litter and in the quality of DOC and DON. In particular, differences in the tissue chemistry of roots versus leaf litter may impact the quality of DOM produced by those litter types. For example, compared to leaf litter, fine roots of trees generally have higher lignin concentrations (Hobbie et al., 2006, 2010). In a companion study, root litter decomposed more slowly than leaf litter, respiring less and leaching less DOC per unit mass during simulated field conditions in Mt. Shasta soil (Uselman et al., 2007a).

In this study, we compare DOM originating from roots versus leaves because roots are such an important part of net primary production in forested ecosystems (Schlesinger, 1997). Furthermore, during primary succession at the Mt. Shasta Mudflows ecosystem chronosequence, the ratio of fine root production to leaf litter production increased by a factor of 6.9 across the chronosequence (Uselman et al., 2007b). We also compare the quality of DOM from leaf litter of different species that represents a shift in species composition from predominantly ponderosa pine to a mixture of conifer species and oak along the chronosequence (Dickson and Crocker, 1953; Uselman et al., 2009). Data on concentrations of N and P in solid litter are more commonly available in the literature than concentrations of soluble N and P from litter. Therefore, we examine correlations between these variables to determine if solid N and P concentrations can be used to predict soluble N and P concentrations. Similarly, we determine whether the concentrations of individual chemical constituents in DOM (i.e., soluble monomeric carbohydrates, proteins, and polyphenols) among different species can be predicted by DOC and DON concentrations. We further characterize the DOM produced following a widely used DOC fractionation procedure (Leenheer, 1981) because it separates all of the DOC into categories that have been experimentally related to both sorption in soil and biodegradability (Kalbitz et al., 2000; Qualls, 2005). Comparison of the DOC fractions to specific chemical constituents allows us to determine the relative importance of specific constituents in the categories of the fractionation procedure.

Our specific hypotheses were that:

(1) The quality of DOM originating from freshly senesced root litter would be lower than that from leaf litter,
(2) The quality of DOM originating from freshly senesced leaf litter would differ among different species,
(3) The concentrations of total N and P in freshly senesced solid leaf litter could be used to predict DON and soluble P among different species,
(4) The concentrations of DOC and DON from freshly senesced leaf litter could be used to predict concentrations of individual chemical constituents (i.e., soluble monomeric carbohydrates, proteins, and polyphenols) of extracted DOM among different species, and
(5) Specific biochemical assays (i.e., soluble monomeric carbohydrates, proteins, and polyphenols) would be correlated with specific fractions of DOC in a widely used comprehensive DOC fractionation procedure.

2. Materials and methods

2.1. Study area and experimental design

The study area is located within the >850 yr-old ecosystem of the Mt. Shasta Mudflows Research Natural Area in the Shasta-Trinity District of the U.S. National Forest, about 6 km northeast of McCloud, California, USA. The >850 yr-old ecosystem is part of an ecosystem chronosequence, composed of mudflows of 77, 255, 616, and >850 years old in 2001 (see Dickson and Crocker (1953), Lilienfein et al. (2003), and Uselman et al. (2007b)). The mudflows are all derived from andesitic bedrock and volcanic ash from glacial outwash, originating from Mt. Shasta. Topography and climate are uniform across the chronosequence. The two younger soils are Typic Haploxerepts and the two older soils are Humic Vitrixerands. The flows are first covered by a ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forest, which later develops into a mixed-conifer forest during primary succession (Dickson and Crocker, 1953; Uselman et al., 2007b). The >850 yr-old ecosystem site can be described as a mixed-conifer forest, with well-drained soils, and climate that can be generalized as a winter precipitation – summer drought temperate climate. Precipitation averages 1300 mm, mainly as snow between November and March. The average annual air temperature is 9.9 °C, varying between 1.4 °C in January and 20 °C in July (Lilienfein et al., 2003).

Five plots (10 × 10 m) were randomly located along a transect within the >850 yr-old mudflow. More detailed information about the study area can be found in Dickson and Crocker (1953), Sollins et al. (1983), Lilienfein et al. (2003), and Uselman et al. (2007b).

2.2. Sample collection and processing

We collected freshly senesced fine roots from root ingrowth cores that we used to measure total fine root production (Uselman et al., 2007b). These roots were freshly senesced fine roots, as opposed to simply dead fine roots, because we attempted to collect roots that had recently died. These roots also had an upper age limit of 5–7 months since first growing into the core, because we only used roots from the first harvest of root ingrowth cores (placed in April and removed in November). As a comparison to freshly senesced fine roots, we also collected live fine roots from the root ingrowth cores. Vitality was determined by resilience, elasticity, and color. To help calibrate our visual and physical criteria, roots