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Carbohydrates and thermal properties indicate a decrease in stable aggregate carbon following forest colonization of mountain grassland

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ABSTRACT

In mountainous areas of Europe, the abandonment of grasslands followed by forest expansion is the dominant land-use change. Labile (i.e. easily decomposable) litter represents the major source for soil microbial products, which promote soil aggregation and long-term C stabilization. Our objective was to investigate changes in the content and origin of soil C components involved into aggregate stabilization (i.e. carbohydrates) following forest expansion on abandoned grassland in the Alps, where only few studies have been conducted.

Changes in carbohydrates and thermally labile C were assessed along a land-use gradient in the Southern Alps (Italy) following analysis of carbohydrate monomers and thermal analysis of mineral soil and physical soil fractions. The land-use gradient comprised managed grassland, two transitional phases in which grassland abandonment led to colonization by *Picea abies* (L.) Karst., and an old forest dominated by *Fagus sylvatica* L. and *P. abies*.

Grassland abandoned for 10 years tended to have higher levels of carbohydrate and thermally labile soil C than managed grassland and old forest, presumably caused by differences in the quality and amount of litter input. Carbohydrates and thermally labile C showed similar patterns in bulk soil, suggesting that thermal analysis can be used to complement chemical analysis although a straightforward relationship could not be established. Following forest expansion on abandoned grassland, ratios of microbially to plant-derived carbohydrates and thermally labile to resistant components decreased in bulk soil and soil fractions. Forest expansion entailed decreasing amounts of microbially derived compounds known to be important for aggregate stability, and corresponded to decreased soil C allocation to stable aggregates.

The combination of carbohydrate and thermal analyses revealed a lower abundance of microbially derived C components after forest colonization on abandoned grasslands, thus resulting in lower physical protection of soil C considering that carbohydrates of microbial origin actively promote soil aggregation.

1. Introduction

Abandonment of agricultural land is a global phenomenon, which has been taking place in recent decades due to socio-economic changes (Brown et al., 2005; Grau and Aide, 2008; Zhang et al., 2010; Fuchs et al., 2013). The abandonment of grasslands followed by forest expansion is the dominant land-use change in mountainous areas of the European Alps (Tappeiner et al., 2008; Zimmermann et al., 2010). Due to changes in the

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amount and quality of carbon (C) input to soil, microclimatic conditions and decomposer community (Nosetto et al., 2005; Macdonald et al., 2009; Hiltbrunner et al., 2013), forest colonization of grasslands can affect soil organic carbon (SOC) storage and stability. Contrasting directions and magnitude of changes in SOC stocks have been reported following forest expansion on abandoned grasslands, with responses ranging from SOC losses to accumulation (Thuille et al., 2000; Thuille and Schulze, 2006; Montane et al., 2007). Previous investigations of forest expansion on abandoned grassland in the Southern Alps (Trentino, Italy) showed that mineral SOC stocks (0–30 cm) decreased while SOC in the organic layers increased, thus resulting in unchanged total SOC stocks (Guidi et al., 2014a). Physical SOC protection in the mineral soil declined, while the allocation to particulate organic matter (POM) increased (Guidi et al., 2014b), thereby enhancing accessibility of SOC to microbes (Dungait et al., 2012).

Changes in physical SOC protection can be linked to labile plant litter inputs, i.e. high carbohydrates and low lignin-to-N ratio (Cotrufo et al., 2013). Such labile litter inputs decompose quickly during initial decay stages (Silver and Miya, 2001; Zhang et al., 2008) but eventually lead to long-term organic matter (OM) stabilization given their enhancing effect on soil microbial activity and microbial use efficiency (Dungait et al., 2012; Cotrufo et al., 2013). Therefore, labile litter represents the dominant source for microbial products in soil, which are known to increase soil aggregation (Oades, 1984; Roberson et al., 1995; Cotrufo et al., 2013). A lower proportion of labile plant inputs, together with a higher proportion of components with a higher stability against decomposition (e.g lignin) (Montane et al., 2010; Hiltbrunner et al., 2013) would reduce the production of microbial compounds involved in aggregate stability following forest colonization of mountain grasslands. Moreover, forests generally show higher above-than belowground C input allocation than grassland sites (Jobbagy and Jackson, 2000; Jackson et al., 2002; Guo et al., 2008), thus affecting the overall ecosystem C distribution (Guidi et al., 2014a) and the localization of microbial processing within the soil layers (Helfrich et al., 2006). Changes in litter quality, together with modifications in above- and belowground C allocation, the cessation of manure application (Aoyama et al., 2000), and decreases in soil temperature (Nosetto et al., 2005) would therefore cause a decrease in microbial OM processing and be responsible for the observed decrease in aggregate stability following forest expansion on grassland (Guidi et al., 2014b). Previous studies showed lower soil microbial biomass and activity in afforested sites compared to pasture sites (Ross et al., 2002; Macdonald et al., 2009), thus supporting the hypothesis of a decrease in microbial OM processing following forest expansion. In addition, changes in aggregation depend on differences in root morphology and mycorrhizal associations, as shown by Jastrow et al. (1998) and Rillig et al. (2002). It is likely that the decrease in fine root input in forests compared with grasslands (Guo et al., 2007; Solly et al., 2013) contributed to lower aggregate stability following forest succession, considering the enhancing effect of fine roots on aggregate stabilization (Jastrow et al., 1998). Aggregate stability can also be affected by the increasing abundance of ectomycorrizal (ECM) vs. arbuscular mycorrhizal (AM) associations, as reported following conifer afforestation of grasslands (Macdonald et al., 2009). The development of ECM associations leads to the production of SOM degrading enzymes (Ekblad et al., 2013; Phillips et al., 2013; Clemmensen et al., 2014), while on the other hand the lower abundance of AM fungi leads to decreased production of glue-like substances that promote aggregate stabilization, e.g. glomalin (Wright and Upadhyaya, 1998; Rillig et al., 2002).

However, it is not well understood how soil C components that are involved in aggregate stabilization respond to forest succession on abandoned grasslands. Among soil C components, carbohydrates provide the major source of energy for soil microbial processes (Cheshire, 1979; Martens et al., 2004). Carbohydrates are easily decomposable outside the soil matrix but especially those synthesized by microorganisms can be preserved for many decades and become physically and chemically protected within fine soil particles (Derrien et al., 2006; Rumpel et al., 2010; Dungait et al., 2012). While structural carbohydrates in plants are not directly involved in aggregate stabilization, root mucilages and especially microbial polysaccharides function as glues that increase soil organic matter (SOM) stabilization, thus their abundance was found to be indicative of high aggregate stability (Puget et al., 1998). The prevalent origin of carbohydrates in SOM pools is indicated by the relative abundance of specific carbohydrate monomers (Oades, 1984). While pentoses (arabinose and xylose) are mainly derived from plants, deoxy sugars (fucose and rhamnose) and hexoses (galactose and mannose) are largely considered microbially derived (Murayama, 1984; Guggenberger et al., 1994), although hexoses are also abundant in the hemicelluloses of conifers (Schädel et al., 2010).

Thermal analysis has the potential to complement chemical analysis, through quantification of thermally labile vs. resistant components (Rovira et al., 2008; Creamer et al., 2012; Pérez-Cruzado et al., 2014). Several indices have been developed to describe the relative abundance of organic materials with different thermal stabilities (Plante et al., 2009), based on the size and position of particular exothermic regions produced upon thermal SOM degradation. For example, the first exothermic region detected around 300–350 °C is typically attributed to the burning of carbohydrates and aliphatic compounds, whereas the second exothermic region, detected around 400–450 °C, has been attributed to the oxidation of aromatic compounds (Dell'Abate et al., 2002). Therefore, indicators derived from specific exothermic regions may qualify as proxies for the abundance of SOM components such as soil carbohydrates.

Despite the ongoing and widespread process of grassland to forest succession in European mountains, the mechanisms leading to changes in SOC are not well understood. Exploring changes in the content and origin of soil C components involved into aggregate stabilization, i.e. plants or microbial products, can help to unravel the mechanisms leading to changes in SOC content and stability following forest succession on former grasslands, as former studies showed that carbohydrates of microbial origin positively related to aggregate stability (Roberson et al., 1995; Puget et al., 2000).

The main objective of this study was to investigate changes in the content and origin of soil C components involved into aggregate stabilization following forest expansion on abandoned grassland in the Alps. We tested the hypothesis that decreased aggregate stability following forest expansion on grassland (Guidi et al., 2014b) corresponds to a decrease in the relative content of carbohydrates and thermally labile C, and especially to decreased abundance of carbohydrates of microbial origin in mineral soil layers. To address this hypothesis, we combined analysis of soil carbohydrate monomers, determined by acid hydrolysis followed by chromatography, and analysis of thermal SOM stability, measured by differential scanning calorimetry (DSC). Our specific objectives were to evaluate: (i) carbohydrate C and thermally labile C in bulk soil and physical soil fractions; (ii) carbohydrate origin in bulk soil and physical soil fractions; (iii) if thermally labile C can be used as a proxy for changes in carbohydrate C; and (iv) if changes in carbohydrate C and thermally labile C can explain the decline in aggregate stability following forest expansion as observed previously. We studied a land-use gradient located in Trentino (Southern Alps, Italy) that has previously been investigated for changes in SOC content (Guidi et al., 2014a) and aggregate stability (Guidi et al., 2014b), comprising managed grassland, two transitional phases in