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Controls on wood and leaf litter incorporation into soil fractions in forests at different successional stages

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ABSTRACT

In this study, we examined the response of surface soils to increased leaf and wood litter input within adjacent successional forests recovering from agricultural disturbance at the Smithsonian Environmental Research Center (SERC), Maryland, USA. Previous studies at this site demonstrated an arrested development of O-horizon, even after 130 years of forest growth, and an annual loss of leaf litter in forests with the highest abundance of invasive earthworms. Biogeochemical indices of plant biopolymer dynamics, i.e. extractable lignin and substituted fatty acids (SFAs), were applied to soil physical fractions in order to assess the fate of 5 years of increased Tulip poplar (*Liriodendron tulipifera* L.) wood and leaf litter into O-horizon and mineral soil particles of purportedly different protection levels in this recovering forest system. Our results showed that in this continuously-disturbed recovering system the pattern of litter incorporation into soil varied with both litter type and forest age. For example, young successional forests, that also contained higher abundances of soil feeding endogeic earthworms, incorporated wood amendments deeper into soils and in a predominantly particulate organic matter (POM) form than older successional systems with predominantly litter and surface dwelling earthworms. Soil lignin concentration increased sharply with wood amendments in both forest stages, but young successional forests exhibited incorporation of fresher lignin into both POM and silt and clay (SC) fractions over 0–5 cm and 5–10 cm depths while old forests only increased in POM in the 0–5 cm depth. We attribute these differences to the higher rates of physical mixing from soil feeding endogeic species and potentially lower fungal activity in young successional forests. However, despite nearly 2.5 times of background annual leaf litter input over 5 years, neither total C content nor SFA concentration in soil fractions increased, a phenomenon we attribute to full decomposition of leaf litter amendments. These results demonstrate how the chemical trajectory of soils and litter layers in recovering forests can be a function of both legacy and current disturbance.

1. Introduction

The composition and incorporation rate of surface litter to soil horizons in forests can vary with forest type, climate and ecosystem disturbance (Jobbagy and Jackson, 2003). The process of afforestation of agricultural lands is generally accompanied by the gradual accumulation of a litter layer and the rebuilding of organic horizons due to increased aboveground litter production, altered litter composition and the slow development of the litter decomposing system (Richter et al., 1999; Paul et al., 2002; Cerli et al., 2006; Wang et al., 2006). However, in forest ecosystems with a high abundance of invasive litter consumers and soil mixers, like earthworms, annual litter fall can be consumed and translocated into mineral soil horizons and thus the observed recovery process of the forest floor and O-horizon could be largely impeded (Foote and Grogan, 2010; Ma et al., 2013). The lack of O-horizon development and subsequent carbon (C) down-flow into soil layers in those forests may fundamentally alter the subsequent utilization pattern of litter-derived C by microbes and other micro- and meso-fauna (Nicolai, 1988; Hendriksen, 1990; Field and Lettinga, 1992), thus leading to a different ecological and chemical trajectory during forest succession.

Lignin, a phenylpropenoid structural plant biopolymer, as well as the substituted fatty acids (SFAs) from leaf-derived cutin and

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root and bark-derived suberin are important chemical contributors to the intermediate and long-term stabilized cycling soil C pools in forest soils depending upon the nature of microbial, physical, and chemical protection mechanisms dominating a particular soil (Baldock and Preston, 1995; Nierop, 1998; Mikutta et al., 2006; Kleber, 2010). Many studies have demonstrated how the relative input and chemistry of these biopolymer components to soils can be directly controlled by the selective consumption of litter by soil animals but also controlled by secondary processes resulting from the disruption of fungal and microbial communities by those same detritivores (Zhang et al., 2000; Filley et al., 2008; Dempsey et al., 2011; Ma et al., 2013). In fact, lignin incorporated into soil by physical mixing processes has been shown to be of a lower oxidized state compared to lignin components transported by leaching/adsorption processes that dominate in forests that lack soil mixing fauna (Hernes et al., 2007; Ma et al., 2013).

The analysis of soil fractions, separated by size and density into particles relating to theoretical physical and chemical protection mechanisms of soil organic matter (SOM), has been widely used to estimate the stability and turnover of SOC under ecosystem disturbance (Cambardella and Elliott, 1992; Jastrow, 1996; Six et al., 2000, 2002a; Kaiser and Guggenberger, 2003). Particulate organic matter (POM), composed of relatively undecomposed or partly degraded plant residue as well as seeds and microbial debris, is usually biologically and chemically active and is part of the fast cycling pool of SOM (Cambardella and Elliott, 1992; Solomon et al., 2002; Six et al., 2002b). In contrast, mineral associated OM has a mean residence time (MRT) that is much longer than POM, due to limited microbial accessibility (Hassink, 1997; Marschner et al., 2008; Kögel-Knabner et al., 2008) and strong chemical interactions (Kleber, 2010). The inclusion of particulate carbon into physically aggregated structures increases the probability that decomposing soluble fragments become associated with minerals for binding. The activity of many soil feeding invertebrates, including earthworms, directly increases the association of plant and mineral organic matter (Bossuyt et al., 2006; Ma et al., 2013). Thus, inclusion of plant litter into mineral associated soil fractions is a key component of long-term stabilization of SOM.

At the Smithsonian Environmental Research Center (SERC, Edgewater, MD), five-year long, increased litter amendment plots were established in five forest sites that varied in age (60–132 yrs) of successional recovery from agriculture. SERC forests represent typical deciduous forests that cover a large area of the mid-Atlantic and southeastern U.S., with stands in various stages of post-agriculture or logging recovery. Previous studies at this site demonstrated an impeded development of O-horizon even after 130 years of forest growth and an annual loss of leaf litter in forests with the highest abundance of invasive earthworms (Szlavecz and Csuzdi, 2007; Xia, 2012; Ma et al., 2013). Biogeochemical indices of plant biopolymer dynamics, i.e. extractable lignin and substituted fatty acids (SFAs), were applied to soil physical fractions in order to assess the fate of 5 years of increased inputs of Tulip poplar (*Liriodendron tulipifera* L.) wood and leaf litter into the O-horizon and mineral soil particles of purportedly different protection levels in this recovering forest system. With the addition of both leaf and wood litter that are much higher than background litter fall, we introduced a biogeochemical signal which allowed us not only to investigate the response of different age forests with high abundance of invasive earthworms to increased aboveground litter input but also trace the fate of lignin/SFA incorporation into specific soil fractions and the implication to SOM formation and stabilization.

After 5-years of enhanced leaf litter and punctuated woody debris input we expected to see that: 1) Five years of increased application of leaf and wood litter would result in accumulation of forest floor thus an incipient O-horizon dominated by *Liriodendron tulipifera* chemistry as the new input rate would exceed the capacity of the forest floor biota to process the litter; 2) Cutin-derived SFA concentration in soil would increase under enhanced leaf amendment, while lignin concentration would increase with wood amendment in all sites; 3) young successional forests with higher rates of physical mixing, higher pH, and potentially lower fungal activity would exhibit selective accumulation of lignin carbon from aboveground litter amendments in soil compared to older successional forests; and 4) with high soil feeding earthworm in young successional forests, aboveground litter amendments would be incorporated deeper into soils and would be more associated with soil mineral matter (silt and clay).

2. Methods

2.1. Site description

This study was conducted at the Smithsonian Environmental Research Center (SERC), (38°53′ N, 76°33′ W), which lies along the Rhode River and the Chesapeake Bay, Maryland USA. In 2003, five plots, each 3 × 3 meters, were established in two groups of stands that differed in forest successional stages: three young successional stands (60–74 years) and two old successional stands (113–132 years) (Filley et al., 2008; Crow et al., 2009; Ma et al., 2013) (Table 1). In young successional forests, the dominant tree species were tulip poplar (*Liriodendron tulipifera* L.), sweet gum (*Liquidambar styraciflua* L.). Red maple (*Acer rubrum* L.), white oak (*Quercus alba*), American beech (*Fagus grandifolia*) and red/black oaks (*Q. falcata*, *Q. coccinea*, *Q. velutina*, and *Q. rubra*) are the secondary species. In old successional forests, tulip poplar alone is the dominant species, while white oak, red/black oaks (*Quercus* spp.), American beech, and hickories (*Carya* spp.) are the secondary tree species (G. Parker, unpublished data). The mean precipitation in the region is 114.6 cm and the mean annual temperature is 13 °C (D. Correll, T. Jordan, and J. Duls, unpublished data). At SERC, leaf litter input rates range from approximately 330–450 g m^{-2} $year^{-1}$ with high and low rates ranging from 272 to 525 g m^{-2} $year^{-1}$, with the average background coarse woody debris (CWD) input estimated at 190 g m^{-2} $year^{-1}$ (G. Parker, unpublished data).

Soils at the study sites are classified as Collington sandy loam (fine-loamy mixed, active, mesic Typic Hapludult), Monmouth fine sandy loam (fine, mixed, active, mesic Typic Hapludult), or Donlonton fine sandy loam (fine, mixed, active, mesic Typic Hapludults). The soils among all the sites had similar textures with minor variations (Ma et al., 2013; Table 1).

At the experimental sites, soil invertebrate surveys have been conducted, including isopods, millipedes, earthworms, enchytraeid worms, slugs, ants, termites, and other insects (Szlavecz unpublished data). Although they all feed on leaf litter and soil organic matter, earthworms with their highest biomass remain the major agent in surface removal of leaf litter, and the only significant group in soil mixing. Twelve earthworm species of which three are native and nine are non-native were identified in SERC forest sites. Non-native earthworms were present at all sites (Szlavecz and Csuzdi, 2007; Szlavecz et al., 2011). In general, young successional forests exhibited higher total earthworm abundances and higher abundances of soil feeding/burrowing (endogeic) species compared to old successional forests (Szlavecz and Csuzdi, 2007; Xia, 2012).

2.2. Plot manipulation

The litter manipulation plots were divided into 36 equal 0.5 × 0.5 m grids and in the center of each grid square a 25 cm diameter, 5 cm high, slotted, plastic ring was placed in which the